Motor Patterns in Walking

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Despite the fact that locomotion may differ widely in mammals, common principles of kinematic control are at work. These reflect common mechanical and neural constraints. The former are related to the need to maintain balance and to limit energy expenditure. The latter are related to the organization of the central pattern-generating networks.

Walking is a form of locomotion used by limbed animals on land. It involves the coordination of numerous muscles to provide forward progression while maintaining body balance and limiting energy expenditure. Neurophysiologists tend to focus on the principles of organization of the central networks that generate the patterns of rhythmic muscle activity (8, 10, 11). Exercise physiologists, on the other hand, focus mainly on the mechanics of gait, including limb and body kinematics, kinetics, and energy cost (1, 6). Historically, these two approaches have remained relatively distant, and the conclusions reached in one field often have not found direct application in the other. However, to answer the question of how the nervous system controls gait mechanics, a link between the two approaches must be established.

Central pattern generators

The term central pattern generator (CPG) designates the spinal networks that can generate patterns of rhythmic activity for locomotion even in the absence of external feedback or supraspinal control (Fig. 1A, see Refs. 8, 11, 14). Normally, however, these spinal networks are modulated by peripheral and supraspinal inputs. It is thought that CPGs are organized according to similar principles in many vertebrates, including mammals (8, 10). Most current CPG models assume that each limb of an animal is governed by a separate network, interlimb coordination being achieved by coupling these networks together. According to these models, each network is...
comprised of multiple unit burst generators (unit CPGs or unit oscillators) that directly control the muscle activities of a limb. The flexor muscles at one joint are driven by one unit, and the extensor muscles by another unit. Reciprocal inhibitory synaptic interactions exist between flexor and extensor units. Interoscillator coupling can be modified by changing the synaptic strength (or polarity) of the relative spinal connections. As a result, unit CPGs can be coupled in phase, out of phase, or with a variable phase, giving rise to different behaviors, such as speed increments, transition from walking to running, or reversal of gait direction (from forward to backward). Supraspinal centers may drive or modulate functional sets of coordinating interneurons to generate different walking modes (or gaits).

**Walking mechanics**

During each walking step, the center of body mass vaults over the supporting limb like an inverted pendulum (Fig. 1B). Human walking is sometimes described as a controlled falling. At slow speeds, walking is characterized by static stability when the center of body mass remains within the polygon of support formed by the legs in contact with the ground. At faster speeds, dynamic stability results from the summation of the support forces, momentum, and inertial forces. During progression, not only does the system maintain balance, but it also attempts to limit energy expenditure. Conservation of the total mechanical energy of the body also depends on control of the motion of the center of body mass. Thus the main mechanism for energy conservation during walking consists of the exchange between the forward kinetic energy and the gravitational potential energy of the center of body mass, as this point decelerates in the forward direction when rising and accelerates in the forward direction when falling (6). In contrast with an ideal pendulum, the recovery of mechanical energy is incomplete, and muscles must perform work to replace the energy lost as heat. An additional mechanism for energy recovery depends on the elastic storage in muscles and tendons; this contribution is small in walking but substantial in running (6).

**The degrees of freedom of muscle activity do not match those of the center of body mass**

If one wants to relate theories on the CPGs’ functional organization to theories on walking mechanics, one is faced with the problem that the former deal with far more degrees of freedom than the latter. The center of body mass is a virtual point (it lies in the trunk, the heaviest body segment) with two degrees of freedom of linear motion (horizontal and vertical translation) in the sagittal plane. By contrast, the degrees of free-

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dom of muscle activation are vastly more numerous. There are more than 50 different muscles in one limb only, and each muscle is characterized by multiple functional actions (even monoarticular muscles may act at multiple joints because of the dynamic interactions between different limb segments; see Ref. 14). Moreover, the mechanical advantage of any given muscle and the effects of its contraction on the whole body depend in a complex manner on the geometric relationships with other muscles and joints. In contrast, limb movements depend not only on active muscle torques but also on gravity and dynamic interaction torques. Thus walking does not involve a simple sequence of alternating contractions in pairs of antagonistic muscles but involves complex and variable patterns of activity (7, 11). Rossignol (11) has stated that “describing in detail the normal pattern of EMG [electromyelogram] from published records is like describing the little twigs of trees in a forest.” Also, Grillner (8) noted that “there is no way to predict the movement of a limb segment from a knowledge of only the overall EMG signals in all the muscles controlling the segment.” The complicated EMG patterns are not reduced to simple alternation between flexors and extensors, even in spinal cats or after deafferentation of walking mesencephalic cats (8, 11).

An intermediate level of kinematic control might match the muscle patterns to the pattern of motion of the center of body mass

The position of the center of body mass in space depends on the combined rotation of all lower limb segments. During walking, the pelvis, thigh, shank, and foot swing back and forth, and in so doing they carry the trunk along and shift the center of body mass (Fig. 1). Monitoring the center of body mass directly and computing exactly how much work needs to be done for its motion may not be an easy task for the nervous system. However, monitoring the kinematics of the limb segments is considered to be a normal task for CPGs (8, 10). If the nervous system could control a pattern of covariation between limb segment rotations that reduced the degrees of freedom to those of the center of body mass, the motion of the latter would be specified implicitly. In other words, a neural law that coupled together the angular motions at the individual limb segments would uniquely determine the spatial trajectory (as well as its time course) of the center of body mass: the angular rotation of the lower limb segments through a given excursion would result in a corresponding translation of the center of body mass in the sagittal plane. In the end, the control of limb kinematics would help to ensure mechanical stability and energy saving at the whole body level.

Such a kinematic covariation between limb segment rotations has been recently uncovered in both cat (12) and human (3, 4, 7) locomotion. In contrast with the patterns of muscle activity, the corresponding patterns of limb segment angular motion are remarkably simple and consistent (Fig. 2). Each segment of the lower limbs oscillates forward and backward, with a waveform that differs mainly in timing and amplitude among different segments. The variables plotted in Fig. 2 are the elevation angles of the limb segments with respect to the vertical and forward directions.

The similarity of these waveforms in cat and human locomotion is remarkable if one considers the wide differences in the postural attitude in these two species (see Fig. 2, top). The overall base of support of the body is relatively shorter in bipeds than in quadrupeds, but foot support is digitigrade in cats and plantigrade in humans. A crouched (semiflexed) posture of the hindlimbs gives high mobility to cats as to other small quadrupeds, whereas a more upright posture (fairly extended limbs) of larger mammals, including humans, limits musculoskeletal strains and stresses that would otherwise increase with body mass.

Note that the movement of limb segments in a step cycle is customarily represented in terms of joint angles (as in Phillipson’s scheme of cat locomotion) rather than in terms of elevation angles. This is because it is generally assumed that muscle contractions directly affect joint angles and that muscle receptors sense changes in muscle length and joint angles. In fact, as noted above, muscles generally act on whole limb motion, and muscle receptors can sense the elevation angles and the joint angles with the same accuracy (13). Moreover, during walking the joint angles are affected by a greater variability (4, 7) and a more complex relationship with the gait cycle compared with the elevation angles (12).

Different kinematic representations highlight different aspects of the same behavior. These representations may or may not be mutually interconvertible. Thus joint angles can be derived by subtraction from the elevation angles of adjacent segments. However, elevation angles cannot be derived from the joint angles alone, but an internal representation of an absolute reference outside the limb is needed, say the vertical or the body axis. This external reference could be sensed by foot mecanoreceptors, by graviceptors in the body, or by labyrinthine cues.
A planar law of intersegmental coordination

The temporal changes of the elevation angles of lower limb segments do not evolve independently of each other, but they are tightly coupled (4). The bottom panels of Fig. 2 illustrate the kinematic law described for human and cat walking. When the elevation angles are plotted one versus the others, they describe regular loops constrained close to a plane. This represents an attractor plane common to both the stance and swing phase. In this graph, paths progress in time in the counterclockwise direction, heel contact and toe-off phases corresponding roughly to the top and bottom of the loops, respectively. The specific orientation of the plane of angular covariation reflects the phase relationships between the elevation angles of the lower limb segments and therefore the timing of the intersegmental coordination. Because the degrees of freedom of limb angular motion in the sagittal plane are reduced to two by the planar con-
straint, they match the corresponding degrees of freedom of linear motion of the center of body mass. In other words, the coupling of the angular motion at the different limb segments dictates the spatiotemporal trajectory of the center of body mass. In locomotion, therefore, the control of limb segment rotations is tantamount to a control of the position of the center of body mass.

In humans, the planar law is not an obligatory outcome of any movement of the lower limbs, because it is not associated with either voluntary kicking movements or passive manipulations. Remarkably, however, it is shared by a walking mode that differs drastically from normal forward walking in terms of mechanical characteristics and patterns of muscle activity, namely, walking backwards (7). Stance is characterized by an inverted plantigrade-digitigrade sequence in the two movement directions. The anatomic and functional asymmetry of the foot and leg along the antero-posterior axis also imposes different biomechanical constraints on forward and backward gait. Forward thrust is provided mainly by ankle plantar flexors, whereas the backward thrust is provided by hip and knee extensors. Despite all these differences, the planar covariation of the elevation angles in backward locomotion is essentially identical to that of forward locomotion, and the gait loop is traversed in the opposite direction (clockwise instead of counterclockwise). This depends on the fact that the waveforms of the elevation angles in backward gait are a time-reversed copy of the corresponding waveforms in forward gait.

The planar law of kinematic covariation described for locomotion is closely reminiscent of that described for the postural responses to static and dynamic perturbations in cats (9). Rotations of the support platform in the sagittal plane evoke compensatory responses of the limb segments. All paths described by these responses are confined close to a plane of angular covariation. The existence of laws of intersegmental coordination, common to the control of posture and locomotion, presumably contributes to the maintenance of dynamic equilibrium during forward progression and the anticipatory adaptation to potentially destabilizing factors by means of coordinated kinematic synergies of the whole body.

Kinematic patterns are good predictors of the mechanical energy expenditure

What is the relationship between the limb kinematics and the mechanical energy of the body? We noted above that conservation of the mechanical energy of the whole body during walking depends to a large extent on the exchange between the forward kinetic energy and the gravitational potential energy of the center of body mass. In this context, the hypothesized selection by the nervous system of the elevation angles of each limb segment with respect to the direction of gravity and that of forward progression as the controlled variables may help in predicting the energetic consequences of the desired kinematics. Moreover, as we noted, the planar covariation of the elevation angles is instrumental in reducing the degrees of freedom of limb motion to those of the center of body mass, where most mechanical energy is expended in walking.

There is an additional mechanism embedded in the law of kinematic coordination that contributes to the control of mechanical energy expenditure. The net mechanical power tends to increase rapidly with speed (Fig. 3). This is because the changes in potential energy are roughly independent of speed, whereas the changes in kinetic energy increase with speed and therefore less and less energy is conserved by means of the energy exchange at the center of body mass. However, there is a compensatory mechanism that reduces the oscillations of the center of body mass (3). The phase coupling between the instantaneous changes of the elevation angles of the limb segments shifts systemati-
cally with increasing speed in both humans (3) and cats (12). In humans it has been shown that the phase shift translates in a reduction of the increment of the net mechanical power with increasing speed (3). This mechanism is not equally developed in all human subjects, however. Trained subjects (such as that denoted by yellow points in Fig. 3) generally exhibit a more pronounced phase shift with increasing speed than untrained subjects (such as that denoted by red points). Accordingly, the mechanical power output at intermediate and high speeds is significantly lower in the former than in the latter subjects (2).

One can prove that the intersubject variation in the recovery of mechanical energy at higher speeds depends on different kinematic strategies, rather than different biomechanical characteristics (such as a more or less advantageous mass distribution), by creating chimerical subjects and simulating their mechanical behavior (2). Thus grafting the kinematics of an energy-saving subject into the body of a less economical subject results in an energy-saving chimera, whereas grafting the body mass and the mass distributions, leaving the kinematics unchanged, does not.

In summary, the described correlation between kinematics and mechanical energy output suggests that the specific tuning of the phase of intersegmental coordination can be used by the nervous system for limiting energy expenditure, for instance, to maximize endurance or simply to walk in a smooth and effortless manner.

A new hypothesis on the operation of CPGs

Despite the progress in understanding the general principles of operation of CPGs, the nature of the control waveforms that are putatively encoded is poorly understood. As we remarked at the beginning of this review, the simple view that mutually inhibiting extensor and flexor half-centers control immutable patterns of muscle activity at each single joint is not valid in mammals. The relationship between muscle activity and whole body mechanics is too variable and complex to allow direct control of the latter without an intermediate kinematic representation.

We propose that CPGs may control limb segment motion by encoding the waveforms of the elevation angles. In response to these kinematic reference signals, the appropriate muscle synergies would be determined in a subordinate and flexible manner to adapt to the current mechanical constraints. The significance of muscle redundancy would then be to allow the same movement to be carried out by means of different combinations of muscle activity under different environmental circumstances, for instance, to cope with fatigue or changes in load.

The kinematic waveforms could be output in either direct or time-reversed form (like a motor tape) depending on the direction (forward or backward) of gait (7). The planar law of intersegmental coordination might derive from the dynamic interaction of segmental oscillators between each other and with limb mechanics. The plane of angular covariation reflects the phase relationships between the elevation angles of the lower limb segments and, therefore, the timing of the intersegmental coordination. Speed increments are accompanied by a progressive phase shift (3, 12). In this context, the phase plays a role of global control variable similar to that previously hypothesized for the network of CPGs (8).

Although by definition CPGs can generate rhythmic motor patterns in the absence of afferent input (11), afferent feedback has several roles in regulating the production of these motor patterns, such as establishing details of the temporal order of motor activity, controlling transitions from one phase of the movement to another, and reinforcing ongoing motor activity (10). Inputs from muscle spindle afferents (particularly from proximal hip muscles) can reset the fictive locomotor rhythm. The transition from stance to swing is triggered by afferent signals from the hip region when the hip is extended near the end of stance. Swing is initiated when the leg is extended (stretching flexor muscles) and unloaded (reduced force in extensor muscles sensed by Golgi tendon organs of the extensor muscles). Thus proprioceptive signals regulate the timing of reversal from backward to forward rotation of the limb during the gait cycle. As noted above, the timing of the intersegmental coordination represents a control variable in CPGs.

The degree of autonomy of spinal CPGs in producing the described kinematic law independent of supraspinal control is unknown. However, preliminary observations in our laboratory indicate that the planar covariation of limb segment angles is preserved, although in a degraded form, in paraplegic patients (with incomplete section of the spinal cord at thoracic level) trained to walk on a treadmill with body weight support. Spinal cats also exhibit a limb kinematics roughly comparable to that of intact cats (11).

It is likely, however, that in intact mammals the spinal CPGs interact extensively with the other networks involved in the control of locomotion. In particular, it is known that the activity of both ventral (VSCT) and dorsal (DSCT) spinocerebellar neurons is rhythmically modulated with the different phases of locomotion. These neurons send to the cerebellum an efferent copy from spinal loco-

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motor networks and afferent information from the moving leg. The integrative role played by DSCT neurons in encoding whole limb parameters has been recently uncovered in cats (5). Thus these neurons encode linear combinations of the limb elevation angles during changes in limb geometry. These authors have proposed “that the DSCT responses to perturbations may reveal a utilization at the spinal level of a coordinate system that is similar to that deduced from the behavioral studies. Moreover, this coordinate representation of proprioceptive sensory information would have the proper form to provide the basis for segmental feedback that may be essential for the fine tuning of motor strategies to control limb geometry” (5).

Conclusions

We showed that a similar control of limb segment rotation occurs in two very different forms of walking, quadrupedal (cat) locomotion and bipedal (human) locomotion. The law of intersegmental coordination we have described may emerge from the coupling of neural oscillators with each other and with limb mechanical oscillators. Muscle contraction intervenes at variable times to reexcite the intrinsic oscillations of the system when energy is lost. The hypothesis that a law of coordinative control results from a minimal active tuning of the passive inertial and viscoelastic coupling among limb segments is congruent with the idea that walking has evolved according to minimum-energy criteria (1, 6).

References