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GEORGE ELLETT COGHILL

1872–1941

BY

C. JUDSON HERRICK

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George Ellett Coghill was a philosopher before he was a biologist. At Brown University he followed the conventional classical course, graduating in 1896 with the A. B. degree. At twenty-five years of age, without professional training in philosophy, psychology or biology, during several months of solitary meditation he pondered the issues of a naturalistic philosophy which was consonant with his own way of thinking. The problems with which he struggled were essentially psychological; accordingly, he resolved to try to penetrate to the root of the matter and devote himself to an inquiry into the natural history of the human mind.

He realized at the outset that the biological approach offered promise, for the key factors probably lie in the nervous system. It was also evident that one lifetime is too short for that professional training in philosophy, psychology and biology requisite to round out the program. The obvious answer was to begin at the beginning and qualify himself as a biologist. This he did. Though most of his published research is strictly biological, the philosophical interest never waned and he was alert for the psychological meaning of his findings. His reading covered a wide field and was directed toward psychological interpretation and philosophical integration, as testified by voluminous notes, extracts and comments, all systematically filed and indexed. This background perhaps explains the curious fact that, though he was expert in neither philosophy nor psychology, his work received wider recognition in the psychological field than among his biological colleagues.

He was born at Beaucoup, Illinois, on March 17, 1872, the fifth of a family of seven children of John Waller and Elizabeth Tucker Coghill. He was reared on a farm near Roseville, Illinois. On September 13, 1900, he married Miss Muriel Anderson and to them five children were born, Robert DeWolf, James Tucker, Louis Waller, Muriel, and Benjamin Anderson. He is survived by these children and their mother.

He attended Shurtleff College for two years, then transferred to Brown University. His biological training began at the University of New Mexico, which he entered as a graduate student in 1897 and left with the rank of assistant professor of biology in 1900; it was continued at Brown University, 1900 to 1902, when he received the Ph. D. degree in biology. During several collegiate appointments from 1902 to 1913 and as professor of anatomy in the University of Kansas from 1913 to 1926 a secure factual foundation was laid by unremitting observation and experiment and this accumulation of data continued until his death at Gainesville, Florida, on July 23, 1941. During the decade, 1926 to 1936, he held a research appointment as member and professor of comparative anatomy at the Wistar Institute of Anatomy and Biology, Philadelphia, and during this period the chief conclusions reached were formulated in lectures and brief published papers. He was elected to membership in the National Academy of Sciences in 1935.

The years 1936 to 1941 were spent in retirement. Though broken in health and at times completely incapacitated, these years were productive. He continued his research as strength permitted, aided by grants from the Josiah Macy, Jr. Foundation, and had in preparation a comprehensive work to be entitled, "Principles of Development in Psycho-organismal Behavior" designed to present a psychological and philosophical synthesis of his studies on organismic development and the significance of mentation in these vital processes. Unfortunately this manuscript was left unfinished.

The nervous system was envisaged as a going concern the business of which is to maintain efficient coordination of the internal activities of the body and to ensure appropriate adjustment of the animal with its environment. Anatomical structure is meaningless apart from what it does. In all of his work this attitude is manifest. Every detail of structure and every observed activity was consistently examined in its relations with the organism as a whole. The program was so purposefully planned that every line of inquiry begun was directed toward a definite end and was set in its appropriate place without fumbling or lost motion.

The most significant outcome of this series of researches is the impressive demonstration of the unity and integrity of the organism and the dominance throughout life of the "total pattern" over "partial patterns" of behavior. Most behavior results from local and transient disturbance of this equilibrated system. There are many subordinate centers of dominance with more or less local autonomy, but these develop and continue to operate within the frame of the organismic whole and any permanent distortion of balanced interaction within this hierarchy of integrated units is abnormal. The nervous system is the chief, though by no means the only, agency employed in the maintenance of normally balanced vital functions, and the research program was directed primarily to the discovery of the actual apparatus involved.

These generalizations may be formulated as one views the program in retrospect. They matured slowly in Dr. Coghill's mind, not as logical deductions from philosophic premises, but from the evidence accumulated as the research progressed. There is no evidence of any philosophic "system" at the start. On the contrary, problems were attacked with an open mind singularly free from preconceptions and distrustful of dogma, conventional methods and traditional formulations. This is illustrated by a remark in his early account of the behavior of Triturus larvae in 1909, where he writes, "tabulated schemes for rapid recording were tried in my first experiments of 1906, but it soon became apparent that such forms could not be adhered to, for they were necessarily based upon presumptions of some sort and were, therefore, a hindrance rather than a help to alert observation."

The original purpose was to find out what animals do with their nervous systems. Direct observation of the nervous tissues in action was impossible. At that time no technique was available for this, but overt behavior was observable. The problem was to find some way to correlate this behavior with the nervous tissues which activate and regulate it. Some progress had already been achieved by indirect methods of experiments on animals and by neuropathological studies, but a more direct approach was sought.

About forty years ago he resolved to attack this problem genetically. The late Stewart Paton was at that time (unknown to Coghill) investigating reactions of vertebrate embryos and associated changes in the nervous system; but his objective and methods were radically different from Coghill's, for he dismissed the study of specific reactions as impractical and aimed to discover how far the behavior in general is dependent upon "the functional activity of a nervous system." This specific relation is exactly what Coghill proposed to investigate.

Doctor Coghill's plan was to select some primitive and generalized species of animal with simple behavior and a nervous system which is correspondingly simplified, though not beyond the limit where comparison with human structure is practicable. The first step would be to follow the development of this animal from egg to adult, recording the sequence of changes in patterns of overt behavior from the first muscular movements. These observations made on statistically adequate numbers of specimens at each stage in the elaboration of the behavior pattern would establish for the species studied a norm or standard of developmental stages from the simplest to the completed action system of the adult. The records would include both spontaneous behavior and responses to various standardized methods of stimulation. The next step would be the preservation of large numbers of specimens each of which was known by test to have reached a particular and definable stage of physiological development. Microscopic study of these specimens would, it was hoped, reveal a series of changes in bodily structure correlated with the physiological stages previously established. Finally when the physiological and the anatomical data are assembled and fitted together the bodily organs concerned with successive phases of the functional development are revealed. With each increment of the developing complexity of the behavior pattern some specific activity is seen in sharp relief for which a corresponding change in bodily structure would be sought.

This program obviously would be exceedingly laborious and exacting and it should be carried on cooperatively by a team of qualified investigators; nevertheless Coghill resolved to attempt it single-handed. To this resolve he steadfastly adhered for the remainder of his life, with industry, insight and productiveness rarely equalled. The results have justified the labor and sacrifices—and these were very large. The obstacles encountered would have been insuperable to a man of less intensity of purpose and indomitable persistence. During the years 1902 to 1913 he held appointments in small colleges with a heavy teaching schedule and no assistance of any kind. The tedious physiological experiments and the preparation of enormous numbers of serial sections had to be done with his own hands after long days of fatiguing duty.

As objects of study he selected the salamanders, whose eggs are abundant, easily reared and observed, and tolerant of a wide variety of experimental procedures. Among these Amblystoma was an especially fortunate choice, for during the span of forty years of his labor this has proved to be the most serviceable type for a wide range of experimental researches at the hands of numberless other investigators. The common frog has been the handmaid of physiology for centuries, beginning even before that memorable day when Galvani hung some frogs' legs on an iron railing with brass hooks and saw them twitch from the electrolytic currents generated; and Coghill's first observations were upon anuran tadpoles. He promptly transferred his attention to the salamanders, which since that time have displaced the frogs from their preeminence in the field of experimental embryology. Here he broke new ground in both objective and methods of work.

With Dr. Coghill the total behavior of the animal was under observation and knowledge of the anatomical structure of the body as a whole was essential for its interpretation. In this connection the subject chosen for his doctor's dissertation is significant—"The Cranial Nerves of Amblystoma tigrinum." In this, his first major scientific contribution, he gained the necessary familiarity with the structure of the animal whose development he later studied.[1] This paper is not descriptive anatomy of the traditional sort, but each peripheral nerve is analyzed microscopically into its components as functionally defined and in his subsequent studies the development of each of these components is separately described. This dissertation laid a secure foundation for all subsequent work. His program included, in addition to study of the differentiation of the nervous system in correlation with the sequence of development of behavior patterns, also parallel descriptions of the development of blood vessels, organs of digestion, excretion, etc. Some of the latter studies were begun in collaboration with his students, but not carried to completion. In view of the great amount of research which has been done on Amblystoma, these studies should be continued, and this would seem to be the next step toward the realization of Dr. Coghill's ideal.

Doctor Coghill's first teaching positions were in Oregon, where Amblystoma was not readily available. It would have been possible to secure the eggs from the east, for they survive shipment very well. This was not tried, and fortunately so, for later experience taught him that, though Amblystoma eggs grow apparently normally after long shipment, their subsequent behavior is atypical. The first physiological observations were made upon Triturus (Triton, Diemyctylus) torosus and these were later repeated with Amblystoma. The findings were similar, and this is explained by the fact, recently demonstrated by Dr. G. P. DuShane, that the pattern of development of Triturus closely resembles that of Amblystoma. The cranial nerves of Triturus were described by Dr. Coghill at this time (1906) from specimens of T. tæniatus which were given to him by Dr. Th. Boveri, with whom he studied in Würzburg in 1902.

It was not then known whether the earliest movements of these embryos were haphazard and disorderly or performed according to some observable system. This question was soon answered and an orderly sequence of reactions to stimulation and of spontaneous movements was described in the paper of 1909.

The preliminary experiments showed that the most useful criteria for staging the developing embryos physiologically were their reactions to tactile stimulation. A fine human hair was brushed lightly over the skin and reactions recorded. He early noted that "the extreme sensitiveness of some very young embryos is remarkable" and took special precautions to distinguish between "reflex," i. e., neuromuscular responses, and myogenic movements called forth by direct pressure upon the reacting muscles. The neglect of these precautions by some subsequent students of embryonic behavior has resulted in much confusion. In these amphibian embryos the distinction between neurogenic and myogenic responses is sharp and clear at the hands of a careful and experienced observer.

In the course of further experimentation the spontaneous movements of these embryos were carefully observed and their sensitivity to electrical, chemical, visual and other stimuli was explored. In the staging of the younger specimens responses to light tactile stimulation of the skin continued to be the chief reliance. At more advanced ages a large variety of other criteria were employed as the patterns of behavior changed.

In the paper of 1909 the sequence of changes in response to light tactile stimulation was recorded, but the growing embryos were not grouped in named or numbered physiological stages. In later reports, after the observations had been repeated with Amblystoma and amplified, the following physiological stages were defined: (1) premotile, including all early stages which exhibit no movement of somatic muscles; (2) nonmotile, with only myogenic movements executed spontaneously or resulting from direct stimulation of the muscles; (3) early flexure, characterized by the first neuromuscular responses; (4) coil, when the embryos execute spontaneously or in response to stimulation spasmodic unilateral contractions resulting in a tight coil; (5) S-reaction; (6) early swimming. These stages are demonstrable in the embryos and are clearly defined. The staging of larvae after hatching from the eggs presents more serious difficulties and these problems are even now still under investigation.

During this period Dr. R. G. Harrison had been engaged upon a morphological staging. A series of specimens of Amblystoma from the unsegmented egg to the first feeding reactions was separated into 46 stages, representatives of which were carefully drawn. Though these pictures have not been published, photographs of them have been supplied to other workers in this field and frequent references to Harrison's stages are in the literature. In 1933 Dr. W. T. Dempster published observations on the growth of Amblystoma in early stages, and from 1937 to 1941 the present writer issued a series of papers describing the internal differentiation of the brain from the coil stage to the adult, with a provisional correlation of Coghill's and Harrison's stages. Currently Doctors DuShane and Hutchinson are engaged upon a more critical study of the growth of Amblystoma under rigidly controlled conditions which it is hoped will clarify a confused situation.

From all of these studies it is clear that the growth and differentiation of Amblystoma under natural environmental conditions cannot be reduced to any single series of formulae. Coghill's physiological series does not run exactly parallel with Harrison's morphological series, and in the differentiation of internal structures the various organs do not keep step with one another or with the development of external form. In view of these rather wide deviations from any single standard or norm of development and the number of unknown variables, the only practicable procedure has been to select some particular criterion of structure or function and stage the specimens under investigation with reference to it. Thus Coghill writes, "after locomotion by swimming is established, the development of behavior in Amblystoma may be regarded as following two courses towards different goals: the one leading to the capture of prey and swallowing it; the other to terrestrial locomotion by walking." These two courses do not necessarily run parallel, but may vary independently, and Coghill's later studies were devoted to the development of the limbs as organs of locomotion and specifically to the relation of these "partial patterns" of movement to the "total pattern."

The stages from swimming to feeding were grouped as early swimmers, strong swimmers, late swimmers and, preceding the first feeding reactions, short periods of active avoiding and non-responsiveness. Movements of the limbs begin shortly before the time of the first feeding reactions, and the sequence of this development was outlined to me in a letter of May 26, 1926:

"Following swimming, events come in the following order:

gill movement coordinated with trunk movement, discrete gill movement (along with fore limb movement), fore limb movement coordinated with trunk movement, discrete arm movement, elbow flexion coordinated with arm movement, discrete forearm movement, hand movement integrated with arm movement, hind leg movement integrated with trunk movement, knee flexion integrated with leg movement, discrete knee flexion, toe movement integrated with leg movement."

From this he concludes (in a statement published ten years later—J. Genetic Psychol., vol. 48, p. 6):

"Terrestrial locomotion, like the aquatic, is also a total action pattern in Amblystoma. . . . In the beginning of the walking gait, therefore, the limbs function wholly as integral parts of a total pattern of action without any intervention of local reflexes. Local reflexes of the limbs appear later, as the limbs become a factor in orientation of the animal with reference to a surface."

Doctor Coghill's conception of the "total pattern" has been frequently misunderstood, even by his own disciples and sympathetic critics, with resulting confusion. If authors use the same word with different meanings, controversy is almost inevitable regarding both factual description and interpretation. In his earlier papers this expression was used in a restricted sense which was not clearly defined. His later references indicate a broader connotation, but unfortunately the relations between the larger total pattern and the subordinate patterns are not explained in sufficient detail and misunderstanding has resulted. The apparent ambiguity disappears when the earlier condensed statements are read in the light of the subsequent discussions of the apparatus of integration.

As already pointed out, the mature organism is regarded as an hierarchy of local units, each with some measure of autonomy and all bound together as an integrated whole. During the maturation of the neuromotor apparatus these local units are so interconnected that the first overt movements to appear are orderly sequences of behavior, not haphazard nor convulsive action. In subsequent stages, with increase in the complexity of the local apparatus, these "partial patterns" remain throughout life under the control of the "total pattern" of the organismic whole. The apparatus of integration takes various forms —nervous and non-nervous—but in the normal animal the dominance of the total pattern is never lost. Thus Coghill wrote in 1940, "'Pattern' connotes organization, and 'total pattern' expresses the organization of the whole individual for purposes of behavior."

In a study of the embryogenesis of animal behavior these two factors must always be kept in view, for they are indissociable—the presence of local and more or less autonomous organs and the dominance of the organism-as-a-whole over all of them. These factors are sometimes antagonistic, but they are not mutually exclusive. Without this dominance orderly development would be impossible and without some measure of local autonomy differentiation cannot go on. The problems of organogenesis and total integration go hand in hand.

In the development of Amblystoma this relationship appears with unusual clarity. According to widely current theory the complicated action system of the adult is built up by combining simple reflex units into progressively more and more complex systems. But when Dr. Coghill watched the development of salamanders and followed the successive steps in the elaboration of the action system of the skeletal musculature, he found no simple local reflexes. On the other hand, the first neuromuscular responses to appear were contractions of large masses of the muscle of the trunk, the mass increasing as the nervous and muscular organs matured, until in response to a single stimulus practically all of the trunk musculature was involved in an efficient swimming movement. This is a total pattern of behavior resulting in aquatic locomotion.

At this "early swimming stage" there are no limbs and all visible somatic movements are at first of total pattern type. As limbs develop and their movements are individuated, these movements emerge within the total pattern and as parts of it. Movements of the limb as a whole and of the separate parts of it are progressively emancipated from immediate participation in total movement and the aquatic type of locomotion is transformed into the terrestrial type, with separate action of the limbs and their members. In Amblystoma this emancipation of the partial patterns of the limbs is never complete and adult walking normally involves some total bodily movement of the swimming type. Even in birds and mammals, where limb movements may be executed quite independently of any visible overt movement of the trunk musculature, it remains true that the local activities of the limbs are to some extent subordinate to and under the control of the total pattern of the organization, for flying and walking are usually directed some whither and this direction does not reside in the members which execute the movements.

The preceding description applies to Amblystoma and only to the development of somatic movements of the trunk and limbs. For these it seems to be well validated; but it does not follow that the same sequence of events will appear in the development of other systems in Amblystoma, say of eye movements or visceral movements, or of limb movements in all other animals. The last point was investigated incompletely by Dr. Coghill in some fishes, reptiles and mammals. These studies were unfinished and the details are unpublished, but they convinced him that fin movements in killifish and toadfish and limb movements in reptiles and opossums in early stages of development are integrated with trunk movements much as in Amblystoma.

In these facts Dr. Coghill found no support for the current doctrine that complex behavior patterns are synthesized by accretion of discrete reflexes. Quite the contrary, the integration is primary and the analytic functions are secondarily developed within the total pattern. These partial patterns, in turn, may subsequently be synthesized into an indeterminate type of behavior of infinite variety, again under the influence of higher "supra-sensory and supra-associational centers" of integration (Proc. Nat. Acad. Sci., vol. 16, 1930, p. 642).

The evidence for this conclusion was presented, for Amblystoma, in detail up to maturation of the swimming movement, together with an account of the correlated development of the anatomical structures involved. The history of the individuation of limb movements is quite different and study of the structural changes involved was in process at the time of his death. Had he been permitted to carry these studies to conclusion, it is probable that his formulation of the relations between partial patterns and total patterns would have been amplified in form different from the concise and over-simplified statements in the earlier papers.

At the beginning he was confronted with the necessity of clearing the ground of some misconceptions in current doctrines of reflexology. He found in early stages no discrete local reflexes and no isolated reflex arcs. The present writer, who has devoted considerable attention to the histological structure of the brains of these salamanders, reports that even in the adult animal there is no such thing as a discrete reflex arc anywhere. The apparatus of the action system is not built of such units, but the structural specifications are according to a different plan in which the apparatus of integration is paramount and local individuation is at a minimum as compared with more highly differentiated brains.

Doctor Coghill, accordingly, emphasized the point at issue—the primacy of the integrative functions and total patterns—which comes out more clearly perhaps in his material than in any other vertebrate species which might have been chosen. In generalizing this conclusion in the broad biological terms laid down here he is on safe ground; but it is not safe in any particular instance to anticipate that the process of individuation of any organ will follow the same lines in detail. He was not unmindful of this point and it is unfortunate that he did not give it more explicit emphasis in his published writings.

During the developmental process, up to and including the adult, the partial patterns are initiated, differentiated and operated within the total organismic pattern and influenced by it. This influence may be manifest in overt behavior, as in the entire history of limb development of Amblystoma, or the process of emancipation may be accelerated in the central nervous adjustor so that the first overt movement of the limb is a local reflex.[2] In both cases the limb mechanism is never entirely free from some measure of subordination to the total organismic pattern.

Now to recur to the question of definitions. If one defines the concept of total pattern broadly in organismic terms, as Coghill evidently did, it is probable that few competent biologists or psychologists would controvert the thesis that the whole is greater than the parts and that in the living body the parts are under some measure of control by the organism-as-a-whole, i.e., that all partial patterns are subordinate to the total pattern. This total pattern is a complex hierarchy of local centers of dominance over subordinate parts with varying grades of autonomous activity. In any experimental program some particular component of this complex is selected for intensive study out of its total context, such as, for instance, aquatic or terrestrial locomotion. "Total" and "partial" are here relative terms to be interpreted in the light of the context in which they are used. In the context before us they are restricted to visible overt movement of skeletal musculature.

This is explicitly so stated in the manuscript of an unpublished lecture delivered at the University of Minnesota in April of 1930, where he wrote, "There is nothing immaterial in mind when I use the term pattern. I try to use it consistently to designate configuration or form of action or inhibition. When all overtly mobile parts of the animal appear to be in action I call the performance a total action pattern. When only a part of the overtly mobile animal is in action I call the performance a partial action pattern." In the monograph of 1940 Dr. Coghill says, "the whole individual probably acts in every response, either in an excitatory or inhibitory way. Therefore, while overtly the individuated part acts apparently independently of the total pattern, the latter participates in its performance by inhibition."

In this restricted sense there are instances, like the limbs of Amblystoma, where the partial pattern is at first tightly bound to the total pattern and in later stages progressively emancipated from these bonds. These instances were critically studied and described in detail by Dr. Coghill because they supply easily demonstrable factual data in support of his main thesis that the living body is not an assemblage of particulars built up by accretion, but an integrated unity from beginning to end. The patterns here demonstrable are not unique, but are found to recur with more or less variation in many other situations. These patterns, accordingly were regarded as typical illustrations of his larger conception. He would not have claimed that the development of all partial patterns must conform with the paradigm here laid out, though his own program had not advanced far in the exploration of other types of development.[3]

Most of the factual material published after his appointment in the department of anatomy at the University of Kansas is included in the twelve parts of his "Correlated anatomical and physiological studies of the growth of the nervous system of Amphibia" published from 1914 to 1936. These papers are models of close, accurately controlled observation and clear description, but they are not easily read, for the technical details are recondite and intricate. Skillful analysis marshals the evidence in intelligible and convincing form. The present writer has verified many of the observations upon the younger stages, using the original preparations, and he has confirmed and extended the descriptions of more advanced stages upon other material prepared by different methods. Other collaborators make similar reports. The accuracy of Coghill's descriptions is amply validated.

These papers cannot be summarized here, nor is this necessary, for their author has reviewed their salient features and has interpreted them more clearly and graphically than any commentator could hope to do. These studies, he says, "were undertaken with a view to correlating specific structure, in particular animals, with known physiological characteristics of those animals," and the measure of his success in this difficult enterprise exceeds that of any of his predecessors or successors.

The topics treated include an analysis of the afferent systems, central and peripheral, at successive stages of physiological development, a similar analysis of the efferent systems, and detailed accounts of the development of the apparatus of correlation and integration. Paper 10 of the series (1931) discusses some corollaries of the study of early development to the swimming stage. Papers 11 (1933) and 12 (1936) begin a new series of studies on the differentiation of the limbs and the relation of their local functions to the total pattern of behavior. It is hoped that these unfinished studies may be continued by some of his younger colleagues who collaborated in this program.

The ten papers of the first series deal with the development of the embryo up to the stage when locomotion by swimming is acquired. "During this period," he says, "the behavior pattern is an integrated unit, and the structural development of the nervous system is such as to maintain this integrity through the growth of functional neurons." Another important finding is the demonstration of the precocious differentiation of the motor systems and the early maturation of these and also of the sensory and correlating apparatus by intrinsic agencies in advance of any peripheral influence.

Clear and concise summaries of the observations recorded in the twelve "studies" are available in several of the published lectures, together with interpretations and applications to specific biological and psychological problems. The titles of these brief papers as listed in the accompanying bibliography reveal the scope of his interests and their content expresses profound and incisive thinking. Special mention should be made of two of these publications: (1) the lectures delivered in London on "Anatomy and the Problem of Behaviour" (Cambridge University Press, 1929), and (2) the presidential address before the American Association of Anatomists on "The Neuro-embryologic Study of Behavior: Principles, Perspective and Aim" (Science, vol. 78, 1933).

The psychological significance of the facts brought to light in this series of studies on embryogenesis had not been systematically formulated before Dr. Coghill's untimely death, though fragmentary suggestions are scattered through his later papers and lectures. Typical of these is the concluding passage of paper 10 of the "Studies."

"My object in this discussion is to show that . . . . spontaneity of nervous action, in the sense that it has been presented above, is projected into the life of the individual through an indeterminate period, and that, therefore, sensorimotor response should not be regarded as constituting the whole function of the nervous system. Overt behavior actually occurs in some species as an expression of the intrinsic dynamics of the organism as a whole, and, in so far as the correlation of nervous structure and function in the development of the individual has been carried, structural provision has been found for the perpetuation of spontaneity, autonomy, or initiative as a factor in its behavior. Any theory of motivation, therefore, that attributes this function wholly to the environment (Troland, '28) is grossly inadequate."

In this passage there is adumbrated a psychological principle to which he devoted much thought in his later years. Several years earlier (July 27, 1926), in reply to some comments upon the sixth paper of his "Studies," he wrote to me:

"In my opinion the most important thing in it is the demonstration of the wonderful capacity for growth that is retained by the nerve cell after it has become functional as a conductor. I am sure of the soundness of the observation histologically and see it amply corroborated in the development of movements in the limbs. . . . . . . I don't believe there is any break whatever between embryonic and adult performances, and that so long as adaptation to new conditions is possible functional nerve cells are growing somewhere in the nervous system in the same way that I see them growing in the ventral nerve roots."

This implies, as he later expressed it, that "learning is essentially growth, and mental hygiene is grounded in the growth of the nervous system." The spontaneous movements of the youngest motile embryos are internally activated and the pattern of their expression is determined by an intrinsic organization which is not dependent upon any sensori-motor excitation. "The organism," he says, "first acts on the environment and only later reacts to the environment." "The sensori-motor response, designated as the S R by psychologists, is a secondary form of behavior. Its primary function is orientation of the animal so that the action will be directed toward the appropriate end. But the sensory component of the system soon acquires the further role of activating and conditioning behavior." Thus we see that the later stages of intrinsic growth are modifiable by sensori-motor experience, but the internally generated spontaneity is not thereby reduced; on the other hand, it is amplified as the central adjustors increase in complexity of organization and integrative efficiency.

"The individual, certainly in the early stages, has much more nervous organization than can express itself in immediate behavior; and the higher the species in the animal scale, the larger is this supra-sensory and supra-associational component of the nervous system" (Conference on Adolescence, Cleveland, 1930). These remarks remind one of Wm. James' writings on "The Energies of Men," and it is a pity that they were never amplified in print by Dr. Coghill.

If space permitted many similarly pregnant passages might be cited in justification of the words spoken by Dr. R. G. Harrison on the occasion of the award of the Elliot Medal of the National Academy of Sciences to Dr. Coghill on April 24, 1934:

"Dr. Coghill's pioneer work has won for him a place of high distinction. . . . . . . Progressive changes in reaction have been followed by Dr. Coghill step by step in individual embryos, and at each stage cases taken immediately after their reactions had been tested were preserved and studied microscopically. In this way the actual state of differentiation of the nervous system in each individual has been correlated with its behavior. . . . . . .

"Associated with differentiation, but in a certain sense antagonistic to it, is the process of growth, the study of which has required the counting of thousands of cells and charting their positions in the spinal cord and brain at various stages of development. This has involved an immense amount of painstaking work which would all have been to little purpose had the task not been approached by a man of broad knowledge and subtle insight. From all this has developed a new conception of the origin of nervous function. At no time does the nervous system work as a collection of independent reflexes, which later become integrated. On the contrary, at each stage it functions as a whole, expanding from stage to stage, and as development proceeds, various partial functions arise within it as more or less discrete reflexes. These investigations of Dr. Coghill will have a lasting influence in psychology and physiology as well as in embryology."

This summary may be further condensed into a few words taken from a letter written by Dr. Coghill on Feb. 8, 1930:

"For my own thinking the two important results of all my juggling with Amblystoma are the reality of a total-pattern mechanism, and a scientific basis for the conception of spontaneity, autonomy or initiative of the individual in behavior. In these two principles I get a different conception of motivation than I get from any other source."

NOTES

In the preparation of this memoir free use has been made of appreciations published in *Science,* Aug. 29, 1941, *Journal of Comparative Neurology,* Oct. 15, 1941, and *Anatomical Record,* Feb. 25, 1942, and May 25, 1942.

The aim here is to present a concise summary of Dr. Coghill's scientific contributions, with some commentary. The more intimate details of a personal biography and intimations of the philosophic motivation of his work, with extracts from his published and manuscript papers, are reserved and may be published elsewhere.

[1] In the published thesis (Journal of Comparative Neurology, vol. 12, 1902) the ages of the specimens described are not recorded, but Dr. Coghill later informed me personally that the descriptions are based on serial sections of adults after metamorphosis and advanced larvae from 8 to 13 cm. long. The figures are from a larva 12 cm. long.

[2] Compare Donald H. Barron's statement: "The later in ontogeny a sensory nerve makes functional connexions with the central nervous system, the more restricted the motor response it elicits when stimulated may be expected to be."—The functional development of some mammalian neuromuscular mechanisms, Biological Reviews, vol. 16, 1941, pp. 1-31.

[3] See Dr. Coghill's discussion of Tracy's work in his presidential address, Science, 1933. Barron's comprehensive review (1941) already cited is of interest in this connection.

BIBLIOGRAPHY

KEY TO ABBREVIATIONS

Am. J. Psychol.—American Journal of Psychology
Anat. Rec.—Anatomical Record
Arch. Neurol. and Psychiat.—Archives of Neurology and Psychiatry
J. Comp. Neur.—Journal of Comparative Neurology
J. General Psychol.—Journal of General Psychology
J. Genetic Psychol.—Journal of Genetic Psychology
Ohio J. Sci.—Ohio Journal of Science
Proc. Am. Philos. Soc.—Proceedings, American Philosophical Society
Proc. Nat. Acad. Sci.—Proceedings, National Academy of Sciences
Proc. Soc. Exper. Biol. and Med.—Proceedings, Society for Experimental Biology and Medicine
Psychiat. en Neurol. Bladen—Psychiatrische en Neurologische Bladen
Psychol. Rev.—Psychological Review
Trans. Am. Neurol. Assoc.—Transactions, American Neurological Association

1898

The somatic equilibrium and the nerve endings in the skin. (With C. L. Herrick). J. Comp. Neur., vol. 8, pp. 32-56.

1899

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ADDENDUM

The following title appears in Doctor Coghill's own manuscript bibliography, accompanied by a carbon copy:

Flexion spasms and mass reflexes in relation to the ontogenetic development of behavior. Festschrift in honor of Prof. A. I. Heymanovich, U. S. S. R.

This paper was prepared for publication in Russia in 1933 or 1934, but a reference has been unobtainable. The complete paper will appear shortly in the Journal of Comparative Neurology.