11
The Bernstein Perspective: II. The Concept of Muscle Linkage or Coordinative Structure

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The puzzle of the control and coordination of movement as seen by Nicolai Bernstein can be expressed succinctly: How can the many degrees of freedom of the body be regulated systematically in varying contexts by a minimally intelligent executive intervening minimally? A reasonable hypothesis is that nature solves this puzzle by keeping the degrees of freedom individually controlled at a minimum, and by using "units" defined over the motor apparatus that automatically adjust to each other and to the changing field of external forces (Gel'fand, Gurfinkel, Tsetlin, & Shik, 1971). In accordance with this hypothesis we introduce and explore the concept of muscle linkage or coordinative structure, defined as a group of muscles often spanning several joints that is constrained to act as a single functional unit.

Consider the contrast between a person who is a novice at shooting a gun and a person who is highly skilled. What makes these two people different? Imagine that you aim a gun and try to zero in on a target. And imagine that a light is attached to the end of your gun so that, when you aim, the beam focuses in the region of the target. The beam of light will not remain motionless at one spot, but rather it will wander around the target area. This is because, when you aim, your body in general and your arm in particular are not perfectly motionless. Now, in the case of the skilled marksperson, the light will wander around, but generally it will remain very close to the target; that is, the "scatter" is within a limited area around the target. In the case of an unskilled marksperson, however, the light will wander over a wide range around the target. So a skilled marksperson—not surprisingly—keeps the gun on target much better than the unskilled. What we want to know is how the skilled marksperson is able to do this. The question is, how has the person organized the body with reference to the specific problem of

aiming a gun. Two differences between the skilled and the unskilled marksperson are evident. Whenever a person lines up to fire the gun, there is some oscillation of the body—the center of gravity is moving. The first thing we can observe about the skilled marksperson is that in comparison with the amateur the oscillatory movement is less. She or he has found some way of "freezing" the muscles, restricting their freedom, so as to keep the body's center of gravity more stable. The second difference we can observe is the following. While aiming the gun, any change of the wrist or shoulder joint will cause the gun to deviate from target. In the unskilled marksperson, movement at one joint is not compensated by a change at the other joint, thus throwing the gun off target. The joints are relatively independent of each other. But in a skilled marksperson, the story is very different. The two joints are constrained to act as a unit such that any horizontal oscillation in the wrist will be matched by an equal and opposite horizontal oscillation in the shoulder (Arutyunyan, Gurfinkel, & Mirsky, 1969). It appears that the joints relate among themselves (see Fig. 11.1) according to some equation of constraint, just as the two points in Fig. 10.3b of the previous chapter relate to each other by the equation of constraint for the connecting line. In the unskilled performer the pieces of the body relevant to the skill vary in a relatively independent fashion, which can be interpreted to mean that no equation of constraint applies. The joint at the wrist is unrelated to the joint at the shoulder, so that whenever there is any oscillation at one joint the other joint follows or remains fixed. In either case the gun moves off target. The difference, then, is that the skilled performer has found a way of constraining his or her muscles to behave as a single unit, that is, as a coordinative structure. And we may suppose that, in part, learning any skill entails a similar discovery of relevant constraints over the muscles used in the skill.

Let us consider another example. When a person breathes, inhaling and exhaling pulls and pushes the spine backward and forward. The mechanics of the body, the biokinematic linkage of head and spine, dictate that the head should move with the spine; curiously, the head is stable throughout the cycle of spinal movements. The stability of the head arises as follows. With inhalation the thoracic region of the spine is pushed backward, but the pelvic girdle and the cervical region move forward by just the degree needed to preserve the head's position (see Fig. 11.2). It appears that there is a functional grouping over the muscles of the cervical-thoracic-pelvic groups (Gurfinkel, Kots, Pal'tsev, & Fel'dman, 1971), because the muscles relevant to inhalation are anatomically quite separate from those relevant to the movements of the hip and anatomically separate from those relevant to the movements of the upper part of the spine. It is as if an equation of constraint has been written over these elements. A change at one joint necessarily entails a particular kind of change at the other. The preceding depicts the control principle identified at the outset of this chapter: Muscles are not controlled individually but are functionally linked with other muscles so as to form autonomous systems—coordinative structures. What pre-
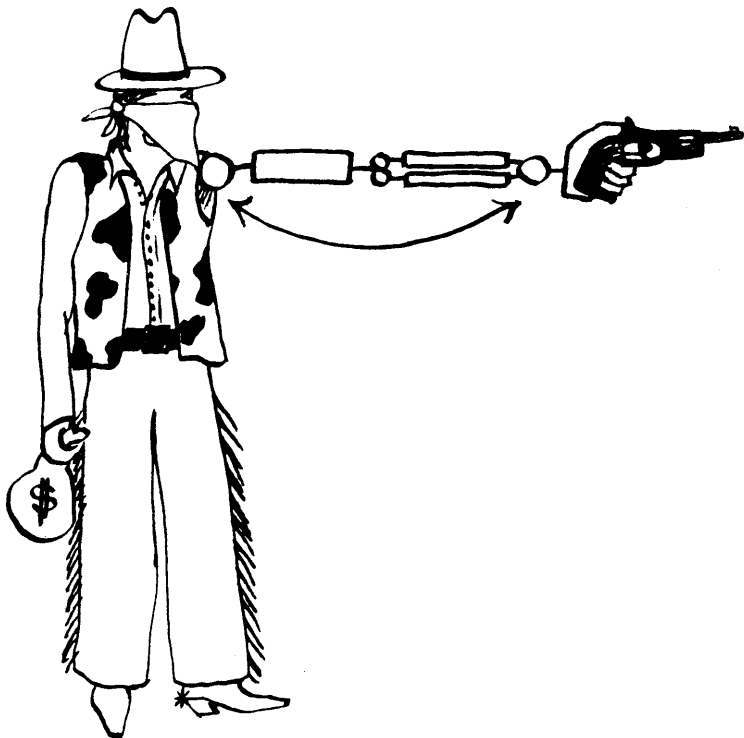
FIG. 11.1. In a skilled marksperson, any movement at the wrist is matched by an equal and opposite movement at the shoulder. This constraint over the joints keeps the gun on target.

viously was an aggregate of many degrees of freedom becomes a system of fewer degrees of freedom.

If you have ever tried to do a handstand, you can readily appreciate the need for organizing the separate parts of the body. One of the things you are trying to discover in learning how to stand on your hands is a way of linking or constraining those muscles involved so they become just a single entity. A change in one part of the body, the shoulders, must be perfectly matched by a change at the hips. If it isn't, you keep falling over. In part, learning to handstand is discovering the right kinds of constraint over the separate parts of the body. In the discovery of such constraints, effective control of the musculature is achieved through the reduction in the number of degrees of freedom that must be controlled independently. Let us explore this concept further using a detailed example.
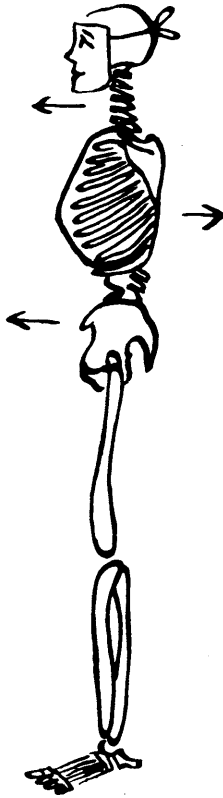
FIG. 11.2. When a person breathes, the backward movement of the thoracic region of the spine is matched by forward movement of the pelvic and cervical regions. This constraint over the relevant muscle groups keeps the head stable.

Imagine an aircraft having two wings, each with one aileron. The ailerons are used to control the roll of the aircraft. On the horizontal part of the tail fin are the left and right elevators that control the pitch of the aircraft. There is also a rudder that controls the aircraft's yaw. The rudder can move to the left or to the right, and the elevators and aileron can be raised or lowered. In short, the plane has five independent parts: two ailerons, two elevators, and a rudder (see Fig. 11.3). For simplicity, assume that these independent parts can each adopt one of nine positions at any time. The zero position is when the part is in its neutral position, for example, flush with the wing in the case of an aileron, flush with the tail fin in the case of the rudder. An aileron or an elevator can go four positions up (+4) and four positions down (−4). The rudder can move four positions to the right (+4) and four positions to the left (−4).

Imagine that you were the pilot of such a plane and had to control these pieces independently. You have five buttons in front of you with which you must control at any point in time the positions of both ailerons, both elevators, and the rudder. Obviously, controlling such a plane is not going to be easy—rapid adjustments in the flight pattern in order to accommodate to new conditions (say, an evasive maneuver) may prove impossible.

What is needed is a way of organizing the parts of the airplane so as to simplify its control without losing its desirable maneuverability. One way to do this is to link parts of the system together (see Fig. 11.3). Firstly, the aileron and the rudder can be linked into a functional relationship; when the aileron on the left goes up by one position, the rudder goes to the right by one position. This is a simple equation of constraint that says that the position of the left aileron equals the position of the rudder ($La = r$). Next, the right aileron can be linked to the rudder so that when the right aileron moves up the rudder moves to the left. In this case we have an equation of constraint that says that the position of the right aileron equals the position of the rudder but with opposite sign ($Ra = -r$). Think of what we are attempting to do. We are trying to make the airplane manageable. We want the airplane to be something that a pilot could actually fly. Initially, the airplane has five independent parts each capable of assuming nine different positions. A pilot would have great difficulty controlling this system. Now three of those parts have been banded together into a single entity, the aileron–rudder subsystem. The way that a beginner learns a skill is to "freeze out" some of the free variation of the body, so that it is not used, that is, not allowed into the activity. Our task is to make it possible for a pilot to be skillful
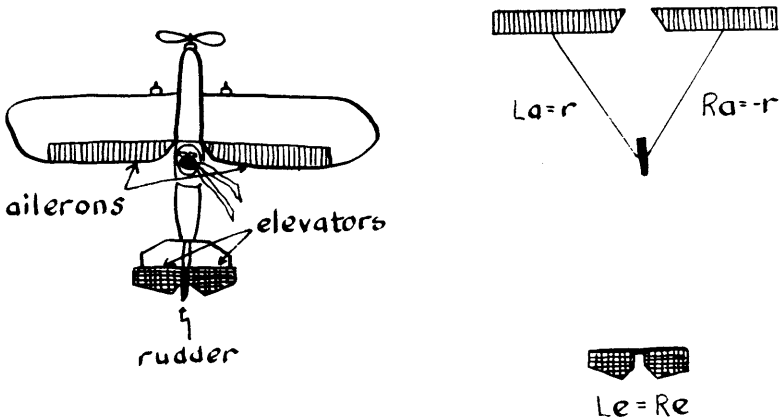

FIG. 11.3. An airplane of five freely moving parts (left) and how they might be linked by equations of constraint (right).

with this plane by likewise "freezing out" some degrees of freedom. This is accomplished by linking the ailerons and rudder with two equations of constraint. Very simply, when the left aileron moves up, the rudder moves to the right by the same amount; when the right aileron moves up, the rudder moves to the left by the same amount. In brief, there are two equations of constraint that apply to the aileron-rudder subsystem of the airplane.

Now let us recall and apply the formula for capturing the degrees of freedom of any system: $ND - C = df$. Remember that N stands for the number of elements. In the system being discussed here there are three elements—the two ailerons and the rudder. The dimensionality, D, of this system is 1; one coordinate or one dimension is needed to identify the position of an element. In other words, each element can move along only one axis going either above zero or below zero. As we just saw, this system now has two equations of constraint, C. So the number of degrees of freedom of the aileron-rudder system is 3 (elements) times 1 (Dimension), minus 2 (equations of constraint), or, in short, a system of one degree of freedom.

The concept that we are pursuing, that of muscle linkage or coordinative structure, suggests that muscles are brought together into similar types of collections; a number of relatively independent muscles are constrained to act as a unit. What does this achieve? In principle, it creates an autonomous (self-regulatory) entity. The skilled marksperson has found a way of organizing the muscles so that, when going into the aiming position, he or she "adopts" a particular equation of constraint over the joints. As in the analogy of the airplane, this constraint means that when the wrist joint goes so many degrees to the left, the shoulder joint must go so many degrees to the right, keeping the gun on target. A particular kind of equation of constraint has been "written," as it were, over the free parts of the body.

Returning to the airplane, the pilot's task can be simplified further by linking the elevators. If the left elevator goes up, the right one goes up by the same amount so that the position of the left elevator equals the position of the right elevator ($Le = Re$). This linkage produces another subsystem and results in an airplane that is even more manageable.

The procedure of making the airplane controllable through linkages can go a step further. The two subsystems, the aileron-rudder subsystem and the elevator subsystem, can be linked by using another equation of constraint. As the organization of the airplane now stands, these two subsystems are free to vary independently of each other; the elevator system can adjust independently of the aileron-rudder system. But they can be related to each other in a precise fashion by writing another equation of constraint. For example, let the positions in the aileron-rudder system always be some constant proportion of the positions in the elevator system, $ar = k(e)$. This simple constraint says that the elevator system must change in some constant ratio of changes in the aileron-rudder system. A link has been forged between the two subsystems. For the five elements that

originally comprised five degrees of freedom, we now have four equations of constraint—two for the aileron-rudder system, one for the elevators, and one linking each of these two subsystems—thus leaving us with only one degree of freedom. We see, in short, that as the variable parts of the airplane are linked together the parts are no longer free to vary. Importantly, the procedure of linking can serve to eliminate as possible states those combinations that would result in potentially uncoordinated movements of the airplane (remember the many futile combinations of wheel positions of the car that were discussed in the previous chapter.

Now let us pull the strands of this story together. We have underscored two main problems. The first problem is the large number of degrees of freedom of the body that must be regulated. The second problem is what we have called context-conditioned variability, whether anatomical, mechanical, or physiological in source. When taken seriously these problems can be shown to have strong implications for how coordinated activity is achieved. One implication that we have been examining is that control and coordination cannot be in terms of individual muscles; they must be in terms of something larger—collections of muscles. Moreover, when these collections are constrained, they must compensate automatically to preserve the relationship of muscles within the collection, just as the position of the rudder and right aileron change automatically with a change in the position of the left aileron.

Let us now see how these slowly developing ideas are realized in a fairly complex form of real-life activity—locomotion. In discussing how locomotion is organized, we see the many concepts we have been wrestling with come into play.

Consider the step cycle of a single limb. Various positions of the limb during the step cycle are diagrammed in Fig. 11.4. In position A, the body weight is directly over the foot. In position B, the back leg is extended and the body weight is transferred so that it is centered forward of the foot. Next, the leg flexes as shown in position C, and finally it is extended in front of the torso (position D). So, starting at position A, the leg extends backward, flexes, extends forward and lands, the weight moves over the body, and the cycle starts again. These positions delineate four phases of the single-step cycle (see Fig. 11.5). Going from position B to position C is called flexion (F). Position C to position D marks off the first extension phase (E 1). From position D to position A is the second extension phase (E 2), and from position A to position B is the third extension phase (E 3).

In order to take a detailed look at the step cycle, we also need to distinguish between the support phase and the transfer phase. The support phase is when the leg is supporting the body weight, and it consists of E 2 and E 3. The transfer phase is when the shift from one position of support to the next occurs, and it consists of F and E 1.

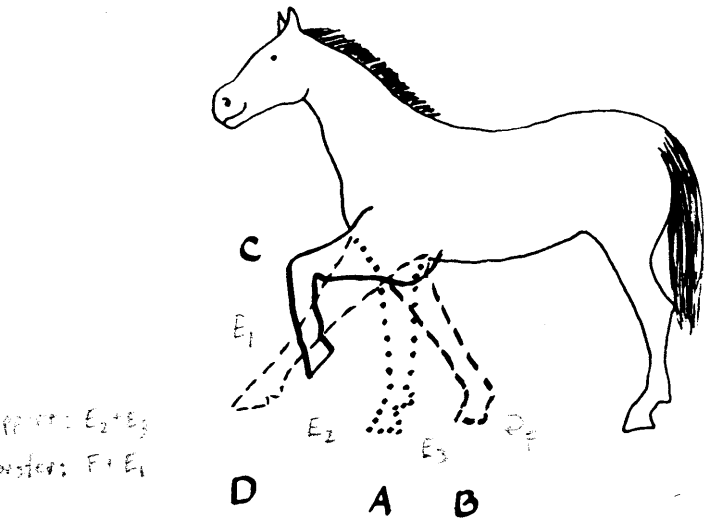Within the constraints imposed by the anatomy of a limb, the muscles of the

FIG. 11.4.   The step cycle of the single limb. See text for details.

hip, knee, and ankle may relate in many ways. One can jump, squat, or sit and wiggle the leg. But once locomotion starts, a remarkably systematic arrangement over the joints occurs, as can be appreciated by the equations of constraint that coordinate the extensors and the flexors of the limbs.

If you record the activity of the extensor muscles (those responsible for extending the leg) at each of the joints during locomotion, there is a constant
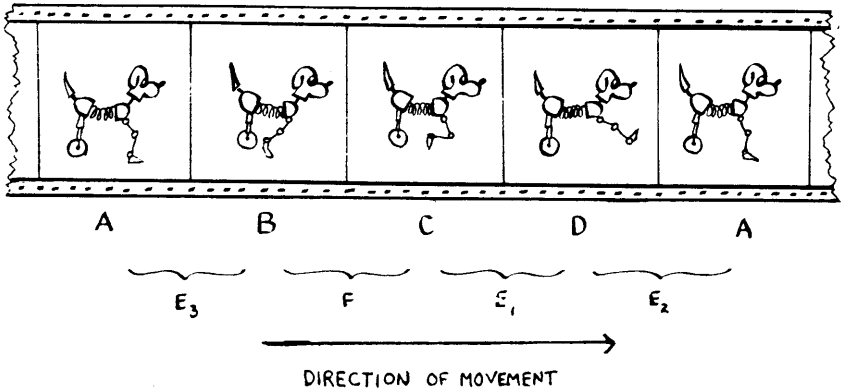

FIG. 11.5.   The step cycle of the single limb partitioned into phases of extension (E_1, E_2 and E_3) and flexion (F). See text for details.

relationship of the activity among the muscles, regardless of the speed of locomotion (Grillner, 1975). It is as if an equation of constraint is written over the extensors of the limb, preserving this invariant relationship. As the actual amounts of EMG activity in the extensor muscle groups change with velocity, the ratio of activity among those groups does not change. Suppose the extensor muscle group at the hip shows X amount of activity during locomotion, the group at the knee has Y amount of activity, and the group at the ankle has Z amount of activity. No matter how fast the animal is running, although the absolute values of X, Y and Z will change, the ratio of activity among the three muscle groups is always the same.

It is remarkable that, as the animal runs faster and changes gait, very few details of the step cycle undergo any change. This can be seen by breaking the step cycle into its component phases. Consider a simple plot in which the abscissa represents velocity of running and the ordinate represents amount of time spent in each phase (see Fig. 11.6). As the animal runs faster, the time spent in the transfer phase does not change, whereas the time taken in the support phase decreases considerably. In fact, the E 3 phase of support is the *only* part of the cycle that changes significantly (see Fig. 11.7). It gets shorter as the animal runs faster. The flexion activity of the step cycle is remarkably automatic; it will always bring the leg from position B to position C in approximately the same amount of time regardless of running speed. The duration of E 1 and E 2 change only slightly: it is only during the end of extension, at the boundary of the support
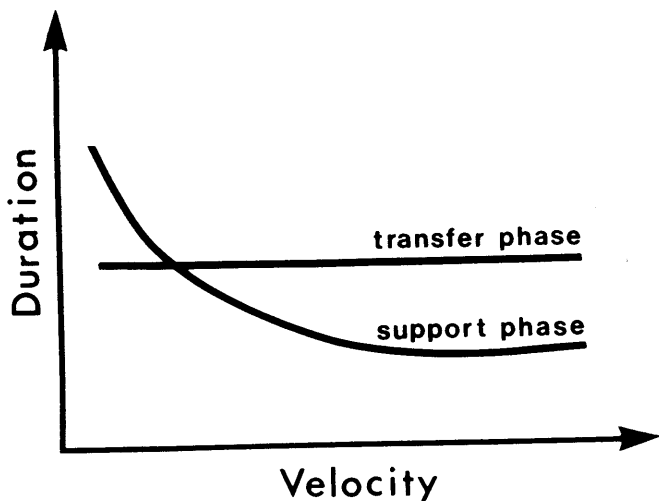

FIG. 11.6. As the velocity of running (x) increases, the duration (y) of the transfer phase remains essentially unchanged, but the duration of the support phase decreases markedly.
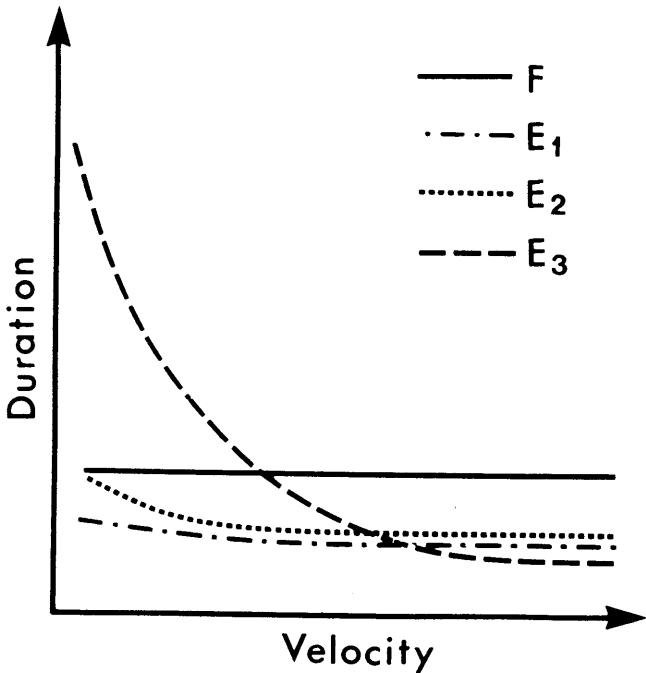
FIG. 11.7. As the velocity (x) of running increases, the durations (y) of flexion (F), flexion to extension (E_1), and extension to landing (E_2) do not change. However, the duration from landing to the next flexion (E_3) decreases considerably as velocity increases.

and transfer phases, that some variation occurs. At that point the system can be modified. In fact, what we see is that running speed seems to be increased by applying more force during E_3, causing its total duration to shorten (Shik & Orlovskii, 1976).

Now let us turn to the notion of the nesting of coordinative structures. When we discussed the airplane organization, we wrote two equations of constraint to form the aileron–rudder subsystem and a third equation of constraint to form the elevator subsystem. Another equation of constraint written over the two subsystems allowed the "nesting" of these automatisms. With respect to locomotion, the discussion thus far has been limited to the systematic behavior of a single limb, and how that systematic behavior can be described in terms of muscle linkages—equations of constraint. We now turn to the systematic behavior of two and four legs in the locomoting of a four-legged animal and ask how this systematic behavior might be understood. Again, we find the airplane example to prove useful.

There are a number of gaits, or styles of coordination, available to the four-legged animal. These different styles can be characterized as different nestings of the single-limb step cycles. One style is the alternate-step gait in which the legs are one-half cycle out of phase. This is the gait used by humans for walking and running. When a four-legged animal uses an alternate-step gait, any given limb is always half a cycle out of phase with the other limb of the same girdle. So in an alternate-step gait (see Fig. 11.8), the two limbs at the shoulder are always half a cycle out of phase with each other. In effect, an equation of constraint links the two limbs such that, whatever the position of a given limb, the other limb of the same girdle must be in a specified position as defined by that equation. This is directly analogous to our airplane example—if the aileron is in one position, the rudder must be in some specific position defined by the equation. Experiments have been performed where an animal is running with one leg on one treadmill and the other leg on a faster treadmill; the second, faster limb is running in a shorter cycle than the first, yet the .5 out-of-phase relationship is preserved (Kulagin & Shik, 1970). In alternate-step gaits it is as if an equation of constraint functionally binds the limbs of a girdle, holding the limbs in a specified relationship.

We have considered an equation of constraint linking the muscles of a single leg, and an equation of constraint linking the two limbs of the same girdle. Consider a form of running in which both these equations of constraint are preserved. An additional constraint must hold to coordinate the two girdles. In the trot, the opposite limbs of the different girdles are synchronized so that, for example, the right limb at the hip girdle and the left limb at the shoulder girdle go through their cycles together. The cross limbs of different girdles are syn-
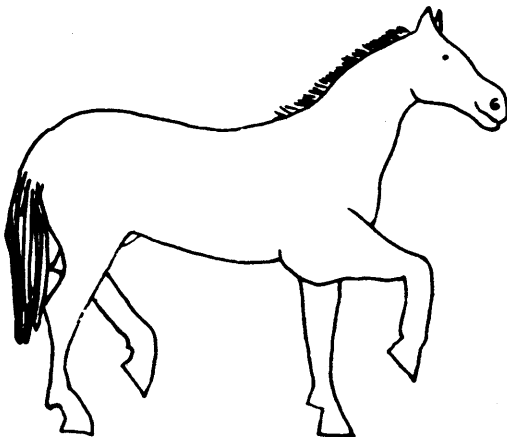

FIG. 11.8. In the alternate-step gait, any given limb is always one-half cycle out of phase with the other limb of the same girdle.

chronized in trotting, whereas the limbs of the same girdle preserve a half-cycle out of phase relationship between them. As the animal switches into the (rack) or pace, the limbs of the same side (and hence different girdles) are synchronized. Think now what that means. To do the trot, the opposite legs of different girdles are linked so as to be in phase; to do the pace or rack, the same-side limbs of different girdles are linked so as to be in phase (see Fig. 11.9).

We now have a family of equations of constraint. In alternate-step gaits only two equations of constraint are used at any one time. One constraint is needed over limbs of the same girdle and one constraint over limbs of different girdles. If we now break the constraint on limbs of the same girdle, just eliminate it, then the animal goes into a gallop. Notice in a (gallop) limbs of the same girdle now move approximately in phase with each other, whereas limbs of the shoulder girdle and limbs of the hip girdle move approximately out of phase with each other (see Fig. 11.10). When an animal gallops, it is no longer necessary that the
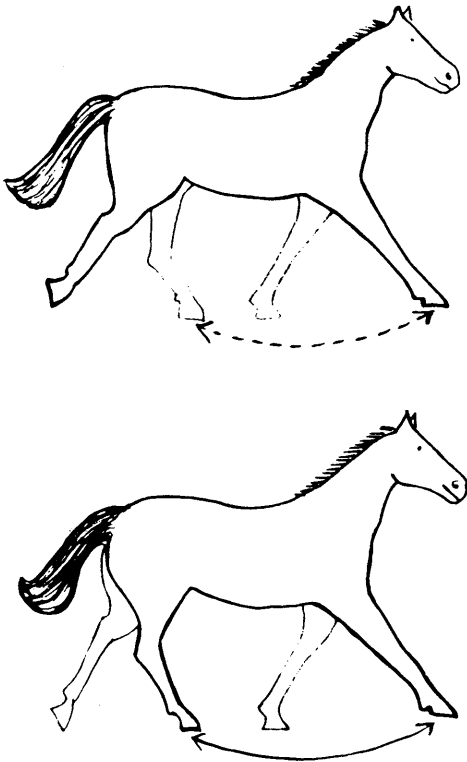

FIG. 11.9. (Top) In the trot the opposite limbs of different girdles are synchronized.
(Bottom) In the rack, or pace, the limbs of the same side are synchronized.

two limbs on the same girdle be half a step out of phase. However, if you have ever closely watched a galloping animal, you will notice that the animal actually does not land with both limbs simultaneously. One limb lands very slightly before the other. It may be the case that a gallop is actually a synthesis of the two larger constraints—the one that defines the rack (ipsilateral, or same-side limbs synchronized) and the one that defines the trot (contralateral, or opposite-side synchronized). It may be that the combination of these two equations of constraint results in a gallop (see Fig. 11.10).

In these examples, a set of elements (muscles, joints, or limbs) are linked by means of a set of equations of constraint. Linking elements in this fashion reduces the number of degrees of freedom that must be controlled independently. This number is always smaller for a set of constrained elements than for a set of elements that are free to vary independently. Essentially, establishing linkages or constraints produces a system in which effective coordination of elements is possible. We now go a step further and ask: What *kind* of system or device is produced when elements of the motor apparatus are linked by equations of constraint? A major clue is provided by the fact that a coordinative structure is a device which adjusts itself automatically to changing external conditions in the sense of reaching the same final position from any initial position.

There is a very simple and commonplace device that exhibits the property just noted—a mass-spring system. A mass-spring system is simply a spring attached at one end to a fixed support and at the other end to a mass (see Fig. 11.11).
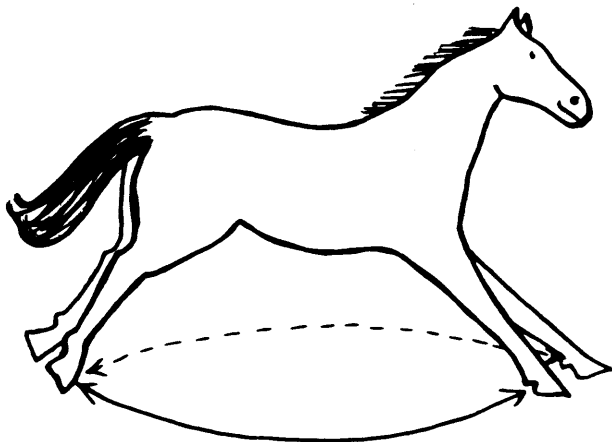

FIG. 11.10.   In the gallop, limbs of the same girdle are in phase with each other. The constraint linking limbs of different girdles appears to be a synthesis of the rack (same-side limbs synchronized) and the trot (opposite limbs of different girdles synchronized).
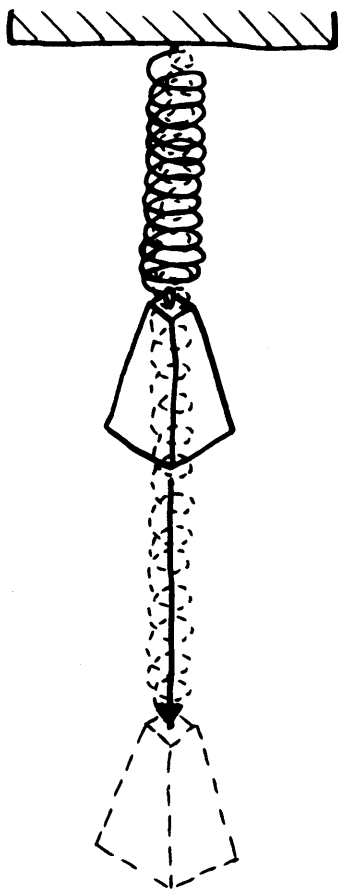
FIG. 11.11. A mass-spring system, consisting of spring attached at one end to a fixed support and at the other end to a mass.

When the mass is pulled it stretches the spring. When let go, the mass (and spring) oscillates eventually coming to rest at some position. When the mass is pushed it compresses the spring; releasing the spring again causes the mass (and spring) to oscillate. However, the system will eventually come to rest at exactly the same equilibrium position as it assumed after the spring was pulled. Given a mass-spring system displacing the mass by pulling or pushing does not affect the final equilibrium position, the length of the spring at rest. Nor is this final equilibrium position affected by the *amount* that the mass is displaced. In sum, the system equilibrates at some constant length of spring regardless of initial conditions.

Notice another characteristic of the mass-spring system: Not only does it get to where it is going regardless of initial conditions, but it does so without any

"homunculus" or external controller directing it. The spring adjusts automatically to changes in its context. Picture the situation in which the adjustments of the spring are not automatic but must be controlled directly by the "little man in the head" introduced in Chapter 10. The homunculus sitting outside the mass-spring system must detect the changes in initial conditions and compare the present location of the mass spring to some reference value representing the desired final position of the spring. The homunculus must compute the necessary correction of the mass-spring trajectory and then relay appropriate commands to the mass spring so that the "error"—the distance from equilibrium—is reduced. A system of this sort places an enormous burden of computation on the controller of the spring. Unfortunately, any information that is available to the controller will always arrive too late to be useful. By the time the controller receives information concerning where the spring is in its trajectory, the spring will have already moved into a new position. Thus, the controller would have to correct for more than the discrepancy between where the spring is and where it should be. The controller would also have to correct for the discrepancy between its information about the position of the spring, and the position to which the spring has moved since that information was sampled.

The reality of the mass-spring system, and other oscillatory systems, is that no such "error-correction" is necessary. The system adjusts itself automatically without choice or computation and without increasing the number of degrees of freedom that must be regulated independently. No controller or tracking device is necessary. The parameters of the system, the length and stiffness of the spring and the weight of the mass, uniquely determine the equilibrium position of the mass spring.

Do normal movements of a biological system exhibit the same properties as oscillatory systems? Some experiments suggest that they do: Movements at the elbow (Fel'dman, 1966) and finger movements (Kelso, 1977), for example, act analogous to a mass-spring system. In one experiment subjects moved their forefinger some distance of their own choosing. Their finger was then passively moved by the experimenter to some other location. The subjects' task was to reproduce either the final position or the amplitude of the first voluntary movement. Let us consider this experiment (Kelso, 1977) in some detail.

Suppose that your finger is in a position forming a 180° angle with respect to the palm of your hand (S_1 in Fig. 11.12). You are now instructed to produce a finger movement of your own choosing and let us say that you move the finger to a position that is at a 130° angle with respect to your palm (P/A in Fig. 11.12). This movement can also be described as being of a certain amplitude, that is, a movement of 50°. The experimenter then moves your finger to some starting position different from the original angle of 180°, say 200°, and asks you to reproduce either the final position of a 130° angle, or to reproduce the movement amplitude of 50°. The task is complicated by the fact that two sources of information that are normally available to you have been removed. You cannot see your
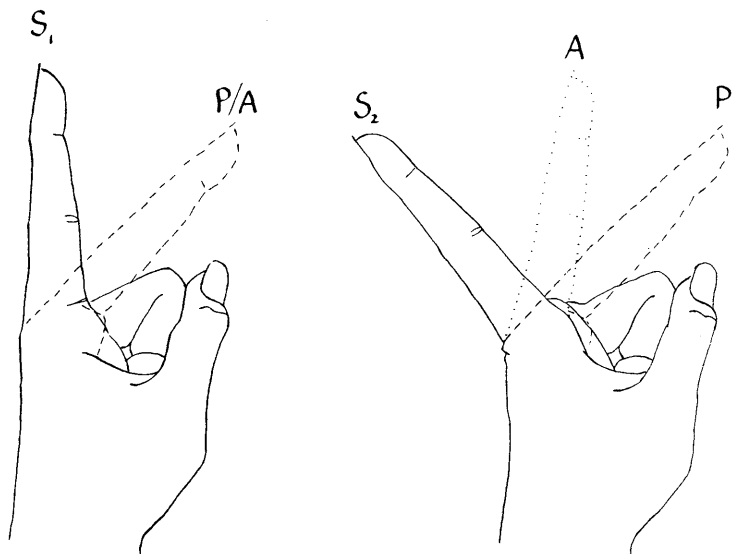
FIG. 11.12. In the experiments by Kelso (1977), subjects moved their forefinger from an initial starting position (S_1) to some location of their own choosing. Their finger was then passively moved to a different starting position (S_2). The subject's task was to reproduce either the amplitude (A) or the final position (P) of the first movement.

finger, nor can you feel your finger's location. Information from your joint and skin receptors has been eliminated by inflating a cuff around your wrist until the blood flow to the finger is blocked.

So, you attempt to reproduce the amplitude or final position of your previous movement without being able to see or feel what you are doing. As it happens, you will not be very accurate at reproducing the amplitude of your movement. But you will be very accurate at reproducing the final location of your movement. In fact, your ability to reproduce the final position under the conditions of sensory deprivation is as good as when normal skin and joint receptor information is available to you.

The major thing to be appreciated is that your finger movements are not impaired by context-conditioned variability; specifically, they exhibit the property of equifinality. Regardless of where your second movement starts from, you can still reproduce the final position accurately. Moreover, the final position is achieved automatically. It seems unlikely that the distance of the finger from the desired position is computed by a homunculus or other controller with the necessary adjustments relayed as commands to the relevant muscles. After all, no

information is available as to where the finger is, and no "error-correction computation" is possible.

To summarize: We have used the analogy of an oscillatory system to illustrate the kind of device produced when muscles are linked by equations of constraint. This device has many advantages over the individual control of free variables. The advantage we have underscored here is that it is able to equilibrate at some invariant position, adjusting automatically for changing initial conditions.

But there are other advantages of this identity between coordinative structure and oscillatory system that may well be of greater significance. We have been speaking of a constrained collection of muscles as a mass-spring system. It happens to be the case that there are a variety of oscillatory mechanisms of which the mass-spring system is just one, and it is a task for science to determine precisely what kind of oscillator best defines a coordinative structure. In these concluding remarks we wish to simply hint at the possibility that coordinative structures are not strictly oscillators of the familiar mass-spring type but oscillators of a somewhat different kind called limit-cycle oscillators (Kugler, Kelso, & Turvey, in press). The reader need not be bothered by the very formal distinctions that mathematicians and physicists draw between these two kinds of oscillators; it is only important for present purposes to note that limit-cycle oscillators have a property of some consequence for understanding the coordination and control of movement that oscillators of the typical mass-spring type do not possess. Limit-cycle oscillators are mutually synchronizing; that is, where two or more limit-cycle oscillators are interacting, they can influence each other's behavior such that eventually they behave as one. This phenomenon of mutual synchronization—or *entrainment* as it is most commonly called—was first observed serendipitiously (that is, by chance!) by Huygens in the 18th century. He noticed that, when two clocks (and a clock, it should be highlighted, is an oscillatory mechanism with *sustained* oscillations) running at different speeds were both hung on the same thin backboard, they became synchronized and kept identical time. Apparently, the ticking of one clock was transmitted through the thin backboard to the other clock, and vice versa, until eventually the two clocks synchronized. This phenomenon of entrainment appears to occur in movement. Consider, for example, a dog locomoting in one of the gaits described previously. If the step cycle of one limb is perturbed for a brief moment so that it is out of phase with the three other limbs, the step cycles of the three other limbs will change, until, within a few, full cycles, all four limbs are again in the phase relations appropriate to the gait (Shik & Orlovskii, 1965). Entrainment may also be manifest as a "limitation" on activity. Witness the difficulty of performing simultaneously two different rhythms, one with one arm and one with the other. There is an impression of one of the rhythms dominating the other or of the two rhythms converging on a compromise rhythm (von Holst, 1973).

At all events, if constrained collections of muscles are instances of limit-cycle oscillators, then the property of mutual synchronization provides a means by

which a good deal of coordination among coordinative structures can be maintained "for free," as it were, without burdening an executive system. In short, entrainment as a property of neuromuscular systems would help to resolve the puzzle of Bernstein, identified at the outset of this chapter.

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REFERENCES

Arutyunyan, G. H., Gurfinkel, V. S., & Mirsky, M. L. Investigation of aiming at a target. *Biophysics,* 1969, *13,* 536–538.

Fel'dman, A. G. Functional tuning of the nervous system during control of movement or maintenance of a steady posture—III: Mechanographic analysis of the execution by man of the simplest motor tasks. *Biophysics,* 1966, *11,* 766–775.

Gel'fand, I. M., Gurfinkel, V. S., Tsetlin, M. L., & Shik, M. L. Some problems in the analysis of movements. In I. M. Gel'fand, V. S. Gurfinkel, S. V. Fomin, & M. L. Tsetlin (Eds.), *Models of the structural-functional organization of certain biological systems.* Cambridge: MIT Press, 1971.

Grillner, S. Locomotion in vertebrates: Central mechanisms and reflex interaction. *Physiological Reviews,* 1975, *55,* 247–304.

Gurfinkel, V. S., Kots, Ya. M., Pal'tsev, Ye. I., & Fel'dman, A. G. The compensation of respiratory disturbances of the organization of interarticular interaction. In I. M. Gel'fand, V. S. Gurfinkel, S. V. Fomin, & M. L. Tsetlin (Eds.), *Models of the structural-functional organization of certain biological systems.* Cambridge: MIT Press, 1971.

Holst, E. von. *The behavioral physiology of animal and man: The collected papers of Erich von Holst* (Vol. 1). London: Methuen Ltd, 1973.

Kelso, J. A. S. Motor control mechanisms underlying human movement reproduction. *Journal of Experimental Psychology,* 1977, *3,* 529–543.

Kugler, P. N., Kelso, J. A. S., & Turvey, M. T. Coordination and control in naturally developing systems. In J. A. S. Kelso & J. C. Clark (Eds.), *The development of movement coordination and control.* London, New York: Wiley, in press.

Kulagin, A. S., & Shik, M. L. Interaction of symmetrical limbs during controlled locomotions. *Biophysics,* 1970, *15,* 171–178.

Shik, M. L., & Orlovskii, G. N. Coordination of the limbs during running of the dog. *Biophysics,* 1965, *10,* 1148–1159.

Shik, M. L., & Orlovskii, G. N. Neurophysiology of locomotor automatism. *Physiological Reviews,* 1976, *56,* 465–501.