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COORDINATION AND INTEGRATION IN THE HINDLEG STEP CYCLE OF THE RAT: KINEMATIC SYNERGIES

ILANA GANOR and ILAN GOLANI

Department of Zoology, Tel Aviv University, Tel Aviv (Israel)

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SUMMARY

The kinematics of the hindleg step cycle of the rat in the vertical domain is composed of 7 synergies. Additionally, a global spatiotemporal principle ensures that each segment of the leg is never displaced backwards.

The concepts of flexion and extension are inadequate for the description of step kinematics. As a limb segment changes its orientation, it does so in relation to the next serially connected limb segment or else in relation to gravitation. We call these two aspects of kinematics 'movements' and 'displacements' respectively, and describe segment kinematics in these terms.

Of the 7 kinematic synergies, 5 involve a specific invariant interplay between 'movements' and 'displacements'. Together with the two additional parts they form the skeleton around which the step is organized. The flexible and regulatory nature of the step is obtained by the superposition of biasable properties on top of this skeleton. These include the durations, amplitudes, and initial and final positions of movements-displacements.

The formalization of the step cycle kinematics represents explicitly intralimb coordination and integration. It also specifies the demand made upon the muscular and neural background organization that mediates the kinematics in a language which is appropriate for neurophysiological investigation.

INTRODUCTION

Locomotion is of interest to a variety of scientists: for ethologists it represents a relatively stereotyped, phylogenetically ancient behavior, appropriate for the study of comparative morphology. In the neurosciences it is used for the study of neural coordination and integration.

Progress has been made in the study of locomotion by abstracting particular features of the step: angles in joints[7], force configurations[8], trajectories of joints[1], and muscular activity[3]. Although useful, the extensive work has been elusive, in that it did not yield a qualitative understanding of locomotion, and did not provide a natural language of both behavior and its presumed central representations[10].

This study examines intralimb coordination and integration. It proposes a natural organization of the kinematics of the hindleg step of the rat. As will be shown, the concepts of flexion and extension are insufficient for a full account of the step's kinematics in the vertical domain. They are replaced by a conceptual framework which stems from a redefinition of the coordinate systems in which motor behavior is examined.

An appropriate description of motor behavior should disclose the fact that as a limb segment changes its orientation, it does so in relation to the next serially connected segment, and/or in relation to gravitation. Therefore, kinematic management is represented in relation to these two frames of reference, in two separate polar coordinate systems. Description is obtained by the use of the Eshkol–Wachmann Movement Notation* (ref. 4), already employed in studies of motor behavior[5,6].

Another aspect not fully considered previously is the effect of firm contact with the ground on the freedom for displacement for each segment of the leg. Whereas in swing the movements of distal segments have no effect on the kinematics of proximal ones, in support they do affect the kinematics of proximal segments. To represent this reversal in mechanical interdependence, kinematics are described during swing from pelvis to toes and during support from toes to pelvis[4]. This powerful descriptive principle might have implications for the control of motor behavior.

METHODS

Free walking on an open wooden table of three adult rats was filmed at 64 fps. Only the parts in which the rat walked perpendicularly to the camera were analyzed. Thirty steps were notated and analyzed using a 16 mm stop-frame projector. The vertical orientations of the limb segments of the hindleg were notated in two separate coordinate systems. In the 'bodywise' coordinate system, orientation of a segment was defined by the angle between its longitudinal axis and the longitudinal axis of the next serially connected segment. The distal segment was used for reference during support and the proximal during swing. The record was divided into (a) movements in which there was a continuous change of the angular relationship, and (b) bodywise positions which bound the movements.

In the second, 'absolute' coordinate system, the reference was the direction of gravitation. The angle between the 'absolute' vertical and the longitudinal axis of a segment was described as its orientation in absolute space. We have termed a change in orientation of a limb segment in relation to the vertical a 'displacement'. The record was divided into (a) displacements, in which there was a continuous change of the orientation of a segment, and (b) absolute positions which bound the displacements.

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* The Eshkol–Wachmann movement notation publications can be obtained from the Movement Notation Society, 75, Arlozorov St., Holon, Israel.

Although somewhat redundant, the two-fold description in terms of 'movements' and 'displacements' is necessary because it discloses two different essential kinematic aspects: when a displacement, i.e. a change in orientation of a segment in absolute space, is examined separately, it is impossible to know whether the change is due to the segment's own movement in relation to the next serially connected segment, or due to the movements of other segments on which it is carried, or both. Similarly, lack of change in orientation in absolute space may be due to total lack of movements, or due to antagonistic movements of two or more serially connected segments. Thus, the displacement of a segment is an algebraic sum of its own movements and the movements of all the segments distal to it in support and proximal to it in swing.

The evaluation of segment orientation was done by visual examination of film projected on graph paper. Data on each segment were recorded separately. The description in the two coordinate systems was made independently at separate times. The reliability of the notation was checked by comparing the two descriptions.

The degree of resolution employed was 1/16th of the circle; smaller amplitudes were recorded as 'minimal'. This degree of resolution was chosen because: (a) it yielded robust organization — the organization that might be discovered by the use of a finer resolution should fit into the one described in this study and should not invalidate it — and (b) pushing for a finer resolution reduces reliability and results in an only apparent increase in exactitude.

RESULTS

Establishment of contact of the foot with the ground divides the step into two distinct phases — support and swing. These are further divided into 7 relatively independent kinematic parts. Five form subsystems characterized by specific invariant properties. Continuous forward flow is ensured by a global spatiotemporal organisation imposed upon the 7 parts.

Support phase

(a) Carrying along I

During this part of the step the foot is in full and firm contact with the ground. Since the leg revolves around it, movements are described from phalanges to pelvis.

Metatarsus, whether initially in contact or not, moves around the fixed phalanges–metatarsus 'joint'. During its movement the angles of ankle and knee joints are maintained constant, resulting in the lower and the upper leg being carried along. Thus, a change in the absolute orientation of three segments involves an actual bodywise movement of only the distal segment (Fig. 1a).

Often, after the beginning of the carrying along part, the lower leg starts to move actively on the metatarsus in a direction opposite to the metatarsus movement (Fig. 1b). The antagonistic direction of the movement counteracts the change in absolute orientation of the lower leg that would have occurred had the lower leg not moved in the opposite direction. Be it full or partial carrying along, the sum total of the movements is such that the lower leg arrives at the absolute horizontal.

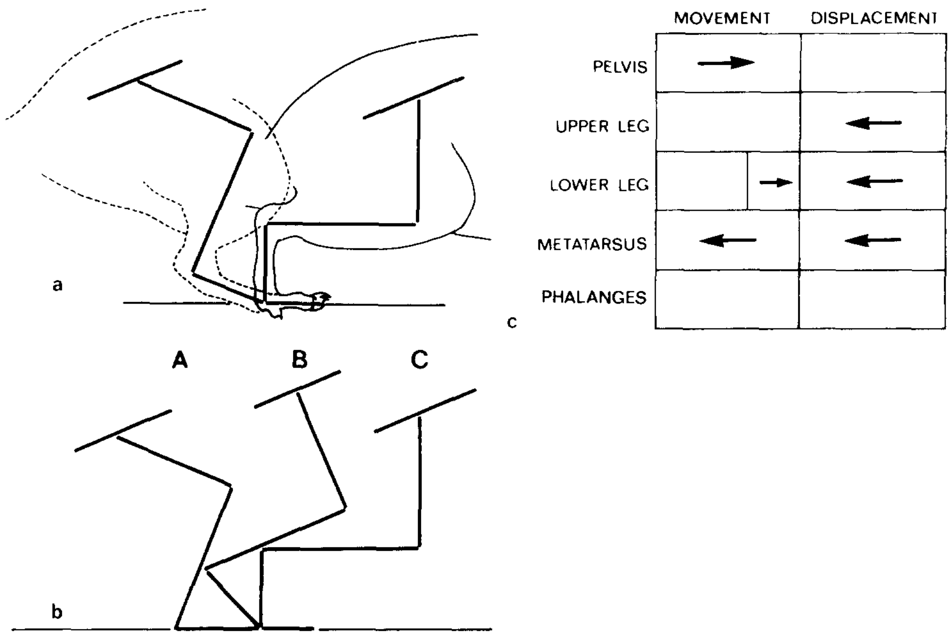

Fig. 1. Carrying along I. Bars stand for axes of segments, indicating boundaries of subsystem during specific steps. Note orientation of each segment in relation to next distal segment and in relation to gravitation. a: full carrying along. b: stick diagram of carrying along I which involves an antagonistic movement of lower leg towards the end of the subsystem. c: formal summary of movements–displacements. Vertical line within entry indicates that the event on its left must occur and the one on its right is optional. Temporal order within entry is from left to right.

The pelvis maintains actively its absolute orientation by moving simultaneously with equal amount in an opposite direction to the displacement of the upper leg (fixation in the absolute).

Kinematic invariance. The carrying along part is described as a separate subsystem because it constructs itself in every step by a specific invariant interplay between movements and displacements (Fig. 1c). It may be formulated as follows: phalanges, in firm contact, do not move, as metatarsus moves and is displaced, as lower leg and upper leg are merely displaced, as pelvis moves in the opposite direction and is not displaced. The lower leg has an option to move in opposition to the metatarsus.

This chord of movements–displacements is so organized as to converge to a specific absolute orientation of the lower leg.

The next two subsystems are superimposed on top of each other.

(b) Fixation

After arriving at the horizontal, the lower leg maintains this position actively, until the end of the support phase. It means that any movement of the metatarsus and/or phalanges is compensated for by a simultaneous opposite movement of an appropriate amount of the lower leg. The upper leg and the pelvis maintain their absolute and bodywise orientations as they are carried along on top of the fixated lower leg (Fig. 2a).

Kinematic invariance. On top of the phalanges–metatarsus subsystem (to be described later), the lower leg moves in a direction opposite to the displacement of the metatarsus while not being displaced, as the upper leg and the pelvis neither move nor are displaced (Fig. 2b).

(c) Phalanges–metatarsus subsystem I

This subsystem operates simultaneously with the fixation subsystem, following carrying along I. The phalanges move around their tips starting either at, or after the beginning of the fixation part. The metatarsus, which moves until the end of carrying along I, may perform a large number of possible movements within this subsystem. It may continue its movement into the present subsystem singly, before the phalanges join in, or it may be carried along on the phalanges once they start to move, (Fig. 2c, A–B). Then, it may move in the opposite direction, partly buffering out the

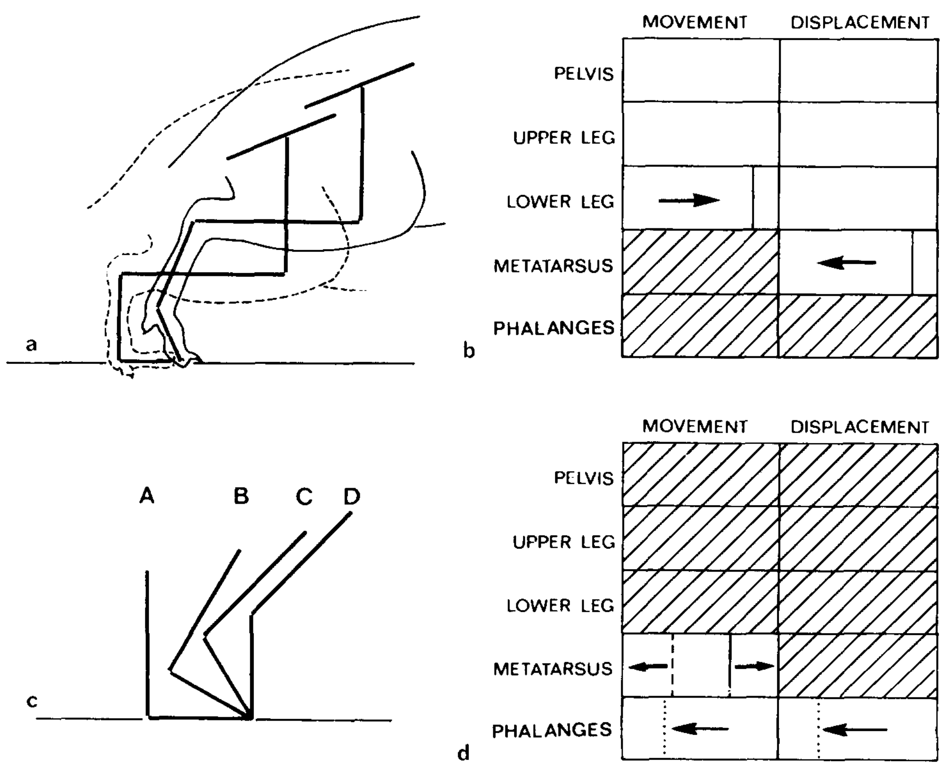

Fig. 2. Fixation (a and b) and metatarsus–phalanges I (c and d). Interrupted outline of hindleg in a indicates initial, and continuous outline final, boundary of subsystem. Hatched area in b represents phalanges–metatarsus I subsystem on top of which the fixation occurs. For further explanation see legend to Fig. 1. c: bars stand for phalanges and metatarsus in a specific step. A–B, carrying along; B–C, partial carrying along; C–D, fixation. d: formal summary of phalanges–metatarsus I. Signs as in Fig. 1c. Interrupted line within entry indicates that events on both sides of it are optional. Dotted line indicates that event on left of it is optional and event on right must occur.

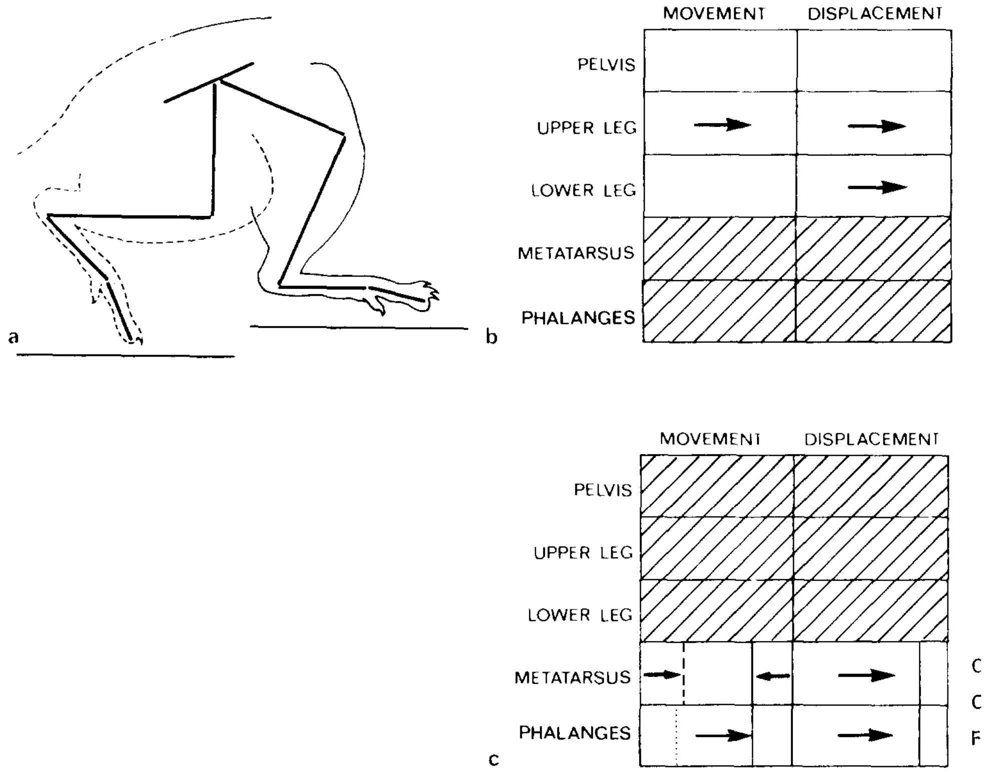

Fig. 3. Carrying along II and metatarsus-phalanges II. a: initial and final positions of segments in the two subsystems in a specific step. b and c: formal summaries of the two respective subsystems. Legend for signs as in Figs. 1 and 2.

displacement imposed upon it by the phalanges (Fig. 2c, B–C). Ultimately, it may fully compensate for the movement of the phalanges, and fixate in the absolute (Fig. 2c, C–D). The metatarsus performs any of the above described movements singly or in any combination, with the constraint that the above order is obeyed.

The large number of possible combinations between phalanges and metatarsus movements endows the end of support with a significant regulatory flexibility.

Kinematic invariance. The phalanges move either throughout the process or after it starts. The metatarsus is displaced throughout this process with an option for a short position holding at the end. The involvement of the movements of the metatarsus in its displacement diminishes throughout the process, starting with a positive and ending with a negative contribution that ultimately absorbs the displacement (Fig. 2d).

Swing phase. Release of contact reverses the mechanical interdependence of the segments of the leg: in swing, movement of the proximal segments has kinematic consequences on more distal segments and no such consequences on more proximal ones. This implies that an adequate representation of movement will add the movements of distal segments on top of movements of proximal ones.

(d) Release of contact

During this part, the metatarsus moves at first on top of the phalanges, then the mechanical interdependence reverses and the phalanges move on top of the metatarsus. The angle between the two increases from less to more than 180°.

The next two subsystems are superimposed on top of each other.

(e) Carrying along II

Upon release of contact the upper leg moves on top of the pelvis, carrying along the lower leg, metatarsus and phalanges. The angle at the knee is maintained fixed during this subsystem and throughout the step (Fig. 3a).

Kinematic invariance. Upper leg moves and is displaced as the bodywise fixed lower leg is only displaced, carrying along the metatarsus and the phalanges (Fig. 3b).

(f) Phalanges–metatarsus subsystem II

Metatarsus, which is carried along by the movement of the upper leg via the lower leg from a variety of absolute orientations, always arrives at the end of this movement at a horizontal position. It means that it usually must move bodywise: as a rule, at the onset of upper leg movement the metatarsus may enhance the change of orientation imposed on it; may then be carried along; then may start moving in the opposite direction, and ultimately may resist fully the change in orientation imposed on it, and fixate in absolute space. The metatarsus performs any of these movements singly or in combination but the above order is obeyed.

Metatarsus arrival at the same final position indicates that either the kinematics of all the segments proximal to it as well as its own are taken into account, or its absolute orientation is sensed separately, or both. The phalanges may move, enhancing their own displacement, but never crossing the horizontal.

Kinematic invariance. Metatarsus is displaced with an option of a fixation at the absolute horizontal at the end. Its involvement in its displacement diminishes gradually, so that it may start with a movement in the same direction of displacement and end with a movement in the opposite direction that ultimately absorbs the displacement. The phalanges are displaced, having an option to move in the direction of displacement (Fig. 3c).

(g) Establishment of contact

Contact is established due to movements of the metatarsus and phalanges. At the end of carrying along, metatarsus is horizontal and phalanges are either in horizontal or lower. This configuration is followed either immediately or after an intermediate configuration, by planti- or digitigrade contact. Contact is established simultaneously with the whole surface so that the sole, the bases, or the tips of the toes, never bump into the ground.

Global organization

Up to now, organization was shown to prevail only synchronously, within each subsystem. No clue was given as to an order which makes the step a unitary kinematic

TABLE I

Global (diachronic) organization of support and swing phase

Each segment may perform some or all of the kinematic events, but always in the prescribed order. Phalanges may violate principle during swing. mad, movement and displacement in same direction; c.a., (carrying along) no movement while being displaced; p.f., antagonistic movement involving partial fixation; f, antagonistic movement involving fixation; n.m.an.d., no movement and no displacement.

Support		*Swing*
Pelvis	f; n.m.an.d.	
Upper leg	c.a.; n.m.an.d.	mad
Lower leg	c.a.; p.f.; f; n.m.an.d.	c.a.
Metatarsus	mad; c.a.; p.f.; f.	mad; c.a.; p.f.; f
Phalanges	mad	(mad; c.a.) or (c.a.; mad)

process. It will be shown that a global spatiotemporal invariant is imposed upon the synchronous organisation.

Table I presents the kinematic options during support and swing. Each segment may perform some or all of its options, but always in the prescribed order. The ordering principle is the same for all segments.

The involvement of the movements of each segment in its own displacement decreases during each of the phases: during support a segment may move on top of the segment distal to it, then may not move and be carried along, then may move in the opposite direction thus buffering out some of the displacement imposed upon it by more distal segments, then may fixate in the absolute performing no displacement at all, and finally it may stop moving on top of the adjacent distal stationary segment. This order is always followed, but some options may be skipped. In other words, the transition is from agonist to antagonist movement with an option for no movement in between. However, whereas the agonist always enhances displacement, the antagonist may at the most fixate the segment in the absolute: a segment is never displaced antagonistically throughout the step. The same applies for swing, this time relating to more proximal segments. This principle ensures a continuous forward flow.

The biasable properties of subsystems

There are kinematic properties that differ from step to step and from one sequence to another, depending on the prevailing environmental and motivational circumstances: a rat walks plantigrade in a previously unexplored environment, digitigrade in a familiar one. It can walk slowly or quickly, low or high, using small or large steps.

Since observations were made in an open field rather than on a treadmill, the velocity and type of step were uncontrolled. In spite of, or rather due to, the observed variety, we have found that the rat always performed the invariants described previously. The biasable properties within each subsystem, which endow it with its flexibility, are (a) the durations of movements and (b) their amplitude. A detailed metric description is beyond the scope of this paper.

DISCUSSION

Previous representations of the kinematics of the step involved the concepts of flexion and extension. These concepts ignore the mechanical interdependence between segments and the reversal from phalanges to pelvis in support and vice versa in swing. They do not make a distinction between a moving segment and a segment on top of which movement occurs, and thereby fragment the essentially coordinated kinematics of a linkage of segments into seemingly isolated events.

Had mechanical interdependence between segments been taken into account, it would have represented explicitly only the management of segment orientation in relation to the next segment (bodywise movement); it would still have ignored the change of orientation of segments in relation to gravitation (displacement), thereby omitting an essential kinematic aspect.

On the one hand, displacements can be viewed as the algebraic summation of bodywise movements of segments on top of each other; on the other hand, displacements constrain the bodywise movements and impart to them their specific kinematic significance. Flexion, for instance, may have some 10 qualitatively different kinematic effects on the moving segment (proximal in support and distal in swing), depending on the direction and amount of displacement of the segment on top of which it occurs (e.g. with the same amount of flexion the segment may be fixated, its displacement may be accelerated or reduced, etc.). All these considerations explain why the concepts of flexion and extension which conceive of angular changes in isolation, do not yield meaningful elements of coordination and integration.

Apart from the fact that the concepts of flexion and extension should be abandoned on kinematic grounds, there is now some evidence that the classification of muscles as flexors and extensors is inappropriate. Wetzel et al.[10], citing Gambaryan, point out that 'sometimes a muscle would contribute to opening a joint and sometimes to closing it, by functioning either to stabilize or else actually move the bones'. Others show a complex division of labour between limb muscles rather than a simple classification of a muscle as extensor or flexor[2,3], or observe subtle mutability of EMG activity depending on the kinematic context[9]. Finally, Wetzel et al.[10] point out that 'the complexity of EMG patterns suggests that a central stepping generator for even a single limb must account for far more than simple flexion or extension'.

In order to represent management of orientation of a segment as part of the totality of relevant kinematic events in other segments, the concepts of flexion and extension had to be replaced by a redefinition of the coordinate systems within which motor behavior takes place. This yielded descriptions in terms of movements and displacements and the concept of mechanical interdependence. An appropriate representation of kinematics must be comprised of at least these two descriptions.

A formulation in terms of movements versus displacements has resulted in the isolation of relatively independent, self-regulatory processes. Each of these demarcates itself in the flow of the step as a morphogenesis of a structural invariance. The invariance is formulated as a specific recurrent interplay between movements and displacements — a kinematic synergy.

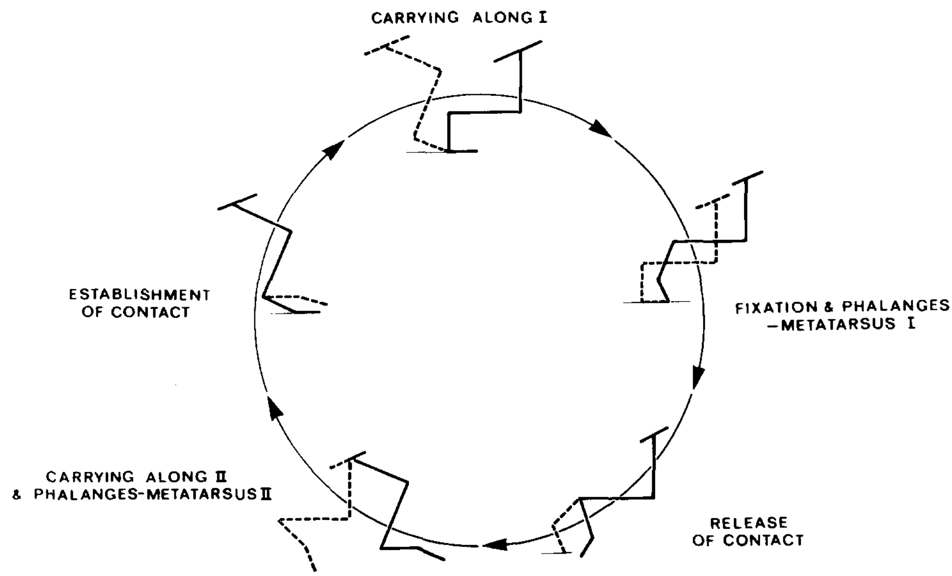

Fig. 4. Schematic representation of the rat's hindleg step cycle. Interrupted lines in stick figures represent initial and continuous lines final boundaries of subsystems.

The step cycle, so to speak, dissociated itself, yielding 7 parts, 5 of which were demonstrated to be biasable subsystems. These 7 parts comprise the skeleton of the step. Of the 5 subsystems, carrying along I, fixation, and carrying along II, follow each other in succession. Together with the parts of establishment and release of contact, they partition the step. Two additional subsystems, phalanges and metatarsus I and II, are imposed on the fixation and carrying along II subsystems, respectively. The labels of subsystems should not be interpreted as focusing on one aspect as more important than another in the chord which they represent. Activity is distributed throughout the linkage (Fig. 4).

A global invariant is imposed on the 7 synchronous parts. It is so structured that the involvement of a segment in its own displacement diminishes in swing and support. Since all the segments of the leg follow this ordering principle, continuous forward progression is assured.

The formulation of invariance provides a specification of the demand made upon the nervous system in a representation that suggests several options for motor control. Clearly it is impossible to visualize a situation in which the underlying organization would be found to contradict the behavioral one. Therefore it is firstly suggested that a functional classification of muscles be re-examined within the framework of the present proposed subsystems. Secondly, a formulation in terms of movements–displacements raises questions about the nature of the neural representations that mediate motor behavior: is there a multiplicity of neural representations of motor behavior which could be classified according to the distinction between movements and displacements? Is it conceivable that disposition for action undergoes a series of transformations from displacements to movements and vice versa at several anatomically and physiologically distinct levels? The languages of such presumed successive representations could bear different relative weights of at least two kinematic aspects: management of segment orientation in relation to the next segment and in relation to gravitation.

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