

## From Muscles to Motivation

*Three distinct kinds of elementary units of behavior combine to form complex units whose coordination by selective potentiation and depotentiation yields motivated behavior*

There is a conceptual chasm between muscles and motivation. We understand a great deal about the contraction process in muscle and about the mechanisms that convey contraction-initiating signals to muscle along axons and across synapses. We also understand something about how these signals are patterned by neural circuitry in the spinal cord. Together these materials form the core of modern courses in neurophysiology. They are the terra firma on one side of the chasm. On the other side is our understanding of the physiological variables and neural substrates for elementary motivational processes—thirst, hunger, and concupiscence. This material forms an important part of modern courses in physiological psychology. Here, too, there is a certain amount of terra firma. The chasm yawns when we ask how the motivational signals that arise in and around the region of the brain known as the diencephalon (see Fig. 1) eventuate in the intricately patterned muscular activity that we call motivated behavior.

This essay attempts to bridge the chasm, proceeding by sections. The first section distinguishes between

elementary and complex units of behavior, behavior being understood to mean any naturally occurring muscular or glandular action or pattern of action. I argue that there is an explicit way to decide whether or not a neurobehavioral entity is a unit of behavior, and if it is, whether elementary or complex. The second section presents three distinct types of elementary units: the reflex, the oscillator, and the servomechanism. These units are neurobehavioral entities that can be characterized both in behavioral terms and through describable neural circuitry that makes possible their behavioral properties. By building on these foundation stones, it is possible to link the concept of motivation in behavior to an explicit conception of the underlying neurophysiological structures and processes.

The third section briefly considers some principles that govern the interaction of elementary units of behavior when, as is almost always the case, several units are active simultaneously. A grasp of one of these principles—the principle underlying oscillator coupling—is a necessary background for the ensuing portrait of a complex unit. The fourth section uses the modern neurobiological understanding of the processes underlying locomotion to show how elementary units of behavior may be combined by coordinative circuits to create complex units of behavior. These complex units may exhibit a consistent function (for example, forward progression) achieved by means of diverse outputs (for instance, diverse stepping patterns) on diverse occasions. Each of these outputs is generated by the same underlying mechanism; their diver-

sity is achieved by varying only one parameter.

A fifth section elaborates on the properties of complex units of behavior and the light these properties throw upon some longstanding problems in behavioral and neurobehavioral analysis. This leads to the sixth section, which points out that higher-level circuitry coordinates the activities of the lower circuits primarily by regulating their potential for activation, a phenomenon I term selective potentiation and depotentiation. Five examples of this phenomenon carry us from a very low level in the hierarchy of neurobehavioral units to a very high level—a level at which motivational processes are being described. In this way it is possible to progress from the muscle to the motor neuron, and thence to elementary neurobehavioral circuits, to complex coordinations, and finally to the controlled deployment of many complex coordinations that we call a motivated pattern of behavior.

### Units of behavior

The first step is to take the concept of units of behavior seriously, as Sherrington (1947) did near the outset of his great work, where he gives a clear definition of elementary and complex units of behavior:

The reflex-arc is the unit mechanism of the nervous system when that system is regarded in its integrative function. The unit reaction in nervous integration is the reflex, because every reflex is an integrative reaction and no nervous action short of a reflex is a complete act of integration. The nervous synthesis of an individual . . . resolves itself into coordination by reflex action. But though the unit reaction in integration is a reflex, not

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every reflex is a unit reaction, since some reflexes are compounded of simpler reflexes. Coordination, therefore, is . . . the compounding of reflexes. In this coordination there are therefore obviously two grades [the elementary reflex or elementary unit of behavior and the compound reflex or complex unit of behavior] [p. 7; italics in original].

I adopt Sherrington's criterion for identifying elementary and complex units of behavior: a neuromuscular or neuroglandular circuit mediates a unit of behavior if it contains within it all the functional elements necessary to explain the occurrence of muscular contraction or relaxation or glandular secretion under some natural (nonexperimental) conditions. The necessary functional elements are those Sherrington recognized: an effector, a conductor, and an initiator. For example, a reflex arc is a unit of behavior. Muscle is the effector, the axons and synapses in the arc are the conductor elements, and sensory receptors are the initiator elements. By contrast, a motor unit, in Paul Weiss's definition (1941), is not a unit of behavior. A motor unit consists of a motor axon and the muscle fibers it innervates—an ensemble containing an effector and a conductor but no initiator. Signals do not naturally arise in vertebrate motor axons in the absence of input from presynaptic neurons. This unit, like an isolated receptor unit such as a rod in the retina, is a subbehavioral unit of analysis, just as a quark is a subatomic unit of analysis.

The heart, on the other hand, contains a complete unit of behavior. Within the heart itself are all three of the elements that comprise an elementary unit of behavior: effector, conductor, and initiator. Oscillatory electrochemical processes that generate the rhythmic contraction of heart muscle take place in specialized pacemaker cells within the heart (and also, to varying degrees, in the muscle tissue itself). These pacemaker cells are the initiator. The rhythmic signal propagates to the heart muscle (the effector) over cells specialized for conduction. The rhythmic contraction of the heart is an example of the output of an oscillatory unit of behavior.

Now that we have a criterion for deciding when we are dealing with a unit of behavior, how do we determine whether such a unit is elementary or

complex? Again I follow Sherrington: a unit of behavior is complex if it may be broken down analytically into constituents that are units of behavior in their own right. A unit of behavior is elementary if it cannot be further broken down into units that are still units of behavior. This principle for distinguishing between elementary and complex units is used in other sciences as well. In chemistry, a substance is elementary if it cannot be broken down into anything that is

havior, properly so called, the separable operations of the constituents are integrated to produce a function that no one constituent performs by itself. Superordinate neural circuitry exerts a coordinative influence on the circuits subserving the constituent units, creating a functionally cohesive pattern in the operation of the constituents. One example, elaborated on below, is the gait of a walking cockroach. The rhythmic steppings of each leg are locked into a limited set

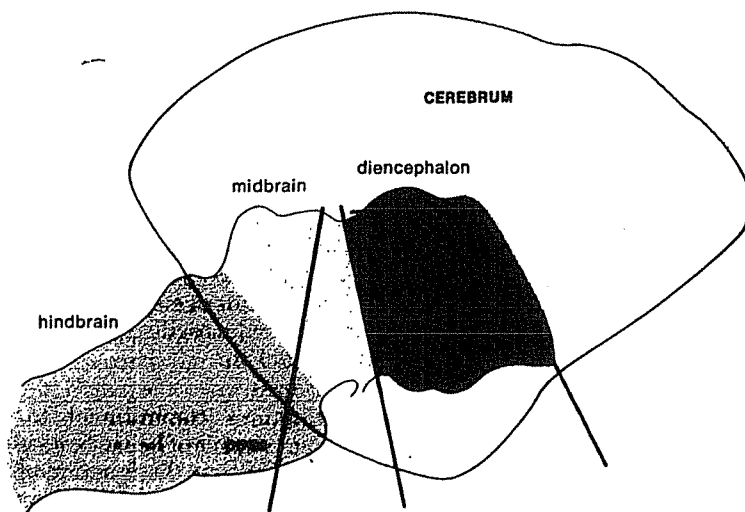


Figure 1. In this view of the three classic transections (black lines), the cut at the left produces the so-called "hindbrain" cat, whose behavior shows many fragments of the actions seen in intact cats; however, these fragments are not integrated to form simple acts of the whole animal such as locomotion or grooming. The middle transection results in the "midbrain" cat, which performs many simple acts but does not integrate these acts to form motivated behavioral sequences. The cut at the right creates the "diencephalic" cat, which

exhibits the kind of motivated behavioral sequences that lead us to speak of hunger, thirst, fear, rage, and concupiscence. The conclusion that the function of neural tissue in and around the diencephalon is to organize motivated behavioral sequences is further confirmed and amplified by experiments in which discrete loci within this region are either destroyed or electrically or chemically stimulated (see Gallistel 1980, Chap. 9). (Figs. 1-4 and 6 are from Gallistel 1980, by permission of Lawrence Erlbaum Associates, Inc.)

still a substance. Hydrogen and oxygen are elementary substances because they cannot be broken down into other substances; water is a complex substance because it can be broken down into hydrogen and oxygen.

But what is the justification for calling certain collections of elementary units of behavior complex units? Is a randomly chosen set of elementary units entitled to be called a complex unit? No. In a complex unit of be-

of phase relationships by the superordinate circuitry that controls walking.

The existence of processes that constrain a set of elementary units of behavior to operate in accord with one or a few among many possible patterns is a sine qua non for recognizing a complex unit of behavior. A second property of the true unit, while not essential, is extremely common. This is the tendency of the unit to appear in many different be-



havioral contexts, that is, in combination with many other units of behavior. Again, walking illustrates the point unusually well. The coordination of six legs that we call walking in the cockroach appears in an enormous variety of behavioral contexts. There is hardly a behavior of the roach as a whole that does not have walking as one of its constituents.

This rationale for recognizing a complex unit is in no way peculiar to neurobehavioral analysis, but can be found also in chemistry, physics, and linguistics, to mention only a few of the sciences in which complex units are recognized as such. Take, for example, the sentence—a complex unit in linguistics. A sentence is a particular combination of noun and verb phrases, which are complex units in their own right—particular combinations of certain kinds of words in a certain order. A given noun phrase may appear in many different simple sentences, and a given simple sentence may be recognized as a constituent of many different complex sentences. Similar observations may be made about complex units in biochemistry (for example, peptides and nucleotides) or about complex particles in particle physics (for example, neutrons and protons).

## Elementary units

This analysis parts company with Sherrington in recognizing more than one kind of elementary unit. For Sherrington there was only one kind—the reflex. In Sherrington's day and since, the term "reflex" has been used in so many ways that it would be impossible to advance a definition that accorded with everyone's usage. I adopt here a narrow definition, one that I think follows most directly from Sherrington's concept of a reflex arc. A reflex is a neural circuit, commencing with sensory receptors and ending with muscular or glandular effectors, whose action satisfies two conditions: (1) The output to a unimodal stimulus is unimodal. That is, the response to a stimulus whose intensity rises to a single peak and falls away is a contraction (or relaxation, or secretion) that likewise rises to a single peak and falls away, although not necessarily with the same time-course as the stimulus. In other words, in a reflex unit of behavior, repetitive effector action occurs only when there is a re-

petitive stimulus. (2) In a reflex unit, the relation between effector output and receptor input either does not normally exist or, if it does normally exist, may be altered without altering the behavior of the unit.

To see how restrictive this definition is, note that the first condition means that the scratch reflex has been misnamed. In the typology here suggested, it is not a reflex, because—as Sherrington emphasized—it involves a nonrepetitive or arrhythmic stimulus (the itch) that elicits a repetitive rhythmic effector action (the scratching). By the second condition, the optokinetic reflex (or reaction), a rotation of the eyes in response to rotation of the visual field, is also not a reflex. The output in this unit of behavior normally has a dramatic effect on the input, and altering this effect profoundly alters the behavior of the unit, as discussed in detail below. In short, I restrict the term "reflex" to exclude units that I believe ought to be recognized as distinctly different kinds of elementary units of behavior—the oscillator and the servomechanism.

Sherrington's commitment to the reflex as the unit of behavior grew out of his belief that the function of the nervous system was to be understood entirely in terms of the conduction of neural activity: "From the point of view of its office as integrator of the animal mechanism, the whole function of the nervous system can be summed up in the one word, *conduction*" (p. 8; italics in original).

Although Sherrington knew about the endogenous rhythm of contraction in heart muscle (indeed, Harvey had remarked on it in his famous treatise), he, like nearly all of his contemporaries, never seriously considered the possibility that neurons originate patterned discharges in the absence of sensory input. To concede that the neural activity underlying functionally patterned muscular activity could have a purely endogenous origin in the central nervous system no doubt sounded too much like vitalism, against which the nascent science of behavioral neurobiology was still struggling.

We now know that the pacemaker cells found in the heart are not peculiar to the heart: analogous cells are found in the central nervous systems

of many, if not all, species. When these pacemakers initiate rhythmic discharges in motor neurons that eventuate in rhythmically patterned muscular contractions, we are dealing with a different kind of elementary unit: an oscillator. In other words, in a reflex the initiator element is a receptor, in an oscillator it is a pacemaker.

A notable development in motor-system neurobiology over the past decade has been the broadening awareness of the importance of central pacemakers in the timing of motor outputs (cf. Herman et al. 1976). A growing body of electrophysiological data (cf. Kennedy and Davis 1977) has brought a long-overdue appreciation of von Holst's seminal work (1937) on the mechanisms of oscillator coupling and the role of coupled-oscillator systems in behavior (see Gallistel 1980 for elaboration).

In a reflex, the form and amplitude of the output are determined by what happens to the signal generated at the receptor as it is conducted around the arc. The behavior of a reflex unit as defined here is completely characterized as soon as the relation between receptor input and effector output is described. In linear systems terminology, the transfer function from receptors to effectors is the only transfer function it is necessary to know in order to compute an output, given an input.

This view is inherent in the reflex concept. It had almost the character of a self-evident truth in the thinking of Sherrington and his many followers. There are, however, elementary neurobehavioral circuits, consisting of receptors, conductors, and effectors, whose output cannot be even approximately calculated given only the input and the "neural transfer function," that is, the transfer function from receptors to effectors. These neurobehavioral units are servomechanisms, or servocircuits.

The defining properties of an elementary servomechanism are: (1) In normal operation there is negative feedback from its output to its input. That is, the output tends to reduce the input that caused that output in the first place. (2) The parametric properties of the neural circuitry that translates the input into an output



are comprehensible only when this negative feedback is taken into account. Because of the negative feedback, the neural circuit will not achieve its intended behavioral function unless it has certain parametric properties—properties that would make no functional sense if the circuit were conceived of as a reflex. One such property, described below, is high gain.

Recent work in behavioral neurobiology makes it possible to illustrate the distinction between a reflex and a servomechanism with unusual precision. Baarsma and Collewyn (1974) used linear systems methods to determine the transfer functions for both the vestibulo-ocular reflex and the optokinetic reaction in the rabbit. The first of these neurobehavioral units is a reflex, while the second is a servomechanism, yet they have nearly the same function and employ the same motor neurons and muscles. The vestibulo-ocular reflex is a counter-rotation of the eyes; it occurs when receptors in the vestibular apparatus adjoining the middle ear sense a rotation of the head. The optokinetic reaction is a rotation of the eyes in the same direction in which the visual field rotates; it occurs when circuits in the retina sense the image of the field moving across the photoreceptive surface. Both the vestibulo-ocular reflex and the optokinetic servomechanism serve to reduce the rate at which images sweep across the retina when the rabbit rotates.

In experiments testing the vestibulo-ocular reflex, a rabbit is strapped to a turntable and rotated back and forth in a dark room (so that there is no visual input and the optokinetic reaction is inoperative). The amplitude of the back-and-forth excursions is held constant but their frequency is varied. The angular accelerations and decelerations during the back-and-forth rotation excite the rabbit's vestibular system, producing counter-rotation of the eyes, which is then measured. The rotation of the eyes, of course, has no effect on the input seen by the vestibular system. That is, we are dealing here with a reflex, not a servomechanism.

In order to conduct a comparable experiment on the optokinetic unit, it is necessary to prevent eye rotation from having any effect on image velocity. Ordinarily there is feedback

from output to input in this reaction. The rotation of the eyes slows down the slippage of the image across the retina, which is the proximal stimulus for the reaction. The negative feedback effect of eye rotation on image velocity is prevented by anchoring the eye that sees the visual field so that it cannot rotate. The other eye is covered so that it does not see the visual field but is free to rotate. Its amplitude of rotation is measured while the visual field (the vertically striped interior of a cylinder) is rotated back and forth. Thus the input falls on one eye while the other eye produces the output.

The most striking difference between the reflex circuit and the servocircuit is seen in their gains. The reflex circuit has a gain of about .8 at the optimum back-and-forth frequency. That is, the velocity of the eyes' counter-rotation is eight-tenths of the velocity of the head's rotation. The gain of the optokinetic circuit, on the other hand, ranges from 20 to 100! When the image moves across the retina of the fixed eye at .05° of visual angle per second, the unfixed eye rotates at 1° per second or faster.

Both of these elementary units of behavior have the same function—slowing the rate at which the image of the visual field sweeps across the retina when the rabbit rotates. The amplification characteristics of the two circuits differ by more than an order of magnitude because one unit is a reflex and the other a servomechanism. The vestibulo-ocular reflex operating by itself with a gain of .8 would reduce the slippage of the visual field across the retina by a factor of five. A head rotation at a velocity of 1° per second results in an image slippage of .2° per second, the other .8° per second being canceled by the counter-rotation of the eyes. In order to achieve a similar efficiency, the neural portion of the optokinetic servocircuit must have a gain of four! When the eyes rotate in response to the slippage of the image, their rotation reduces the slippage. But the slippage of the image is the stimulus for the eyes' motion. It is inherent in a servosystem that the negative feedback from output to input reduces the stimulus for action. To overcome this, a little stimulus must produce a lot of action, that is, gain must be high. The high gain in the neural circuitry subserving the opto-

kinetic reaction is dictated by—and is functionally comprehensible only in the light of—the negative feedback from output to input. It is to be expected in a unit that is a servomechanism rather than a reflex.

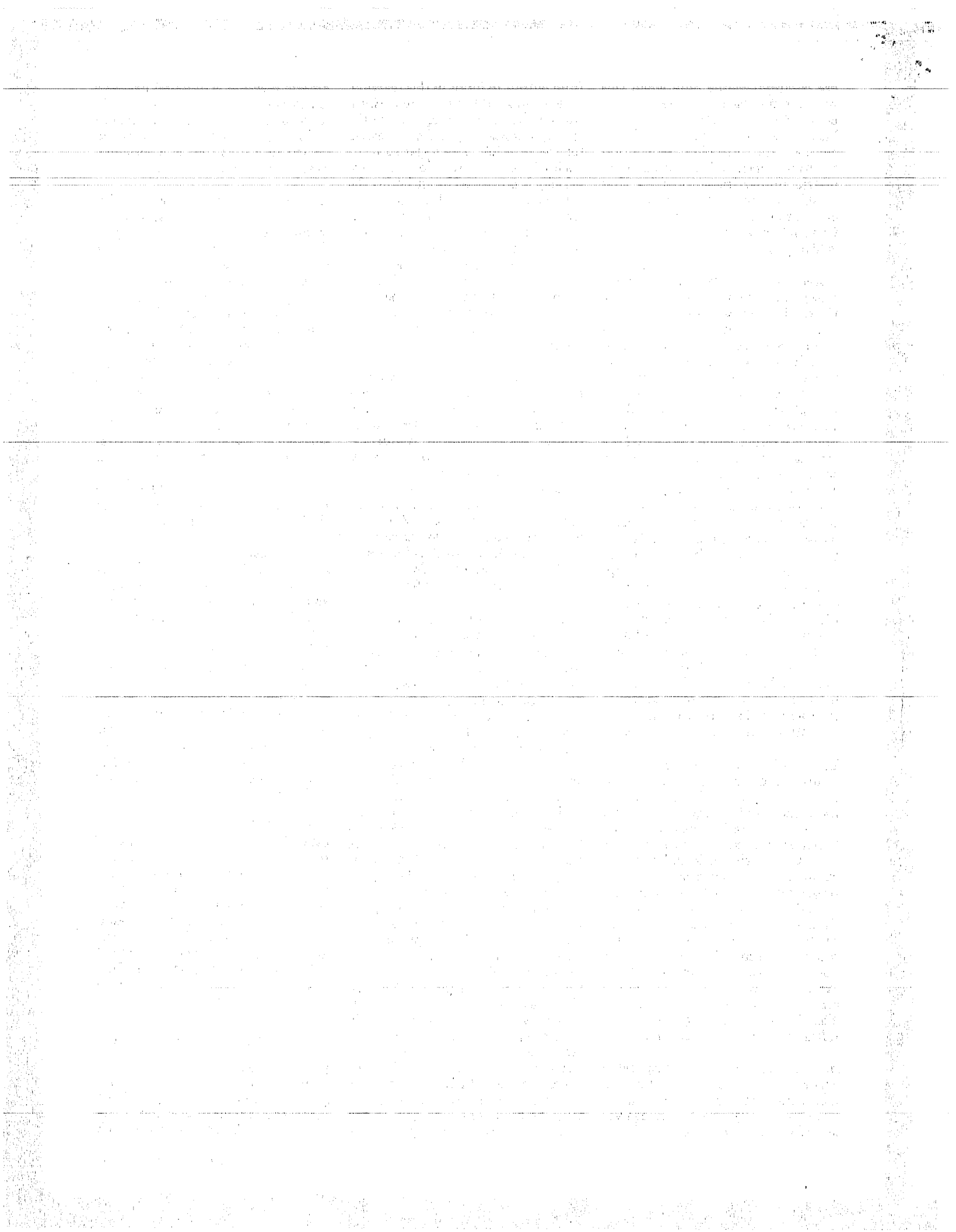
Another important difference between the two circuits is seen in the maximum acceleration they can produce. The servocircuit is more sluggish than the reflex circuit; hence it responds very poorly when the frequency of back-and-forth rotation is high. The sluggishness of the optokinetic circuit is dictated by two aspects of its situation: (1) the output feeds back on the input; and (2) there is (in both units) an unavoidable delay on the order of 100 msec between a change in input and the onset of an answering change in output. The sluggish acceleration (poor high-frequency response) is necessary in order that the servo-unit not display unstable, nonfunctional oscillations in response to high-frequency jitter in the image of the visual field.

In sum, although both reflex units and servo-units have neural circuitry consisting of receptors, conductors, and effectors, there are cogent reasons for treating servocircuits as a distinct kind of elementary unit of behavior. The properties of a servocircuit, such as its gain and acceleration, and the behavior that the unit will display are comprehensible and predictable only when the relation between output and input is taken into account. This relation need not be considered in analyzing a reflex circuit and predicting the behavior it will display.

I think it likely that there are still other kinds of elementary units of behavior in addition to the three I have just defined, but not a great many more—a number nearer 10 than 100. In any event, we can safely assume that the reflex, the oscillator, and the servomechanism are prominent among the elementary units of behavior. Many complex units of behavior can be seen to be compounds of these three kinds of units.

## Principles of interaction

When elementary units function simultaneously or in immediate sequence there are distinct principles that mediate their interaction. Sherrington identified at least three such





principles: reciprocal facilitation between agonistic units, reciprocal inhibition between antagonistic units, and reflex chaining. Along with the recognition of other kinds of units has come the recognition of other kinds of interactions.

Oscillators, for example, interact by what von Holst (1937 and 1973) termed the magnet effect, which is observed when one pacemaker sends an entraining or coupling signal to another and the recipient responds with phase-dependent acceleration or deceleration. That is, the receiving pacemaker either speeds up or slows down, depending on its phase at the moment the signal is received. The response of marchers to the beat of a drum is phase-dependent in this way. A marcher slows his step if the drum beat is heard after his foot strikes the ground but speeds his step if the beat is heard before the foot makes contact. The neural pacemaker that times the rowing motion of a crayfish swimmeret responds in just this way to the coupling signals it receives from pacemakers controlling other swimmerets (Stein 1971).

Phase-dependent responses to coupling signals sent back and forth between pacemakers are the means by which an assemblage of oscillators entrain one another, that is, establish and maintain either a fixed *phase relationship* or a fixed *temporal relationship* between their rhythmic outputs. Take, for example, the pacemakers on either side of the ganglion that controls the hind limbs of a cockroach. These pacemakers run 180° out of phase with one another, with the result that the opposing legs always step in alternation. The fixed phase relationship between the pacemakers is maintained by an exchange of coupling signals.

Take as a further example the three pacemakers arrayed along the side of a cockroach, one for each of the three legs on a side. To a first approximation, there is a fixed temporal relationship in the outputs of the same-sided pacemakers. The stepping pattern along one side of the forward-moving roach runs from back to front: first the hind leg steps; at a fixed interval thereafter the middle leg steps; after another fixed interval the front leg steps. When the slowly walking cockroach turns on the speed by increasing the frequency of

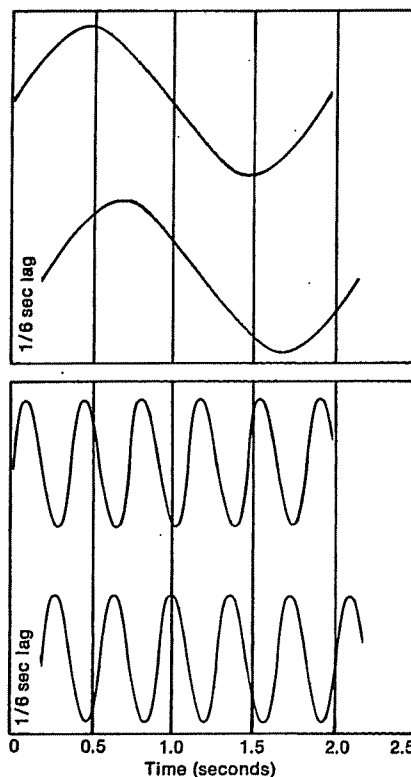


Figure 2. When the temporal lag between oscillators is fixed, the phase difference depends upon how rapidly the oscillators are cycling, because the phase difference is equal to the lag divided by the time required to complete one cycle. If the oscillators complete a cycle once every 2 seconds and one lags behind the other by  $\frac{1}{6}$  of a second (above), the phase difference is  $\frac{1}{12}$  of a cycle, or 30°. If they complete a cycle once every  $\frac{1}{3}$  of a second (below), then the phase difference is half a cycle, or 180°.

stepping, these intervals remain almost constant. Hence the phase relationship between same-sided legs changes (Fig. 2). This changing phase relationship explains the different gaits, or footfall patterns, observed in insects (cf. Wilson 1966 and Fig. 5). It is likely that the fixed temporal relationship between the outputs of same-sided pacemakers is maintained by circuits that carry coupling signals from pacemaker to pacemaker (cf. Stein 1971).

Entrainment by means of coupling signals that produce phase-dependent acceleration or deceleration, then, governs interactions between oscillators. A principle that may govern interactions among units of any kind is the cancellation of refference by efference copy—a principle given its clearest formulation in

the classic paper by von Holst and Mittelstaedt (1950). In the course of producing output, a unit of behavior invariably generates sensory input. Self-generated sensory input is called refference because it is a result of the animal's own action. (Sensory input generated by external events is termed exafference.)

Reafference is potentially troublesome, since it is likely to trigger other responses that are functionally counterproductive. The occurrence of such responses is, however, anticipated and prevented by means of efference copy. An efference copy is a copy of the command that caused the refference-generating action. The refference, since it is generated by the action, may be predicted from the command that initiates the action. A suitably scaled copy of the command signal may therefore be used to nullify the refference that the action generates, preventing units whose action would be counterproductive from "seeing" the refference.

## The complex unit

In the course of his work on the development of coordination, Paul Weiss (1941) provided compelling demonstrations of the unitary character of complex coordinations, particularly the coordination of the limbs in locomotion. He interchanged the two front limbs of larval salamanders so that in the mature salamander the front limbs were oriented backward with respect to the rest of the body. If the front limbs stepped in the way that would ordinarily propel the salamander forward, the effect was now to propel the salamander backward. The muscles of the interchanged limbs were reinnervated by the motor neurons appropriate to the normally positioned limb. The result was that the interchanged front limbs behaved at cross purposes to the normally positioned hind limbs. When the salamander's tail was pinched, the hind limbs stepped forward but the front limbs stepped backward. When the salamander's nose was poked, the opposite patterns ensued; the hind limbs attempted to propel the animal backward, while the front limbs tried to propel it forward.

As Weiss's experiment demonstrates, the salamander has two complex units of locomotory coordination, one for advancing and one for retreating.



What the salamander lacks is the neural circuitry required to dissolve these units into constituents and to recombine the constituents into an ensemble that works when the front limbs are oriented the wrong way. If the salamanders in Weiss's experiments had been able to command their front limbs to walk backward while commanding their back limbs to walk forward, the animal as a whole would have been able to run away from the beast that had grabbed its tail. But the animal has no circuitry for implementing this unusual interlimb coordination. Although both forward and backward locomotion may be broken down experimentally into simpler constituents, they present themselves as units to the higher levels of the salamander's nervous system.

In recent years, the neural control of locomotion has been the focus of a great deal of research (cf. Grillner 1975; Hermann et al. 1976; Shik and Orlovsky 1976; Stein 1978; Wetzel and Stuart 1976). From this research, principles have begun to emerge that account for the coordination of locomotion in animals as diverse as the cat and the cockroach (cf. Pearson 1976). This work underlies the following schematic rendering of the complex units controlling forward and backward locomotion.

The basic building block in locomotion is the circuitry that controls the stepping of a single leg (Fig. 3). This circuitry is a complex unit of behavior incorporating all three types of elementary units of behavior described above. The elementary unit at the core of this complex unit is an oscillator. Pacemaker neurons (or possibly pacemaker circuits) periodically trigger a swing of the leg by exciting a short burst of firing in the motor neurons activating the muscles that lift the leg off the ground and swing it. During this swing phase of the stepping cycle, the otherwise steady discharge of the opposing motor neurons is inhibited. The discharge of these opposing motor neurons during the stance phase of the cycle presses the leg down to support the animal and pulls the leg back to propel the animal (cf. Pearson 1976).

The strength of the stance-phase discharge is regulated by a servocircuit that adapts it to the load to be moved. This load is greater when the

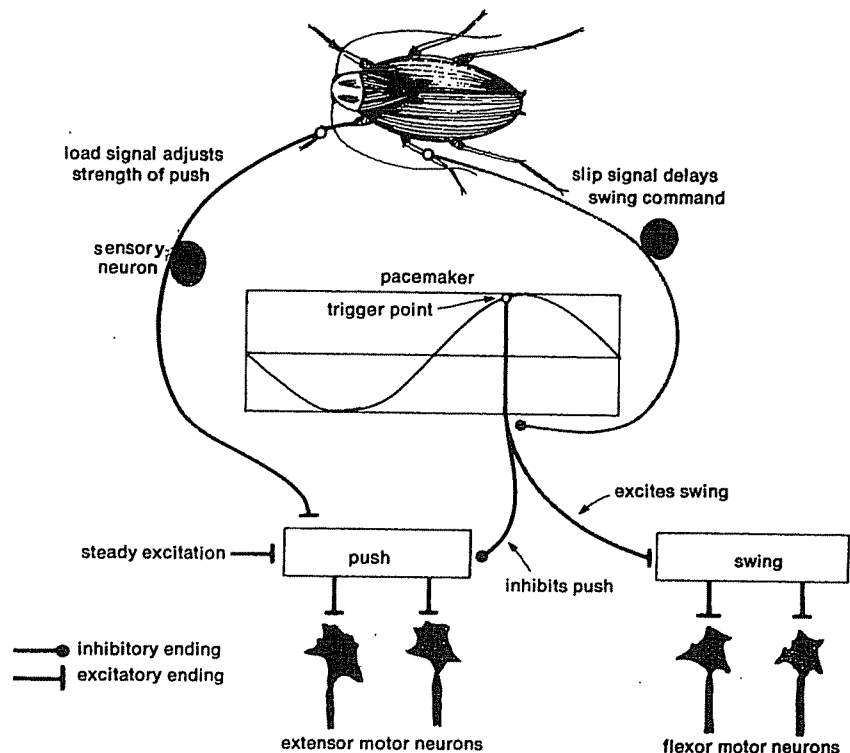


Figure 3. The complex unit controlling the stepping of the left front leg of a cockroach is made up of three elementary units. The extensor motor neurons are active during the stance, or push, phase of the stepping cycle, when the leg holds the cockroach up and propels it forward. The activity of these neurons is promoted by a steady excitatory input, whose action is inhibited periodically by a signal from a pacemaker. This signal simultaneously excites a brief burst of activity in the flexor motor neurons, which lead to the muscles that swing

the leg up and forward. The circuitry described thus far (color) constitutes one elementary unit of behavior—an oscillator. Two other elementary units cooperate with the oscillator: a servocircuit (black line) adjusts the strength of the activity in the push system to compensate for variation in load; and a trigger-delay reflex (gray line) senses failure of the middle leg to take up the load and inhibits the swing-triggering action of the pacemaker. Similar complex units control each of the cockroach's other legs.

animal moves uphill than when it moves downhill. The servocircuit senses leg position and velocity and increases or decreases the discharge in the appropriate motor neurons whenever these variables depart from normative values. These increases or decreases in motor-neuron discharge alter leg position and velocity in such a way as to reduce the sensed discrepancy (cf. Wendler 1966).

The timing of the swing phase is altered by a trigger-inhibiting reflex. If other legs fail to take up the load of the leg about to be swung, as will happen when another leg slips or trips, the resulting sensory message inhibits the swing phase (Pearson 1972). This inhibitory override prevents the robot-like removal of the animal's sole means of support. The reflex circuit, like the servocircuit,

makes intelligent moment-to-moment adjustments in the rhythmic action of the oscillator, adapting the action to the vicissitudes of locomotion.

An animal has as many leg-stepping units as it has legs. These units are combined to form a locomotory unit by oscillator-coupling circuitry that conveys timing signals between pacemakers (Fig. 4). The receiving pacemakers make phase-dependent accelerations or decelerations whose parameters are such as to yield the following two relationships: (1) oscillators on opposite sides of the same body segment operate 180° out of phase (that is, in strict alternation); (2) oscillators along the same side of the body operate at fixed lags. For example, as the cockroach moves forward the rear leg swings first, the



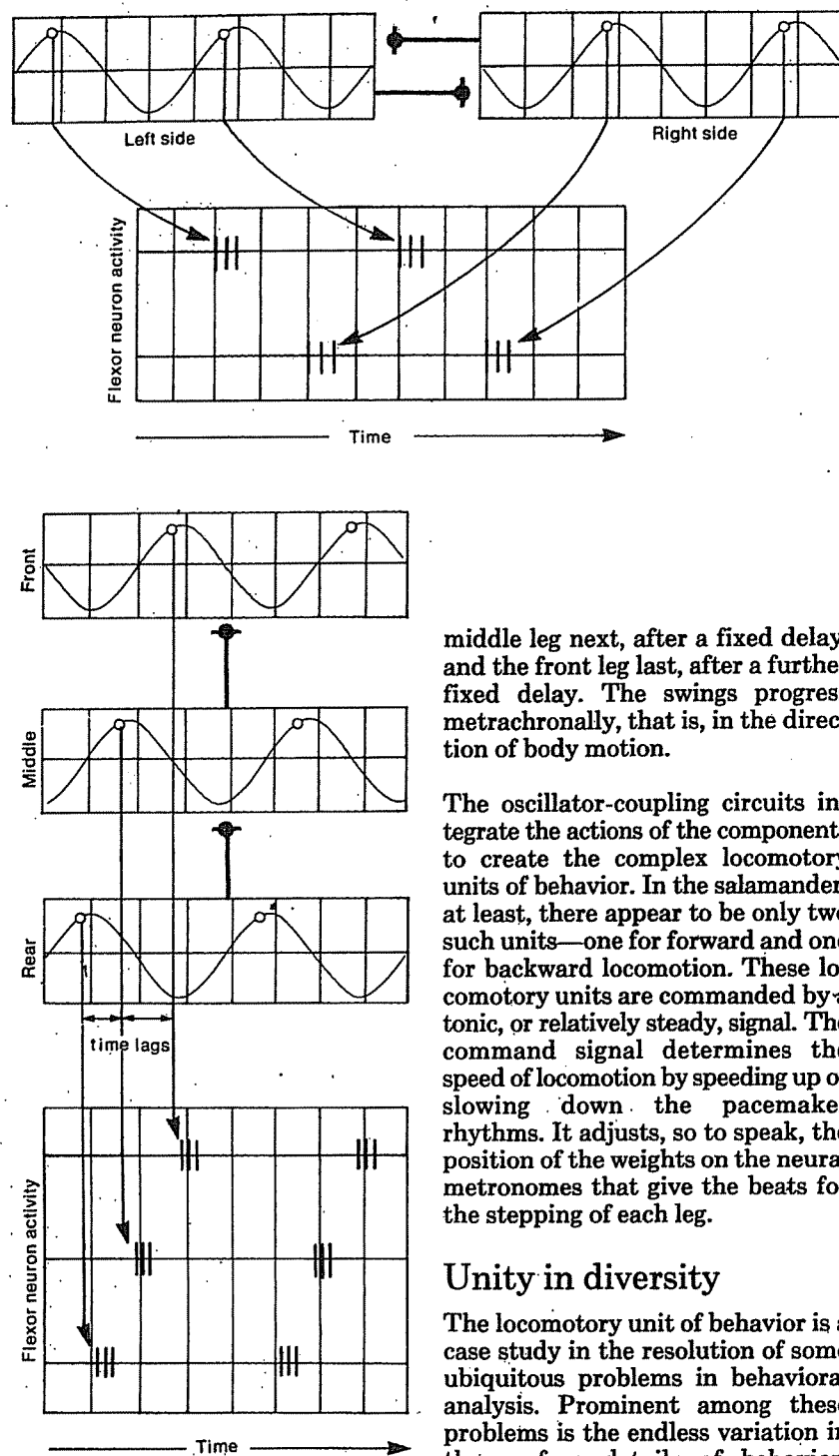


Figure 4. Oscillator-coupling circuitry integrates the pacemaker rhythms to create patterns of stepping, here seen from two perspectives. The two oscillators on opposite sides of the same body segment (above) are coupled in such a way that they operate 180° out of phase. The oscillators ranged along one side of the body (below) are coupled in such a way that each oscillator lags behind the one to its rear by a fixed temporal interval. The symbol at the end of each pacemaker-coupling pathway combines the symbols for excitation and inhibition, because signals in these pathways excite (accelerate) the pacemaker if they arrive during certain phases but inhibit (decelerate) it if they arrive during other phases.

middle leg next, after a fixed delay, and the front leg last, after a further fixed delay. The swings progress metrachronally, that is, in the direction of body motion.

The oscillator-coupling circuits integrate the actions of the components to create the complex locomotory units of behavior. In the salamander, at least, there appear to be only two such units—one for forward and one for backward locomotion. These locomotory units are commanded by a tonic, or relatively steady, signal. The command signal determines the speed of locomotion by speeding up or slowing down the pacemaker rhythms. It adjusts, so to speak, the position of the weights on the neural metronomes that give the beats for the stepping of each leg.

## Unity in diversity

The locomotory unit of behavior is a case study in the resolution of some ubiquitous problems in behavioral analysis. Prominent among these problems is the endless variation in the surface details of behavior. Whereas the operation of most man-made machines is identical from one occasion to the next, the running of even so lowly a creature as the cockroach varies from occasion to occasion. The linguist Chomsky (1965) is hardly alone in arguing that diverse surface manifestations of behavior derive from the operation of one and the same underlying process.

The locomotory unit illustrates one way of obtaining seemingly very dif-

ferent outputs by varying a single parameter in the operation of underlying neural machinery. Figure 5 compares the gait of a slowly moving insect with that of a scurrying insect. The two gaits could hardly appear more different, yet both are generated by the machinery described above. All the surface differences between the two gaits derive from a single underlying difference—a difference in the stepping frequency (the reciprocal of the interval  $e$  in Fig. 5).

The locomotory unit also displays the rudiments of intelligence, at least as Bartlett (1958) conceives of it. Bartlett begins his analysis of thinking with a consideration of skilled action. What he finds intelligent in skilled action is the rapid adoption of new responses that maintain the function of the behavior in the face of altered circumstances. The scurrying of a cockroach after experimental amputation of its middle legs displays just this sort of adaptation. As can be seen in Figure 5, the scurrying roach normally swings the front and rear legs on a given side in phase. That is, both these legs are off the ground at the same time, during which time the middle leg supports the side. This gait will not work after amputation of the middle legs. Remarkably enough, the post-operative roach behaves *immediately* as if it knows this. It scurries off like a four-legged salamander, swinging the front and rear legs on each side 180° out of phase.

The discovery by von Buddenbrock (1921) and Bethe (1930) of the seemingly insightful response of insects to amputation of the middle leg led to a good deal of fanciful scientific prose in which whiffs of mysticism might be detected. The system sketched above explains this intelligent adaptation as a consequence of the trigger-delaying reflex. The recurring failure of the middle legs to take up the load results in a recurring delay in the triggering of the swing of the front legs. The delayed triggering of the front legs explains the change in the phase relationship between front and rear legs. (Another likely mechanism, not mutually exclusive with the one suggested, is that altered sensory input from the middle-leg region slows down the stepping frequency of all the legs. Any slowing of stepping frequency will shift the front legs out of phase with the rear legs.)



The explanation of this particular piece of intelligence cautions against our tendency to equate the capacity to respond intelligently with the capacity to learn.

Another lesson to be drawn from a study of locomotory units is that different complex units of behavior may be created by combining the same set of more elementary units in different ways. For example, it is likely that the system underlying backward locomotion uses the same motor neurons, the same pacemakers, and—to some extent—the same oscillator-coupling circuitry (e.g. the coupling circuitry that keeps pacemakers on opposing sides of the same body segment running  $180^\circ$  out of phase) as are employed in forward locomotion. However, in backward locomotion the pacemaker excites a different combination of motor neurons during the swing phase—a combination that swings the leg up and backward rather than up and forward.

It also seems likely that the pacemakers ranged on one side of the body are coupled by different circuitry in backward locomotion, with the result that the sequence of leg swings progresses from front to back instead of from back to front. (A careful analysis of interleg phasing in backward locomotion has not been done, as far as I know.) Work by Sherman and his co-workers (1977) suggests that the same pacemakers and coupling system are employed in the leg movements that a cockroach on its back makes in order to right itself. It also appears that the same pacemakers and motor neurons are used in producing the leg movements by which the roach grooms itself. In both cases, the relations between the circuit elements at different levels of the hierarchy are altered to achieve a different basic pattern.

The use of the same elements in different combination is commonly found when two or more behavior patterns of comparable complexity are broken down into their constituents. I have termed this the principle of the lattice hierarchy, because when the control by higher units over lower units is diagrammed, the diagram looks like a ramshackle lattice (Gallistel 1980). Sherrington recognized this mode of organization; he called it the principle of the common path, because a given lower unit is used by

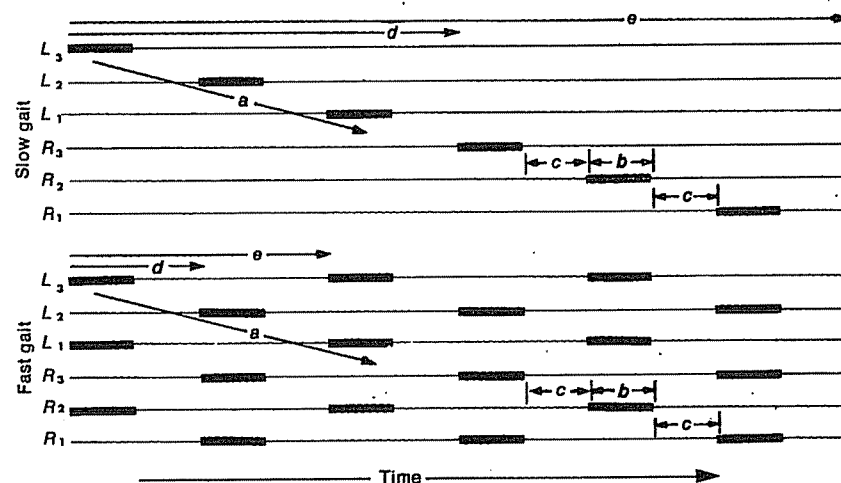
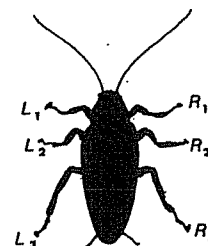


Figure 5. Black bars indicate the sequence of leg swings on the left ( $L_1, L_2, L_3$ ) and right ( $R_1, R_2, R_3$ ) sides in slowing-moving and scurrying insect gaits. Both gaits conform to four motor constancies: (1) the sequence of leg swings on a given side progresses from back to front (arrow  $a$ ); (2) the duration of a leg swing is fixed (interval  $b$ ); (3) the lags between hind- and middle-leg swings and between middle- and front-leg swings are fixed (interval  $c$ ); (4) opposing legs swing  $180^\circ$  out of phase (the ratio  $d/e = 1/2$ ). The specification of the period from one swing of a leg to the next (interval  $e$ ) exhausts the degrees of freedom in the parameterization of these gaits, given the constraints imposed by the four constancies. All other



differences follow from this specification. The stepping frequency is  $1/e$ . (After Wilson 1966.)

many different higher units to convey their output to muscle.

Another aspect of locomotory units is that they may be controlled from above by signals that are both few and simple. The outputs that may be generated by a locomotory unit are diverse and complex, and they adapt intelligently to sudden, unforeseeable variations in circumstances. Nonetheless, the higher circuits that coordinate behavior patterns of which locomotion is but a constituent can call upon the services of this resourceful unit by means of a few signal pathways. These control pathways carry primarily tonic signals whose simple temporal and spatial patterning in no way reflects the complexly patterned signals that will issue forth to the motor neurons.

We have already encountered one of these control signals: the command signal that sets the rate at which the pacemakers beat. The other control signals are commonly also tonic, and their average value determines some

property of the controlled circuitry. For the most part they determine which pathways within the controlled circuitry are allowed to be active and which are not. They do not usually engender activity within the controlled elements; they only vary the potential for activity. For this reason, I term this kind of controlling influence selective potentiation and depotentiation (Gallistel 1980).

## The link to motivation

Selective potentiation and depotentiation is the final span that links the concept of hierarchically ordered units of coordination to the concept of motivated behavior patterns. In what follows I give five examples of this principle. The first example is at a very low level of the motor hierarchy; the last two are clearly at motivational levels of function.

A "low spinal cat" is a cat whose spinal cord has been cut through in the chest region, thereby isolating the neural circuitry in the bottom half of





the spinal cord from the influence of anatomically (and for the most part functionally) higher circuitry. When such a cat is supported with its hind paws on a treadmill, the hind legs can walk. A tap delivered to the back of a hind paw during such walking elicits one of two opposing reflexes, depending on the phase of the leg's stepping cycle. If the tap is delivered during the swing phase, it elicits flexion of all the leg joints. This flexion lifts the paw up and over the obstacle against which the swinging paw has struck. The same stimulus delivered during the stance phase causes the opposite pattern of muscle activation. It elicits an extension of all the leg joints, hastening the moment when the paw may safely be lifted out of the way of the moving object that threatens to sweep the cat's paw from beneath it (Forssberg et al. 1975).

It would seem that the pacemaker that sets the stepping rhythm also controls the potential for action in the competing reflex arcs. During the swing phase the flexion reflex is potentiated and the extension reflex is depotentiated; during the stance phase the reverse is true. In neither case does the pacemaker set these arcs in action. Sensory input—the tap on the paw—plays that role. The pacemaker, however, controls the potential for action in these arcs, the pacemaker coordinates the operation of the reflexes with the operation of other units of behavior, insuring that at any given moment only the reflex action consonant with the other actions then taking place is allowed.

Selective potentiation and depotentiation do not generate activity in lower units, but rather control the flow of signals generated by other factors. In so doing they determine which units of behavior may be active and in what combinations. For example, when a salamander walks forward, the swing-triggering signal from the pacemaker must be routed to the muscle that lifts the leg (the elevator), the muscle that flexes the elbow (the flexor), and the muscle that swings the leg forward (the abductor). When the salamander walks backward, the same signal must be routed to the elevator, the flexor, and—rather than the abductor—the adductor, the muscle that draws the leg back (see Weiss 1941). I suggest

that descending control signals potentiate the path from pacemaker to abductor when the higher levels want forward locomotion and from pacemaker to adductor when they want backward locomotion.

If I am correct in assuming that during backward locomotion the direction of phase lags between oscillators on the same side is reversed, then a different set of coupling pathways must operate during backward locomotion. The control signals that specify which unit of locomotion is to operate realize their function by potentiating one set of coupling pathways and depotentiating the other. Thus the higher circuits that select walking forward or walking backward as part of a larger pattern of behavior do so largely by directing the flow of signals between pacemakers, and from pacemakers to motor neurons.

Taxes are servomechanisms that maintain an animal's orientation with respect to some directional stimulus such as light (phototaxis), gravity (geotaxis), or wind (anemotaxis). When these orienting units operate concurrently with a locomotory unit, directed progression results. In a paper published many years ago, Fraenkel (1927) showed that the taxes of the coastal snail, *Littorina*, are controlled by potentiation and depotentiation in such a way as to produce a major behavior pattern.

*Littorina* are usually found in crevasses about 3 to 8 meters above the waterline of rocky coasts, where they feed on algae when the crevasse is dampened by spray and estivate when it is dry. Fraenkel's work shows that snails dislodged from their crevasse by a storm may find their way back from shallow water near the shore to an appropriate crevasse by the following set of taxic progressions.

Except under special conditions, to be noted in a moment, these snails are negatively phototactic (they crawl toward the dark) and negatively geotactic (they crawl upward). In general, the path to the coast will be both darker than and higher than the path to the open sea, which explains why the snails crawl toward and up the coastal cliffs. A problem arises when they encounter underwater crevasses, however. They crawl into the dark depths of these crevasses

under the influence of negative phototaxis, up the back wall by negative geotaxis, and onto the ceiling. But how are they to progress farther? They are upside down, with gravity pulling perpendicularly to the surface they are on, so that geotaxis cannot guide their progression. To crawl farther under the guidance of negative phototaxis is impossible, because they are at the darkest point already.

It happens, however, that when—and only when—a coastal snail is both upside down and under water, the circuitry subserving negative phototaxis is depotentiated, while the circuitry subserving positive phototaxis is potentiated (see Fig. 6). Hence the snail crawls out along the ceiling of the underwater crevasse under the guidance of positive phototaxis. It then resumes its progression up the cliff under the guidance of negative geotaxis. The fact that the depotentiation of the negative phototaxis and the potentiation of the positive one occur only when the snail is under water (and upside down) explains why the snail's journey ends in the first crevasse above high tide.

This example shows how appropriately timed potentiation and depotentiation of selected lower-level circuitry may create complex purposive behavior patterns. We have already seen how the ingenuity with which the lower-level circuits are structured provides for the intelligent adaptation of details of the behavior to circumstances prevailing at the moment of its execution. We come now to examples of potentiation and depotentiation at motivational levels of function.

But why do we speak of motivation in behavior? Because, I submit, we see in behavior certain complex, goal-directed patterns that are adapted in such a way as to accomplish the overall function despite variations in circumstances. This sustained, functional cohesiveness of behavior cannot be accidental; it must be the outcome of processes that promote this cohesiveness. These processes are what we allude to when we mention motivation. The examples of potentiation and depotentiation just presented have therefore carried us from the simple neural circuits that control elementary responses to the other side of the chasm—the motivational processes that determine the overall



direction of behavior. Two final examples from work on the motivational function of the diencephalon anchor the bridge to the other side of the chasm.

It has been known since the pioneering work of Hess (1954) that electrical stimulation of discrete sites in and around the diencephalon can induce motivated behavior. Work by Flynn and his collaborators (Flynn 1972; Flynn et al. 1971) on stimulation-induced predation in cats shows that the mechanism of inducement is selective potentiation. When a non-predatory cat is touched on the cheek, it turns its head away; when touched on the lips, it purses them. In the predatory cat these reactions are depotentiated, and opposing reflexes are potentiated. Now a touch on the cheek elicits a turn toward the touch, and a touch on the lips elicits opening of the jaws. When an otherwise non-predatory cat is rendered predatory by mild electrical stimulation at a specific site on one side of the diencephalon, these predatory reflexes are potentiated on one side only! When touched on one side the cat reacts in a predatory fashion; when touched at the same place on the other side of its body it does not (MacDonnell and Flynn 1966). The unilaterality of this potentiating effect argues for the existence of quite specific neural pathways linking the site stimulated to the neural circuits subserving these elementary predatory reflexes. By means of these paths, the stimulation-generated neural signals potentiate the reflexes. By means of other paths emanating from the same site, these signals potentiate the spectrum of behaviors that together constitute predation.

The examples of potentiation given so far involve relatively elementary and probably inborn, unlearned units of behavior. The work of Beagley and Holley (1977) extends the unilateral potentiation phenomenon to a learning-dependent behavior. This extension makes it possible to argue that the account of motivation offered here applies to all motivated behavior, whether or not that behavior depends on learning.

Beagley and Holley surgically installed electrodes in the diencephalons of rats, positioning the electrodes in such a way that stimulation induced feeding. At the same time, they

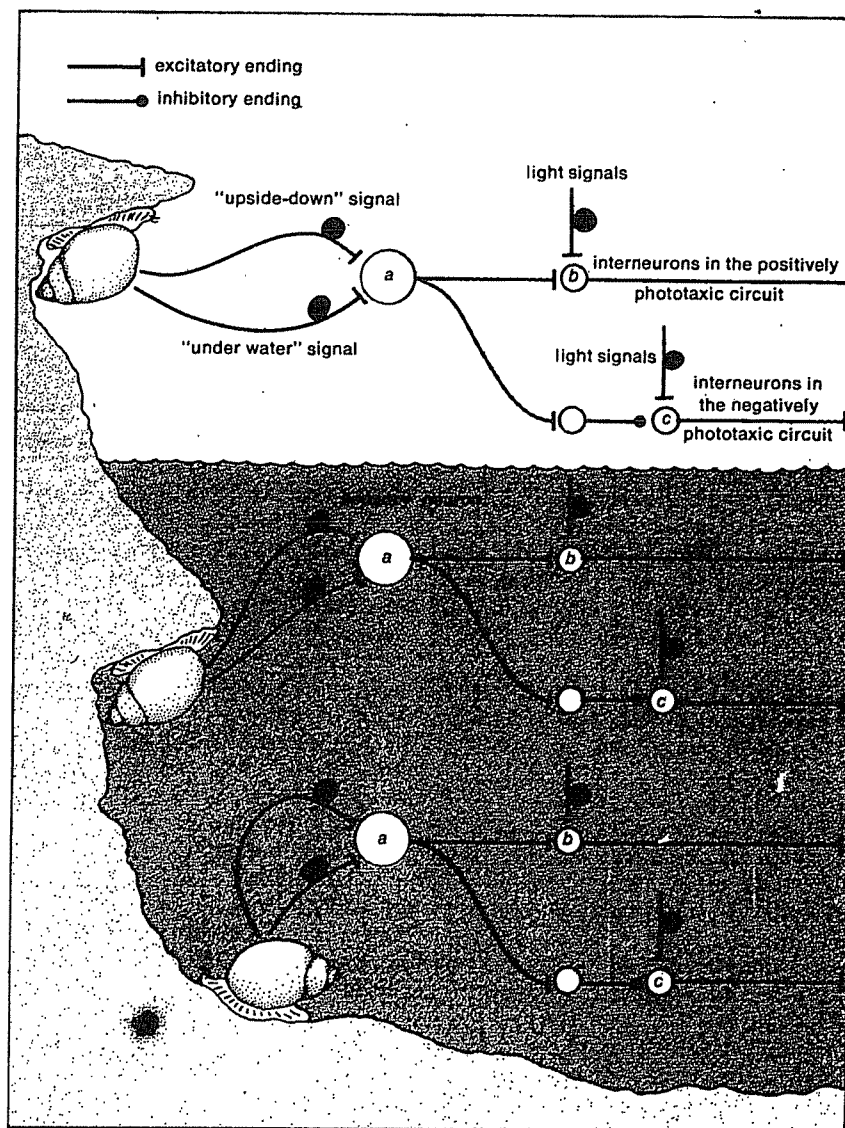
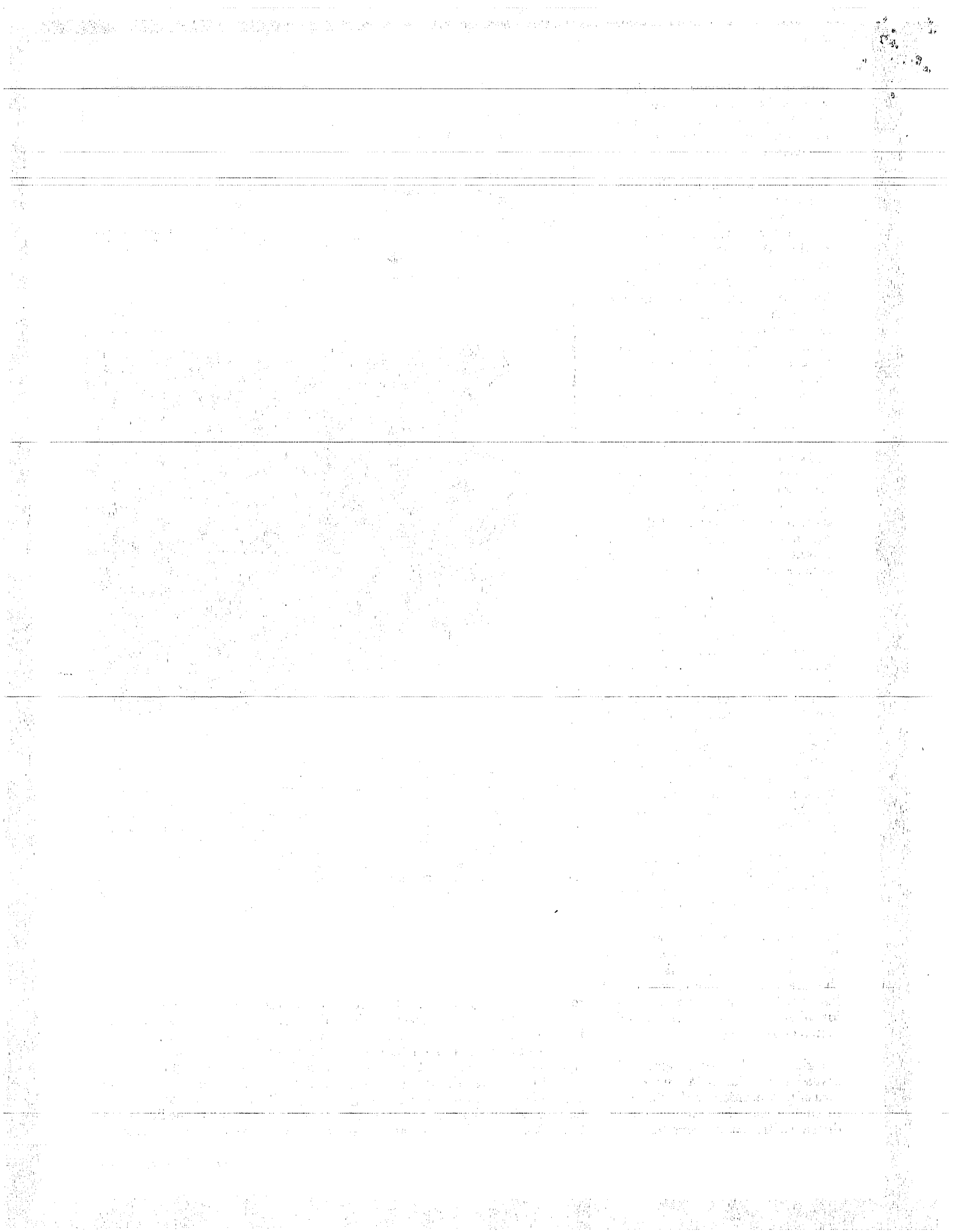


Figure 6. This highly conjectural neural circuit demonstrates that the principles of synaptic function elucidated by Sherrington can explain how the snail's positive light taxis becomes operative only when the snail is upside down and under water, while his negative light taxis is operative at all other times. The operation of the circuit is shown at three stages in the snail's progress from the ocean bottom to a suitable niche above the water. Activity of the sensory neurons (i.e. transmission of signals) at a given stage is indicated by colored lines, inactivity by

black lines. In the top and bottom stages interneuron *a* is inactive, hence interneuron *b*, which would be potentiated by *a*, is also inactive. Since the inactive *b* is a crucial component of the circuit mediating positive phototaxis, the snail has no functional positive phototaxis. In the middle stage, interneuron *a* is active, because both its inputs are active. Hence *c* is depotentiated, or inhibited, and *b* is potentiated. Now the positive phototaxis is functional and the negative is not, enabling the snail to continue its journey.

mounted two tiny lights on stalks secured to the rats' heads, so that the light on the left side was visible only to a rat's left eye and the light on the right was visible only to its right eye. They then trained the hungry rats to press a bar to obtain food in a nearby hopper. When the rats had learned this, Beagley and Holley arranged

matters so that presses of the bar delivered food only when the tiny lights were on, and the rats learned to press the bar only then. If a rat was hungry and either one or both lights came on, then the rat would go to the lever and press. When the rats were satiated they did not attend to the lights. Regardless of whether one or both lights



were on or off, they pressed infrequently.

Beagley and Holley then induced feeding behavior in *satiated* rats by stimulating a site on one side of the diencephalon. This stimulation potentiated the rats' response to the light, but only to the light on one side—the side opposite to that stimulated, since the right side of the brain controls the left side of the body and vice versa. When the light on the side opposite to that receiving electrical stimulation came on, therefore, a rat would press the lever and eat the food thus obtained. But the rat ignored the light on the other side, just as it normally did when satiated. In short, on one side the rat looked at the world through the eye of a hungry rat, while on the other it looked at the world through the eye of a satiated rat.

This procedure was inspired by the MacDonnell and Flynn experiment, in which the unilaterality of the potentiating effect also argued for specific pathways running from the site of diencephalic stimulation to the neural circuitry that coordinates the behavior. In the Beagley and Holley experiment, however, the form of the potentiated behavior depended on the rat's having learned the relationship between the lights, the pressing of the lever, and the appearance of food in the hopper. It may be concluded that motivated behavior, whether or not its form happens to depend on learning, is goal-directed behavior whose functional cohesiveness is produced by the selective potentiating and depotentiating effects of neural and hormonal signals arising in and around the diencephalon.

## Crossing the bridge

The conception of motivation put forward in this essay is not new. Ethologists have always thought of motivation in this way (see e.g. Lorenz 1937; Tinbergen 1951, Chap. 5), as have many physiological psychologists (Lashley 1938; Stellar 1960). Morgan (1943), for example, speaks of central motive states as establishing "a set or potentiality for presenting various patterns of behavior when the appropriate stimulus conditions in the external environment are available" (p. 461; italics in original).

By potentiating a coherent spectrum of possible behaviors, a central motive state establishes an overall direction to behavior, but leaves it to the potentiated circuits to determine how that direction shall be maintained given the circumstances attending the execution of the behavior. Motivational processes set up an array of behavioral options, all tending to the same end. Other factors determine which options are exercised. In this way motivated behavior acquires the dual characteristics of purposiveness and intelligent adaptation to unforeseeable circumstances.

What I have tried to do here is integrate this view of motivation with work on lower-level mechanisms of coordination. As long as one sticks to the notion that the reflex is the only elementary unit of behavior, there is no prospect of understanding the baffling degree of variation to be found in the surface detail of behavior. Recognizing the existence of other kinds of elementary units, the oscillator and the servomechanism in particular, leads in many instances to an explanation of this variation.

Systems of coupled oscillators produce a great many different outputs when one or a few parameters are varied. This is illustrated by the modern understanding of how the diverse gaits of insects are generated. Those familiar with the synthesis of trajectories by Fourier techniques, that is, by the concurrent execution of two or more sinusoidal trajectories, will realize that any trajectory whatsoever may be closely approximated by superimposing the outputs of a modest number of oscillators running at different frequencies (cf. Bernstein 1967, p. 37).

Complex units of behavior, composed of oscillators, servomechanisms, and reflexes, have an inherent capacity for producing many variations on the basic output pattern. This capacity is extended by the repeated use of the principle of selective potentiation to insure that the elements operate in appropriate conjunction. This last point is illustrated by the role of selective potentiation and depotentiation in integrating the operation of opposing stumble-preventing reflexes within the cat's stepping cycle.

The principle of selective potentiation and depotentiation is used at

every level of the motor hierarchy. When it is used at the highest levels, to integrate the operation of many complex units of behavior, we call the result motivated behavior.

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