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KINEMATIC CONTROL OF WALKING

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INTRODUCTION

The work reported in this brief review has been carried out along lines stemming from the holistic approach to motor control pioneered by Carlo Terzuolo many years ago. Traditional approaches to the study of posture and movement have emphasized the role of chain of reflexes starting from different peripheral sensors and directed to specific muscle effectors as the basic building blocks of motor mechanisms. Carlo Terzuolo was among the first neuroscientists to realize that, because a coordinated motor action results from the complex fusion of concurrent inputs from multiple sources, it cannot be effected muscle by muscle but is aimed at the control of more global goals. He first applied the integrative approach of systems analysis to quantify the behaviour of the stretch reflex in cats (34, 36), monkey (40) and man (41), and of the vestibulo-spinal reflexes in cats (2). Together with his pupils and colleagues he then proceeded to identify some of the more general control principles that may underlie the execution of complex motor behavior in man, such as typing (42), drawing and handwriting (29, 39).

In the early eighties he gave us impetus to address the problem of postural control in behaving cats (12). At that time the classical notion was that postural control can be simply equated with the stabilization of the body against gravity, that is with a problem of force control (kinetics). Because animals are statically balanced when the vertical projection of their centre of mass (*CM*) falls within the support area, it was assumed that *CM* is the main variable regulated in stance (7, 28, 32, 35). However a different perspective emerged from a series of studies dealing with the behavior of intact cats trained to stand freely on a platform tilted in the sagittal plane (pitch rotations) by variable angles (between -30° and +30° from the horizontal, 27). In these conditions, the distribution of ground contact forces and joint torques can be idiosyncratic to a given animal and condition (26), but the geometry of both forelimbs and hindlimbs is much more stereotyped (26, 27). Thus the length and the angle of orientation of the limb axis change very little despite wide changes of platform tilt (26, 27) or loads (23, 24). Cats who stand at the preferred interfeet distance align the axis of both fore- and hindlimbs with the vertical, and keep the forelimbs relatively extended and the hindlimbs more flexed. Moreover, even when a load (corresponding to 20% of the animal's weight) is applied, limb geometry is preserved unmodified at the expense of a marked shift of CM and of an abnormal dis-

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tribution of forces between forelimbs and hindlimbs (23, 24). These observations led us to hypothesize that the maintenance of postural geometry of the limbs takes precedence in the control hierarchy, whereas the control of *CM* and ground contact forces is determined in a subordinate manner (24, 26). Interestingly, limb length and orientation are faithfully encoded in the responses of DSCT neurons to applied changes in limb posture in the anesthetized cat spinal cord (6).

Length and orientation specify the position of the limb endpoint (the foot) relative to the proximal joint (scapula or hip) in a global manner, leaving the detailed geometric configuration undetermined (21, 31). There is an additional processing stage that transforms limb length and orientation into the angular coordinates of the joints (24, 25). The changes of these angles under both static and dynamic conditions are not independent, but covary close to one plane (24, 26). The orientation of this plane is essentially the same in all cats (despite wide differences in their biomechanical parameters), and is also the same at the forelimbs and at the hindlimbs. The latter invariance is especially remarkable, considering that the forelimbs differ considerably from the hindlimbs in terms of the length and orientation of the individual corresponding segments. The described planar covariation involves either absolute angles of orientation relative to the vertical at the proximal limb segments and relative angles of flexion-extension at the other joints, or absolute angles at all limb joints. A related planar co-variation has recently been found in the case of whole-body motion in man (19). In fact, even though the work summarized above pertains to cat posture, similar kinematic strategies have been found for postural responses evoked by external perturbations and the anticipatory responses associated with the voluntary movements of the trunk involved in axial bending (32). Thus, postural geometry is accurately controlled also in humans and the general principles of control do not differ substantially from those found in quadrupeds (28, 32).

Kinematic co-ordination in locomotion.

Emphasis has often been placed on the control of *CM* and ground contact forces also in the case of quadrupedal and bipedal walking (8, see however 44 for pioneer studies of limb kinematics). This is because the behavior of *CM* tends to be simple and stable. During each walking step, *CM* vaults over the supporting limb like an inverted pendulum (1, 8, 22, see Fig. 1). At slow speeds, walking is characterized by static stability when *CM* 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 a control of *CM* motion. Thus, the main mechanism for energy conservation during walking consists in the exchange between the forward kinetic energy and the gravitational potential energy of *CM*, as this point decelerates in the forward direction when rising and accelerates in the forward direction when falling (8). 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.

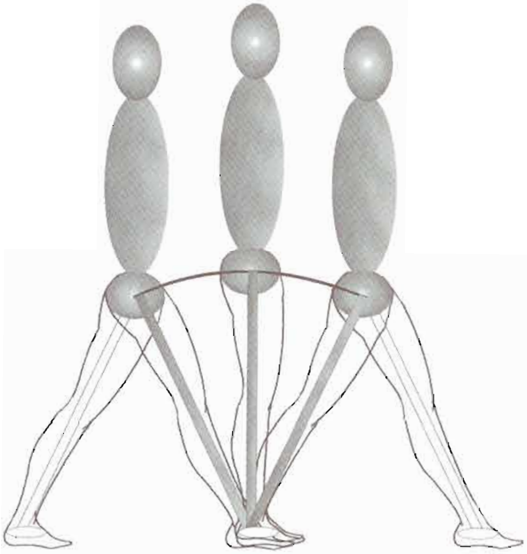

Fig. 1. - *During each walking step, the center of body mass vaults over the supporting limb like an inverted pendulum.*
Gravitational potential energy is smallest during the double support phases, when the center of body mass is lowest, and potential energy is greatest when the center of body mass passes over the supporting foot. Forward kinetic energy fluctuates out of phase with the changes in potential energy, and as a consequence a significant proportion of the former is converted into the latter during each gait cycle.

The problem is that *CM* has no anatomical or functional autonomy; it is a virtual point lying somewhere close to the ilium, but this location can change widely depending on body posture or the presence of loads. Monitoring *CM* position 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 *CM* position depends on the combined rotation of all lower limb segments. Thus if the nervous system could control a pattern of co-variation between limb segment rotations that reduced the degrees of freedom to those of *CM*, 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 determine uniquely *CM* space-time trajectory: the angular rotation of the lower limb segments through a given excursion would result in a corresponding *CM* translation in the sagittal plane. In the end, the control of limb kinematics would help to ensure mechanical stability and energy saving at whole body level.

A kinematic co-variance between limb segment rotations has been found in both cat (38) and human locomotion (4, 5, 22). The patterns of limb segment angular motion are remarkably simple and consistent (Fig. 2A). Each segment of the lower limbs oscillates forward and backward, with a waveform that mainly differs in timing and amplitude among different segments (Fig. 2B). The temporal changes of the elevation angles of lower limb segments do not evolve independently of each other, but they are tightly coupled (4, 5). When the elevation angles are plotted one versus the others, they describe regular loops constrained close to a plane, common to both stance and swing phases (Fig. 2C). 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 inter-segmental coordination.

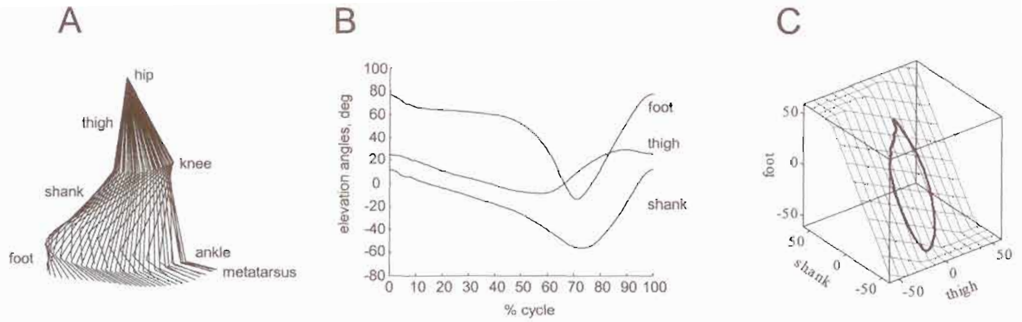

Fig. 2. - *Kinematic patients*. - *A*: stick diagrams for one complete gait cycle are plotted aligned on the hip joint. The elevation angle of each limb segment in the sagittal plane corresponds to the angle between the segment and the vertical. *B*: time course of the elevation angles during one gait cycle. Limb segments rotate backward (smaller angular values) during stance and forward (larger angular values) during swing. *C*: planar co-variation of the elevation angles at the thigh, shank and foot during one gait cycle. Path progresses in time in the counterclockwise direction, heel contact and toe-off phases corresponding roughly to the top and bottom of the loops, respectively. Grid corresponds to the best-fitting

Because the degrees of freedom of limb angular motion in the sagittal plane are reduced to two by the planar constraint, they match the corresponding degrees of freedom of linear motion of *CM* (22).

Relation to energy expenditure.

Saving the mechanical energy of the body during walking depends to a large extent on the exchange between the forward kinetic energy and the gravitational potential energy of *CM* (8). The selection 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 predicting the energetic consequences of the desired kinematics (22). Moreover, the planar co-variation of the elevation angles is instrumental in reducing the degrees of freedom of limb motion to those of *CM*, where most mechanical energy is expended in walking. There is an additional, important mechanism embedded in the law of kinematic co-ordination that contributes to the control of mechanical energy expenditure. The net mechanical power tends to increase rapidly with speed, 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 (8). However, there is a compensatory mechanism that reduces the oscillations of *CM* (3, 4). The phase-coupling between the instantaneous changes of the elevation angles of the limb segments shifts systematically with increasing speed both in man (4) and cat (38). In man it has been shown that the phase-shift translates in a reduction of the increment of the net mechanical power with increasing speed (3, 4). This mechanism is not equally developed in all human subjects, however. Trained subjects generally exhibit a more pronounced phase shift with increasing speed than untrained subjects. Accordingly, the mechanical power output at intermediate and high speeds is significantly lower in the former than in the latter subjects (3, 22).

Interaction between posture and locomotion.

Human erect locomotion is unique among living primates. Evolution selected specific biomechanical features that make human locomotion mechanically efficient. These features are matched by the motor patterns generated in the central nervous system. But what happens when humans walk with bent postures? Are normal motor patterns of erect locomotion maintained or completely reorganised? We studied walking in bent postures, either knee-flexed or knee- and trunk-flexed (17). These postures imply large differences in the position of *CM* as compared with the standard erect posture: *CM* is displaced downward and forward (outside the body) and its oscillations are reduced because the legs cannot fully extend. Thus the exchange of kinetic and potential energy is much more limited than usual.

Ground reaction forces differ prominently in bent posture erect posture, displaying characteristics that are intermediate between those typical of walking and those of running (17). Amplitude and waveforms of the muscle activities also are deeply affected by the adopted posture. By contrast, the waveforms of the elevation angles along the gait cycle remain essentially unchanged irrespective of the adopted postures (17). Thigh, shank and foot angles covary close to a plane in all conditions but the plane orientation is systematically different in bent vs. erect locomotion. This is explained by the changes in the temporal coupling (phase shift) among the three segments.

An integrated control of gait and posture is made possible because these two motor functions share some common principles of spatial organisation (16, 28, 32). The frame of reference for the kinematic coordination for both postural responses and locomotion seems to be anchored to the vertical. Also, the planar law of intersegmental kinematic coordination applies to both tasks (see Introduction). It is not surprising to find that similar laws of inter-segmental coordination apply to the control of posture and locomotion. Locomotion must assure a forward progression compatible with dynamic equilibrium, adapting to potentially destabilizing factors (e.g. changes in body posture or load, uneven terrain, obstacles, etc.) in an anticipatory fashion by means of co-ordinated synergies of upper limbs, trunk and lower limbs (11, 20).

Development of kinematic co-ordination in children.

Integrated control of gait and posture is not yet in place at the onset of unsupported locomotion in toddlers, but develops rapidly over the first following weeks. Walking children were monitored from 11 to 144 months of age, some of them from the very first unsupported steps (9, 10). Both the general pattern of the inter-segmental coordination of the lower limb segments and the stabilization of the trunk with respect to the vertical are immature initially, but they develop in parallel very rapidly in the first few weeks of walking experience. By contrast, the maturation of the individual kinematic waveforms of each segment and their convergence toward waveforms that are more typical of adults is much slower, being acquired over a period of months to years.

These results support the view that the planar covariation reflects a coordinated, centrally controlled behavior, in addition to biomechanical constraints. A planar covariance is not an inevitable mechanical consequence of a system of linked segments that are cross-coupled by passive inertial and visco-elastic forces. In fact, some toddlers can perform successfully their very first steps even though the coordination pattern of the lower limb segments deviates very significantly from the standard planar loop observed in adults. The refinement of the planar covariation while morphological variables change drastically as the child grows implies a continuous update of the neural command based on changes in the internal model of limb mechanics (10).

According to current views, the network of burst generators (central pattern generators or CPGs) is already in place at birth (13, 30). However, the phase coupling between the CPG units driving different limb segments may change during development, for instance because of the maturation of supra-segmental control of the locomotion pattern. This is consistent with our results that indicate how the phase-coupling between different limb segments changes progressively with age. A stable and mature covariation plane can be achieved by tuning muscle activity patterns that appropriately modify the passive biomechanical coupling among limb segments.

Adaptation in adults: changes in body load.

We have seen above that limb kinematics is unaffected by the addition of extra-loads in cats standing on a tilted platform (23). It has recently been shown that body weight unloading is compatible with accurate control of limb kinematics in human locomotion (17). Subjects walked on a treadmill while the amount of body weight support (BWS) was modified in steps between 0 and 100% of body weight. Changing BWS between 0 and 95% resulted in drastic changes of kinetic parameters, but in limited changes of the kinematic coordination. In particular, the peak vertical contact forces decreased proportionally to BWS; at 95%-BWS they were 20-fold smaller than at 0% and were applied at the forefoot only. Also, there were considerable changes of the amplitude of EMG activity of all tested lower limb muscles and a complex re-organization of the pattern of activity of limb muscles. By contrast, the corresponding variation of the parameters that describe shape and variability of the foot path was very limited, always < 30% of the corresponding values at 0 BWS. Moreover, the planar co-variation of the elevation angles was obeyed at all speed and BWS values. At 100%-BWS, subjects stepped in the air, their feet oscillating back and forth just above but never contacting the treadmill. In this case, step-to-step variability of foot path was much greater than at all other BWS levels, but was restored to lower values when minimal surrogate contact forces were provided during the "stance" phase. Thus the data indicate that the detection of minimal contact forces is sufficient for accurate limb trajectory control.

Adaptation: reversal of walking direction.

Reversal of walking direction from forward to backward represents a key test to study locomotor patterns. According to the influential scheme put forth by Grillner (18), backward walking could be produced by switching the sign of the phase coupling among unit oscillators. As a result, the controlled output patterns would be simply the time-reversed copy of those of forward gait.

If we consider the patterns of the muscle activities, there is no way we can superimpose those of BW gait onto those of FW gait, whether the waveforms are looked in direct time or they are time-reversed (15, 43). This is perhaps not so surprising given that the mechanical requirements of BW walking are very different from those of FW walking. Stance is characterized by an inverted plantigrade-digitigrade sequence in the 2 movement directions. Forward stance begins with heel contact and ends with toe-off. Backward stance begins with toe contact and ends with heel off. The anatomical and functional asymmetry of foot and leg muscles along the antero-posterior axis also imposes different biomechanical constraints on forward and backward gait. Forward thrust is mainly provided by ankle plantar-flexors, whereas the backward thrust is provided by hip and knee extensors.

However, the time-reversed waveforms of backward gait are almost perfectly superimposable onto those of forward gait (15). Accordingly, also the planar co-variation is the same; the loop is simply traversed in the opposite direction due to a switching of thigh-shank phase. Thus kinematic patterns follow Grillner's predictions of a phase-switch among unit oscillators. It appears as though the same kinematic templates can be output by CPGs in either direct or time-reversed form (like a motor tape) depending on the direction (forward or backward) of gait.

SUMMARY AND CONCLUSIONS

The planar law of inter-segmental co-ordination we described may emerge from the coupling of neural oscillators between each other and with limb mechanical oscillators. Muscle contraction intervenes at variable times to re-excite the intrinsic oscillations of the system when energy is lost. The hypothesis that a law of co-ordinative control results from a minimal active tuning of the passive inertial and visco-elastic coupling among limb segments is congruent with the idea that movement has evolved according to minimum energy criteria (1, 8).

It is known that multi-segment motion of mammals locomotion is controlled by a network of coupled oscillators (CPGs, see 18, 33, 37). Flexible combination of unit oscillators gives rise to different forms of locomotion. Inter-oscillator coupling can be modified by changing the synaptic strength (or polarity) of the relative spinal connections. As a result, unit oscillators can be coupled in phase, out of phase, or with a variable phase, giving rise to different behaviors, such as speed increments or reversal of gait direction (from forward to backward). Supra-spinal centers may drive or modulate functional sets of coordinating interneurons to generate different walking modes (or gaits).

Although it is often assumed that CPGs control patterns of muscle activity, an equally plausible hypothesis is that they control patterns of limb segment motion instead (22). According to this kinematic view, each unit oscillator would directly control a limb segment, alternately generating forward and backward oscillations of the segment. Inter-segmental coordination would be achieved by coupling unit oscillators with a variable phase. Inter-segmental kinematic phase plays the role of global control variable previously postulated for the network of central oscillators. In fact, inter-segmental phase shifts systematically with increasing speed both in man (4) and cat (38). Because this phase-shift is correlated with the net mechanical power output over a gait cycle (3, 4), phase control could be used for limiting the overall energy expenditure with increasing speed (22). Adaptation to different walking conditions, such as changes in body posture, body weight unloading and backward walk, also involves inter-segmental phase tuning, as does the maturation of limb kinematics in toddlers.

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