The isolated action of a lower unit of behavior will not usually serve any purpose for the animal. Suppose, for example, that the unit controlling the stepping of a single leg were active all by itself. What good would that do the cockroach? A single leg, stepping all by itself cannot propel the roach anywhere. It can only waste energy. Other units must be active at the same time in order that the action of a leg-stepping unit may make a useful contribution to behavior. Nor can these be just any collection of other units. Insects use their front legs for grooming as well as walking. They rhythmically stroke their front “feet” (tarsi) over their head and down their antennae. There is also a distinctive pattern of leg movement when the roach is on its back and trying to right itself. It obviously will not do to have some legs stepping, some grooming, and some making righting motions all at the same time. In order that diverse lower units may act in concert to generate a coherent behavior of the whole animal, there must be higher levels of organization, levels that permit only those actions that fit together.

An elementary functional unit, when it is permitted to act, directly controls the motor neurons to the muscles, the final common paths for the expression of all behaviors. But, any given elementary unit is only permitted to act some of the time. The elementary unit that underlies the positive light orientation of the coastal snails, when it is allowed to act, directly controls the motor neurons that determine direction of turning. However, it is only allowed to act—it is only potentiated—when the snail is upside down and underwater. When the snail is right side up and/or out of water, the positively phototactic mechanism is depotentiated—not allowed to act. Control over the motor neurons passes to the negatively phototactic mechanism.

The example of the positive and negative phototaxes in the coastal snail displays a three-level hierarchy. At the lowest level are the motor neurons. They directly activate and deactivate the muscle fibers that comprise a muscle. At the second level are the positive and negative phototaxes. These neural circuits do not control muscle fibers directly; rather, they control the pattern of firing in the motor neurons to the muscles. At the third level we have a “decision” circuit. Its control over muscle fibers is twice removed; it determines whether the positively phototaxis or the negatively phototaxis circuit is potentiated. The potentiated taxis controls the firing in a subset of motor neurons, and the motor neurons in turn control the contraction and relaxation of muscle fibers. The decision circuit controls behavior by way of the control it exerts over lower level units (the orienting units), much as a general controls the footsoldiers by way of the control he exerts over their commanders. This layering of control processes is what one means by hierarchical organization in action. And, the pattern of neural connections which determines that the decision circuit controls the phototaxes but not the geotaxis is what one means by the structure of the hierarchical control system. The structure of the system determines what controls what.
WEISS'S APPROACH

forward and backward working in coordination.

The hierarchical structuring of action.

The bottom-up approach of action.

The top-down approach of action.

The interaction of the two approaches of action.

The action of selection and planning.

The action of execution and monitoring.

The action of evaluation and correction.

The action of decision making and control.

The action of adaptation and learning.

The action of communication and coordination.

The action of representation and understanding.

The action of motivation and emotion.

The action of memory and forgetting.

The action of attention and perception.

The action of consciousness and awareness.

The action of survival and adaptation.

The action of evolution and development.

The action of interaction and cooperation.

The action of collaboration and coordination.

The action of competition and conflict.

The action of power and authority.

The action of leadership and management.

The action of governance and administration.

The action of policy and strategy.

The action of law and order.

The action of justice and fairness.

The action of rights and responsibilities.

The action of equity and equality.

The action of freedom and democracy.

The action of peace and security.

The action of prosperity and welfare.

The action of culture and identity.

The action of nature and environment.

The action of society and community.

The action of economy and business.

The action of technology and innovation.

The action of science and research.

The action of education and training.

The action of health and welfare.

The action of sports and leisure.

The action of arts and culture.

The action of religion and spirituality.

The action of ethics and moral.

The action of justice and fairness.

The action of freedom and democracy.

The action of peace and security.

The action of prosperity and welfare.

The action of culture and identity.

The action of nature and environment.

The action of society and community.

The action of economy and business.

The action of technology and innovation.

The action of science and research.

The action of education and training.

The action of health and welfare.

The action of sports and leisure.

The action of arts and culture.

The action of religion and spirituality.

The action of ethics and moral.

The action of justice and fairness.

The action of freedom and democracy.

The action of peace and security.

The action of prosperity and welfare.

The action of culture and identity.

The action of nature and environment.

The action of society and community.

The action of economy and business.

The action of technology and innovation.

The action of science and research.

The action of education and training.

The action of health and welfare.

The action of sports and leisure.

The action of arts and culture.

The action of religion and spirituality.

The action of ethics and moral.

The action of justice and fairness.

The action of freedom and democracy.

The action of peace and security.

The action of prosperity and welfare.

The action of culture and identity.

The action of nature and environment.

The action of society and community.

The action of economy and business.

The action of technology and innovation.

The action of science and research.

The action of education and training.

The action of health and welfare.

The action of sports and leisure.

The action of arts and culture.

The action of religion and spirituality.

The action of ethics and moral.

The action of justice and fairness.

The action of freedom and democracy.

The action of peace and security.

The action of prosperity and welfare.
forward the effect was instead to propel the salamander backward. In this way, Weiss developed a clear and experimentally documented conception of the intermediate functional units in the hierarchically structured neural machinery. He showed that the coordination of front limb stepping with hind limb stepping depended on the organizing effect of a central programming unit that specified a particular, centrally mediated pattern of interaction between the lower units controlling the individual legs. The coordination between legs was not achieved by way of the kind of peripherally mediated process posited by chained-reflex theories of coordination. The stepping of the front legs was not triggered by sensory signals resulting from the mechanical effects of the stepping movements of the hindlimbs (and vice versa). Rather, the units controlling the hind limbs and the units controlling the front limbs were constrained by some central program to interact in such a way as to produce one or another pattern of stepping across all four limbs. The great merit of Weiss's experiments was to show that these higher order constraints operated whether or not the resulting four-limb stepping patterns were functional. The centrally coordinated interaction between the units that control the individual limbs was in some ways as rigid and blind as the computer programs that relentlessly call up the prescribed series of subroutines even when the input to the computer is such that the computations carried out by the subroutines no longer make sense.

At the time Weiss wrote, we had little grasp of what the units controlling individual legs might be and even less grasp of how a higher unit could constrain these lower units to interact in a particular way. Now, however, it seems likely that the lower units are the oscillator-dominated units discussed in Chapter 5. The higher unit—the unit that coordinates walking—constrains the interaction between these oscillators by controlling the flow of coupling signals from one oscillator to the other. This idea will be spelled out in more detail at the end of this chapter.

The lengthy paper by Weiss that follows is remarkable for the incisive introduction to the general nature of the problems posed by the phenomena of motor coordination. As he points out early on, the subject is frequently discussed in a maddeningly vague way. His introduction is also remarkable for its concise and critical review of the major schools of thought—the preformistic structural (innate connections), the heuristic (learned associations), and the systemic (Gestalt) schools.

IN DEFENSE OF CONNECTIONISM

Weiss goes to some lengths to point out the deficiencies in the preformistic structural school of thought, the school which holds that coordinated action is determined by genetically specified patterns of connections between

neurons. The most common objection to this school of thought concerns the ontogenetic aspect—the assertion that the basic determinants of coordination are genetically specified. This is emphatically not Weiss's objection; a central argument in the complete version of Weiss's paper is that the basic determinants of coordination are indeed inherited (or, better, self-differentiated). Weiss is too subtle a developmental biologist to use the vague and confusing term "inherited." He prefers the subtler, but more precise and defensible term "self-differentiated," that is, "differentiated in their essential characteristics independently of the actual intervention of function" (p. 223).
WSESS BASIC PATTERNS OF COORDINATION

SELF-DIFFERENTIATION OF THE NERVOUS SYSTEM

The problem of coordination may be estimated from a recent paper by Vroman in the Psychologische Zeitschrift, vol. 17, no. 1 (1917). His paper treats the problem of the coordination of the nervous system, and a recent paper by Vroman in the Psychologische Zeitschrift, vol. 17, no. 1 (1917). His paper treats the problem of the coordination of the nervous system.


text continued...
of this paper is to present direct experimental proof that the basic patterns of coordination arise by self-differentiation within the nerve centers, prior to, and irrespective of actual experience in their use. In addition, experimental data will be reported indicating what coordination consists of, and how it is laid down in the centers. So specific and articulate has this experimental information been that we would forego the full benefit of its instructiveness if we were to report it in the general inarticulate language in which the problems of coordination are conventionally treated. Since the experiments have produced answers much more differentiated and detailed than any of the questions commonly being asked, we must prepare the ground for their presentation by reformulating the questions with greater precision. One cannot discuss "coordination" profitably so long as the term is kept on the abstract level; ill-defined, and noncommittal in regard to concrete implications. We, therefore, shall try to dissect the general concept of "coordination." By breaking it down into more tangible issues, we make it tractable and give experimental analysis a chance to substitute knowledge for conjecture.

Thus, with a view to discontinuing the practice of speculating about "coordination" without a clear mental picture of just what it implies, we shall first review the facts and reformulate the problems, and only then proceed to present the experiments and, in their light, scrutinize the existing theories of coordination. The notable confusion about terms and facts in this field would justify a much more thorough reconsideration of the whole subject than can here be afforded. However, such an ambitious attempt had better be postponed until more concrete building stones for a good and sound theory of coordination have been gathered than are now available. It is only a few of these building stones that the present paper aims to contribute.

There is a striking disproportion between our knowledge of the physiological properties of nervous elements and our understanding of the operation of the nervous system as the coordinator of those elemental activities in the service of the organism. While the combined efforts of electrophysiological, histological, biochemical and mathematical studies have produced a great wealth of data concerning the elemental activity of the neurone, our conception of the systematic activity of their organized totality has essentially remained pegged to the level to which it had been raised by Sherrington's classic work on the "Integrative Action of the Nervous System." We do not mean to imply that some progress has not been made here and there. Brain physiologists and neurologically-minded psychologists, in their efforts to interpret behavior in terms of the function of the nervous system, naturally had to focus on the system as such. From their studies, they were led to conclusions which partly supplemented, partly discredited, the synthetic conception of the nervous system to which preoccupation with the nervous elements had led. Yet, although they succeeded in pointing the direction toward a more adequate theory of central functions, the actual progress made thus far appears small when contrasted with the spectacular growth of our information about the nervous units during the same period. A mere comparison between the volume of attention currently paid to the issue of synaptic transmission—whether chemically or electrically mediated—on the one hand, and the almost complete neglect of the problem of how central transmission has come to be so discriminatory and selective as to lead to coordinated responses, rather than to unorganized convulsions, on the other, puts the situation into sharp relief. A restoration of sounder proportions should be attempted, of course, not by detracting from the current vigorous trend toward the isolated elements, but by reviving interest and revitalizing research in matters which concern the integrative aspects of the nervous system. If such course is to be followed with profit, it will pay, at the outset, to examine the possible reasons of its lag in the past.

A few explanations suggest themselves quite readily. The most obvious one is the infinitely greater difficulty and complexity of the task facing the student of the nervous system. This may be a challenge to inquisitive minds, but it certainly does not predispose the subject for mass attack by routine methods. So long as one clings to the study of elements, one is dealing with well-circumscribed units, a well-defined subject, presenting clearcut problems, and one can call on familiar and approved methods of analysis. As soon as one raises the eye from the unit to the whole system, the subject becomes fuzzy, the problems ill-descript, and the prospect of fruitful attack discouraging in its indefiniteness. This may explain why a considerable number of able experimental workers prefer to circle around the focal problems at a respectful distance rather than heading straight at them. It also explains why discussions of central nervous function operate so much more liberally with words than with facts; for it is remarkable how general the tendency is in this field to cover up factual ignorance by verbalisms. The average attitude is somewhat like this: the "whole" gets a large share of one's thought and talk, but the elements get all the benefit of one's actual
The hierarchical structuring of action

When we think about the structure of actions, we often consider the hierarchical nature of these structures. At the highest level, we have broad goals or intentions that guide our actions. These goals are then broken down into more specific sub-goals, which in turn are further refined into specific actions. This hierarchical structure helps us organize and prioritize our actions effectively.

Within this framework, the selection of actions is guided by the overall goal. Each action is chosen based on how well it aligns with the goal and how it contributes to achieving it. This process is recursive, with higher-level actions shaping the selection of lower-level actions.

The hierarchical structuring of action is also reflected in the neural systems that support these processes. Different areas of the brain are involved at different levels of the hierarchy, with some areas responsible for goal selection and others for action execution.

The hierarchical structuring of action is not only a fundamental aspect of human behavior but also a key feature in the design of artificial intelligence systems. Understanding this structure helps in the development of more effective and efficient decision-making algorithms and robotics systems.
be found—by his neighbor. In this sense, the denial that the central nervous system presents problems *sui generis*, has undoubtedly been a potent deterrent from a vigorous attack on those problems.

It is not to be questioned that the attempt to identify in the central nervous system properties familiar from peripheral nerve elements has met with spectacular success. In fact, faith in the fundamental identity of both has been rewarded by discovery in the peripheral elements of properties which had formerly been known only to occur within the centers (see Gasser). However, by confining attention to those phenomena which the peripheral and central systems have in common, we plainly relegate the specifically central phenomena to continued obscurity; by “specifically central” we mean the ones that are not recoverable from peripheral investigations. *Coordination* is a case in point, and this brings us to our immediate subject.

Even though we can interpret other central phenomena, such as reaction time, summation, rhythmicity, inhibition, irradiation, fatigue, etc., in terms of known properties of neurones, the specific *order* in which the units are brought into play so as to produce effects serviceable to the organism, is nowhere accounted for in this scheme. It is this order that is commonly referred to as “coordination,” with implications that are not always clearly realized. Coordination means the *selective* activation of definite groups of units in such combinations that their united action will result in an organized peripheral effect that makes sense. But what principle is there in operation in the centers to make the appropriate selection? And in what terms is the choice being made? Here is a question aimed at a “specifically central” phenomenon, evidently of fundamental importance, and yet one that is hardly ever asked explicitly, and still more rarely answered in anything but the most general of terms. Really only a very few have taken the trouble of penetrating beneath the surface of the problem, and although, as we shall show below, none of their efforts have as yet yielded wholly acceptable results, they have at least emerged with some definite suggestions that can be put to test and serve as points of departure for further clarification. In addition to the few who have given the matter mature thought, practically every biologist and psychologist carries in his mind some sort of notion, specific or hazy, of the mechanism of coordination, which he has usually acquired unconsciously and by accident.

Disregarding their various shades, we can class these notions, both rational and instinctive ones, into three different groups: the *preformistic*, the *heuristic*, and the *systemic* theories. All three start from the fact of the transmissibility of excitation from one nerve element to another, and go on to explain why transmission in the normal nervous system does not occur indiscriminately, ending up in mass contraction of all muscles, but remains confined within certain channels, yielding an orderly and differentiated response. For the time being, we may ignore the fact that by stamping the problem as purely one of controlled transmission we subject our search to an unwarranted limitation from the very start. Inasmuch as most speculations on coordination have tacitly accepted this limitation, they do not essentially differ on that point. From here on, however, they diverge.

**THEORIES OF COORDINATION**

The Preformistic-Structural Concept

The first and most popular interpretation of coordination is the reference to stereotyped inherited anatomical neurone connections in the centers. It is based on the study of reflexes, the observation that in many simple reflexes there is a fairly definite and constant relation between the point of stimulation and the nature of the response ("reflex-arc"), and the assumption that the chain of events leading from stimulus to response is anatomically preformed in a chain of neurones leading from the sense organ through the centers to the effector. The biological adequacy of the response, according to this concept, is a result of the correct construction of the anatomical apparatus, that is, among other things, of the suitable distribution of the peripheral and intracentral neurones, suitable arrangement of the central switches among neurones, suitable arrangement of the muscles on the skeleton and suitable form of the joints; “suitable” in the sense of making the whole response come out as of service to the organism. In other words, the body has its coordination built in.

In designating this concept as “preformistic,” we do not use the term “preformation” in the sense in which it is used in embryology. There it refers to the existence of organized patterns in the egg prior to the onset of *development*, while in the present connection it merely implies the presence of definitely organized innervation patterns in the centers prior to the onset of their actual *operation*. Developmentally speaking, these patterns have, of course, been differentiated according to the same principle of progressive (epigenetic) determination which dominates embryonic development in general (P. Weiss, 1939). Only in functional regards may we call them “self-differentiated,” that is, differentiated in their essential characteristics independently of the actual intervention of function.
That most judicious student of the anatomy of the central nervous system, had to say in this connection (1950):

No complication of separate and insulated reflex arcs, each of which is conceived as giving a one-to-one relation between stimulus and response, and no interconnection of such arcs by elaborate switchboard devices can conceivably yield the type of behavior which we actually find in higher vertebrates. These facts are regarded as incompatible with the traditional dogmas of reflex physiology, with its precisely localized and well-insulated reflex arcs and centers of reflex adjustment. The mechanisms of traditional reflexology seem hopelessly inadequate (p. 845).

However, even if the concept of a rigid anatomical neurone linkage were adequate to explain the single pendulum-like action of a hinge joint, it must utterly fail as a basis of coordination in any more general sense. For most joints are constructed so as to allow of more than one degree of freedom and, therefore, require more than two sets of muscles, inserting and acting in different planes.

A ball joint, such as the shoulder joint, can be moved in any plane laid through its center (Fig. 8.2b). The direction in which it actually moves at any given moment, is determined by the resultant of muscular tensions acting from all sides. Depending on the combination of active muscles and the relative strength of their contraction, an infinite variety of positions can be assumed. Variety of movement is thus made possible by varying the combination of muscles called into action. While it is easy to separate the muscles of a hinge joint sharply into agonists and antagonists, such classification is no longer applicable to a ball joint. Any two muscles may facultatively operate as agonists or antagonists. The following example, which refers to a specific case dealt with later in this paper, will help to make this clear.

Let us consider the shoulder joint of a tetrapod. Ignoring the finer details of the distribution of its muscles, we recognize four main groups converging upon the humerus from four different directions, schematically along the four edges of an imaginary pyramid (Fig. 8.2b and 8.3). Acting individually, these muscles—listed in counterclockwise order—would pull the humerus upward, forward, downward, and backward, respectively, and they may be designated accordingly as elevator (El), abductor (Ab), depressor (De), and adductor (Ad). Through their graded contraction in proper combinations the humerus can be made to describe a full circle, eight representative stages of which are reproduced in Fig. 8.3. To bring

![Fig. 8.3. Eight positions of the ball joint of Figure 8.2b, assumed through the contraction of its muscles in the combinations listed in Table 8.1. The posture in which all muscles are evenly contracted is pictured in phase 0; it is indicated throughout the following phases by dotted lines, the arrows showing the direction of the excursions.](image-url)
The Heuristic Concept

Weiss/Basic Patterns of Coordination

---

Table 8.1 The Hierarchical Structuring of Action

<table>
<thead>
<tr>
<th>Action</th>
<th>Resulting</th>
<th>Phase</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dorsal</td>
<td>PA</td>
<td>7</td>
</tr>
<tr>
<td>Cranial</td>
<td>PA</td>
<td>6</td>
</tr>
<tr>
<td>Opharyngeal</td>
<td>PA</td>
<td>5</td>
</tr>
<tr>
<td>Palatine</td>
<td>PA</td>
<td>4</td>
</tr>
<tr>
<td>Cervical</td>
<td>PA</td>
<td>3</td>
</tr>
<tr>
<td>Thoracic</td>
<td>PA</td>
<td>2</td>
</tr>
<tr>
<td>Abdominal</td>
<td>PA</td>
<td>1</td>
</tr>
</tbody>
</table>

Note: PA stands for "Progression Action."
wholly tentative grouping of the muscles through which it is brought about. Whether the trials in this "trial-and-error" procedure are entirely random, or whether they show some method and direction; whether the drive to move is produced within the organism or furnished by external stimulation; whether the "associations" are to be viewed as nerve fiber connections, or whether—following behavioristic maxim—one had better refrain from such attempts at visualization; all these are relatively minor matters compared with the basic tenet in which all heuristic theories agree: that the central nervous system is a plastic mold upon which experience gained in actual performance gradually inscribes the patterns of coordinated behavior, with the adequacy of the effect for the organism as a whole serving as the standard of rating. This concept has been advanced for the lowest (Jennings, 1931) as well as for the highest forms of animals (Pavlov, 1927), and it has been variously applied to the development of nervous coordination from the highest cortical acts down to the most elementary motor functions.

The Systemic Concept

The systemic theories of coordination have in common with the heuristic theories the assumption of practically unlimited plasticity of the nervous system. However, instead of letting coordination become built up bit by bit through trial and error methods, they concede to the nervous system a primordial dynamic ability to respond to any change in the external stimulus situation by a total response of maximum adequacy for the organism as a whole. According to this view, entirely novel stimulus situations, neither provided for in the organization of the animal nor previously experienced, can be met by a primary response of great suitability. This view, shared by many Gestalt psychologists, has been particularly elaborated by Bethe (1931) and Goldstein (1939). The contrast between the heuristic and systemic concept can perhaps be expressed as follows: according to the former, partial reactions (elementary sensomotor responses) of no definite directiveness are variously recombined until they finally compose a chain the resultant direction of which has affirmed its value for the organism; whereas, according to the latter, resourceful dynamics of the central nervous system lay down the general direction of the total response as a sort of frame through which the partial reactions necessary for its execution are forced in channels consonant with the general "intention." In this view, the drive toward a certain real or visualized goal would directly produce the proper muscular innervation necessary to attain that goal.

SUMMARY

Reduced to the terms of the preformistic-anatomical (1), heuristic (2), and systemic (3) theory, respectively, the coordinated advance of the organism toward a desirable goal, and its coordinated retreat from a harmful situation, could be expressed as follows:

1. Beneficial and nocuous stimuli enter through different adequate receptors, activate each a system of separate pre-arranged lines which, in turn, engage a pre-arranged selection of muscles in a pre-arranged time order, the combined action of which then becomes manifest as a motion of advance or withdrawal. The appropriateness of the response is based on the appropriateness of the inherited pre-arrangements; the individual itself deserves no credit for it.

2. Either kind of stimulus evokes ubiquitous random reactions, including excursions of limbs and trunk of continuously varying patterns, which are tried and discarded and repeated and altered, until eventually the correct composition and sequence is discovered; the animal is to be given credit for its resourcefulness in producing ever changing assortments of undirected responses, as well as for its faculty to choose and retain those that prove to lie in the right direction.

3. Any stimulus produces a general response the character of which is directly determined by the constellation of the external field of stimuli and the internal state of the centers, resulting in a primarily directed movement; the centers get credit for their ingenuity.

To reduce the various theories of coordination to such simple formulae, admittedly involves a great deal of abstraction and oversimplification. Moreover, many authors, in discussing these matters, have failed to take an explicit stand, which puts it up to the interpreter to extrapolate their basic beliefs from casual remarks; which is a doubtful task. Again, some have taken compromise attitudes, contaminating one theory with admixtures from another, which makes a strict classification of their views impossible. Hence, no more than practical significance should be attached to the attempt of the preceding pages to group all existing theories of coordination into the three outlined categories. The justification for that attempt
Weiss/Basic Patterns of Coordination

333

The Experimental Study of Coordination

be subjected for coordination and thus project the experimental results, which they

must
then
produce
the
experience
and
inference
of
the
voluntary
actions,
the
methods
in
which
to
explain
the
issue
in
the
coherent
coordinated
processes
and
the
behavioral
patterns
of
action.
offered. Some pertinent experiments were made on the coordination of eye movements after muscle translocation in mammals (Marina, 1912), but the results have remained controversial (Dusser de Barenne & de Kleyn, 1929; Olmsted, Margutti & Yanagisawa, 1936). An isolated report of reorganization of limb coordination in the frog (Manigk, 1934) was shown to have arisen from a faulty interpretation of the underlying experiments (Taylor, 1936). But in spite of this lack of convincing experimental proof, the view seems to prevail that the locomotor apparatus of an animal can undergo essentially the same kind of adjustable "re-education" which has been demonstrated in man.

Critical experiments on amphibians, however, have contradicted this view decisively. As will be reported below in greater detail, these animals show no trace of readjustment of muscle coordination under comparable circumstances. To avoid misunderstandings, it may be added that while the basic coordination mechanisms through which all locomotor acts must be executed are in themselves quite unmodifiable in amphibians, the total behavior of these animals can be somewhat modified by training. They can learn to advance or retreat on different occasions, but they cannot learn to change their manner of walking or retreating. Similarly, recent experiments on the rat have definitely shown that the time pattern of coordination of the hind limb muscles of these animals, too, is rigidly fixed and remains incorrigible even after the crossing of antagonistic muscles resulting in permanent reversal of movements (Sperry, 1940). There may be a trace of re-adjustment after transposition of muscles in the fore limb of the rat (Sperry, see below), and as we extend the examination to higher and higher mammals, we may expect to find a growing faculty for such corrective measures of the nervous system. The essential point, however, remains that this faculty is a very late evolutionary acquisition of the central nervous system, practically still absent in as high an animal as the rat, and consequently entirely unfit as a model of the principle of coordination in general. (See p. 264–268.)

We must once and for all renounce the idea that the type of muscular control with which we are most familiar, namely, our own, or at least that part of it of which we are consciously aware, represents the fundamental type of vertebrate coordination. Man can learn to engage individual muscles independently, but most animals cannot. This is why the anthropocentric approach to the general problem of coordination is misleading and has failed to produce results of general applicability whenever attempted.

The issue has often been further obscured by ill-defined and unverified generalizations of the concept of "learning." "Learning," that is, an adaptive modification of behavior in response to recurrent stimulus situations, has been demonstrated to occur, at least in traces, in most branches of the animal kingdom, from the lowest forms up. However, the strict constitutional limitations of this learning ability do not seem to be generally realized, or if so, have certainly not received due emphasis. There is agreement that the total motor performance of an animal can be modified by experience, but since the total performance is an integrated act, involving shifting combinations of partial performances of more elementary character, it remains to be demonstrated whether the modification concerns those elementary acts—the building blocks of behavior, as it were—as such, or merely their combination into more complex actions on a higher level. The mere assertion that the response mechanisms of the animal as a whole are not absolutely rigid but provide for some degree of adaptation, does not reveal whether this plasticity extends to all parts of the behavioral mechanism alike or is a privilege of certain components only, and if so, of which. Adaptive behavior presupposes functional reorganization somewhere; but where? Is the whole nervous system one vast pool of equivalent elements whose functional relations can be infinitely varied by experience, or is adaptability confined to some of its divisions or some of its functions only, while the rest are immutable?

The question is no longer whether learning is a common faculty or not. The answer to this has become a matter of course. What we need, is to know precisely what functions are amenable to change and what others are not; further, what functional elements, or groupings of elements, remain constant and unmodifiable even as the behavior pattern of which they form integral parts changes. Behavior results from the activities of a hierarchy of functional levels, each of which may or may not be adaptable. Plasticity on any one level neither implies nor precludes plasticity on any other level; the only means to test their capacities is by way of experiments.

Let us briefly illustrate the various levels.2 Confining ourselves to metazoans possessing a differentiated nervous system, we may dismiss subcellular entities and start right at the cellular level. There we find as the lowest recognizable elements to which a measure of functional stability may be conceded, the individual motor units, the

---

2This list is more pertinent than one published on an earlier occasion (P. Weiss, 1925).
Weiss/Basic Patterns of Coordination

236

...
several limbs in the acts of locomotion should not be equally adept at changing the rhythm of the several muscles within the limb, if in last analysis it all comes down simply to rearranging neurone linkages.

However, this view is strictly contradicted by the facts. We have already quoted evidence to show that in amphibians, and even the rat, the time order according to which muscles execute a limb movement is unalterably fixed, while at the same time the total behavior of these animals is amenable to reconditioning by training and other regulatory adjustments. In the light of these facts, the distinction between rigid and plastic functional levels assumes great significance, as indeed the neglect of the hierarchical principle would lead, and has led, to serious confusion. In brief, the fact that an animal can learn (on levels S and W) to use its limbs differently in moving the body, does not necessarily imply that it can likewise learn (on levels O and G) to use its muscles differently in moving a limb. Adaptive functional reorganization is a prerogative of certain functional levels only. Therefore, in raising the question of learning separately for each level, we merely give expression to realities.

The preceding pages may suffice to bear out our contention, that progress in the study of coordination has been held up both by lack of restraint in extrapolating from higher mammals to animals in general, and by lack of precision in the application of the principle of learning. In this state of affairs it is not surprising to find the changes observed after tendon transposition, muscle transplantation, nerve crossing, sectioning of central tracts, destruction of brain portions, and similar interferences, lumped together indiscriminately under the common headings of re-education, regulation, functional restoration, reconstitution, reparation, reorganization, readjustment, and the like. If in the future more discretion will be exercised in the use of these terms and if the mere statement, that a behavioral change has occurred, will be amplified by precise information as to what this change has consisted of and where it has taken place, the gain for our understanding of nervous function will be enormous. Then, all the mentioned interferences, instead of merely serving to tell whether or not "functional recovery" can occur, become discriminative assay methods, revealing the degree in which the various functional levels participate in the noted "adjustment." It is in this assaying capacity that the transplantation experiments to be discussed below have been used, and since this method invites much wider application, a few comments on general methodology seem appropriate.

Experimental Methodology

As all biological experiments, those dealing with the nervous system fall essentially into three classes: defect experiments, isolation experiments, and recombination experiments (compare P. Weiss, 1939, p. 147 f.). Given a system Y, consisting of parts A, B, C, D, and so forth, the experiment aims at establishing the relations between the system and its parts, as well as among the constituent parts, by severing the existing relations. Singling out, for instance, part A, the isolation experiment determines the properties and capacities of A, when completely released from the rest of the system, while the defect experiment, complementary to the former, ascertains the properties and capacities of the remainder of the system (Y minus A). In both cases the relations between the system and the parts are permanently interrupted. It is left to the recombination experiment to supply the positive part of the story by restoring connection and relations between the severed components, however, with such added variations from the original condition that it will be possible to discern whether and in what respect the relation between the system and part A differs from its relation to parts B, C, and so on. Part B is supplanted for part A, and vice versa, and the subsequent conduct of the altered system is studied. If the system behaves as before, we conclude that A and B are equivalent; if it behaves differently, the change is ascribed to the differential between A and B.

In the past the defect experiment has been by far the predominant method in the study of nervous function. The value of the isolation experiment is increasingly appreciated; witness the work on isolated nerve fibers and isolated brain parts. The recombination experiment, however, has been largely neglected. Yet, its instructiveness greatly exceeds that of the defect experiment. In what respect, can be easily shown.

Let us quote an example. We cut a tendon and note subsequently that limb movements are changed. Now, the operation has altered a number of conditions in one stroke: It has caused trauma, produced a gap in the elastic continuity of the tissues, interrupted the transmission of pull from muscle to skeleton, abolished stretch reflexes from the affected muscle, and, as a result, changed the mechanical and innervatory balance of other muscles. What each one of these factors contributes to the common defect, cannot be immediately discerned. Their effects can be separated, however, by resuturing the tendon stumps in various modifications—under slack
AN ANALYSIS OF COORDINATION IN AMPHIPHIA

WEISS/BASILICS PATTERN OF COORDINATION


AN ANALYSIS OF COORDINATION IN AMPHIPHIA

THE General Problem of Analyzing Motor Coordination in AMPHIPHIA

innervation for these transplants by diverting to them some motor nerve branch from one of the normal host limbs. The amount of deviated nerve fibers can be held to such insignificant proportions that no perceptible change in the function of the host limb results. This small nerve source is fully adequate to assure complete reinnervation of the transplant, inasmuch as nerve fibers in the course of regeneration undergo profuse branching. The experiments were so devised as to assure that the muscles of the transplants would be reinnervated for the most part or wholly by nerves with which they formerly had no relations. After transmissive connections between the regenerated nerve fibers and the grafted muscles had been restored, the supernumerary muscles began to exhibit regular and strong contractions whenever the host limb, from which their nerve supply was derived, moved.

The stress, however, lies not so much on the fact that the transplanted muscles had become re-engaged in functional activity, but on the peculiar time order in which they were found to operate. Extensive studies, under a great variety of conditions, of the precise times when a transplanted muscle starts to contract and ceases to contract, as well as of the degree of its contractions during that active period, has revealed a principle of such definiteness and constancy that it amounts to a law. The phases of activity of an extra muscle correspond precisely to the phases in which the muscle of the same name, or synonymous muscle, is found to be active in the host limb innervated from the same plexus of the spinal cord. Whether the transplant consists of a single muscle, or a group of muscles, or a whole limb, each individual muscle as such duplicates the action of the synonymous muscle in the normal limb nearby. This phenomenon has been described, and ever since been referred to, as "homologous response" of synonymous muscles. The term signifies that if a body district is provided, instead of with a single muscle of a given kind, with two, three, or even four homologous muscles of the same kind and name, all of them will act in unison, the contractions beginning at the same moment, developing the same proportional tension and subsiding at the same time; the only prerequisites being, that all of them receive their nerve supply from the same side and the same general level of the spinal cord (e.g., limb level in the case of limb muscles), and that the transplantation be done in young, preferably metamorphic, animals.

Now, what does this phenomenon of "homologous response" actually mean? In spite of the ample attention given to it in the past, it does not seem that the majority of authors have succeeded in seeing it in the correct light. Many authors, while reporting the phenomenon correctly, yet have missed the point which it so clearly proves, namely, the existence of correspondences of a specific kind between nerve centers and individual muscles. Thus, the phenomenon was variously described as demonstrating almost unlimited "plasticity of coordination," "learning capacity" even at the lowest level, "adjustments" of the nervous system to the introduction of a new organ, integrative action of the spinal cord, and so forth. Some of these interpretations are strictly incorrect, others merely besides the point. It would be idle to try to fix the blame of these misinterpretations. Part of it can probably be ascribed to lack of clarity in the earlier descriptions of the phenomenon, as well as to misleading terminology, part to the fact that the problem of coordination, to which the phenomenon offered a clue, was not usually presented in the correct light. It thus becomes necessary once more to explain the intrinsic meaning of this phenomenon of "homologous response" of synonymous muscles.

To begin with, to emphasize the fact that the transplanted muscle and the synonymous muscle act in unison, is already putting the wrong slant on the phenomenon, because in stressing the association of the two peripheral parts, we give prominence to a rather irrelevant aspect. We make it appear as if the transplanted muscles, or rather their centers, have in some way learned to imitate the synonymous normal muscles, even though it would be difficult to find any plausible reasons why they should have done so. To avoid this misconception, it must be stressed that in all these experiments the normal muscles simply serve as indicators of the hidden activities of the central nervous system, and that their actual presence is in no way required for the appearance of the phenomenon. Even if all muscles of the normal limb are removed, the transplanted muscle keeps on functioning at precisely the phases when the removed synonymous muscle would have functioned if it were still present. But so long as a normal limb is available, we use it as a detector to tell us which combination of muscles the central nervous system tends to activate in any given phase of a locomotor act.

Let us now forget for a while that effective limb movements are of service to the animal, and let us consider them simply in their service to the observer as convenient instruments for the visible registration of the content of the varying central commands. To be used for this purpose, movements must be resolved into muscle actions. This can be done directly or indirectly—directly, by connecting the muscles with mechanical or electrical recording devices, as is commonly done in the study of simple reflexes with fairly constant stimulus-response relations; indirectly, by taking cinematographic records of the
The term "coordination of action" refers to the facilitation of the interaction between the various components of the body in order to perform a specific task. This coordination is achieved through the integration of feedback from various sensors, such as joint position and force sensors, and the central nervous system's ability to interpret this information and generate appropriate motor commands. The coordination process is also influenced by the body's current state, such as its velocity and acceleration, and the context in which the movement occurs, such as the desired trajectory and the desired endpoint of the movement. The coordination of action is a dynamic process that takes place in real-time, allowing for the adaptation of the movement to changing conditions.
is an important concept. The model of the output probability framework is a key factor in the determination of the output and input probabilities, which are derived from the input observations. The output probabilities are used to update the model parameters, which in turn are used to predict future observations. This process is repeated in an iterative manner until the model parameters converge to a stable state.

The iterative nature of the process allows for the self-correction of the model, improving its accuracy over time. The model parameters are updated based on the differences between the observed and predicted values, which are used to adjust the parameters in a way that minimizes the error. This process is repeated until the error is minimized, at which point the model is considered to be trained.

The trained model can then be used to make predictions on new data, with the predictions being based on the updated parameters. The predictions are made by inputting new data into the model and using the updated parameters to predict the output values. This process is repeated for each new data point, allowing for the model to be continuously updated and improved over time.

The flexibility of the model allows for it to be applied to a wide range of problems, including classification, regression, and clustering. The model's ability to handle complex data structures and relationships makes it a powerful tool for a wide range of applications. The iterative nature of the process also allows for the model to be easily adapted to new situations and environments, making it a versatile and robust tool for solving a wide range of problems.
motor neurons are unable to find their way to the displaced muscle, then the muscle never again becomes functionally active. Other motor neurons will not command the biceps muscle, only “biceps” motor neurons will.

As Weiss himself emphasized, however, the manner in which myotypic responses are achieved has no bearing on the implications of the myotypic response principle for our understanding of the general nature of coordination. The fact remains that coordinated action depends ultimately on elementary functional units that contract and relax specific muscles in certain patterns, regardless of the functional effect those patterns may or may not have. The patterns realizable through the elementary functional units are the raw materials that the higher levels must work with. The higher levels may select one or another elementary pattern of muscular activity, but the higher levels cannot (in lower animals) produce just any pattern that circumstances may require. Even in higher animals, where there is some capacity for reprogramming even very elementary patterns of muscular activation, there is reason to believe that at any given time the higher levels must synthesize complex actions out of a limited set of elementary units that command particular patterns of muscular activation. The primate, like the salamander, may readily change the occasions on which it advances or retreats, but it cannot readily change its manner of advancing or retreating. The elementary units and intermediate units controlling the pattern of muscular activity in locomotion delimit the primate’s options with respect to the manner in which it walks.

---

**MYOTYPIC RESPONSE AS ASSAY METHOD**

Having established the general validity within known limits of the principle of myotypic response, we may pass on and use it to assay central coordination. How, will become clear from the following example.

Let us consider what is conventionally described as a flexion reflex. A stimulus applied to the toes results in the withdrawal of the foot and leg. This reaction occurs essentially on the level O of the hierarchical scale, implying operations on the subordinate levels G, M, and N. In terms of the top level (W) it can be rated as part of an escape reaction from a harmful stimulus. In terms of the organ level (O) it means approximation between base and tip of the limb. In terms of the muscle group level (G), it amounts to reducing the angles of the ankle and knee joints, commonly designated as “flexion”; and on the level of the individual muscle (M), it simply means contraction of these muscles which happen to be inserted on the flexor sides of the joints (e.g., hamstring at the knee; tibialis at the ankle). Our problem is to decide in terms of which of these levels the coordination of the withdrawal reflex is laid down.*

It is here that the assay function of a transplanted muscle can prove its value. For we can transplant a flexor muscle in such a fashion that it will have the mechanical effect of extending the joint instead of flexing it, as it did before. Thereby we alter the relation between the M level and all higher levels. When a “flexion” reflex is now elicited, will the response still be “flexion,” or will it be a contraction of what used to be the “flexor” muscle now producing extension? Or can we change the insertion and orientation of a whole limb with regard to the body in such a manner that, while the muscles will continue to produce the normal kinetic effects within the limb, the net result of the limb action for the body as a whole will become quite different from what it was before. Thereby we upset the relation between level O and the higher levels S and W. Will coordination patterns within the limb thereafter remain as they were before, perpetually in discord with the needs of the body, or will they be remodeled and re-integrated with the levels S and W in such a way as to restore harmonious operation of the whole?

Applying these experimental tests, it was found that a stimulus which normally yields a “flexion” reflex will invariably lead to a contraction of the hamstring muscles and the tibialis group, no matter whether the resulting movement comes actually out as flexion, or, owing to transposition of the muscles, as extension, rotation, or any other joint excursion, irrespective also of whether or not the resulting flexion or extension, as the case may be, leads to an effect which can be considered adequate from the standpoint of the body.

Now, let us go one step farther. Let us change the nerve supply of a “flexor” muscle, either one that still flexes, or one that has been transposed to the extensor side, by substituting an “extensor” nerve for the original “flexor” nerve. As we have outlined before, the result will vary with the age of the animal at the time of operation. Late operations will lead to neurotypic response; that is, the muscle will contract during “extensor” phases only and, hence, not take part in the “flexion” reflex (cf. Sperry, 1941). Early operations, however, will result in continued myotypic response, that is, a “flexion” reflex will

*Editor’s footnote: The reader will note that this is the same question that arose in connection with the Wicken’s conditioned finger “withdrawal” experiment.
bring in the "flexor" muscle even though it is now innervated from an "extensor" nerve and may have been switched over to the extensor side so as actually to produce extension. Whatever we do to it, the muscle with the "flexor" constitution will be the one to respond in the so-called "flexion" reflex (see Table 8.2).

Such being the situation, it would seem much more to the point to speak of a "tibialis-semimembranosus-semimembranosus" reflex, rather than of a "flexion" reflex, and to describe the "flexion" reflex about as follows: A stimulation of sensory fibers from the skin of a toe sets off a central discharge pattern, which selectively engages all motor neurones, however much scattered over the central district, which bear the specific "tibialis," "semimembranosus," and "semimembranosus" tags previously acquired from their respective muscles, with no regard to the actual kinetic and biological effects of the resulting contractions. The fact that the contraction of the hamstrings produces flexion, which has given the reflex its name, is, physiologically speaking, pure coincidence; fortunate from the standpoint of the animal and, of course, fixed by virtue of that very fact during the phylogenetic evolution of the species, but entirely dependent on the skeletal attachments of the muscles being and remaining what they are. If we disrupt this anatomical wisdom, we note no tendency of the centers to maintain the integrity of the response in terms of its effect ("flexion," "withdrawal"), but a blind continuance of the inherited central impulse scheme, delivered in terms of muscle-specific calls, in spite of the adversity or, at best, indifference to the individual of the resulting effects.

We have chosen a reflex as our first example because reflexes are usually conceded to be sufficiently rigid to fit into this picture. Therefore, the statements of these last pages do not exact much revision of current thinking, except in so far as they show that the response called for in a given reflex is not due to firmly set central connections, but that the nerves are conditioned for their response by their muscles. All the other conclusions could have been reached without knowing about the myotopic principle. It is only on the level of the more complex motor activities that uncertainties arise which it might not have been possible to clear up without the aid of the myotopic test.

A transplanted supernumerary limb can be of no use to the body unless possibly in the very special case where it has been inserted exactly in the same orientation as the nearly normal limb so that the pair can execute parallel action. In all other cases the actions of the transplant are sheer waste from the standpoint of the body. Conditions can even be created in which the action of the transplant...
is distinctly harmful in that it counteracts the normal limb (P. Weiss, 1937a). No adjustment or elimination of the wasteful action has ever been observed. It was suggested by Bethe and Fisher (1931, p. 1119) that the disturbance caused to the animal by the extra limb might not have been sufficiently vital for the centers to do something about it. It was argued that so long as the host limbs could continue in their normal function, the incentive to change the functional pattern might not have been strong enough. This criticism, however, has been invalidated by later experiments in which the nuisance value of the transplant was so aggravated that it created a serious predicament for the animal. Since these experiments illuminate the problem of coordination most clearly, we shall recount them here briefly, adding a number of comments that were not contained in the original publication (P. Weiss, 1937b).

UNMODIFIABILITY OF LOCOMOTOR SCORES

In larval salamanders possessing developed and functional limbs, the two fore limbs were mutually exchanged under preservation of their original dorsoventral orientation. Since the two limbs are mirror images of each other, this operation amounts to replacing one limb by another limb which has the same assortment of muscles but in exactly the reverse arrangement. A comparison between the insets of Fig. 8.5 and 8.6 explains the situation. Of the six muscles which represent the limb in our myochronograms only the elevator (Δ) and the depressor (X) have retained their normal positions relative to the body, while the adductor and abductor of the shoulder, and likewise the extensor and flexor of the elbow, have traded places. Adductor (⊙) and extensor (●) now lie at the anterior instead of the posterior border of the limb and abductor (⊙) and flexor (●) lie on the posterior instead of the anterior side.

After being re-innervated by regenerating nerves, these limbs resume function. The characteristics of this function are outlined in Fig. 8.6, in which six phases of a full walking cycle have been reproduced diagrammatically. Strips of the moving pictures from which these diagrams were reconstructed have been reproduced previously, and the reader may be referred to the earlier publication (P. Weiss, 1937b) for further details. The functional effect of the anteroposterior reversal of the whole muscle apparatus was so obvious that it seems hardly necessary to add much to the story, as it unfolds itself in a comparison between Fig. 8.5 and 8.6 (pp. 246-247).

All movements of the trunk, hind legs, and other parts which have been left untouched by the operation, are identical with those of a normal animal in the act of progression. Hence, we can use these normal parts to identify the successive phases of locomotion and to line them up with the corresponding phases of the normal animal in the diagram. This being done, we realize immediately that the position of the transposed fore limb (Fig. 8.6) and those of the normal fore limb (Fig. 8.5) are precise mirror images for each corresponding phase of the body movement. If we resolve the movement again into its component muscular contractions, we note that at any one moment the combination of muscles active in the reversed limb is identically the same as the one that would be active at that particular moment if the limb were a normal unreversed one. Using the myochronogram as index of the central impulse pattern, we thus learn that the centers have continued to call up the individual muscles in the same rhythm, sequence and intensity as they had done when they were still operating normal legs with unreversed musculature. In doing this, however, they lead to peripheral effects which are exactly the opposite from what would serve the organisms: instead of progression, they produce regression. This is explained in the diagram (Fig. 8.6).

In phase 1, the reversed limb on the right side has taken hold on the ground. During phases 2 and 3 the extensor (●) and adductor (⊙) muscles contract—the same muscles which are active during phases 2 and 3 in the normal animal (Fig. 8.5). This swings the body backwards (see arrow), while the arm on the left side reaches backward owing to the contraction of its elevator (Δ), flexor (●) and abductor (⊙). In phase 4, this free arm, in turn, takes hold on the ground, and the following contractions of its adductor (●) and extensor (●) bring the body still further backward through phases 4, 5, and 6. Thus, the muscles of the reversed limbs, while going through precisely the same cycle of innervation which their synchronous muscles would go through in the normal limbs, move the body backward instead of forward.

Actual regression occurs only if other means of progression, such as the tail and hind limbs, have been removed or paralyzed. If the hind limbs are present, however, the resultant effect is a constant struggle between the hind limbs and the fore limbs, the former striving to advance the body and the latter cancelling the effect by moving the body backwards by the same amount. The net result is that the animal swings back and forth without ever moving from the spot. It is almost pathetic to see how helpless the animals are about
repelling stimulus, and, biologically speaking, the result is as absurd, if not even more so, as in the case of forward locomotion: In their attempts to recede, they bring themselves closer and closer to the stimulus which they tend to avoid. For us the observation proves that even reversed fore limbs can efficiently contribute to forward locomotion of the body if only their muscles are activated in a time pattern appropriate for the purpose. In purely anatomical regards, the reversed fore legs are, therefore, as adequate for forward as for backward motion; hence their persistent failure to cooperate in the total locomotion of the body cannot be ascribed to mechanical incompetence.

A comparison of the myochronograms of ambulation and retreat at the same time permits us to define precisely what changes in the pattern of locomotion would have been necessary in order that the animals with reversed fore limbs might have learned to employ their limbs more judiciously. There are two ways in which the functional incongruity between the normal hind limbs and the reversed fore limbs could have been removed. One would have been to make the adductor and abductor phases trade places in the central time score of progression at the fore limb level, and the other would have been to combine the hind limb fraction of the time score of progression with the fore limb fraction of the time score of retreat. Both changes would have led to essentially the same net results, namely, a transformation at the fore limb level exclusively of the myochronogram of Fig. 8.6 into the myochronogram of Fig. 8.7. This would have restored harmony between the fore and hind limbs in that it would have enabled the fore limbs, too, to take part in body propulsion (lower row of Fig. 8.7). In other words, it would not even have been necessary to rebuild the whole locomotor pattern de novo. Most of it could have been left unaltered, with a simple shift of the abductor innervation from the elevator-flexor phase to the depressor-extensor phase, and conversely, of the adductor from the depressor phase into the elevator-flexor phase. This would have involved the time schedule of one muscle pair only. Or the retreat pattern might have been divided into its fore limb and hind limb parts, and the fore limb part alone substituted for the part normally assigned to the fore limbs in progression.

These would seem to be relatively minor changes, and if the amphibian central nervous system had any tendency and power to take into account and to repair inadequate peripheral results, the emergency of the reversed fore limbs should have proved to be a minor problem. As it is, however, it proved to be insurmountable, and neither were corrections effected nor any tendencies at correction, however abortive, ever observed.

The conclusions to be drawn from the reported results are the following: The chronological scores, according to which muscles are called into action when a limb is supposed to move are rigidly fixed. The centers contain a definite repertoire of such fixed and discrete scores; for instance, one for ambulation, one for retreat, one for swimming, one for righting, one for turning, and so forth, each of which can be displayed only as a whole or not at all. The nervous system cannot recombine for simultaneous execution parts of one score with parts of another score, nor can it alter the sequence and associations among the individual muscles within a given score. In other words, coordination patterns from level S down are ingrained in the centers and are not "effect-determined."

Basic coordination is thus revealed to deal exclusively with the central representatives of muscles, regardless of what effects these dealings will entail. So far as the basic scores are concerned, the muscles might be non-existent. Amphibian coordination operates "blindly," reeling off available central scores evoked by the stimulus situation. In fact, it can be predicted that they would continue to do so even after the interruption of all motor nerves, or the amputation of all limbs. If it were technically feasible to direct each muscle free, fully protecting its nerve supply, and then to attach them individually to writing levers, we should expect to obtain a myochronogram reconstructed from the muscle play in a smoothly moving normal limb with all muscles in place. In fact, the result should not be essentially different if we cut all nerves and registered oscillographically the activity of all central stumps. Pieced together, the records should again present the myochronogram of one definite movement or another. This would be true not only of type reflexes, for which our statement is not likely to be questioned because it refers to a standard practice in reflex registration, but also for the much more complex and highly coordinated movements which form the locomotor repertoire of the species.*

It will be noted that in this description a possible determining influence of sensory innervation has been completely left out of consideration. This is fully justified by the facts. While a more detailed discussion of this problem will be presented below, we may already in this place point to the fact that in amphibians the basic

*Editor's footnote. In the recent literature on invertebrate neurobiology, there are numerous instances in which the entire nervous system is removed from the animal and kept in a dish. Recordings from the motor nerve-stumps of these isolated nervous systems show that the nervous system can continue to send out the complex pattern of commands that would produce, for example, feeding or locomotion in the intact animal.
The Hemispheric Theory of Action

According to the hemispheric theory of action, the interaction between the left and right hemispheres of the brain is crucial for the understanding and execution of actions. This theory posits that the left hemisphere, involved in logic and language, is primarily responsible for planning and coordinating actions, while the right hemisphere, associated with spatial and emotional processing, plays a role in the execution of these plans.

In the context of action, it is proposed that the left hemisphere generates a mental representation of the desired action, which is then translated into a physical plan by the right hemisphere. This process involves the integration of sensory information from the environment with the internal representation of the action, allowing for the appropriate selection and execution of movements.

The hemispheric theory of action has implications for a variety of domains, including motor control, decision-making, and creativity. It suggests that the hemispheres work in a complementary fashion, with each hemisphere contributing unique strengths to the overall process of action execution.

Models of hemispheric interaction propose that the left hemisphere initiates and monitors the action sequence, while the right hemisphere provides the necessary adjustments and feedback. This division of labor allows for a more efficient and coordinated execution of actions, leveraging the distinct strengths of each hemisphere.
inherent in the centers, and the units of coordinated behavior are integrated complexes of the kind reflected in a myochronogram, rather than individual neurone activities. This is the basic fact which all theories of coordination will have to keep in view, and compatibility with which will be their test.

[Editor’s note. I have omitted a section that argues for what Weiss termed the resonance theory. This was the theory that a complex signal from the central programs was sent simultaneously and continually to all motor neurons and that different motor neurons were sensitive to different aspects of that signal. The theory was an alternative to the connectionist theory, which holds that the central program sends signals over selected neural pathways to activate specific motor neurons at appropriate times, Evidence presently available favors the connectionist theory, at least at the spinal level.]

I have also omitted several pages at the beginning of the next section. They contain a lengthy discussion of sensory deafferentation studies and what they do or do not prove about the viability of the chained reflex theory of locomotion. Since the literature around which this discussion turns has been superseded by more recent work, we skip the discussion of these now outdated studies and take up with Weiss’s conclusion, which (in the editor’s opinion) is essentially correct.

Plainly there are differences between the movements of a fully sensitive and a de-afferented limb, as well as differences in the behavior of the whole animal, which become increasingly greater as the extent of de-afferentiation increases. The finer polish through which the movements become smooth and are kept in harmony with the changing topography of the environment disappears, and only the crude basic structure of the main patterns is left. But the difference between the polished behavior of the normal animal and the crude performance of the de-afferented animal is so much smaller than the difference between the still highly coordinated function of the latter and a disorganized state of random contractions, which would mark the break-down of coordination, that it becomes practically negligible so far as the problem of basic locomotor coordination is concerned. The step from the irregular twitching of an uncontrolled muscle machine to the coordinated activities observed even in de-afferented animals is so immense, when compared with what sensory control has to add in the way of further accomplishment, that our sense of proportions should revolt against the recurrent attempts to give sensory control full credit for the whole achievement.

However, clarification of the whole issue will be greatly aided, if we abandon such inarticulate utterances about sensory control as that it is “of paramount importance,” “dominant,” “essential,” “vital,” or, on the other side of the picture, “irrelevant,” “practically insignificant,” and so on, and replace them by precise statements as to what phases of motor activity depend upon the integrity of sensory innervation, in what respect, and to what degree. Such a program would make no sense unless the hierarchical constitution of nervous functions is recognized. But if we admit that sensory influx may have different effects with regard to some levels of nervous activity than with regard to others, we realize the necessity of a more differentiated rating of those effects, than merely as a point on a scale from “unimportant” to “highly important.” Without trying to be exhaustive, here is a brief list of known sensory functions as they affect motor behavior.

1. The afferent influx initiates responses by releasing central discharges of definite pattern.
2. It conditions the centers for subsequent excitations by residual effects on central excitability and excitatory state. The total afferent influx thus produces a continuously shifting background of central excitability, which explains much of the latitude of the stimulus-response relation.
3. It decides which response from among the plurality of latent discharge patterns composing the central "repertoire" is actually to go into effect. It also influences direction, intensity, speed and duration of the elicited response.
4. Afferent proprioceptive impulses control the degree of muscular tone, and hence, maintenance of posture against gravity.
5. They also contribute to the precision and smoothness of a movement through local stretch reflexes (myotatic reflexes) acting as "governesses."

Since each major item of this list can be still further subdivided, it will be realized how complex the effects of sensory influx are, hence, how futile it is simply to assert their bearing on motor functions without further qualification. A toad with de-afferented hind limbs moves perfectly well over rough ground; but when it happens to land from a jump with its limbs contorted, no postural correction will ensue until the next locomotor impulse automatically returns the limbs to their normal position. This exemplifies the kind of disturbances to be ascribed to lack of sensation. Other shortcomings are the cruder dosing of the muscular contractions, exaggeration of movements, abnormalities of the tonic background, and so on, none of them serious enough to mask the essential fact that the basic
coordination in man

WESS / BASH PATTERNS OF COORDINATION

COORDINATION IN MAN

The familiar motion of the human eye is a complex movement involving a large number of muscles and tendons. The eye moves in a coordinated manner, allowing for smooth and precise movements. This coordination is achieved through a network of muscles that work together to rotate the eye in different directions. The muscles involved in this movement include the extraocular muscles, which are attached to the sclera (the white part of the eye) and move the eye in a coordinated fashion.

The coordination of these muscles is controlled by the brain, which receives input from the eyes and sends commands to the muscles through the cranial nerves. This process is facilitated by the cerebellum, which plays a crucial role in the coordination of movements. The cerebellum receives input from the eyes and the rest of the body, and uses this information to adjust the muscle activity to achieve smooth and coordinated movements.

In addition to the cerebellum, the basal ganglia also play a role in the coordination of movements. These structures receive input from the cerebral cortex and other brain regions, and use this information to modulate the activity of the cerebellum and other motor areas.

Overall, the coordination of the muscles of the eye is a complex process that involves a number of brain and spinal cord structures. Understanding this coordination is important for the diagnosis and treatment of eye movement disorders such as strabismus and nystagmus.
position is assumed and maintained only for the one specific act for which it has been acquired, namely, the support of the body, while in all other performances the elbow is still moved in reverse. Moreover, frequent relapses occur even during the supporting phase.

In other words, the basic patterns of coordination have not been remodeled, extensor and flexor muscles have not traded their phases of innervation as they would have had to do if the mechanical reversal were to have been compensated for, and in this respect the experiments on the fore limb merely duplicate those of the hind limb. However, in addition and on top of the immutable inherited habit, a trick performance has been established, the locking reaction, through which the old automatic and inadequate response can be temporarily superseded in a manner profitable to the body as a whole. This new performance is neither a permanent substitute for, nor is it in itself a revised edition of, the old pattern. The old stereotyped automatism continues in existence, only intermittently covered up by the action of another nervous apparatus more responsive to the needs of the body.

The adjustment of the fore limb behavior is of a very crude and primitive nature. However, an adjustment it is, nevertheless, and possibly the first faint trace of that capacity for learned coordination, which has reached such high degree in man. Pending proof to the contrary, one would feel inclined to ascribe this incipient adaptive capacity to the beginning evolutionary efflorescence of the motor cortex. Accordingly, the cortico-spinal system would have to be considered as the mediator in these adjustments (see Tower, 1936), and the lack of secondary adjustments of the hind limb movements of the rat could be correlated with the fact that in this animal only a small fraction of the pyramidal system reaches the hind limb centers (Ranson, 1913). Through its short-cut from the cortex to the spinal efferent neurons, this system is obviously enabled to deal with the muscles directly under circumvention of the whole hierarchy of lower centers. Whereas such motor acts as are produced through the mediation of lower centers will continue to exhibit the stereotyped inherited patterns, responses effected over the cortico-spinal system may engage the muscles in new temporal groupings of varying combinations, to be deleted or retained depending on their ultimate success for the body.

Whether these new patterns are established by a trial-and-error procedure, or by virtue of some intrinsic self-regulatory capacity of the cortical system, is impossible to say and also wholly irrelevant from our present point of interest. The main thing is that this cortical activity, or to put it more cautiously, adjutant capacity of higher centers, is limited to setting up new secondary patterns without power to remodel or abolish the primary patterns. This would seem to imply that the primary and secondary patterns are operated by different central mechanisms.

As we go up in the scale of mammals, the wealth of secondary patterns—that is, of acquired performances, learned under the guidance of cortical activity—becomes so enormous that their preponderance tends to obscure the existence of the old primary patterns which dominated the amphibian picture. The presence of basic patterns of the primary unlearned type even in man, has of course been widely recognized. Studies on fetal behavior (Hooker, 1959) and child development (Gesell, 1929, Shirley, 1941) have been particularly suggestive. However, the distinction between primary and secondary patterns was usually based merely on differences of origin: autonomous central maturation of the former, as against peripheral acquisition of the latter by experience. There has been no intimation that the difference may also be one of plasticity. Hence, if we want to homologize the primary innate patterns of man with the basic coordination patterns of the lower vertebrates, we must first prove that they are equally unmodifiable. This is an empirical task which has not yet been accomplished thus far.

The problem is to separate those motor performances in which the chronological scores of muscular contractions are absolutely fixed, and remain so even when they lead to unsatisfactory results for the body, from those in which the muscles can be operated in freely variable combinations so as to yield aimful responses. The most valuable experimental material bearing on the problem is in the hands of orthopedic surgeons, who are studying the recuperation of useful coordination after muscle transplantation in partially paralyzed limbs. Some well analyzed cases have brought to light a real conflict between inherited and unmodifiable patterns on the one hand, and novel patterns learned by experience with the aid of physical therapy, on the other (Scherb, 1938). However, no more than the first step towards a really clearcut classification and distinction in these matters has been undertaken.

Another source of valuable evidence lies in the study of the comparatively rare cases of functional supernumerary appendages in man. One such case has been examined and has yielded some instructive data. A girl with three supernumerary fingers, which could be identified as a third, fourth, and fifth finger, when first tested, showed distinct "homologous response" between each extra finger and the corresponding normal finger of the same hand (P. Weiss, 1938). Thus, obviously, the principle of myotopic response is
CONCLUSIONS

Evaluating the information which they present, the compound scissorial unit in each molecule, which in turn the muscle in a single scissoring order to achieve vertical, the swing, in contrast to the latter, the central nervous system is also inserted. The lower scissoring “contraction” one will remember, not these results. Standard confusion coordination will fall in the light of our standard confusion coordination will result in the context interpretation of the paper.

However, we may briefly examine how the answer to some of the questions based on our confusion and coordination without having to coordinate the specific conditions.

It would be needless speculation to resort to the specific conditions.
period. They are laid down in a hierarchy of functional levels, of
which the lowest, i.e., the one dealing directly with the muscles,
operates in terms of specific signals, one signal for each individual
muscle ("myotopic" principle). That the centers should be able to
differentiate such a variety of specific signals (specific biochemical
processes or specific electric states) is no more surprising than that
different glands should be able to produce different secretions.

Once in operation, these basic patterns of coordination act
"blindly," unconcerned of whether or not their peripheral effects are
of service to the animal. Achievement counts in neither their making
nor maintenance. In normal animals they are serviceable by
predesign—evolution has taken care of that. When disarrangement
of the bodily machine for which they are pre-adapted abolishes their
serviceability, they continue unaltered. This, better than any indirect
evidence, proves their preformed stereotypism. To this extent the
data confirm the preformistic concept.

However, there is a second side to the story of coordination that is
distinctly non-preformistic. The preformed patterns are relatively
crude, and only grossly speaking are they stereotyped. The inherited
repertoire provides an animal only with what we may call an
existential minimum of vital performances. Improvements are called
for and occur in varying degrees.

In this connection it should be pointed out that the inherited
patterns, of course, do not arise all at the same time, nor all in the
embryonic phase. Not only does the metamorphosis of amphibians
furnish many dramatic examples of comprehensive behavioral
changes during the functional life span, but a progressive expansion
of the motor repertoire is plainly observable even in non-
metamorphic animals. There is not the least doubt that this
gradual enrichment has the same non-experiential origin as the
earlier functional endowment, and is nothing but an external
manifestation of the continuous progress in the elaboration of the
central coordination systems by self-differentiation. The inability of
amphibians to readjust primary coordination at any phase in life
seems to dispose of the possibility that coordination patterns first
exhibited in later life may, in contrast to earlier ones, have been
molded by experience.

The inherent repertoire of an amphibian is fully adequate to carry
the individual through life without major changes, and, qualitatively,
the animal must get along with its limited repertoire of
"scores." However, there is room left for improvement on the
quantitative side: in the readiness with which a certain score is
activated, the smoothness and speed with which it is executed, and in

its competitive rating relative to other scores. That is to say, the
behavior of an amphibian can become "conditioned" to the
exigencies of its environment by selective facilitation or inhibition of
existing motor patterns. Within these narrow limits actual experience with the environment then modifies the structure of
behavior—although not the structure of its component scores,— and
within these limits the heuristic concept finds support. So much for
the amphibians.

Vertebrates higher on the evolutionary scale, of more complex
organization and more specific in their requirements, face more
complex tasks. The elasticity of the inherited scores is becoming
increasingly insufficient to meet the accidents of the environment. It
is on this level of the scale that a new method of coordination came
into being: coordination by individual design and discovery, rather
than by predesign and evolutionary tradition. This new development
culminates in man. Man can operate his muscles in ever varying
combinations, can discover and retain successful effects, eliminate
wasteful ones, and thus force his motor apparatus into increasingly
better adapted service. Here non-preformed, "invented," coordina-
tion patterns become so prominent that they obscure the more
ancient stereotyped patterns with which they coexist and overlap. We
have tentatively identified this plastic coordination with the activity
of the cortex, but there is no definite proof that subcortical functions
may not take part in it in higher mammals.

In the lower mammals, this type of coordination is, if present at all,
still in a very rudimentary condition. While both the stock repertoire
of the species and the ability of the individual to adapt the elastic
stock performances to its needs seem to be considerably increased in
the rat over what there is to be found in an amphibian, fundamentally the difference seems negligible as compared with the
tremendous efflorescence of the ability to "invent" coordination
patterns on the way from rat to man. On the other hand, the primitive
trick adjustments of which the fore limbs of the rat are capable (p.
265f) may be a true trace of emergent "inventive" coordination.

Whether this type of coordination attains its effects by trial-and-
error procedure or by more direct means, as suggested by adherents of
a systemic concept (e.g., Goldstein), is entirely beyond the
compentence of the present article to decide. The only positive
statement we can make is that, in contrast to preformed coordination,
the adequacy of the effects is the guiding principle in it, and that it
employs different mechanisms from the ones through which the
preformed coordination patterns are put into effect. As we have
indicated above (p. 268), it does not, for instance, operate through
student's performance can be improved. Focus on the positive aspects of the student's performance can improve self-esteem and reduce anxiety. This can be achieved by setting realistic goals and providing constructive feedback. Additionally, providing opportunities for students to practice and engage in meaningful learning experiences can also enhance their performance.

In summary, improving student performance requires a collaborative effort between teachers, students, and parents. By creating a supportive and encouraging learning environment, teachers can help students achieve their full potential. It is important to recognize the unique strengths and challenges of each student and adapt teaching strategies accordingly. By doing so, we can help students develop the skills and confidence they need to succeed in their academic pursuits.
(Bethe, 1931), while retiming of the muscles within the limbs is yet impossible in all lower vertebrates thus far studied, up to and including the rat. The assumption that the progression system and the retreat system are each an entity, likewise explains the inability of our animals to piece together half of one with half of the other (p. 258). In a more general sense this view can be well reconciled, it seems, with the ideas of Lashley (1937, 1938a) on systemic action of the brain, and with the known facts concerning vicarious action and compensatory regulation in integrative function.

However, we do not propose to go into the subject here any further. We merely wanted to indicate that the negation for lower vertebrates of “plasticity” in the sense of an omnipotent faculty to invent novel coordination patterns to meet emergencies outside of the elasticity limits of the inherited repertoire, and the affirmation of systemic properties of the centers, implying free interplay of forces within the limits of the constitution of the central system, are not at variance. There will be no misunderstanding on this point so long as one keeps in mind that the higher integrative functions are bound to operate through the existing lower functional mechanisms and that the latter, qualitatively determined during the developmental, that is, pre-operational, phase, are inaccessible to reorganization. Only the higher mammals seem to have developed a new superstructure capable of setting up “plastic” coordination patterns by means which are not yet available on the lower levels of the animal scale.

**SUMMARY**

Experiments are described in which the method of transplantation of muscles and nerves was used to analyze the origin and, in certain regards, the operation of motor coordination in amphibians. The results support a preformistic concept of coordination in these forms. A basic repertoire of primary motor patterns develops during the developmental phase. These arise essentially by self-differentiation within the central nervous system, independent of the benefits of sensory control and guidance by experience. They are so predesigned that, when later projected into an anatomically normal peripheral effector system, they produce biologically adequate effects. If confronted, however, with an atomically disarranged periphery, they produce correspondingly distorted effects without signs of corrective adjustment. The relation of these facts to the phenomenon of “plastic” coordination observed in man and higher mammals, and their bearing on the theories of coordination is discussed.

**DIAGRAMMING THE HIERARCHY**

Weiss’s outline of the six lowest levels in the hierarchy of action has never been improved upon. In one respect, however, the thirty some years that have passed since Weiss wrote have added to our perspective. We now can suggest plausible models for the processes that determine the coordinated actions of the higher levels in his hierarchy. Using these models, we can elaborate Weiss’s hierarchical classification of coordinations into a hierarchically organized circuit diagram. In fact, we have already considered such models in some detail. The complex unit that controls the stepping of one leg of the roach (Fig. 5.4) operates at what Weiss called the fourth level of organization—the level at which units coordinate the musculature of an entire limb. The coupling circuitry (Fig. 5.5), by which oscillators for each leg maintain appropriate phase relationships among themselves, forms part of a unit at Weiss’s fifth level of organization, the level that coordinates the musculature of all the limbs. The other part of this fifth-level unit is the command pathway (Fig. 5.6), the pathway that varies the nominal frequency of oscillation. The command pathway and the oscillator-coupling pathways coordinate the stepping cycles of the individual legs to produce gaits—interleg stepping patterns. Finally, the taxes, described in Chapter 6, are an example of Weiss’s sixth level of coordination. The unit that coordinates locomotion operates together with a unit that controls orientation. The result of this coordinated functioning of a locomotory unit and an orienting unit is an act of the organism. Indeed, taxic acts are the kind psychologists are most used to considering—approach responses, as with a positive phototaxis, and avoidance response, as with negative phototaxis.

Now that Weiss has so ably argued the importance of hierarchical organization in behavior, the core ideas of this book are in place. The fact of hierarchical organization is one of the core ideas. In the next chapter, we will examine the innumerable manifestations and consequences of this organization. Another core idea is what Sherrington called the principle of the common path. I have called this principle the lattice hierarchy principle. (See Fig. 8.1 for a schematic rendering of this principle.) It cannot be emphasized too strongly that at every level of coordination, the same unit of coordination (the same neural circuitry) participates in—forms a component of—many different patterns of behavior. Thus, a unit of coordination is always subject to control by diverse and competing higher level units of coordination. At the neural level this means that any given neural pathway or connection may be functional (potentiated) under any of several disparate sets of circumstances and nonfunctional (depotentiated) under a number of other and equally disparate circumstances. The third core idea is the principle of selective potentiation and depotentiation. Higher level units of coordination achieve their ends not primarily by activating lower units but
The lower two levels of the hierarchy

In the lower two levels of the hierarchy, the lower motor neurons are directly connected to the spinal cord. The spinal cord then sends impulses to the muscles, triggering muscle contractions and movements.

FIG. 6. The motor units—cells of muscle fibers controlled by single motor neuron.
two opposing reflexes, a flexion reflex and an extension reflex. Opposing extension and flexion reflexes are the archetypical example of the common path or lattice hierarchy principle. The flexion reflex works by graded recruitment of the motor units to the muscles that flex a leg joint and graded inhibition of the muscles that extend the joint. The extension reflex imposes the opposite pattern of excitation and inhibition upon the graded recruitment circuits for the same two sets of muscles.

At Weiss’s levels 3 and 4, which are, roughly speaking, the levels at which the elementary units of behavior are found, activating conditions enter the picture. The activating condition for a reflex is what Sherrington termed the adequate stimulus, the stimulus that triggers the reflex movement. The particular flexion and extension reflex that I have chosen for the present illustration have exactly the same adequate stimulus. Both of these reflexes are activated by a tap on the top or front of the animal’s foot—the part of the foot that is most likely to strike against something that threatens to trip the animal or sweep its foot out from under it. Flexion and extension reflexes with this common adequate stimulus have been demonstrated in the cat by Forssberg, Grillon, and Rossignol (1975). The flexion reflex, which has the effect of lifting the swinging leg higher off the ground, is seen during the “swing” phase (lift and advance phase) of the stepping cycle. If one taps the leading edge of the cat’s paw as the cat swings its leg forward, the tap elicits flexion of the leg joints—the toe, the ankle, the knee, and the hip. In a movie made of this experiment, one can see that the flexion has the effect of lifting the swinging leg up and over a stick that would otherwise have arrested the swing and tripped the cat. The extension reflex, on the other hand, is seen during the stance phase of the stepping cycle when the leg supports and propels the cat. If one taps the leading edge of the paw during this phase, the tap elicits extension of the leg joints. In the movie, one can see that this extension has the effect of hastening the completion of the stance phase, so that a moving object that would otherwise have swept the cat’s foot out from under it does not do so.

Thus, the reflex effect of tapping the leading edge of the cat’s paw undergoes “phase-dependent reversal”: During one phase of the stepping cycle, the tap elicits flexion of the leg joints; during the other, it elicits extension. This is the archetypical example of the intelligent, highly adapted, flexible quality that behavior acquires from the interaction between potentiating and activating signals. Forssberg et al. (1973) assume, as do I, that the oscillator that generates the stepping cycle potentiates the circuitry for the flexion reflex during the swing phase and depotentiates it during the stance phase. The reverse applies to the extension reflex. Thus, a unit at a higher level of organization (level 4—the whole-limb level) permits the flexion reflex (a level 3 unit) to be active only at certain times, only when the leg is not supporting the cat. Notice that the form of control is permissive rather than commanding. The level 4 unit does not activate the level 3 unit; only the activating condition—the tap—does that. On 999 out of every 1000 swings the potentiated flexion reflex is not in fact activated. But, very occasionally, the swinging leg strikes something and then the flexion reflex produces one of those last minute adjustments that leads us to marvel at the intelligent manner in which animal action adapts itself to fluctuating circumstances.

The intelligence of the reaction is traceable to the integrating effects of selective potentiation. The action is intelligent because it further’s the general pattern of action—the swing—which prevails at the moment. In the absence of selective potentiation and depotentiation the impact of the tripping obstacle could elicit both flexion and extension. Flexion is consonant with what is happening during the swing phase; extension is consonant with what is happening during the stance phase. By potentiating the flexion reflex during the swing phase and the extension reflex during the stance phase the oscillator sees to it that only the consonant reaction may occur. Selective potentiation is the agent of behavioral harmony.

We can, by the way, be sure that the phase-dependent governance of the flexion and extension reflexes is actually mediated at this lowest possible level.
these oscillators are coordinated in accord with the rules laid down by Wilson. The stepping is metachronal, that is, the swing phase of each successive leg progresses along the animal's body in the direction of locomotion. If the animal is moving forward, the rear leg swings first, followed by the front leg. The reverse sequence is observed when the animal moves backward. Stated in terms of phase relationships, the stepping cycle of the front leg lags the stepping cycle of the rear leg when the animal moves forward, and vice versa when the animal moves backward. In either case contralateral legs step 180° out of phase.

The phase-relationship between legs is maintained by coupling signals that pass between the oscillators. Here again the flow of coupling signals must be altered depending upon whether the front oscillator is to lag the rear or vice versa. We must imagine that the central program for forward locomotion potentiates one interoscillator coupling network; whereas the central program for backward locomotion potentiates a different coupling network (Fig. 8.11). Of course, the two networks may have many elements in common. That is, the lattice hierarchy principle, the principle of shared elements, may extend down to a level of neuronal detail that eludes any one-one mapping into behavior. What we regard as distinct circuits from a functional/behavioral standpoint may exhibit considerable overlap at the neuroanatomical/neuropsychological level of analysis.

One attraction of the hierarchically organized coupled-oscillator scheme as it has been portrayed up to this level (Weiss's level 5) is that it explains both the variability seen in normally coordinated walking and the striking stereotypy of basic coordination brought out by Weiss's limb reversal experiments. Weiss notes in passing (p. 248) that in normal locomotion the limbs usually maintain constant phase relations but that it is by no means uncommon for the phase relations between front and rear limbs to be momentarily disrupted by one limb "stepping out of turn." He mentions this variable interlimb coordination as a further difficulty in the way of a connectionist account of limb coordination. It is, however, a difficulty only so long as one adheres to purely reflex accounts. This relative rather than absolute coordination between limbs (or fins) is what led von Holst to the discovery of the role of coupled oscillations in the genesis of repetitive movement sequences. Stepping out of turn, that is, phase drift or relative coordination, occurs whenever the driving oscillators are not sufficiently strongly coupled. One can readily construct connectionist mechanical or electronic models that display this phenomenon (for an example, see von Holst, 1973, p. 135). Von Holst regarded the existence of phase drift in the leg movement sequences of mammals as evidence that locomotion also depended on a system of coupled oscillators. From film strips of a sheepdog walking, von Holst (1973) made a detailed analysis of a sequence in which the dog's hind legs made 25 steps whilst the forelegs made only 20. The variation in step amplitudes at various points in the drift were strikingly similar to the amplitude variations seen in the partially coupled fins of von Holst's decerebrate fish.

While normal walking manifests considerable variation in the relative timing of different limb movements, the basic schemes of forward and backward progression are indissoluble, at least in the salamander. The forward progression scheme at level 5 in the motor hierarchy of the salamander is truly a unit. It cannot be dissolved by a higher level of the hierarchy. A higher level, if it wants forward progression, must call up this scheme in its entirety. Even if this scheme cannot produce forward locomotion, the scheme must be activated in its entirety or not at all. The salamander cannot simultaneously activate half of its forward locomotion scheme and half of its backward locomotion scheme, even when a forelimb
Diagramming The Hierarchy

The Hierarchical Structure of Action

A diagram illustrating the hierarchical structure of action.
As a rule of thumb, the higher the level receiving a sensory input, the more global and diverse will be the possible effect of that stimulus on the animal’s action. As one ascends the hierarchy, stimuli play more and more of a role in determining the general course of action and less and less of a role in determining the particular pattern of muscular activity used to pursue that course at a given moment. A corollary of this principle is that the higher one goes in the hierarchy the more elaborate the sensory-perceptual analysis of sensory signals; or, what is almost but not quite the same thing, the more global the sensory factors that serve as inputs. The generals determine where the armies are to be deployed. In doing so they must respond to the geography of the country and the deployment of the opposing armies. The lieutenants determine where the trenches are to be dug. In doing so, they must respond to the local topography and the disposition of opposing forces in their locales. The sergeants determine where the latrines are to be dug. In doing so, they respond to the distribution of bushes in their immediate vicinities.

Weiss’s level 6 is not the highest level of motor organization. An animal’s individual acts must be integrated into behavior sequences. And behavior sequences must be integrated into the pursuit of long term goals such as the homeostatic regulation of the milieu interne and the production of offspring. Tinbergen (1951, Chapter 5) takes over where Weiss left off. He traces out the hierarchical organization of the behavior sequences that comprise the reproductive behavior of the stickleback. The reader who consults Tinbergen’s elegant “Attempt at an Integration” will realize that the study of motivation, at least as the ethologists conceive of it, is continuous with the study of motor coordination. The drive concept in ethology and physiological psychology refers to internal states (“central motive states”) that determine which stimuli will be effective (Deutsch, 1960; Lashley, 1938; Lorenz, 1937; Morgan, 1957; Stellar, 1960; Tinbergen, 1951). The concept is necessary for the elementary but often overlooked reason that a stimulus that is effective on one occasion at eliciting some response will often not be effective on another occasion. This variation in stimulus effectiveness is not random noise. When the mating drive is strong, whole classes of stimuli, namely, those stimuli that play an important role in mating, become effective elicitors of components of mating behavior. When the mating drive is weak, the same stimuli have no effect on the animal’s behavior (Tinbergen, 1951). When the hunger drive is strong in the blowfly, diverse food-related stimuli become capable of eliciting or guiding diverse food-seeking or ingesting responses. When the fly is not hungry, these responses cannot be elicited: their “adequate stimuli” are no longer adequate (Dethier, 1976). Drives, in other words, are neural and hormonal signals originating high in the hierarchy that potentiate complementary acts, acts that serve a common purpose. But this selective potentiation of functionally coherent subsets of lower units is, as we have just seen, a central principle of motor coordination. It may be observed to operate at the bottom of the behavioral hierarchical and at every intermediate level. Therefore, one may reasonably say that the problem of motor coordination becomes the problem of motivation as one ascends the action hierarchy.

If one had to say where in the action hierarchy one passed from the study of motor coordination to the study of motivation, one might draw the line at level 6. Tinbergen (1951, Chapter 5) observes that below this level, hierarchical integration is at least partially coordinative; it involves the simultaneous potentiation of two or more subordinate units with complementary actions. Above level 6 the units of organization determine acts or behavior sequences on the part of the whole organism. Since organisms can generally only be doing one thing at a time, the units at these higher levels can seldom have complementary organizing roles. Therefore, argues Tinbergen, above level 6, intralevel interactions are generally of a reciprocally inhibitory nature.

If one must draw a line between the problem of motor coordination and the problem of motivation, then Tinbergen’s argument may provide the only rationale for determining the locus of that line. However, if we allow the intrusion of introspective observations, most of us will acknowledge that we often act from mixed motives. We do what we do out of a variety of complementary and sometimes not so complementary motives. Each motive has some influence on the exact manner in which we do what we do. Indeed, the fine art of character analysis lies in the dissecting out of the various motives that shaped the behavior we have observed. It would seem that even at the highest levels of the action hierarchy there is room for the simultaneous functioning of more or less complementary organizing processes. It may not be necessary or even possible to draw a clear line separating the problem of coordination from the problem of motivation.

In any event, the hierarchical structure of the mechanism that generates behavior is an inescapable reality. Equally inescapable, but often overlooked, is the fact that a unit that coordinates an action almost always plays a role in diverse behaviors. In order that the unit play its role at suitable moments, it is subjected to control by potentiation and potentiation. The following chapter traces some of the innumerable manifestations of these principles of behavioral organization.