tion. For working out another special case, I am indebted to Dr. H. P. Robertson.
I was told by the late Prof. E. Hilb of Würzburg, to whom I showed this work several
years ago, that he had seen a paper by a French author proceeding on somewhat similar
lines. However, I was unable to locate that paper.

As an illustration of this theory, I usually demonstrate in my lectures the Wiener
experiment (Ann. Physik, 49, 105 (1883); Kohlrausch, Praktische Physik, p. 254,
Leipzig (1921)) about the propagation of light in a medium composed of a layer of water
over one of glycerine. It can be completely understood with the help of our theory of
section 4 (with glancing incidence) and it is suitable for the determination of the relative
index of refraction of water and glycerine.


THE STRUCTURAL BASIS OF THE INTEGRATION OF BEHAVIOR

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The behavior of embryos has attracted the attention of biologists for
a long time. William Harvey recorded important observations on the
movements of the chick embryo. With the advent of the microscope
Schwammerdam and Leeuwenhoek studied intensively the movements
of snail embryos in the egg. Following their time there were only casual
or isolated observations in this line until 1885 when Preyer published his
work on the general physiology of the embryo, in which he gave large
place to movements. Since Preyer, reports on the subject have been for
the most part fragmentary; but not altogether so. Since 1920 Minkowski
of Zürich has studied the movement of young human fetuses very exten-
sively; and others, particularly Yanase, and Bolaffio and Artom, have
made very important contributions to the knowledge of human fetal
behavior. From all of this work, however, as it stands alone, no unifying
principle or law has been deduced to resolve the knowledge of the de-
velopment of behavior into an intelligible system. This is due, not to
lack of acumen on the part of the observers, but to conditions inherent
in the species studied by them; that is to say, the species have been high
in the scale of evolution or morphological specialization, and have for the
most part permitted of very limited time of observation. For some human
fetuses the time of study has been limited to a very few minutes.

For the discovery of law or order in the development of behavior it is neces-
sary to turn to a species which is relatively unspecialized morphologically
and which can be studied continuously from the beginning of movement till
the adult behavior pattern is established. In a complete historical or
chronological panorama of the development of behavior of such a type the
fragmentary pictures from higher species fit appropriate places with a remarkable degree of conformity, and the conclusion seems justified that, from the lowest to the highest vertebrates, there is a common law according to which the individual attains its progressive adjustment to its environment. This law or pattern of development consists in the expansion of a primarily integrated total pattern of action within which partial patterns arise by individuation through restriction of both the field of motor action and the field of adequate stimulation. This law has been demonstrated in the origin of unconditioned reflexes, and it appears also to apply to the formation of conditioned reflexes, instincts and the so-called process of trial and error. The structural basis for this law is found in the growth of the nervous system; and in this also there appears to be a natural basis for the interpretation of attitude and motivation.

The salamander (Amblystoma punctatum), a morphologically generalized type of vertebrate, lends itself admirably to the study of the development of movement, for a particular individual of this genus can be observed continuously from the earliest muscular contraction till the definitive behavior pattern is established. Until some time after swimming begins this animal has no movable appendages. The earliest movement is a contraction of the most anterior muscles of the trunk. As the animal grows older the contraction becomes more extensive tailward till the whole trunk and tail are involved. The more extensive contractions always begin with the most anterior muscles and progress tailward as a perfectly integrated total reaction. A series of these flexures, alternating to one side and then the other, eventually effects aquatic locomotion. As appendages develop and acquire motility they move for a considerable period only as the trunk moves; and before local reflexes appear in the fore legs, or later in the hind legs, the alternating movement of the limbs in walking is established in coordination with the alternating movements of the trunk. Postural reactions of the trunk and limbs, also, are established before local reflexes of the legs appear. These reflexes gradually emerge from a total pattern of limb-and-trunk movements; and this occurs at about the time that antigravity action of the legs can first be observed. Posture and the walking gait as such are therefore primarily total reactions. Also the rotation of the leg in walking occurs first at the extreme phase of extension as a part of a total pattern of leg action.

The salamander orients itself in space also before local reflexes can be excited. This means that the primary relation of the vestibular system is with total reaction, not with local reflexes. Posture and the pattern of locomotion are, then, total systems. They are not built up synthetically by integration of reflexes. They arise by the expansion of a total pattern of action. Within them local reflexes arise by a process of analysis or individuation, and they appear in time primarily in relation to the
orientation of the animal to surfaces, rather than to space as such. They acquire varying degrees of independence according to the age, physiological condition and type of the animal concerned.

This order of development of behavior is explained by the order of growth of certain parts of the nervous system. The cephalocaudal expansion and progression of movement in the trunk have their origin in a series of motor neurones which develop progressively cephalocaudal and conduct in the same direction. From them the primary motor fibres go out to the trunk muscles. Branches of these fibres are the first motor fibres to the limbs, and at the beginning of movement of the limb these are the only perceptible motor fibres in the limb. As reflexes appear motor fibres from another region in the spinal cord join the primary motor fibres in the nerve roots. These secondary ventral root fibres presumably constitute the final common path for local reflexes, although the full demonstration of this is not yet established. The growth of the central and peripheral motor components of the nervous system, accordingly, involves the expansion of a unitary motor mechanism in which secondary systems emerge in subordination to the primary system; and into which essentially sensory systems (e.g., vestibular) grow and become consolidated or mechanized.

It is well known that, in the development of the reflex, there is a progressive restriction of the stimulogenous zone, or zone of adequate stimulus. In the early stage of development, stimulation at any sensitive point excites a total reaction. Within the total receptor field there emerge relatively large zones within which stimulation may excite a particular local reflex; and as development proceeds this zone of adequate stimulation becomes more and more localized. In the salamander, for example, early leg reflexes may be excited from an area on the trunk near the leg as well as by stimulation on the leg. In man (Minkowski) in early fetal stages the plantar reflex may be excited by stimulation on the dorsum of the foot as well as on the plantar surface, which is the definitive zone of adequate stimulation.

For an appreciable period before a particular receptor field acquires specificity in relation to an appropriate local reflex its stimulation inhibits the total reaction. Inhibition, accordingly, through stimulation of the exteroceptive field, begins as a total pattern. It is then in a field of total inhibition that the local reflex emerges. The reflex may, therefore, be regarded as a total behavior pattern which consists of two components, one overt or excitatory, the other covert or inhibitory. The essential anatomical basis for this is (1) in the mechanism of the total pattern of action, or primary motor system, and (2) in the mechanism of the local reflex, or secondary motor system; the mechanism of the total pattern being inhibited and that of the reflex excited. But since inhibition is not
a static condition but a mode of action, the mechanism of the total pattern
must be regarded as participating in every local reflex.

In the light of these facts of structure and behavior, the fallacy of the
traditional conception of the chain reflex, that one initial reflex stimulates
the next in series, and this the following, etc., is apparent. In such an
act as feeding, which may be regarded as a typical chain reflex, the process
begins in the salamander with the elementary total reaction of swimming,
which is followed in order by action of jaw, gill arches and gullet. But
the motor neurones which excite these several phases of the act are in
organic connection with the motor mechanism of the total reaction. In
the first phase of the performance, the swimming reaction, the muscles
of the jaws, gill arches and gullet, must be set, either by excitation or
inhibition, for their responses in appropriate order. In this respect the
situation is essentially like that of the earliest reflex that it is possible to
elicit in the salamander: it can be excited only as the animal as a whole
assumes a definite posture under the dominance of the mechanism of the
total pattern. The particular acts of feeding, which may appear to be
severally discrete, are actually only phases of a reaction which is funda-
mentally unitary. Chain reflexes are fundamentally total reactions
under the dominance of the mechanism of the total pattern of action.

The conditioned reflex is conventionally regarded as differing essen-
tially from the unconditioned reflex, but this is contradicted by evidence
drawn from the development of behavior. Like unconditioned reflexes,
the conditioned reaction emerges on the motor side from a field of general
activity and on the sensory side the specific stimulus emerges from a
general or wide zone of adequate stimulation. The latter phase of the
development is obvious in a highly specialized form in conditioning to the
metronome: the conditioning is first to the ticking in general and only
later to a specific number of ticks. On the motor side of the conditioning,
reaction is at first general, approximately a total reaction, at least of a
postural nature, and only later does it become specific. Conditioning of
reactions accordingly is accomplished by restriction (narrowing) of the
zone of adequate stimulation and concomitant restriction in the field of
action. The primary structural basis for this is in the mechanism of the
total pattern.

The same interpretation can be applied also to learning by trial and error.
The immediate response of an animal when it is placed in an utterly
strange problem box or cage is general activity; and the stimulus to this
action appears to be the situation as a whole. But within this general
situation there eventually emerge particular features as relatively localized
stimuli, and concomitantly out of the general field of action there emerges
the particular act that is appropriate to the situation. This feature in
the behavior of rats in the maze has been recognized by Professor Lashley.¹
He says: "None of the studies of learning or retention of the mazes after cerebral lesions has given the slightest indication that the maze habit is made up of independent associational elements." And, elsewhere, "Many animals tend to explore the entire box at every trial until they become thoroughly adapted to the routine of training, and the initial improvement is largely due to this." In other words, the animal whose mechanism of the total pattern is particularly responsive to the general situation as a stimulus individuates the appropriate response out of the total pattern more readily than others do. Here again the mechanism of the total action pattern is the key to the process of learning.

Instinctive behavior is conventionally regarded as the result of compounding unconditioned reflexes essentially upon the principle of the so-called chain reflex. It involves the organism as a whole as opposed to the reflex, which is conventionally regarded as involving only a part of the organism. But, so far as is known, reflexes begin as total action patterns in response to a comparatively general field of stimulation and acquire their restricted function or specificity on both sensory and motor sides secondarily. Instincts typically are just such responses—total action patterns in response to relatively general situations. In proportion as they lose their pristine purity they acquire the nature of conditioned responses. Whether pure or modified, therefore, instinctive performances like reflexes have their origin in the mechanism of the total behavior pattern.

It has been explained above that the salamander acquires the ability to orient itself in space by the growth of vestibular neurones into the mechanism of the total pattern; but it should be noted that the vestibular system develops centrifugally, that is to say, the vestibular sense organs are the last elements of the system to maturate. The central relation of the neurones of the postural mechanism must therefore be determined without reference to the peripheral stimulation of the sense organs concerned. The same is true of the optic system. In fact, the major conduction paths of the diencephalon and mesencephalon are established in the salamander before there is any evidence of conduction paths entering these regions from the lower parts of the brain and before there is evidence of stimulation of the system through the olfactory, optic or other sense-organs. This cerebral mechanism, however, has at this pre-sensory period already established relations with the motor mechanism just as the vestibular component of the postural mechanism establishes its relation with the motor mechanism before the vestibular sense organs are developed. By this pre-sensory growth of the vestibular system the attitude which the individual will take toward space is predetermined; later when the vestibular sense organs are connected with this apparatus they merely furnish points of reference for orientation. The pre-sensory
growth of the cerebral mechanism may accordingly be regarded as determining what the attitude of the individual as a whole shall be toward the environment before the organism can take cognizance physiologically of its environment.

The determination of the primary attitude of the organism toward environment is intrinsic. When environment is brought to bear upon this intrinsic apparatus through sense organs, conditioning of behavior begins: the initiative of attitude is primarily within the organism. Not only does this statement hold for the initial response of the organism to sensory stimulation, but according to the mode of growth of the central nervous system, it probably holds also during later life; for after the sensory field has established connections with the motor system, and true sensory-motor processes are in play, neurones continue to develop in the brain outside the zones of simple sensory-motor activity. These neurones are, so to speak, supra-sensory or supra-associational elements. Their fibres always grow into the sensory-motor field of action. Their structure warrants the belief that they are functional conductors. That neurones may activate behavior before they are stimulated directly or indirectly from sensory fields in fishes and birds is well known. The hypothesis is therefore justified that these supra-sensory or supra-associational neurones in the growing nervous system are determiners of attitude or activating factors in behavior. The motivation of the organism as a whole must accordingly be, at least in part, intrinsic. The organism acts first on the environment and only later reacts to the environment. This principle is observed not only in behavior but in the growth of the nervous system. Any theory of motivation, therefore, which ascribes the activation of behavior wholly to the environment is inadequate. In so far as the correlation of structure and function in the development of behavior has been established there is justification for the belief in intrinsic sources of action on the part of the individual. The individual is more than reaction to its environment and it dominates its environment according as there is a growing component of supra-sensory and supra-associational elements in its nervous system. The structural basis for such a factor in behavior has been demonstrated in the salamander, though it is only in higher animals with well-developed cerebral cortex that this tendency comes to full expression.

In this discussion emphasis has been placed upon the organism as a whole and the mechanism of the total pattern. Although the conception of "the organism as a whole" may in a degree be mystical as used by some writers, the demonstration of a specific mechanism that at all times makes the normal individual a unit takes this conception out of the realm of mysticism or vitalism and places it on a scientific foundation. Much remains to be learned anatomically about the mechanism of the total
action pattern, which is the organ of the unity of the individual, but this much is known about it: it is a definite structure in lower vertebrates and it is a growing thing. Primarily it is strictly motor and its growth establishes the early behavior pattern without the intervention of sensory elements. Later elements that are categorically sensory (e.g., the vestibular system) grow into it and become inseparably mechanized with it to determine such a subtle action as the orientation of the individual as a whole in space. It is further known that neurons continue to grow into this mechanism from more and more remote fields until the cerebral cortex itself becomes consolidated with it in greater or less degree.

The mechanism of the total behavior pattern is, then, a growing thing. Its reality as such gives scientific grounds for the interpretation of the development of behavior, or learning, in general, as the expansion of a unitary system within which partial systems arise as dependencies under its jurisdiction: an interpretation that rationalizes the phenomena of behavior as treated under the various accepted categories.