

A NEURAL THEORY OF ASSOCIATION: CHRONAXIC SWITCHING

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It is the purpose of this paper to attempt the development of a theory of association in terms of the temporal functions of the nervous impulse. The most orthodox theory of association perhaps is that involving some form of resistance to conduction of the nervous impulse at the synapse. It assumes that the neural changes taking place in learning involve breaking down the resistance of the limiting membrane at synaptic junctions. This orthodox theory is supported by some neurologists and many educational psychologists.

But the studies of Lashley (1920-1929) have brought the synaptic resistance theory into question. First of all, the results of his studies on cerebral localization tend to show that the frontal region, for example, is more or less equipotential in its capacity for forming associations rather than exhibiting sharply localized points at which such associations may take place. These results would indicate that changes at only the juxtaposed surfaces of synapses in a given neural segment imply too definite and sharp a localization of this function. In the second place, Professor Lashley has made some definite observation and experimentation, the results of which tend to disprove the orthodox theory. For example, in studying certain phases of the neurology of learning he obtained results which indicate that new conditioned pathways may be established under conditions where the passage of significant neural impulses over the arcs in question are experimentally precluded during the whole course of learning. The experiments deal with both centripetal and centrifugal paths, in each of which it was possible to block the peripheral neurons during training and to observe their functioning later in the performance of the habitual acts.

In the first experiment he effectually blindfolded the left eye of a white rat and trained it to react in avoiding the brighter of two lights in the Yerkes brightness discrimination box. This experiment extended over a period of one month. When discrimination was perfect (no error in 30 trials) the blindfold was transferred to the right eye. When the animal became adapted to the new adjustment its discrimination with the left eye was tested. It showed perfect discrimination with this eye which had not been used during the formation of the habit.

Now it is not sufficient to say that this result may be explained by the fact that the fibers from corresponding points of the retinae reach the same central ganglion cells. The corresponding fibers, according to Lashley, do not anastomose and there is no evidence that they have synapses in common.

Lashley repeated the experiment with an animal after destruction of the visual area of both hemispheres (i. e. the occipital third of the cortex). The blindfold was applied immediately after the brain operation, so that there was no possibility of the formation of new common associations through the simultaneous use of the two eyes. The results of the test with this animal were the same as with the normal one; effective performance of the habit with the eye which had been blindfolded during the training process. These facts seem to exclude the theory of a simple connection of cor-

responding points in the two retinae with common ganglion cells and re-integration through the passage of impulses over this final common path.

More striking data with the same implications were obtained from studies of the precentral gyrus in monkey. The right precentral in a cebus monkey gyrus was destroyed by cauterization. A severe paralysis of the left arm and leg followed. The animal was trained to open a variety of latch boxes with his right hand. During the training there was some recovery from the paralysis of the left arm and hand, but these were used only as a stiff prop to support the body during the manipulations with the right hand and at no time during the training did the animal grasp at the latches with his left hand. The animal was kept without further training until the left hand had so far recovered as to seem again to permit of manipulation of the latches. Its ability to open latch boxes was then tested again. In the meantime it had acquired facility in the use of its left hand and the right was now by preference used as a prop.

When confronted with the problem boxes again he fumbled clumsily at the catches of each during a few trials with his right hand, then attacked the fastenings with his left hand and released them *without random movements* and almost as quickly as he had formerly done with his right hand after protracted training. There was almost perfect transfer of the habit to the hand which had been paralyzed during the training.

Here, then, are two types of habit formation which cannot be explained by any wearing down of resistance at the synapse through the passage of nerve impulses. The behavior involved, according to Lashley, is of a complex character approximating what is termed ideational behavior in man. This evidence may not be entirely conclusive but it is certainly significant. The consistency of the results if not their extent seems to strengthen them. It is highly probable that the function involved is so proudly basal that a large number of cases is not required to establish the validity of the results. It would seem, therefore, that an alternative theory of association should be proposed.

Now if such a theory is proposed what are burdens which must be borne by it? There are many, no doubt, but a rather hasty analysis of the problem reveals four which seem to be more or less important. First, a theory which is to explain neurologically what takes place in association must account for the mass, unspecialized, random-like character of response when the learner is placed in a novel situation. Secondly, it must account for the specialized preciseness which is observed in the response after the problem has been mastered or habit has been established. Thirdly, such a theory must explain the retention over an indefinite period of time of this modification of the response. Fourthly, it must account for the loss or partial loss of this modified form of response due to emotional or traumatic shock as in asphasia and amnesia on the one hand and to the discontinuance of practice of the function on the other.

We should like to offer as an alternate explanation one which is based on the temporal characteristics of neural activity. We may call it a theory of *Chronaxic switching*. *Chronaxie* has been defined as follows: First determine the threshold intensity for excitation of a given nerve and call it the *rheobase*. Then the chronaxie of that nerve will be the minimum time required for a stimulus just double the strength of the rheobase to excite

the nerve. This is an arbitrary definition given by L. Lapicque (1910), who has been the outstanding investigator of this problem.

However, before considering the facts that are known about chronaxie let us make a few preliminary statements. First, we admit the neurone theory, that is, that the nervous system is discontinuous, formed of elements distinct and juxtaposed. Neurones are distinct, the one formed from the other, anatomically. Secondly, every nerve has its own individual chronaxie conditioned by heredity. Not only are nerves anatomically distinct but they are different as to their physico-chemical properties. Therefore, the phenomenon of conductivity will vary from neurone to neurone. Thirdly, every neurone has the possibility of modifying its chronaxie as a result of environmental conditions.

Now, what are some of the known facts concerning chronaxie? The following results have been obtained by various investigators: One set of facts, as was indicated above, shows that each neurone may have its own individual chronaxie, as is likewise true of muscles. Whether this is true of glands it has not yet been determined to our knowledge. As examples of characteristic chronaxie of a given nerve Marcell Lapicque (1913a) in one specimen of *Rana Esculentia* found that the chronaxie of a certain sensory nerve was 15 units and for a certain motor nerve it was 30 units. Kucharski (1927), in studying the role of time in auditory excitation, found that the chronaxie of the auditory mechanism for a stimulus of 100 d. v. was 232 σ . For 250 d. v. it was 137 σ .

Another group of facts indicates that there are various conditions which may modify the chronaxie of a given neural segment. Rizzolo (1927a) found that in the dog the first application of nicotine modifies the excitability of the cerebral cortex so as to decrease the original value of the chronaxie from 25 to 50%. After the second application the chronaxie continues to diminish up to 65%, but sometimes there is an increase of the chronaxie, which may exceed the normal. The third application, on the contrary, is always accomplished by an increase of the chronaxie, which may attain 100%. Again, Rizzolo (1927c) found that heating a member, say the paw of the dog, for three minutes would give a diminution of the initial chronaxie of neural segments involved in making the response of moving the paw. Likewise Rizzolo (1928b) found that changes in luminosity would change the chronaxie involved in winking movements. Other investigators, among whom are Marcell Lapicque (1913, 1923) Bourghinon and Laugier (1923), Fredericq (1927), Lapicque (1928a, 1928b), have indicated that there are other conditions which may modify the chronaxic relationships of nerves, such as the effects of strychnine, curare, chloroform and caffeine, the strength of the stimulus, the influence of nerve centers upon peripheral nerves, the influence of one peripheral nerve upon another, the posture of the member to which a given motor nerve is attached, depth of penetration between the reactions of opposed muscles. The chronaxie of flexor muscles of the fore limbs of an animal is shorter than that of the extensors, just as their flexion movements are shorter than extension movements. This ratio of chronaxie of extensor movements to chronaxie of flexor movements in some mechanisms approximates 2 to 1. In the lower limbs the muscles moving the leg forward have chronaxies shorter than those carrying it back. (However, Lapicque and Lapicque (1928b) maintain that this relation is

due to function of neural centers rather than of peripheral mechanisms since it is modified by conditions of sleep and narcosis). The facial muscles used in the expression of joy have a shorter chronaxie than those representing sorrow. But according to the studies of Lapique and Lapique, this relationship again is probably due to the influence of nerve centers and not to the functioning of peripheral mechanisms or nerves. It is experimentally determined that cold and fatigue lengthen chronaxie while adrenin shortens it.

The work of the Lapiques and others also indicates that a nerve may excite another nerve or a muscle under normal conditions only when there is a state of *homochronaxie* or *isochronism* existing between them. However, due to continual stimulation or stimulation with a high degree of intensity a state of *heterochronaxie* may be reduced to one of homochronaxie, thereby permitting the free propagation of the impulse through a segment heretofore closed to it.

Now, how may chronaxic switching account for association? In this connection let us take up the four questions raised earlier in the paper. In answer to the first, it may be said that the organism makes a gross or massed type of response the first time it responds to a novel situation because there is an avalanche of conduction due to the fact that there are many motor neurones which are isochronous with the incoming sensory fibers as well as the intermediating central fibers. This may be due to either innate or acquired organization.

The second question concerning the specialization of responses, as the given mode of behavior becomes perfected, may be answered by saying that a certain motor segment, which has been hitherto somewhat heterochronous with the sensory segment has now become homochronous with it. This may have resulted from either continual stimulation or high intensity of stimulation, the two conditions which may set a state of isochronism, or both.

The third question raised as to the nature of retention may be answered by saying that when a state of homochronaxie has been established between two segments, this modification of chronaxie may be retained over a period of time. This, however, is pure conjecture since there has been no experimental work done in this connection to our knowledge.

The last question can be accounted for by indicating that, first of all, if a given function is not used for a period of time the forced isochronism set up in the learning process has been lost in part or total. This may be due to a tendency of acquired isochronaxie to revert to a state of heterochronaxie as a result of instability. This assumption, again, is only partially substantiated by experimental and clinical evidence, although there is none to the contrary. In the case of loss of memory due to shock and lesions it is quite possible that a state of homochronaxie has been disturbed.

It is granted in conclusion that the experimental evidence is limited in support of this theory. It is limited not in the sense that much of it is negative, but rather that this is a field of apparently very fruitful research which has been grossly neglected by neurologists and psychologists alike. We believe that if the present trends of investigation could be extended and borne out by studies calculated to secure results bearing directly upon the

problems of association, the theory would stand a crucial test. And if it did survive it would obviate the difficulties of the synaptic resistance theory pointed out by Lashley, since the theory based on chronaxic switching permits the interpretation of association facts in terms of widespread neural functions and does not require, through the influence of the cerebrum, a narrow and specific localization of the mechanism of association as is the case with the synaptic resistance theory.

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