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 neurones 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.

[1] Lashley, *Brain Mechanisms and Intelligence*, University of Chicago Press, **1929**. Pp. 134, 141.

LOCALIZATION OF FUNCTION IN THE NERVOUS SYSTEM

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Some functions of the nervous system are clearly localized, typified by the classical conception of the reflex arc. About others we are not so sure, particularly the so-called higher or mental functions commonly ascribed to the cerebral cortex. Can their organs be arranged in mosaic patterns and mapped on the cortical surface like the charts of the old phrenology, or are they diffusely distributed so that they are impaired by loss of cortical substance in proportion to the amount of loss, irrespective of its location?

The unsolved problems of cortical localization may be clarified by an inquiry into the principles of localization in simpler and more primitive subcortical nervous tissue and the genesis of these primitive patterns. This theme may be approached from the standpoint of evolutionary development or of embryological development and the two lines of inquiry yield concordant results. Here we shall cite only the embryological evidence.

Of the numerous studies of development of behavior patterns, the most significant for the present purpose are those of Coghill on the salamander,

Amblystoma; for here we have precise records in statistically adequate number of the sequence of development of reflex patterns, together with the much more laborious histological examination of a series of specimens of tested physiological age. We know the order of appearance of reflex responses to stimulation, and also in considerable detail the structural changes that accompany the emergence of each new pattern of reflex and the exact location of these structures.

Dr. Coghill has pointed out that preceding the first neuromuscular response to stimulation there is an orderly development during which the unity of the organization is maintained by various non-nervous agencies, such as the mechanics of surface tensions, the chemical interplay of elementary hormones, differences in biolectric potential and physiological gradients. The neuromuscular apparatus develops within this unitary system and its earliest configuration is evidently shaped by it. The first nervous responses are integrated from the start; they are total reactions of the organism as a whole. There are no separate local reflexes; these come later.

The history of the emergence of some of the local reflexes from the total pattern has been presented by Coghill.[1] He has shown that the earliest movements of particular bodily members—limbs, jaws and so on—always occur in connection with total bodily movement. The capacity of a limb to respond reflexly to local stimulation independently of a generalized body movement is only gradually acquired. In this way the whole complement of individual local reflexes is slowly built up, these local patterns being successively emancipated from a more generalized type of response.

Parallel with this development of the behavior pattern, interesting changes are going on in the nervous system. The first neuromuscular reactions are executed through the mediation of definitely localized chains of neurons in synaptic relations so arranged that all sensory excitations are converged into the single final common path that discharges into the total body musculature, thus automatically integrating the behavior. This arrangement prevails—with some necessary complication of details—up to the perfection of the swimming reaction. Then follows, as an outgrowth from this integrated nervous system, the innervation of limbs and other apparatus of local movement. The same neurons which participate in the swimming movement ·send collateral branches outward into the growing limbs. The result is that the limb can move only when the body moves.

Up to the time of swimming the response at each stage of the development of the functional pattern is perfectly coördinated and integrated because it is performed by a definitely localized chain of nervous conductors so arranged that no other pattern of response is possible. It is

true that the response may be modified by the non-nervous factors of the total organization, for these are still operative; but no specific nervous machinery for modifiability of behavior has so far been demonstrated at this age.

Now as the local reflexes become emancipated from the total pattern and for each one of them a separate localized reflex arc is differentiated in the nervous system, the problem of the coördination of their activities and the maintenance of the unity of the organization takes on a new aspect. For no complication of separate and insulated reflex arcs, each of which is conceived as giving a one-to-one relation between stimulus and response, and no interconnection of such arcs by elaborate switchboard devices can conceivably yield the type of behavior which we actually find in higher vertebrates. The organism is reacting as a whole to its environment as a whole, and it is doing so in ways that cannot be formulated in terms of an algebraic sum or simple mechanical resultant of the interplay of the simple reflex responses to external stimulation. The behavior exhibits not only reaction, but also synthesis, initiative, originality—things that no combination of our hypothetical, simple, discrete reflexes can give. Even the simple response to a stimulus is not a reaction of a part of the body to a part of the environment. It is a response of the body as a whole (including as one factor the whole of its past experience) to the total situation in which the stimulus in question is set, and this response is fundamentally and primarily a unitary event, not an assemblage of separate sensorimotor components which are somehow and somewhere secondarily fabricated into an adaptive behavior pattern. The exponents of the Gestalt movement in psychology have made this very clear.

These facts are regarded as incompatible with the traditional dogmas of reflex physiology, with its precisely localized and well insulated reflex arcs and centers of reflex adjustment. The fundamental unitary character of this response, the preservation of its basic pattern amidst a kaleidoscopic shifting of the play of stimuli on the sensory field, together with its labile character and ready modifiability—for these and numerous other characteristics, the mechanisms of traditional reflexology seem hopelessly inadequate.

Yet reflex responses and sharply localized and well-insulated reflex arcs are unquestionably present. If it were not so, our present practice of clinical neurology and neurosurgery would be far less efficient than it is. These are the stock-in-trade of the neurologists. But perhaps this stock—as well as that of the psychologists—may be improved by the addition of some other wares without discarding any of those that they already have.

Let us now turn back and resume our examination of the differentiation of the nervous system of the growing salamander. At the stage when

local reflexes of limbs and jaws have become emancipated from their former subordination to mass movements of the body as a whole, histological examination shows that for each of these reflexes there is a definite nervous circuit. And it shows more than this. No one of these arcs is perfectly insulated from the others. There is no one-to-one relation between receptive organ and organ of response.

The neurons of the brain which are linked to form these conductors show remarkable complications. From the axons which form the main lines of direct conduction, innumerable collateral branches are given off. These may again branch repeatedly and run in diverse directions apparently haphazard. They rapidly increase in number, length and intricacy of ramification, and in the fields of their distribution other neurons are differentiated whose dendrites and ramified axons enter the entanglements of the collaterals first mentioned until there results a dense feltwork of finest nerve fibres which everywhere fills the interstices between the original pathways of the main lines of through reflex traffic. This is the "neuropil" within which the reflex arcs are embedded, and in the half-grown amphibian larva the specific and precisely localized reflex arcs are so completely immersed in this neuropil that it requires critical microscopic study to recognize them at all.

In the adult amphibian brain the diffuse neuropil and the nerve cells primarily related with it make up by far the larger part of the brain substance. The primary axons of the main lines of reflex conduction can usually be identified by their larger size, better myelination, or more direct course, but in many cases they can be followed through the diffuse and apparently random entanglements of the neuropil only by very careful study of especially favorable preparations. The separate and well-insulated reflex arc of neurological tradition has no real existence at any time in the history of this differentiation of the amphibian nervous system.

The various members of the body are innervated at first by collateral branches of the neurons of mass movement, and by the time the local reflexes are emancipated from these mass movements, their separate reflex arcs are all bound together through the diffuse neuropil so that no one of them can be activated without some influence being exerted upon the common matrix of all of them.

This diffuse and relatively equipotential neuropil, then, provides the anatomical substratum for the unity of the general behavior pattern, for the enduring individuality of the person, for the direct unanalyzed organismic quality of every separate sensorimotor response, for that plasticity and modifiability which are so characteristic of vertebrate behavior, i.e., for learning, and finally for the retention of more or less stable structural alterations of the reacting tissue resulting from particular patterns of response, i.e., for memory.[2]

The evidence for these sweeping general statements cannot be presented here, but attention may be directed to the fact that everything that is going on in the body is registered in this neuropil; into this tissue there is constant discharge of nervous impulses which overflow from every sensory path that enters the brain, and there is constant discharge from it to lower motor centers.

The neuropil of the adult salamander appears to be nearly homogeneous and physiologically equipotential, but not wholly so, for every part of it receives a preponderance of its nerve fibres from certain more or less specific sensory fields and has lines of preferential discharge toward certain motor fields.   It is the parent tissue from which the specialized correlation centers, including those of cerebellum, thalamus, corpus striatum and cerebral cortex, of higher mammals have been differentiated; and the steps in the progress of this differentiation are preserved for our inspection in the organization of the series of brains from amphibian to human.[3]

The amphibian nervous system exhibits a definite pattern of localization embedded within a matrix of relatively unlocalized tissue serving the more general functions of the body as a whole.   Turning to the human brain, we find this contrast accentuated.   The number of individuated local reflexes is greatly increased and their nervous pathways and centers of adjustment are far more perfectly segregated and insulated.   The result is that the human body has capacity for an immeasurably wider range of adjustments to every situation.   There are more things that can be done about it, because there are more different kinds of response provided for in the stable bodily organization.   Each of these local mechanisms is more highly specialized and is more definitely localized. This makes for greater efficiency in all stereotyped or automatized patterns of behavior.

Parallel with this specialization of the apparatus of local reflexes, there is a far greater elaboration of the integrating apparatus.   Out of the diffuse neuropil there have emerged numerous special centers of adjustment, each of which in turn is more or less precisely localized, like the nuclei of the thalamus and the projection centers of the cortex.   And there remains within these centers and between them an enormous mass of correlating tissue which preserves the primordial undifferentiated and labile character.   This attains its maximum in the so-called associational mechanism of the cortex.   This tissue is highly specialized, but its differentiation is in a direction opposite to that of the sharply localized apparatus of the stereotyped behavior patterns, for its prime function is the integration of these in patterns which fluctuate from moment to moment with every change in the content of the sensorimotor experience.   This integration, moreover, is effected, not in terms of the present phase of

this experience merely, but in view of its own record of all previous experience.

Accordingly, the cortical apparatus of memory, apperception, imagination, invention and all constructive thinking cannot in the nature of the case be expected to be arranged in mosaic patterns whose boundaries can be mapped on the brain surface, like the charts of the ancient and modern phrenologists.

These are not disembodied functions, and the organs which perform them have form and location in space, but the forms which they assume are more like those of a continental system of telephone wires, or perhaps better, of wireless broadcasting, than the conventional pictures of the mosaic of cortical areas of, say, "word-memory" and "symbolic thinking." There are transmitters and receivers, whose location is fixed, but the apparatus connecting these may be as labile and as dynamic as the ether of interstellar space—and as imperfectly understood. The pattern of this apparatus may not be identical in two successive repetitions of the same externally evident sequence of stimulus and response, just as I may get telephone connection from Washington with an office in Philadelphia by way of Baltimore, or, in an emergency, by way of Harrisburg.

There is always some kind of localization of every cortical function. Some of these loci, like that of the electrically excitable "arm center," are tolerably accurately definable in terms of superficial cortical landmarks and they are tolerably constant from time to time. This is the classic mosaic localization. The apparatus of other sorts of cortical function does not submit to that sort of localization. By its very nature, it is widely diffused, inconstant, pliable; its configuration varies from moment to moment with a wide range of alternate or substitutional connections which give comparable, though not identical, results with every successive pulse of similar excitation. In response to a tap at my study door, I may say "come in" ten times in the course of a half-hour, but the chances are that the cortical process will not be identical the first and the tenth time.

Now, obviously, the word "localization" has been used in somewhat different senses in previous controversial literature, and even within the limits of this brief discussion. The anatomical localization of nervous functions of traditional neurology is adequate for clinical purposes up to a certain point. In the conventional reflex arc the terminal points are fixed, the peripheral pathways are fixed, and some, at least, of the central connecting tracts are known to be stable. The clinical diagnosis of a nervous lesion depends upon knowledge of the precise localization of these elements and upon their relative constancy.

But there are inconstant features even of the reflex. The scratch reflex of the dog is perhaps the best known example of a typical reflex,

thanks to the work of Sherrington. Here there is a wide area of skin within which stimulation of any point evokes the reflex and outside of which similar stimulation does not. This "receptive field" can be accurately mapped. The anatomical mechanism of this reflex pattern is so set up that adequate stimulation of any point within this field releases the reaction. In this simple case the locus of the receptor may be inconstant within this field. Then there are inconstant features within the adjusting center—the synaptic field of the spinal cord in this case. The typical response may be modified or inhibited by a variety of alterations of the physiological state of the center; but upon removal of the disturbing agencies the former pattern of performance returns.

De Silva[4] employs Henry Head's theory of "schematization" in an analysis of visual perception of movement in a way that may be helpful here also. The reflex pattern conforms to a schema which has a certain stability. Corresponding to this stable dynamic pattern there is an anatomical configuration of structural elements which, in the case of the scratch reflex, is known and localized. The apparatus of modifiability of the schema is not so well known, but the field within which this apparatus works can be delimited. The receptive field of the scratch reflex has such localization, and within this field the separate excitable points can also be located in each reaction. The synaptic field within the spinal cord, where inhbitions, etc., are effected, can also be delimited, but within this field we are quite ignorant of the configuration and precise location of the structural elements which determine what modification will follow some particular disturbing factor.

We have, then, two kinds of localization: (1) a known localization of stable structural elements whose functions also are known, and (2) a localization of fields within which various recurring patterns of performance, or schemata, are known to be fabricated and within which inhibition, modification, or conditioning of these patterns takes place. The first is the traditional functional localization of neurological practice as applied particularly in clinical neurology. The second is the sort of thing that is usually implicit in current diagrams of cortical localization—with very unsatisfactory results. The failures are due largely to our ignorance of cortical functions, and particularly to futile attempts to apply the criteria of localization of rigid structural elements to the second category of locations of patterns or schemata in fields.

It is possible to find out where the tissue is that yields these dynamic schemata and to delimit it; but these limits cannot be circumscribed on the surface of the brain in simple mosaic patterns. The manifestation of any schema at a particular time is always the function of a configuration of nervous elements which has location in space. But a very similar schema may at another time be exhibited by a different structural con-

figuration whose locus in space is by no means identical with the first. Our present technique is adequate to delimit the fields within which the schemata are operative, but it has not yet clarified the exact mechanism employed. Some of the simpler schemata are very stable, perhaps inherited; but others are evanescent. For the first group more or less of the apparatus can be identified as a stable anatomical pattern of fibre tracts and gray centers, but there is always a residuum whose structural basis is unknown.

We may, therefore, for convenience distinguish a localization of stable structural elements with the correlated localization of simple physiological processes from a localization of dynamic patterns or schemata within assignable fields. The latter may include fields of physiological gradients, fields of ionization or electric polarization, fields of differential chemical susceptibilities to hormones, etc., fields of organization of reflexes, fields of conditioning of these reflexes, fields where schemata of relation are fabricated (larger-smaller, lighter-darker, etc.) and in the human cortex fields of ideation, abstraction and the like.

The details of the mechanics of operation of these labile processes are as yet very obscure. Just what goes on in the associational tissue of the cerebral cortex is especially mysterious, but that this half-litre—more or less—of brain substance is the organ of integration of the personality and of control of behavior, including consciously purposive control, is as well-established empirically as anything in biology.[5] The unknown factors in this situation will probably be brought to light by an indirection, namely, by further study of the mechanics of nervous excitation and transmission and the fundamental properties of living substance in general.

[1] Coghill, G. E., *Anatomy and the Problem of Behavior*, Oxford Univ. Press, 1929. Also *Proc. Nat. Acad. Sci.*, 16, 637–643 (1930).

[2] Herrick, C. Judson, "Anatomical Patterns and Behavior Patterns," *Physiol. Zoöl.*, 2, 439–448 (1929).

[3] Herrick, C. Judson, *Brains of Rats and Men*, Univ. of Chicago Press, 1926.

[4] De Silva, H. R., "An Analysis of the Visual Perception of Movement," *Brit. J. Psychol.* (Gen. Sec.), 19, 268–305(1929).

[5] Herrick, C. Judson, *The Thinking Machine*, Univ. of Chicago Press, 1929.