

The Problem of Serial Order in Behavior

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The previous speakers have approached our common problem by considering the properties of the elementary units of which we believe the cerebral structure to be built up. They have considered the kinds of neural integration or behavior which can be anticipated from those properties. The remaining members of the symposium have in their research been concerned chiefly with the analysis of complex behavior, seeking to derive general principles of neural integration from the infinitely complex products of that integration. Our common meeting ground is the faith to which we all subscribe, I believe, that the phenomena of behavior and of mind are ultimately describable in the concepts of the mathematical and physical sciences. In my discussion here, I have deliberately turned to the opposite extreme from the neuron and have chosen as a topic, one aspect of the most complex type of behavior that I know; the logical and orderly arrangement of thought and action. Our discussion so far has dealt chiefly with the conditions of input and of immediate switching in the nervous mechanism, without explicit consideration of what is already going on within the system.

My principal thesis today will be that the input is never into a quiescent or static system, but always into a system which is already actively excited and organized. In the intact organism, behavior is the result of interaction of this background of excitation with input from any designated stimulus. Only when we can state the general characteristics of this background of excitation, can we understand the effects of a given input.

The unpronounceable Cree Indian word "kekawewechetushekamik-owanowow" is analyzed by Chamberlain (7) into the verbal root, *tusheka*, "to remain," and the various particles which modify it as fol-

lows: *ke(la)wow*, the first and last syllables, indicating second person plural; *ka*, a prefix of the future tense; *we*, a sort of imperative mode expressing a wish; *weche*, indicating conjunction of subject and object; *mik*, a suffix bringing the verb into agreement with a third person subject and second person object; and *owan*, a suffix indicating that the subject is inanimate and the object animate. A literal translation: "You will I wish together remain he-you it-man you" or, freely, "may it remain with you." This difference in structure between Cree and English illustrates an outstanding characteristic of verbal behavior; the occurrence of predetermined, orderly sequences of action which are unique for each language. In English the adjective precedes, in French it follows the noun which it modifies. In English the movement or action of the subject is expressed as early as possible after the subject; in German the expression of action may be postponed until all qualifying thoughts have been expressed. In a sentence discussing this subject, Pick (20) introduces fifty-five words between the subject and the principal verb. Each Chinese word, and to a lesser extent, each English word, stands as an unchanging unit. In the highly inflective languages, such as Sioux, the form of almost every word in the sentence may be altered, according to some attribute of the subject, as when two objects rather than one or several are discussed.

The study of comparative grammar is not the most direct approach to the physiology of the cerebral cortex, yet Fournié (10) has written, "Speech is the only window through which the physiologist can view the cerebral life." Certainly language presents in a most striking form the integrative functions that are characteristic of the cerebral cortex and that reach their highest development in human thought processes. Temporal integration is not found exclusively in language; the coordination of leg movements in insects, the song of birds, the control of trotting and pacing in a gaited horse, the rat running the maze, the architect designing a house, and the carpenter sawing a board present a problem of sequences of action which cannot be explained in terms of successions of external stimuli.

ASSOCIATIVE CHAIN THEORIES

In spite of the ubiquity of the problem, there have been almost no attempts to develop physiological theories to meet it. In fact, except among a relatively small group of students of aphasia, who have had to face questions of agrammatism, the problem has been largely ignored. It is not even mentioned in recent textbooks on neurophysiology or physiological psychology, nor is there any significant body of experimental studies bearing upon the problem. The spinal animal scarcely

exhibits serial activity, so the physiologist may be excused for overlooking the phenomenon. On the other hand, psychologists have been concerned chiefly with the question of whether or not the organizing processes displayed in serial action are conscious, and very little with the organization itself. I have chosen to discuss the problem of temporal integration here, not with the expectation of offering a satisfactory physiological theory to account for it, but because it seems to me to be both the most important and also the most neglected problem of cerebral physiology. Temporally integrated actions do occur even among insects, but they do not reach any degree of complexity until the appearance of the cerebral cortex. They are especially characteristic of human behavior and contribute as much as does any single factor to the superiority of man's intelligence. A clearer formulation of the physiological problems which they raise should be of value, even though a solution of the problems is not yet in sight.

I shall consider first some of the questions raised by the structure of language, then turn to other forms of serial action for indications of the nature of the nervous mechanisms involved.

To the best of my knowledge, the only strictly physiological theory that has been explicitly formulated to account for temporal integration is that which postulates chains of reflexes, in which the performance of each element of the series provides excitation of the next. This conception underlay the "motor theories" of thinking which were advocated by several psychologists early in this century. Watson (26) sought to identify thought with inaudible movements of the vocal organs, linked together in associative chains. The peripheral chain theory of language was developed in greatest detail by Washburn (25). She distinguished what she called "successive movement systems" and, although she drew her examples from memorized series of nonsense syllables, her implication was that such series are typical of all language behavior. She defined a movement system as "a combination of movements so linked together that the stimulus furnished by the actual performance of certain movements is required to bring about other movements." She described speech as a succession of vocal acts in which the kinesthetic impulses from each movement serve as a unique stimulus for the next in the series (25, pages 11 ff.). Attempts to confirm these peripheral theories by mechanical (Thorsen, 23) or electrical (Max, 19) recording of muscular tensions have given no valid evidence in support of them. It should be noted that, at the time when the theories were proposed, it was generally believed that conduction in the nervous system is always downstream from sense organ to muscle, and that muscular contraction must always follow promptly on stimulation. The existence of

reverberatory circuits which could maintain central activity was scarcely suspected.

The introspective psychology which objected to such peripheral theories did not explicitly formulate an alternative neurological theory, but there is implicit in it a view that verbal thought is a simple chain of central processes in which each element serves to arouse the next by direct association. Titchener, for example, maintained that the meaning of a word (or of an auditory image in his system) consists of the chain of associations which it arouses; that it has no meaning until such a sequence has occurred. From this it must be inferred that he was thinking in terms of a simple associative chain, since no other relating process is suggested.

OBJECTIONS TO THE ASSOCIATIVE CHAIN THEORY

A consideration of the structure of the sentence and of other motor sequences will show, I believe, that such interpretations of temporal organization are untenable and that there are, behind the overtly expressed sequences, a multiplicity of integrative processes which can only be inferred from the final results of their activity. There is an extensive controversial literature dealing with this inferred integrative activity. Pick (20) devotes almost his entire book, *Die agrammatischen Sprachstörungen*, to reviewing discussions of the subject. Most of this literature deals with the question of whether or not the integrative processes are conscious. Much of this is irrelevant to the present topic, but the advocates of so-called imageless thought did present a great deal of material indicative of the complexity of the problem of thought structure. From this, and other evidence which I shall present, I believe that the production of speech involves the interaction of at least three, possibly four, major neurological systems which are interrelated but somewhat independently variable.

Let us start the analysis of the process with the enunciation of the word. Pronunciation of the word "right" consists first of retraction and elevation of the tongue, expiration of air and activation of the vocal cords; second, depression of the tongue and jaw; third, elevation of the tongue to touch the dental ridge, stopping of vocalization, and forceful expiration of air with depression of the tongue and jaw. These movements have no intrinsic order of association. Pronunciation of the word "tire" involves the same motor elements in reverse order. Such movements occur in all permutations. The order must therefore be imposed upon the motor elements by some organization other than direct associative connections between them. So, for the individual movements in writing or typing the word, finger strokes occur in all

sorts of combinations. No single letter invariably follows *g*, and whether *gh*, *ga*, or *gu* is written depends upon a set for a larger unit of action, the word.

Words stand in relation to the sentence as letters do to the word; the words themselves have no intrinsic temporal "valence." The word "right," for example, is noun, adjective, adverb, and verb, and has four spellings and at least ten meanings. In such a sentence as "The mill-wright on my right thinks it right that some conventional rite should symbolize the right of every man to write as he pleases," word arrangement is obviously not due to any direct associations of the word "right" itself with other words, but to meanings which are determined by some broader relations.

It has been found in studies of memorization of nonsense syllables that each syllable in the series has associations, not only with adjacent words in the series, but also with more remote words. The words in the sentence have, of course, associations with more remote words as well as with adjacent ones. However, the combination of such direct associations will not account for grammatical structure. The different positions of the word "right" in the illustrative sentence are determined by the meanings which the positions in relation to other words denote, but those meanings are given by other associations than those with the words in the spoken sentence. The word can take its position only when the particular one of its ten meanings becomes dominant. This dominance is not inherent in the words themselves.

From such considerations, it is certain that any theory of grammatical form which ascribes it to direct associative linkage of the words of the sentence overlooks the essential structure of speech. The individual items of the temporal series do not in themselves have a temporal "valence" in their associative connections with other elements. The order is imposed by some other agent.

This is true not only of language, but of all skilled movements or successions of movement. In the gaits of a horse, trotting, pacing, and single footing involve essentially the same pattern of muscular contraction in the individual legs. The gait is imposed by some mechanism in addition to the direct relations of reciprocal innervation among the sensory-motor centers of the legs. The order in which the fingers of the musician fall on the keys or fingerboard is determined by the signature of the composition; this gives a *set* which is not inherent in the association of the individual movements.

THE DETERMINING TENDENCY

What then determines the order? The answer which seems most in accord with common sense is that the intention to act or the idea to be expressed determines the sequence. There are, however, serious difficulties for this solution. There is not much agreement among psychologists concerning the nature of the idea. The structuralist school, under the leadership of Titchener, held that the idea consists of mental images, often the auditory images of words, and the meanings are nothing but sequences of such images. Describing the role of images in his lecturing, Titchener wrote (24), "When there is any difficulty in exposition, a point to be argued *pro* and *con* or a conclusion to be brought out from the convergence of several lines of proof, I hear my own voice speaking just ahead of me." What solution of the lecture problem for the lazy man! He need not think but only listen to his own inner voice; to the chain of associated auditory images. A behaviorist colleague once remarked to me that he had reached a stage where he could arise before an audience, turn his mouth loose, and go to sleep. He believed in the peripheral chain theory of language. (This clearly demonstrates the superiority of behavioristic over introspective psychology. The behaviorist does not even have to listen to his own inner voice.)

Seriously, such positions offer no solution for the problem of temporal integration. Titchener finds his grammar ready made and does not even raise the question of the origin of the succession of images. The chain-reflex theory, while definite, is untenable.

The third view of the nature of the idea was developed by a group known as the "Würzburg School" (see Boring, 4); exponents of imageless thought. It held that some organization precedes any expression that can be discovered by introspective or objective means. Thought is neither muscular contraction nor image, but can only be inferred as a "determining tendency." At most, it is discovered as a vague feeling of pregnancy, of being about to have an idea, a *Bewusstseinslage*. It is not identical with the words which are spoken, for quite frequently no word can be recalled which satisfactorily expresses the thought, and we search a dictionary of synonyms until a word or phrase is found which does seem appropriate.

In his discussion of the relation of thought to speech, Pick (20) accepts this point of view, but he asserts further that the set or the idea does not have a temporal order; that all of its elements are cotemporal. Evidence in support of this conclusion comes, for example, from translation of one language into another which has a

different sentence structure. I read a German sentence, pronouncing the German words with no thought of their English equivalents. I then give a free translation in English, without remembering a single word of the German text. Somewhere between the reading and free translation, the German sentence is condensed, the word order reversed, and expanded again into the different temporal order of English. According to Epstein (9), the polyglot shifts readily from one language to another, expressing the same thought in either, without literal translation. The readiness with which the form of expression of an idea can be changed, the facility with which different word orders may be utilized to express the same thought, thus is further evidence that the temporal integration is not inherent in the preliminary organization of the idea.

THE SCHEMA OF ORDER

The remaining alternative is that the mechanism which determines the serial activation of the motor units is relatively independent, both of the motor units and of the thought structure. Supporting evidence for this may be found in the mistakes of order, the slips and interferences which occur in writing and speaking. For some time I have kept records of errors in typing. A frequent error is the misplacing or the doubling of a letter. *These* is typed t-h-s-e-s, *look* as l-o-k-k, *ill* as i-i-l. Sometimes the set to repeat may be displaced by several words. The order is dissociated from the idea. Earlier, in preparing this paper, I wrote the phrase, "maintain central activities." I typed *min*, omitting the *a*, canceled this out and started again; *ama*. The impulse to insert the *a* now dominated the order. I struck out the *a* and completed the phrase, only to find that I had now also dropped the *a* from *activities*. This example suggests something of the complexity of the forces which are at play in the determination of serial order and the way in which conflicting impulses may distort the order, although the primary determining tendency, the idea, remains the same.

The polyglot, who has become proficient in a secondary language, who thinks in it and even dreams in it, may still tend to use the grammatical structure of his native tongue. If, as in French, that tongue applies gender to inanimate things, the English pronouns referring to them may take the gender of the French equivalents, though the French nouns are not thought. The German postponement of the verb or the Magyar use of the past infinitive may be incorporated in the new language. In such cases, the structuring seems to be dissociated both from the content and from the simple associative connections of the words themselves.

The ease with which a new structure may be imposed on words is illustrated by the quickness with which children learn hog Latin. The form which I learned involved transposing the initial sound of each word to the end of the word and adding a long *a*. Thus—at-thay an-may oes-gay own-day e-thay eet-stray. Some children become very facile at such inversions of words, and re-structure new words without hesitation. From such considerations it seems to follow that syntax is not inherent in the words employed or in the idea to be expressed. It is a generalized pattern imposed upon the specific acts as they occur.

"PRIMING" OF EXPRESSIVE UNITS

There are indications that, prior to the internal or overt enunciation of the sentence, an aggregate of word units is partially activated or readied. Evidence for this comes also from "contaminations" of speech and writing. The most frequent typing errors are those of anticipation; the inclusion in the word being typed of some part of a word or word structure which should properly occur later in the sentence. It may be only a letter. Thus I wrote, *wrapid* writing, carrying the *w* from the second word to the first. Not infrequently words are introduced which should occur much later in the sentence, often five or six words in advance.

In oral speech, Spoonerisms illustrate the same kind of contamination. The Spoonerism is most frequently an inversion of subject and object: "Let us always remember that waste makes haste." But it may be only a transposition of parts of the words: "Our queer old dean" for "our dear old queen." The frequency with which such contaminations occur is increased by haste, by distraction, by emotional tension, or by uncertainty and conflict as to the best form of expression. In some types of aphasia the tendency to disordered arrangement of words is greatly increased, and, in extreme cases, the attempt to speak results in a word hash with complete loss of grammatical organization. Professor Spooner, after whom such slips are named, was probably suffering from a mild form of aphasia. In these contaminations, it is as if the aggregate of words were in a state of partial excitation, held in check by the requirements of grammatical structure, but ready to activate the final common path, if the effectiveness of this check is in any way interfered with.

In his *Psychopathology of Everyday Life*, Freud has given numerous examples of similar contaminations of action outside the sphere of language. We do not need to accept his theories of censorship and suppression to account for such slips. They are of the same order as

misplacements in typing and represent contaminations of co-existing, determining tendencies to action.

Such contaminations might be ascribed to differences in the relative strength of associative bonds between the elements of the act, and thus not evidence for pre-excitation of the elements or for simultaneous pre-excitation. However, the understanding of speech involves essentially the same problems as the production of speech and definitely demands the postulation of an after-effect or after-discharge of the sensory components for a significant time following stimulation. Thus, in the spoken sentence, "Rapid righting with his uninjured hand saved from loss the contents of the capsized canoe," the associations which give meaning to righting are not activated for at least 3 to 5 seconds after hearing the word.* I shall refer later to other evidence for such long after-discharge of sensory excitations. The fact of continued activation or after-discharge of receptive elements and their integration during this activation justifies the assumption of a similar process during motor organization. The processes of comprehension and production of speech have too much in common to depend on wholly different mechanisms.

INTERNAL AND OVERT SPEECH

One other point with respect to the organization of speech: The earlier literature on aphasia emphasized the distinction of internal and overt speech. The aphemia of Broca and the pure motor aphasia of Wernicke and later writers were held to be a loss of the ability to enunciate without loss of ability to think in words and without paralysis of the organs of speech. The brain insult was assumed to affect only the transition from the thought to the enunciation of the word. We may doubt the existence of instances of such "pure" defects and question the reliability of the early clinical examinations in view of the more careful analyses that have been made since 1917, but the distinction of internal and overt speech is still valid and the transition still unexplained. Watson interpreted internal speech as inaudible movements of the vocal organs, and Jacobsen (15) and Max (19) have given evidence of changes in muscular tonus during verbal thinking or thought of movement. This is far from proving that the motor discharge is essential for the internal formation of words, however.

I once devised an instrument to record small movements of the

* Dr. Lashley ingeniously laid the groundwork for this three paragraphs earlier, when he mentions "wrapid writing." The audience all heard, "Rapid writing with his uninjured hand," etc. "Capsized canoe" required a complete and amusing about-face. ERROR.

tongue. Within the limits of its sensitivity, it showed that in silent thinking the tongue usually drops to the back of the mouth and shows no detectable movement. Verbal problems, such as the correct squaring of three-place numbers, could be carried out with no trace of overt movement. If, however, I urged the subject to hurry or if I slapped his face, his tongue came forward and showed movements corresponding to the syllabification of internal speech or of the computation he was performing. This I interpret as indicating that internal speech may be carried out wholly by processes within the nervous system, with some unessential discharge upon the final common path for vocal movements. Facilitation of the motor path, either by increased emotional tension or by "voluntary" reinforcement, increases its excitability until the same central circuits whose activity constitutes internal speech are able to excite the overt movements. This aspect of the language function is irrelevant to the problem of syntax or serial order, but is important as illustrating a further point in the dynamics of the cerebrum. Many activities seem to require for their performance both a specific patterning and also a general facilitation, a rise in dynamic level. There are, I think, indications that hemiplegia and motor aphasia are primarily expressions of a low level of facilitation rather than a loss of specific integrative connections which are involved in the use of language or in the patterning of our movements. A monkey, for example, after ablation of the precentral gyrus may seem unable to use the arm at all, but if emotional excitement is raised above a certain level, the arm is freely used. As soon as the excitement dies down, the arm is again hemiplegic. I have seen something of the same sort in a human hemiplegic. The problem of the availability of memories, which was raised earlier in the discussion here, may find a partial solution in such fluctuations in dynamic level. In many of the organic amnesias the pattern of integration seems to be retained but can be reactivated only by an abnormally intense sensory or central reinforcement.

GENERALITY OF THE PROBLEM OF SYNTAX

I have devoted so much time to discussion of the problem of syntax, not only because language is one of the most important products of human cerebral action, but also because the problems raised by the organization of language seem to me to be characteristic of almost all other cerebral activity. There is a series of hierarchies of organization; the order of vocal movements in pronouncing the word, the order of words in the sentence, the order of sentences in the paragraph, the rational order of paragraphs in a discourse. Not only speech, but all skilled acts seem to involve the same problems of serial ordering, even

down to the temporal coordination of muscular contractions in such a movement as reaching and grasping. Analysis of the nervous mechanisms underlying order in the more primitive acts may contribute ultimately to the solution even of the physiology of logic.

It is possible to designate, that is, to point to specific examples of, the phenomena of the syntax of movement that require explanation, although those phenomena cannot be clearly defined. A real definition would be a long step toward solution of the problem. There are at least three sets of events to be accounted for. First, the activation of the expressive elements (the individual words or adaptive acts) which do not contain the temporal relations. Second, the determining tendency, the set, or idea. This masquerades under many names in contemporary psychology, but is, in every case, an inference from the restriction of behavior within definite limits. Third, the syntax of the act, which can be described as an habitual order or mode of relating the expressive elements; a generalized pattern or schema of integration which may be imposed upon a wide range and a wide variety of specific acts. This is the essential problem of serial order; the existence of generalized schemata of action which determine the sequence of specific acts, acts which in themselves or in their associations seem to have no temporal valence.

I shall turn now to other phenomena of movement which may be more readily phrased in physiological terms and which may suggest some of the mechanisms underlying serial order.

DURATION AND INTENSITY OF NERVOUS DISCHARGE

A consideration of the control of extent and rate of movement supports the view that sensory factors play a minor part in regulating the intensity and duration of nervous discharge; that a series of movements is not a chain of sensory-motor reactions. The theory of control of movement which was dominant at the turn of the century assumed that, after a movement is initiated, it is continued until stopped by sensations of movement and position, which indicate that the limb has reached the desired position. This theory was opposed by a good bit of indirect evidence, such as that accuracy of movement is increased rather than diminished with speed. I had opportunity to study a patient who had a complete anesthesia for movements of the knee joint, as a result of a gunshot wound of the cord (16). In spite of the anesthesia, he was able to control the extent and speed of movements of flexion and extension of the knee quite as accurately as can a normal person.

The performance of very quick movements also indicates their in-

dependence of current control. "Whip-snapping" movements of the hand can be regulated accurately in extent, yet the entire movement, from initiation to completion, requires less than the reaction time for tactile or kinesthetic stimulation of the arm, which is about one-eighth of a second, even when no discrimination is involved. Such facts force the conclusion that an effector mechanism can be pre-set or primed to discharge at a given intensity or for a given duration, in independence of any sensory controls.

CENTRAL CONTROL OF MOTOR PATTERNS

This independence of sensory controls is true not only of intensity and duration of contraction of a synergic muscle group but is true also of the initiation and timing of contraction of the different muscles in a complex movement. The hand may describe a circular movement involving coordinated contractions of the muscles of the shoulder, elbow, and wrist in about $\frac{1}{10}$ second, and the stopping of movement at a given position, of course, is only a small fraction of that time. The finger strokes of a musician may reach sixteen per second in passages which call for a definite and changing order of successive finger movements. The succession of movements is too quick even for visual reaction time. In rapid sight reading it is impossible to read the individual notes of an arpeggio. The notes must be seen in groups, and it is actually easier to read chords seen simultaneously and to translate them into temporal sequence than to read successive notes in the arpeggio as usually written.

Sensory control of movement seems to be ruled out in such acts. They require the postulation of some central nervous mechanism which fires with predetermined intensity and duration or activates different muscles in predetermined order. This mechanism might be represented by a chain of effector neurons, linked together by internuncials to produce successive delays in firing. In some systems the order of action may be determined by such a leader or pace-setter. Buddenbrock (6) has shown for the stick insect, and Bethe (3) for a number of animals from the centipede to the dog, that removal of one or more legs results in a spontaneous change in the order of stepping. Thus, for the insects, the normal order is alternate stepping of the first pair of legs with right first, left second, right third leg advancing together. With removal of the left first leg, the right first and left second alternate and the order becomes right first, left third, right third stepping together, with left second and right second advancing together, instead of alternately. These investigators were interested in spontaneity of reorganization, rather than in the mechanism of coordination, and did not propose any

theory for the latter. They did show, however, that it is necessary to remove the leg completely to get the change in pattern of movement; sensory impulses from a limb stump would prevent it. Such coordination might be explained, perhaps, by a combination of loss of excitability in the centers of the absent limb, by the excitation of the remaining anterior center as a leader or pace-setter, and the spread of alternate waves of inhibition and excitation from the more anterior to the more posterior limb centers. The spontaneous change in coordination shows, however, that the coordination is not due to the action of predetermined anatomic paths but is the result of the current physiological state of the various limb centers.

Such an hypothesis implies also the assumption of a polarization of conduction along the neuraxis, with the order of excitation determined by the spatial arrangement of the centers of the legs. I see no other possibility of accounting for the facts. The examples of circular movement and of finger coordination, involving temporal integration of movements, seem to call for a similar hypothesis. They might be ascribed to an habitual linkage of the movements through a simple chain of internuncials but for two facts. First, such series are usually reversible at any point or can be started from any point. This would require the assumption of a second set of internuncials habituated to conduct in the opposite direction, and this in turn leads to the further assumption of a polarization of conduction. Second, such patterns of coordinated movement may often be transferred directly to other motor systems than the ones practiced. In such transfer, as to the left hand for writing, an analysis of the movements shows that there is not a reduplication of the muscular patterns on the two sides, but a reproduction of movements in relation to the space coordinates of the body. Try upside-down mirror writing with the left hand and with eyes closed for evidence of this. The associative linkage is not of specific movements but of directions of movement. An analysis of systems of space coordinates suggests mechanisms which may contribute to production of such series of movements in a spatial pattern.

SPACE COORDINATE SYSTEMS

The work of Sherrington, Magnus, and others on postural tonus and reflexes has defined one level of spatial integration rather fully, yet it is doubtful if these studies have revealed the effective neural mechanism. The work has shown that the tonic discharge to every muscle in the postural system is influenced by afferent impulses from every other muscle, toward increased or decreased activity, according to its syner-

gic or antergic action. To these influences are added vestibular and cerebellar effects. Diagrammatically these mutual influences of the muscular system may be represented by separate reflex circuits from each receptor to every muscle, as Sherrington (21, p. 148) has done. But no neuro-anatomist would, I am sure, maintain that such separate circuits or paths exist. What the experiments on posture actually show is a correlation of sensory stimulation and of tonic changes in a network of neurons whose interconnections are still undefined. The reactions isolated experimentally have the characteristics of simple directly conducted reflexes, but their combination results in patterns of movement and posture which have definite relations to the axes of the body and to gravity.

This postural system is based on excitations from proprioceptors. The distance receptors impose an additional set of space coordinates upon the postural system, which in turn continually modifies the coordinates of the distance receptors. The dropped cat rights itself, if either the eyes or the vestibular senses are intact, but not in the absence of both. The direction of movement on the retina imposes a directional orientation on the postural system. Conversely, the gravitational system imposes an orientation on the visual field. Upright objects such as trees or the corners of a room appear upright, at no matter what angle the head is inclined. Derangement of the vestibular system can disturb the distance orientation or the orientation of the receptors, as in the apparent swaying of the vertical as a result of the after-images of motion following hours of rocking in a small boat.

There are other, still more generalized systems of space coordinates. We usually keep track of the compass points or of some more definite index of direction by a temporal summation of the turns made in walking, though not always with success. Finally, there is a still more plastic system in which the concepts of spatial relations can be voluntarily reversed, as when one plays blindfold chess alternately from either side of the board.

Explanation of these activities, these complex interactions, in terms of simple isolated interconnections of all of the sensory and motor elements involved seems quite improbable on anatomic grounds and is ruled out by results of our experiments on sectioning of the spinal cord. Ingebritzen (14) studied rats with double hemisection of the cord; one-half of the cord cut at the second, the other at the fifth cervical segment. In the best case only a small strand of the spino-cerebellar tract of one side remained intact. These rats were able to balance in walking, oriented to visual stimuli, scratched with the right

or left hind foot according to the side of the face stimulated, were able to run mazes correctly, and even learned to rise on the hind feet and push down a lever with the forepaws in opening a box.

The alternative to the isolated-path theory of the space coordinates is that the various impulses which modify postural tonus are poured into a continuous network of neurons, where their summated action results in a sort of polarization of the entire system. I shall consider later the integrative properties of such a net. For the moment I wish to emphasize only the existence of these systems of space coordinates. Their influences pervade the motor system so that every gross movement of limbs or body is made with reference to the space system. The perceptions from the distance receptors, vision, hearing, and touch are also constantly modified and referred to the same space coordinates. The stimulus is *there*, in a definite place; it has definite relation to the position of the body, and it shifts with respect to the sense organ but not with respect to the general orientation, with changes in body posture.

Memories of objects usually give them position in the space system, and even more abstract concepts may have definite spatial reference. Thus, for many people, the cardinal numbers have definite positions on a spiral or other complicated figure. What, if anything, such space characters can contribute to temporal integration is an open question. They provide a possible basis for some serial actions through interaction of postural and timing mechanisms.

RHYTHMIC ACTION

The simplest of the timing mechanisms are those controlling rhythmic activity. T. Graham Brown (5) first showed by his studies of de-afferented preparations that the rhythmic movements of respiration and progression are independent of peripheral stimulation and are maintained by a central nervous mechanism of reciprocal innervation. He suggested that this mechanism of reciprocal innervation, rather than the simple reflex, is the unit of organization of the whole nervous system. He thus foreshadowed, in a way, the conception of reverberatory circuits which is coming to play so large a part in neurological theory today. Holst (13) has recently shown that the rhythmic movement of the dorsal fin of fishes is a compound of two superimposed rhythms, that of its own innervation and that of the pectoral fins. These two rhythms are centrally maintained.

Musical rhythms seem to be an elaboration of the same sort of thing. The time or beat is started and maintained at some definite rate, say 160 per minute. This rate is then imposed upon various activities. The

fingers of the musician fall in multiples of the basic rate. If the leader of a quartet speeds up the time or retards, all the movements of the players change in rate accordingly. Not only the time of initiation but also the rate of movement is affected. The violinist, in a passage requiring the whole bow, will draw the bow from frog to tip at a uniform rate for the required number of beats, whether the tempo is fast or slow. With practiced violinists, the rate of movement is extremely accurate and comes out on the beat at the exact tip of the bow.

Superimposed on this primary rhythm is a secondary one of emphasis, giving the character of $3/4$, $4/4$, $6/4$, or other time. The mechanism of these rhythms can be simply conceived as the spread of excitation from some centers organized for reciprocal innervation; as a combination of the principles of Brown and of Holst. There are, however, still more complicated rhythms in all music. That of the melodic line is most uniform. In much music, the melodic progression changes in 2, 4, or some multiple of 4 measures. In improvisation, the performer keeps no count of measures, yet comes out almost invariably in a resolution to the tonic of the key after some multiple of eight measures. Here a generalized pattern is impressed on the sequence, but it is a simpler pattern than that of grammatical structure. It only requires the recurrence of a pattern at certain rhythmic intervals; a pick-up of a specific pattern after so many timed intervals.

There are, in addition, still less regular rhythms of phrasing and emphasis. Parallels to these can be found in speech. The skilled extemporaneous speaker rounds his phrases and speaks with a definite though not regular rhythm.

The rhythms tend to spread to almost every other concurrent activity. One falls into step with a band, tends to breathe, and even to speak in time with the rhythm. The all pervasiveness of the rhythmic discharge is shown by the great difficulty of learning to maintain two rhythms at once, as in three against four with the two hands. The points to be emphasized here are the widespread effects of a rhythmic discharge indicating the involvement of almost the entire effector system, the concurrent action of different rhythmic systems, and the imposition of the rate upon both the initiation and speed of movement. Consideration of rhythmic activity and of spatial orientation forces the conclusion, I believe, that there exist in the nervous organization, elaborate systems of interrelated neurons capable of imposing certain types of integration upon a large number of widely spaced effector elements; in the one case transmitting temporally spaced waves of facilitative excitation to all effector elements; in the other imparting a directional polarization to both receptor and effector elements. These

systems are in constant action. They form a sort of substratum upon which other activity is built. They contribute to every perception and to every integrated movement.

INTERACTION OF TEMPORAL AND SPATIAL SYSTEMS

Integration ascribed to the spatial distribution of excitations in the nervous system has been much more intensively studied than the temporal aspects of nervous activity. Theories of integration are based almost exclusively upon space properties, time entering only in theories of facilitation, inhibition, and after-discharge. In cerebral functions, however, it is difficult to distinguish between spatial and temporal functions. The eye is the only organ that gives simultaneous information concerning space in any detail. The shape of an object impressed on the skin can scarcely be detected from simultaneous pressure, but the same shape can readily be distinguished by touch when traced on the skin with a moving point or when explored by tactile scanning. The temporal sequence is readily translated into a spatial concept. Even for vision it might be questioned whether simultaneous stimulation gives rise directly to space concepts. The visual object is generally surveyed by eye movements, and its form is a reconstruction from such a series of excitations. Even with tachistoscopic exposures, the after-discharge permits a temporal survey, and, with visual fixation, shifts of attention provide an effective scanning.

Since memory traces are, we believe, in large part static and persist simultaneously, it must be assumed that they are spatially differentiated. Nevertheless, reproductive memory appears almost invariably as a temporal sequence, either as a succession of words or of acts. Even descriptions of visual imagery (the supposed simultaneous reproductive memory in sensory terms) are generally descriptions of sequences, of temporal reconstructions from very fragmentary and questionable visual elements. Spatial and temporal order thus appear to be almost completely interchangeable in cerebral action. The translation from the spatial distribution of memory traces to temporal sequence seems to be a fundamental aspect of the problem of serial order.

I spoke earlier of the probability of a partial activation or priming of aggregates of words before the sentence is actually formulated from them. There is a great deal of evidence for such preliminary facilitation of patterns of action in studies of reaction time and of word association. Reaction time, in general, is reduced by preliminary warning or by instructions which allow the subject to prepare for the specific act required. In controlled association experiments, the subject is in-

structed to respond to the stimulus word by a word having a certain type of relation to it, such as the opposite or a part of which the stimulus is the whole; black-white, apple-seed. The result is an attitude or set which causes that particular category to dominate the associative reaction. Whether such preliminary reinforcement is to be ascribed to accumulation of excitatory state, as defined by Sherrington (21), or to some other physiological process, the facts of behavior assure that it is a genuine phenomenon and plays a decisive role in determining the character of the response.

Once the existence of such states of partial activation is recognized, their possible role in temporal integration must be considered. There are indications that one neural system may be held in this state of partial excitation while it is scanned by another. Here is an example. A series of four to six numbers is heard: 3-7-2-9-4. This is within the attention or memory span and is almost certainly not remembered in the sense in which one's telephone number is remembered, for memory of it is immediately wiped out by a succeeding series of numbers. While it is retained in this unstable way, subject to retroactive inhibition, the order of the numbers can be reassorted: 3-7-2-9-4, 3-2-7-9-4, 4-9-2-7-3, and the like. It is as if, in this case, a rhythmic alternation can suppress alternate items, or a direction of arousal can be applied to the partially excited system. Another example which illustrates even more clearly the spatial characteristics of many memory traces is the method of comultiplication, used in rapid mental calculation. In attempts to play a melody backward, we have a further illustration. I find that I can do it only by visualizing the music spatially and then reading it backward. I cannot auditorily transform even "Yankee Doodle" into its inverse without some such process, but it is possible to get a spatial representation of the melody and then to scan the spatial representation. The scanning of a spatial arrangement seems definitely to determine, in such cases, the order of procedure. Two assumptions are implied by this. First, the assumption is that the memory traces are associated, not only with other memory traces, but also with the system of space coordinates. By this I do not mean that the engram has a definite location in the brain; our experiments show conclusively that such is not the case. Rather, when the memory trace is formed it is integrated with directional characters of the space system, which give it position in reference to other associated traces. Second, the assumption is that these space characters of the memory trace can be scanned by some other level of the coordinating system and so transformed into succession.

This is as far as I have been able to go toward a theory of

serial order in action. Obviously, it is inadequate. The assumptions concerning spatial representation and temporal representation may even beg the question, since no one can say whether spatial or temporal order is primary. Furthermore, such determining tendencies as the relation of attribute to object, which gives the order of adjective and noun, do not seem to be analyzable into any sort of spatial structure or for that matter, into any consistent relationship. I have tried a number of assumptions concerning the selective mechanism of grammatical form (spatial relations, the relative intensity or prominence of different words in the idea, and so on) but I have never been able to make an hypothesis which was consistent with any large number of sentence structures. Nevertheless, the indications which I have cited, that elements of the sentence are readied or partially activated before the order is imposed upon them in expression, suggest that some scanning mechanism must be at play in regulating their temporal sequence. The real problem, however, is the nature of the selective mechanism by which the particular acts are picked out in this scanning process, and to this problem I have no answer.

Such speculations concerning temporal and spatial systems do little more than illustrate a point of view concerning nervous organization which is, I believe, more consistent both with what is known of the histology and elementary physiology of the brain and also with behavior phenomena than are the more widely current theories of simple associative chains of reactions.

Nearly forty years ago Becher (2, page 243) wrote: "There is no physiological hypothesis which can explain the origin and relations of temporal forms in mental life; indeed, there is no hypothesis which even foreshadows the possibility of such an explanation." The situation is little better today, but I do feel that changing conceptions of the fundamental organization of the nervous system offer more hope for a solution of such problems than did the physiological knowledge available when Becher wrote. However, we are still very far from being able to form an explicit explanation of temporal structure.

THE FUNDAMENTAL MECHANISM OF INTEGRATION

Neurological theory has been dominated by the belief that the neurons of the central nervous system are in an inactive or resting state for the greater part of the time; that they are linked in relatively isolated conditioned reflex arcs and that they are activated only when the particular reactions for which they are specifically associated are called out. Such a view is incompatible both with the widespread effects of stimulation which can be demonstrated by changes in tonus

and also with recent evidence from electrical recording of nervous activity. It is now practically certain that all the cells of the cerebrospinal axis are being continually bombarded by nerve impulses from various sources and are firing regularly, probably even during sleep. The nervous activity which they in turn elicit depends upon the current physiological state of the neurons with which they are connected. It is probably not far from the truth to say that every nerve cell of the cerebral cortex is involved in thousands of different reactions. The cortex must be regarded as a great network of reverberatory circuits, constantly active. A new stimulus, reaching such a system, does not excite an isolated reflex path but must produce widespread changes in the pattern of excitation throughout a whole system of already interacting neurons.

The facts of cerebral structure support such a view. The cortex is composed chiefly of neurons with short axons. LeGros Clark (8) has found for the striate area of the monkey that Marchi degeneration extends for only a short distance from a point of injury. In the striate area of the rat, I have never been able to trace degeneration beyond three or four cell diameters from the margin of a lesion, and I believe that this lack of long transcortical fibers is true of other areas as well as of the visual cortex. Visual perception reveals close integration of different parts of the striate areas in spite of the absence of long association fibers. In the visual cortex of the rat there are only 19 neurons for each afferent fiber. To produce the animal's visual acuity, all of the afferent fibers must be firing continually. There are approximately 34,000 cell bodies in the lateral geniculate nucleus of the rat, and the minimum number of visual units necessary to produce the visual acuity of the rat is actually above this figure. (The acuity is determined by direct experimental tests.) These figures should be of interest in relation to the numerical values cited by Dr. von Neumann. The number of cells in the visual cortex of the rat is only about 10^6 , and in some of my experiments where I have removed the greater part of the visual cortex the capacity for discrimination of visual forms has been retained when no more than 20,000 cells of the visual cortex remain. There is also evidence that no part of the cerebral cortex except the visual areas is essential for visual perception and memory.

DR. LORENTE DE NÓ: What is the number of afferents in the optic nerve?

DR. LASHLEY: There are 290,000 afferents in the optic nerve of the rat, and the figure is reduced to 34,000 in the lateral geniculate. The

actual numbers are 9,000,000 myoids, 290,000 ganglion cells, and 34,000 cells in the lateral geniculate. That may include cells with short axons also. There are about 125,000 cells in each of the five layers of the cortex. These figures are for one eye and hemisphere.

DR. VON NEUMANN: In the human being the corresponding number is about 125,000,000 for the first, isn't it?

DR. LASHLEY: I know of no figure for that level.

DR. LORENTE DE NÓ: It hasn't been analyzed in any way.

DR. VON NEUMANN: The optic nerve corresponds to the second one?

DR. LASHLEY: Yes. The axons of the ganglion cells pass through the optic nerves. There is an average of 300 visual cells firing into each central pathway. There are fewer than 5 cells in the receptive layer of the visual cortex of the rat for each afferent fiber of the optic radiation and only 19 cells per afferent fiber in the entire visual cortex. Since the visual acuity of the rat requires that all of the 34,000 cells of the radiation be firing constantly, it seems certain that all of the neurons within the striate areas, the visual cortex, must be firing constantly. There is a good bit of evidence that all of the integrative functions of vision are carried out within the striate areas. In the rat, I have removed, from one or another animal, practically every other part of the isocortex without disturbing visual perception or memory. With monkeys I have removed the supposed visual associative areas without producing any significant loss of visual functions.

These facts lead to the conclusion that the same cells in the visual cortex participate in a great variety of activities. Practically all of the cells of the area must be fired by every visual stimulation, and these same cells must be the ones which retain the visual memories. The conclusion follows that differential responses depend upon the pattern of cells which are excited in combination. The visual cortex is a network of cells of short axon without long interconnections between its parts or with other cortical areas. Its integrative functions are an expression of the properties of such a network.

The same conception must be applied to other cortical areas. There are, of course, long association tracts in the cortex, such as the corpus callosum, the superior longitudinal fasciculus, and the temporo-frontal tracts. Once, 26 years ago, I suggested facetiously that these might be only skeletal structures, since I could find no function for them. No important functions of these tracts have yet been demonstrated. Section of the corpus callosum produces only a slight slowing of reaction time, ipsilateral as well as contralateral (Akelaitis, 1); section of occipito-frontal fibers produces, perhaps, a temporary disturbance

of visual attention but no other symptoms. The integrative functions seem to be carried out as well without as with the main associative tracts. The major integrative functions must, therefore, be carried out by the network of cells of short axon. The properties of such networks of cells must be analyzed before the mechanisms of the cerebral cortex can be understood. Something can be inferred from the characteristics of excitability of cells and their arrangement in recurrent loops. If, as seems a necessary conclusion from the histology of the striate area, all of the cells of the network are subject to constant excitation and are firing whenever they recover from the refractory state, then mutual interference of circuits will produce complicated patterns throughout the area, patterns which will stabilize in the absence of differential stimulation, as is perhaps indicated by the regularity of the alpha rhythm. Any new afferent impulses reaching the area can only produce a reorganization of the existing pattern. What happens at any particular point in the system, as at an efferent neuron, is the statistical outcome of the interaction of myriads of neurons, not of the transmission of impulses over a restricted path, of which that efferent cell forms a link. It is possible to isolate parts of the system by operative means or by anesthetics and so to get a one-to-one relation of stimulus locus and responding muscles, from which the reflex mechanism has been inferred. As Goldstein (12) has pointed out, however, the parts isolated in the reflex are influenced by a multiplicity of effects in the intact organism of which there is little or no trace in the isolated preparation.

I can best illustrate this conception of nervous action by picturing the brain as the surface of a lake. The prevailing breeze carries small ripples in its direction, the basic polarity of the system. Varying gusts set up crossing systems of waves, which do not destroy the first ripples, but modify their form, a second level in the system of space coordinates. A tossing log with its own period of submersion sends out periodic bursts of ripples, a temporal rhythm. The bow wave of a speeding boat momentarily sweeps over the surface, seems to obliterate the smaller waves yet leaves them unchanged by its passing, the transient effect of a strong stimulus. Wave motion is not an adequate analogy because the medium which conveys the waves is uniform, whereas the nerve cells have their individual characteristics of transmission which at every point may alter the character of the transmitted pattern.

The great number of axon terminations on every nerve cell has not been considered in theories of integration. It implies, of course, that the cell can be fired by impulses from a variety of sources. But it also

suggests another possibility, more fruitful for understanding of integrative processes. A nerve impulse arriving over a single axon terminal may not fire the cell but may modify its excitability to impulses from other sources. In an elaborate system of neurons such subthreshold effects might establish a pattern of facilitation which would determine the combination of cells fired by subsequent excitations. The space coordinate system and various types of *set* or priming may be pictured as patterns of subthreshold facilitation pervading the network of neurons which is activated by the more specific external stimulus.

Such a view of the mechanism of nervous action certainly does not simplify the problems nor does it as yet provide any clue to the structuring that constitutes the set or determining tendency, or to the nature of such relations as are implied in the attribute-object, opposites, or other abstract concepts. A few relations seem reducible to spatial terms, part-whole, for example, but even for these there is no clear conception of the neural basis of their space properties. These considerations do not, I believe, contradict fundamentally the basic conceptions that have been formulated by Dr. McCulloch. They do, however, indicate a direction of necessary elaboration. The nets active in rhythmic and spatial organization are apparently almost coextensive with the nervous system. The analysis must be extended to the properties of such nets; the way in which they are broken up into reactive patterns in the spread of excitation, to give, for example, directional propagation or its equivalent. I strongly suspect that many phenomena of generalization, both sensory and conceptual, are products, not of simple switching, but of interaction of complex patterns of organization within such systems.

SUMMARY

The problems of the syntax of action are far removed from anything which we can study by direct physiological methods today, yet in attempting to formulate a physiology of the cerebral cortex we cannot ignore them. Serial order is typical of the problems raised by cerebral activity; few, if any, of the problems are simpler or promise easier solution. We can, perhaps, postpone the fatal day when we must face them, by saying that they are too complex for present analysis, but there is danger here of constructing a false picture of those processes that we believe to be simpler. I am coming more and more to the conviction that the rudiments of every human behavioral mechanism will be found far down in the evolutionary scale and also represented even in primitive activities of the nervous system. If there exist, in human cerebral action, processes which seem fundamentally different

or inexplicable in terms of our present construct of the elementary physiology of integration, then it is probable that that construct is incomplete or mistaken, even for the levels of behavior to which it is applied.

In spite of its present inadequacy, I feel that the point of view which I have sketched here holds some promise of a better understanding of cerebral integration. Attempts to express cerebral function in terms of the concepts of the reflex arc, or of associated chains of neurons, seem to me doomed to failure because they start with the assumption of a static nervous system. Every bit of evidence available indicates a dynamic, constantly active system, or, rather, a composite of many interacting systems, which I have tried to illustrate at a primitive level by rhythm and the space coordinates. Only when methods of analysis of such systems have been devised will there be progress toward understanding of the physiology of the cerebral cortex.

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DISCUSSION

DR. KLÜVER: In 1914, there appeared a book which, in the opinion of the author, marked an epoch—since during the remaining years of his life he celebrated the day the manuscript was completed instead of his birthday. The author was von Monakow, and the title of the book was *Die Lokalisation im Grosshirn*. There is a remarkable connection between von Monakow's monumental contribution to neurology in 1914 and Dr. Lashley's presentation today. In my opinion, this is the first time since 1914 that a neurological thinker has presented such a trenchant analysis of the role of the time factor in behavior. If you study von Monakow's book you find that the central concept of his work is the concept of a "chronogenic localization," a concept which has been almost completely ignored during the intervening decades.

It is not possible today to enter into a discussion of the numerous problems raised by Dr. Lashley's presentation. As regards the relation of thinking to temporal organization, we are, it seems to me, confronted with a certain dilemma. Ideas, concepts, and meanings themselves have no reference to time and space, and, yet, the expression, formulation, and identification of ideas are processes proceeding in time and occurring in space. It is the relation of ideas to temporal and spatial factors which is of interest to the physiological psychologist. Even the

fact that the verbal expression of an idea is linked up with a temporal sequence of acoustic events raises intricate questions. I got an inkling of some of the difficulties on a visit to Vogt's Institute for Brain Research, where an investigator utilized the methods of experimental phonetics in studying the speech utterances of neurological and psychiatric patients. He found, on the one hand, that the curves he had obtained could not be interpreted without considering the acoustic events "carriers of meanings" and, on the other hand, that certain forms of expression survived speeding up and slowing down and even the complete reversal of the temporal sequence. I do not know whether any further attempts have been made to utilize the techniques of experimental phonetics.

I should like to comment on only one other point. It is true that the same idea may be expressed in various languages by utilizing a different temporal order of words, just as the same perceptual relation may be recognized on the basis of different relations; but it is also true that the structure of language may prevent us from expressing ideas and thinking along certain lines. The fact that the language I am using now does not possess a word for a rough, wet object undergoing a color change may have the consequence that I overlook such an object or that I do not identify, remember, and think about it. Consequently, such an item may not or cannot enter a temporal sequence utilized in expressing an idea. In this connection Allers' experiments on "word nearness" and "word remoteness" are of particular interest. According to Allers, every attempt to express an idea in words induces a tendency towards selecting items in terms of word nearness. Word nearness and word remoteness may become decisive in determining the temporal sequence and in expressing or not expressing an idea. The line of demarcation between word-near and word-remote elements is subject to marked variations and even varies from individual to individual. No doubt, the sequence of phenomena calling for an expression in words, the sequence of words, and the sequence of ideas are sequences of a different order. The great value of Dr. Lashley's analysis lies in the fact that it exhibits the significant factors involved in the expression of ideas as well as in other instances of serial ordering, and that it utilizes such factors effectively in formulating mechanisms of cerebral activity.

DR. KÖHLER: Dr. Lashley rightly said that human orientation in space is mostly achieved in a sequence of events. We move our eyes, or our attention wanders, and so forth, as we inform ourselves about our environment. Curiously enough, however, while the process of becoming so informed occurs in time, and consists of successive acts, the

result appears almost independent of this temporally extended origin. Apart from objective changes, which we may ignore in this connection, the space in which we live, and the objects around us, appear for the most part perfectly stationary. Dr. Lashley agrees, of course, with this observation. I wonder whether he can tell us how in this case the history of becoming informed disappears so completely from the final information.

DR. GERARD: I tried yesterday, in a brief summary, to remain strictly non-partisan while indicating the various viewpoints that had been presented and which were still to come. Actually, I find it impossible to think through or even towards the complexities of behavior if restricted to atomic units traveling along atomic fibers. Even the work we did on the frog brain, which showed a potential field present in which moving waves of electrical activity could travel and cross complete anatomical cuts, seems inexplicable at that level. My own inclination is to think of the discrete elements and the patterns of their activity as involved in the more particular performances of the nervous system, in the immediate sequences of action, as emphasized, but also as active in the more integrated behavior of the whole of the nervous system. This doesn't mean that, in any way, I am disagreeing with Dr. Lashley's final comment. One can hope, with some confidence, that all the properties of the most complex nervous system will prove to be adumbrated in the properties of the simplest element and connection when we know those properties sufficiently well.

I would like to raise one particular point. Some years ago, Culler and his colleagues reported an observation which may have been elaborated or may have been refuted; I haven't been following that literature. If it is correct, it seems very relevant to this whole problem, and I'd like Dr. Lashley's reaction to it. In dogs, conditioned in some particular way, a circumscribed region of the cortex, not in the area either of the receptor or of the effector, became electrically excitable and produced the conditioned response. When the conditioned reflex was extinguished, that area became inexcitable. There was, thus, a sharp localization of conditioning in that particular case, one of the few striking exceptions to the more general pattern of mass activity. What is the present status of such work?

DR. HALSTEAD: I couldn't help thinking, as I listened to this excellent example of what I would call the higher mental processes, that I could have prevented all this by putting a lesion in a particular part of one nervous system—the anterior portion of Dr. Lashley's prefrontal areas. If instead I had put a lesion in area 19 of Dr. Lashley, certain important elements in his presentation would undoubtedly have been

lacking. Yet we could have removed probably each lobe of the brain individually without disturbing the basic form or organization.

I have been greatly impressed with the case that Dr. Lashley has made for non-specific, non-mosaic representation. I would like to emphasize, and if I am incorrect I hope that he will point it out, that his view is not incompatible with progressive specialization of function. The language functions that he talked about are not disturbed, except when particular areas in the brain are involved. The visual functions that he described are not disturbed, except when particular regions of the brain are involved. The important thing is that, within the region, there seems to be the possibility for equivalence to arise.

DR. LORENTE DE NÓ: It is typical of Dr. Lashley that he places on the board a series of figures that no anatomist had ever determined. Dr. Lashley had to determine them himself in order to go on with his work.

I don't think that I have yet fully appreciated the value of Dr. Lashley's talk. I will have to read it and study it thoroughly, but, while I was listening, there was going through my head a mental picture of the future development of a number of experiments that I intend to perform—suggested to me by Dr. Lashley's speech. One of the problems that Dr. Lashley has suggested to me is very accessible of experimentation in the study and treatment of things of purely central origin. There is one very good situation in which we meet discharges of very long duration, which can be created in the absence of every peripheral influence. You know that stimulation of the labyrinth produces a rhythmical movement of the eye and establishes the fact that this rhythm is not dependent upon the feedback from the eye muscles for its production. Impulses can be recorded directly from the nerves to the eye muscles, and therefore any sensory feedback is eliminated. What the labyrinth sends to the nervous system is a continuous stream of impulses, not interrupted rhythmically. The interruptions are produced in the nervous system, and, furthermore, can be produced when the labyrinths are extirpated. Thus in the usual vector nystagmus, if one labyrinth is extirpated, the spontaneous nystagmus will last some 10 or 12 or 15 days after that, and then the spontaneous nystagmus ceases. If the second labyrinth is then extirpated, the nystagmus reappears and lasts for 7 or 8 days. This is a purely central phenomenon—there are no impulses of any kind coming from the periphery into the centers, and the nystagmus can be recorded from the motor nerves after the extirpation of the eye. Consequently, it is describable as rhythmical activity, and is the type of rhythm that I'm going to investigate as soon as I get to it.

I would also like to make a remark in reference to Dr. Gerard's statement about neural elements in cerebral physiology. We have been, for many years, considering only the transmission of impulses as the natural mode. Now, this potential field of yours is another mechanism by which the nerve cells act upon others. Sometimes neurons act upon others by the transmission of impulses, and sometimes by the potential field of the currents that they establish.

DR. WEISS: The great value of Dr. Lashley's presentation lies in the fact that it places rigorous limitations upon the free flight of our fancy in designing models of the nervous system, for no model of the nervous system can be true unless it incorporates the properties here described for the real nervous system. You will recognize that our current models are far short of satisfying this condition.

Dr. Lashley's theses receive crucial support from the student of development. The embryologist has long been up against a tremendous task. While the physiologist and psychologist deal with the ready-made machine of the nervous system and can add to it as many properties as he thinks necessary, the embryologist must explain just how such an immensely intricate, yet orderly, thing can develop. These studies are still in their infancy, but a few things have already come out which gibe completely with the conclusions that Dr. Lashley has presented here; for instance, the relative autonomy of structured patterns of activity, and the hierarchical principle of their organization. As I said previously, the nervous system is not one big monotonic pool whose elements can be freely recombined in any number of groupings, thereby giving an infinite variety of nervous responses. This used to be the old idea of the associationists, and it is utterly incompatible with what we have learned about the development of the nervous system and its functions in animals. I wouldn't have spoken here if Dr. Lashley hadn't said that he is convinced that whatever happens in the brain of man is foreshadowed, and, in principle, is the same as what happens in the lower organisms. Therefore, assuming that premise, I would now like to add a few comments.

First, we know from the lower organisms that the working of the central nervous system is a hierarchic affair in which functions at the higher levels do not deal directly with the ultimate structural units, such as neurons or motor units, but operate by activating lower patterns that have their own relatively autonomous structural unity. The same is then true for the sensory input, which does not project itself down to the last final path of motor neurons, but operates by affecting, distorting, and somehow modifying the pre-existing, preformed patterns of central coordination, which, in turn, then confer their distor-

tions upon the lower patterns of effectation and so on. The final output is then the outcome of this hierarchical passing down of distortions and modifications of intrinsically preformed patterns of excitation, which are in no way replicas of the input. The structure of the input does not produce the structure of the output, but merely modifies intrinsic nervous activities that have a structural organization of their own. This has been proved by observation and experiment. Coghill has shown that the motor patterns of the animal develop prior to the development of sensory innervation. I have shown, as others have, that the removal of the sensory innervation does not abolish the coordination of motor activities. Moreover, coordinated motor functions of limbs and other parts develop even if these parts have been experimentally prevented from ever becoming innervated by sensory fibers. Therefore, the sensory pathway can have nothing to do with the structure of the motor response. There are still some authors who try to save the old associationist idea that actually the input shapes the structure of the output. I think that they are fighting a losing fight, and I think that today's discussion ought to have given them the coup de grâce. The essential independence of the structure of motor activity is dramatically demonstrated when one exchanges and reverses the limbs of animals and then finds them crawling backwards whenever they aim to crawl forwards, and vice versa. Many of you have seen my film where this had been done in the developed animal, but the same operations have been done in embryos and these animals have then functioned in reverse from the very beginning. What more spectacular expression can there be of the intrinsic primacy of the motor patterns of behavior for which the external input acts only as a selective trigger?

The autonomous development of central functions raises a further question: Are the response patterns preformed as merely static conditions, or are they of dynamic nature, that is, properties of automatic central activities? Lashley has favored the latter view, and, again, experiments in lower animals furnish corroborative evidence. Intrinsic automatic rhythms have been shown, for instance, by Adrian in the brain stem of the goldfish and in insect ganglia, by Prosser in other arthropods, by Bremer and by von Holst in the spinal cord, and by Bethe in jellyfish. I have shown experimentally that any group of bulbar or spinal nerve cells taken from vertebrates, if deprived of their structural bonds of restraining influences and allowed to undergo a certain degree of degradation, will display permanent automatic, rhythmic, synchronized activity of remarkable regularity. Rhythmic activity, therefore, seems a basic property of pools of nervous elements. Whether this automatism is generated by neuron switch works or

rather by the rhythmic waxing and waning of metabolic activity expressing itself in the electric field, as suggested by Dr. Gerard, is a secondary question. The principal point is that the rhythm is not something generated through an input rhythm, but is itself a primary rhythm which may be released and even speeded up or retarded by the input, but is not derived from the input. So we have experimental evidence that autonomy of pattern, rhythmic automatism, and hierarchical organization are primary attributes of even the simplest nervous systems, and I think that this unifies our view of the nervous system. I conclude with expressing my hope that today's discussion will really mark a turning point in the building of neurological theories so that more regard will be given to all the actual facts that we do know about nervous systems.

DR. MC CULLOCH: There is a paper by Wiener, written when he was working with Bertrand Russell, in which he described the space of implications. It is a peculiarly degenerate sort of space. Now I, like many other men, find it difficult to think in motion. When I think about motion, I freeze it in a four-space. If you take Wiener's degenerate space of implication and make yourself a four-space image of it, you can visualize these rhythms as fixed forms. You can practically superimpose large numbers of these forms easily in the mind instead of battling with two or three. That is the first point, and it is merely a technical device.

Second, you remember that I said that on the way down from the cerebral cortex I was utterly unhappy about our knowledge of how the cortex did this or that on account of our ignorance of the lower mechanisms. I want to say a word about two rhythmical affairs that we are now working on. If, in the intact animal, you stimulate the nucleus caudatus, the animal just slumps. If, however, you cut bilaterally the cerebral peduncles, through which all impulses coming from the cerebrum have to go to reach the hindbrain and lower structures, and if you then stimulate the nucleus caudatus, you get beautiful automatically associated rhythmical movements. One, for example, resembles a cat fishing in the gold-fish bowl. Another resembles feline boxing. There is always some part of the body, arm, leg, or face, leading in each of these movements. The sequence of each movement belonging to this group starts in the axial system, then goes to the axio-appendicular, and thence to the appendicular, moving ever outward. I have never seen any evidence of somatotopic localization in the input to the nucleus caudatus. Yet here, in its output, on coming down any one puncture, stimulation at superior positions gives responses beginning in the tail and hindleg, deeper, in the forelegs, and near the very bottom, in the face. From the bottom you get complicated lapping and chew-

ing movements just as you do from the amygdala. You get similar movements from the putamen under these circumstances and always this representational reversal, the lowest part being represented highest. Now, if you go down their descending systems, whether you go down the ansa lenticularis or go into the bunch of fibers that pass into the subthalamus and turns down, you can follow right down, stimulating them with similar results. Let me remind you that your stimulus is just a series of impulses, say 40 or 30 per second. The frequency of the movements increases with the voltage of stimulation, to a maximum less than 10 per second. You continue to get these rhythmical movements as you proceed downstream until you reach the pneumotaxic center, when, instead of other movements, panting supervenes. Downstream of the pneumotaxic center, just as you get only torsion to the right or else to the left, so you get only inhalation or else exhalation, or only facilitation or else relaxation. Now the interesting thing is that these rhythmical movements increase in frequency as you increase the voltage of stimulation up to a limiting value of nearly 10 per second. Above that, you never get them, for hypertonus begins to come into the background and stops the movement.

This system, whatever else it does, takes a stream of impulses from the basal ganglia, which is merely a continuous stream, over more or fewer parallel paths and produces rhythmical performances. Thus, whatever makes the rhythm is downstairs; it need not be in the cerebral cortex or in the basal ganglia. These rhythmical movements originate downstream. By destruction upstream, you may release the same thing.

DR. LINDSLEY: Dr. Lashley's discussion of the temporal schema imposed upon the motor system, was of considerable interest to me. I don't know whether the spontaneous rhythms of the cortex have any relationship to this temporal schema, but there are a good many suggestive things that we can pick up in a rather superficial look at cortical activity. We can get, through the electroencephalogram, things which have been rather impressive to me. No one has been able to demonstrate conclusively that any of the cortical rhythms of spontaneous character has a direct relationship to the resting tremors of the normal, or, for that matter, the neurologically abnormal person, despite the fact that their frequencies may be similar in range. However, in the brain waves of new-born infants and even of fetal infants, it is possible to demonstrate rhythms, particularly in the motor area of the cortex, and they seem to be at least grossly correlated with some of the serial and sequential orders of motor activity. The correlation must remain a very rough one at the present state, because we have rather inadequate techniques for investigation.

The frequency that one finds in the fetus or in the new-born infant over the motor areas of the brain is much slower than that in the adult stage. Whether this has any relation to the similar lack of sequential organization which one finds in these early stages of development, I do not know.

Another thing which has been impressive to me is the nature of the frequencies that one records from the central nervous system—the multiple or submultiple character of the rhythms one encounters, not only as a developmental feature of the maturing brain, but in the matured individual when the normal spontaneous rhythm breaks up and multiplies itself or divides in half. Just what relationship these changes in rhythm bear to actual behavior, again I do not know.

I have been particularly interested in trying to devise experiments to help get a better correlation between these superficially observed electrical phenomena of the cortex and the behavioral activities of the motor system. I find this very difficult to deal with in terms of sequential activities which are continually flowing along. It is very hard to devise a system which will do more than suggest possible correlates. On the other hand, there are phenomena we encounter both in the normal and the abnormal individual, which seem to bear some relationship to this serial order. I'd like to have Dr. Lashley comment if he will on whether the breaks in a sequence may not perhaps give us clues to some of the relationships. By this I refer to various types of blocking that one encounters, the blocking in the tapping of a motor rhythm, the blocking in the speech pattern of normal individuals and stutterers, the blocking in color naming, and a variety of others. Some of them (for example, in free associations) represent a longer time scale of blocking, but will do essentially the same thing. I have tried in some instances to correlate certain phenomena of the alpha rhythm with these patterns, such phenomena as the blocking of the alpha rhythm, or the out of phase character of the usually synchronized activity of the two cerebral hemispheres. I found, in some instances, very suggestive correlations, but I must confess that the proof that alpha blocking and the out of phaseness in the two hemispheres are related to blocking in behavior has not yet satisfied me.

DR. LASHLEY: I have been rather embarrassed by some of the flattering remarks made today. I think that here we must also consider background effects. Boring has pointed out that no progress is ever made until the time is ripe for that progress, and that the individual who makes the contribution is a very minor matter. If one doesn't, another will very shortly. What I have said today is really scarcely more than a compilation and summary of the thoughts of the people who have

studied the aphasia problem. I have summarized again a series of problems which have confronted the students of aphasia for many years, to which Monakow and many others have contributed, Pick especially, and I have found their views helpful in considering such problems.

I have also been very much impressed with the similarity of the problems with which the behaviorist is confronted, and the problems with which the student of embryology must deal. The problem of form seems to me to be too similar in the two cases to be altogether due to different kinds of mechanisms.

There have been perhaps too many problems and questions raised here for me to attempt to answer them in detail. With regard to Professor Halstead's remark about the removal of my frontal lobes: In fantasy, I have thought perhaps that my most important contribution when I reach retirement age would be to have my frontal lobes removed and see what I could do without them. I have less confidence than Dr. Halstead that it would preclude the production of something of interest. We have little experimental evidence of intellectual defect from uncomplicated removal of the prefrontal lobes.

The conception of cerebral organization that I have sketched here is the result of repeated failures to confirm simpler hypotheses. Attempts to trace the course of conditioned reflex arcs or to discover the location of the traces of specific habits have been repeatedly unsuccessful. They have revealed areas specialized for different functions, but within those areas the parts have proved to be equivalent or equipotential for a great number of functions. Analysis of effective stimuli and of adaptive responses has shown that these are not dependent upon particular neurons but upon the spatial and temporal relations of excitation within shifting fields of nervous activity. Attempts to develop theories of neural integration in terms of chemical gradients or electrical potentials are difficult or impossible to relate to the established facts of axon conduction, however well they may seem to account for the facts of behavior.

I agree thoroughly with Dr. McCulloch that the transmission of excitation by the individual neuron is the basic principle of nervous organization. However, the nervous activity underlying any bit of behavior must involve so many neurons that the action of any one cell can have little influence upon the whole. I have come to feel that we must conceive of nervous activity in terms of the interplay of impulses in a network of millions of active cells.

In perception, in action, and in the preservation of memory traces there are systems or anatomic structures whose parts seem to be equi-

potential. The equipotential systems of which we have more definite knowledge all work by reduplication of elements or parts, of molecular or gross mechanical structure. The problem of how a reduplication of functional units might arise in the nervous system has seemed to me a basic one in neurology. The analogy with wave form and interference patterns is an attempt to meet that problem. In wave interference, patterns are reduplicated in different parts of the field, and I think it likely that nerve impulses, spreading at definite rates through a nerve net, may also produce reduplicated interference patterns. These would make possible the production of structural changes constituting memory traces at numerous points throughout the system. Such a concept is highly speculative, difficult to apply to concrete instances of behavior, but is as far as I have been able to go toward a solution of the problem of equipotentiality.

I mentioned briefly the problem of the dynamic level of nervous activity and the probable role of non-specific facilitation in the production of the shift from internal to overt speech or in determining the availability of memories. There are certainly other variables which affect the level of activity: changes in the chemical environment and the metabolic activity of the neurons. I believe that many of the symptoms following cerebral trauma or disease are due to such widespread chemical changes, resulting perhaps from vascular damage, rather than to actual destruction of nervous tissue. Aside from sensory defects, clinical symptoms more often suggest changes in dynamic level than the loss of specific integrations.

Dr. Köhler has raised the question of the stationary state of the world around us. I have tried to deal with this in terms of the constant space coordinates maintained by the postural system. The conceptual construct of the data obtained by scanning is closely integrated with this space system. I confess that I can form no clear picture of the actual physical mechanism.

Dr. McCulloch has given a beautiful illustration of the spatial determination of rhythmic activity by spread of excitation from a focal point of stimulation. I wish that such a mechanism were applicable to the problems of the syntax of action with which I have been dealing but I see no way in which such a simple mechanism can be used to account for the more complicated behavior. As for the mathematical representation of time as a fourth dimension: This may help to conceptualize motion, but the actual functions of the brain are carried out by a three-dimensional system. How is time or temporal order represented within the three dimensions? Mathematical symbolization of time as a fourth dimension does not suggest a clue.

Functional Differences between the Occipital and Temporal Lobes*

WITH SPECIAL REFERENCE TO THE
INTERRELATIONS OF BEHAVIOR AND
EXTRACEREBRAL MECHANISMS

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I shall first briefly consider certain behavior alterations following bilateral removal of the occipital lobes in subhuman primates, more particularly, the changes observed in rhesus monkeys.

FUNCTIONS OF THE OCCIPITAL LOBES

I shall not describe the techniques I have developed for testing such animals (34-37, 40). Nor shall I bother you with the details of the experimental analysis. I shall simply point out that such animals in which the geniculostriate system has been eliminated have been studied for a long time before and after the operations. In some instances, thirty to forty-five trials per day have been given for more than 2000 days after the lobectomy. In studying the behavior of the bilateral occipital monkey I have been chiefly concerned with analyzing the responses of the dark-adapted animal to luminous stimuli differing in brightness, area, shape, color, and/or distance from the eye as well as the responses to intermittent light stimuli differing in light-dark ratios and flash frequencies per second. The results of this laborious analysis may be briefly summarized by saying that all or practically all differential reactions of the bilateral occipital monkey to visual stimuli can be understood by assuming the effectiveness of differences in the density of luminous flux at the eye or, expressed otherwise, differences in the quantity of light entering the eye (39, 41, 43). The eye of such

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