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On the Role of Cerebral Facilitatory Set
in Learning and Memory¹

R. W. Sperry²

National Institute of Neurological
Diseases and Blindness

Consider the brain of the dog recently trained by electric shock reinforcement to lift its left forepaw at the sound of a bell. It is clear that the neural mechanisms of the dog's brain have undergone some sort of alteration as a result of the conditioning process in that the auditory impulses from the bell now set off a specific forelimb response which ordinarily they would not do and did not do before the training.

What kind of cerebral alterations are responsible for deflecting the sensory impulses from the bell toward the particular motor patterns of the conditioned response? Or, what kind of traces have been left in the brain by the training experience and in what type of pattern are the memory traces or engrams implanted? We can use this

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²After January 1, 1954, Hixon Professor of Psychobiology, California Institute of Technology.

latter for a simple statement of the primary problem with which we shall be concerned, namely, "In what kind of pattern are the neural engrams of a conditioned reflex laid down?"

This restriction in scope to a simple example of conditioned reflex learning may mean that much of what follows will not be applicable to other fundamentally different types of learning, if there be such. However, a restricted attack has the advantage of making for concrete illustration and for the avoidance of confusion in a subject already extremely complicated even at its simplest. In any case, we can rest assured that a satisfactory physiological explanation of even the simplest conditioned reflex would greatly illuminate the entire engram problem and perhaps at the same time many other obscurities of cerebral function.

In approaching the above problem, it will be helpful if we put aside our conditioned dog for the time being and turn our attention temporarily to a somewhat different but related experiment in which one of our scientific colleagues, rather than an animal, serves as the experimental subject. Suppose we strap our human subject firmly into an experimental version of the electric chair and place his left hand upon the electrically wired arm of this chair. When our friend is settled in position, let us then warn him that if he does not lift his left hand promptly at the sound of the bell which we plan to ring in a moment, he

will receive in the hand a severely painful electric shock of 50 volts or more.

When we sound the bell a few seconds later, we find, of course, that our subject's hand comes up instantly; in fact just as promptly, if not more promptly, than does the paw of the conditioned dog. For purposes of comparison, let us suppose that we use the same bell to signal our human subject that was used for conditioning the dog, so that the sensory stimulus and the motor response in the two cases are virtually identical. Then, for this voluntary response as for the conditioned response, we can again ask: What is the nature of the alterations left in the brain from prior experience that cause the bell stimulus to evoke this particular motor reaction? (The prior experience in this latter instance, of course, is merely the verbal warning that preceded the bell by a few seconds.)

In the case of our human subject, the new S-R linkage between the bell and left hand movement is hardly to be accounted for in terms of any kind of new structural alterations in the brain pathways. There has been no long training, no repeated pairing of the bell and the shock stimuli, no grooving of the fiber pathways between the specific receptor and effector centers of the cortex. In fact, it is entirely possible that the particular cerebral excitation pattern set off by the

sound of the bell in this case may never have occurred before, even once, in the entire lifetime of our subject.

Under these circumstances we say that our human subject, as a result of the warning, is mentally prepared and anticipates the bell and the shock. Accordingly, he gets himself all ready physiologically, or, he gets himself "all set" to make the proper response at the first sound of the bell. Rather noncommittally we can say that the brain pathways for arm flexion are temporarily open in our subject while those for innumerable other possible reactions that might otherwise be made, are temporarily closed. The prevailing distribution of excitation and inhibition in the neural circuits opens the way for the appropriate sensory stimulus to release instantly that response for which the circuits are set. Extraneous sensory excitation tends to be absorbed without effect and incompatible reactions excluded.

As our human subject sits in his experimental chair tensely awaiting the sound of the bell, it is the central patterning of the dynamic states of facilitation and inhibition in the brain circuits that directs the impulses from the bell toward the specific limb response in question. Thus the novel response effect of the sensory input derives, not from any new pattern of structural pathways but rather, from a new pattern of

background excitation or facilitation in the old pathways. We may refer to such a transient dynamic adjustment of the brain mechanisms as a "cerebral facilitatory set" recognizing that the inhibitory phases of the brain process may be just as important as the facilitatory.

It is worth noting at this point that our human subject, if so forewarned, could just as easily set himself to make the reverse or antagonistic response (i.e. depression of the hand instead of elevation). In this case, the complete sensorineuromotor sequence set off by the bell would discharge just as rapidly into the reverse reaction. Likewise our subject could set himself to respond with his foot, or with the opposite hand, or to shout instantly at the sound of the bell any one of hundreds of different passwords we might give him. He could also respond alternately to repeated sounding of the bell at one minute intervals with first one and then the other of two quite different responses. In each case, the specific and immediate motor effect of the incoming auditory impulse is determined by the particular facilitatory set that dominates or prevails in the brain at the time the sensory excitations enter.

We may note further that the directive facilitatory set may be generalized or specific in its organization on both sensory and motor side. For example, our subject could set himself to respond only to bells of a low pitch and not

to bells of a high pitch. Or, his set might be so nonspecific that any loud noise would set off the reaction; even a sudden tactile stimulus might suffice. Similarly on the motor side, a single response may be rigidly predetermined, or a choice of two responses made possible, or any of a given category. The less predetermined the motor pattern, however, the greater the response latency.

The main point to be emphasized in this digression to the voluntary reaction in ^{the} human subject is the fact that a purely transient, dynamic setting of the brain circuits, in terms of active facilitation and inhibition, is quite capable by itself of causing ~~the~~ ^A bell stimulus to set off a particular limb movement without the need for any new structural connections. It can readily be seen that the same response, or other responses, could be directly coupled in a similar manner to any neutral stimulus (of the type employed in conditioning) simply by an appropriate dynamic adjustment in the cerebral facilitatory set.

We are now ready to return to our trained dog and to the problem of the nature of the neural traces implanted by conditioning. For, in the facts of learning and conditioning there is much to suggest that the changes in the brain of the dog must be largely the same as those depicted above for the human subject. In other words, what it takes only a moment to convey to the brain of

man with the aid of language, may require hours or days to instill into the brain of the dog by the more roundabout method of example and experience.

Eventually as a result of training, the dog will come to anticipate the bell and the shock so that by the time the bell sounds, the dog already will be actively prepared in advance--like the human subject--to make the correct forelimb response. In fact, the thoroughly trained dog probably anticipates the whole bell-shock situation a long time before the bell sounds, perhaps as soon as the scientist makes his daily appearance in the animal room to fetch the dog down the hallway to the conditioning chamber. Certainly by the time it is being strapped into its conditioning harness, the trained dog is well aware of what is about to follow, and his preparatory set is already becoming organized.

One can conclude that by the time the bell sounds, there is present in the brain of the conditioned dog a well-organized facilitatory set. It is this special pattern of central facilitation--absent before training and developed during training--that is directly responsible for deflecting the sensory impulses from the bell, so to speak, into the proper motor channels for the conditioned response. To state it more generally, the new S-R linkage is achieved in conditioning, not by the establishment of new sensorimotor pathways in the brain, but through a

dynamic readjustment in the intermediary patterns of central facilitation.

As yet our knowledge hardly touches the physiology of these central facilitatory sets or the laws of their organization and readjustment during learning. The continuing controversy over mere 'contiguity' versus some kind of 'effect' or 'belongingness' as the critical factor for establishing new associations in learning (6) ~~becomes~~^{is} a problem essentially of the dynamic organization of the facilitatory sets.

Establishment of the above conditioned forelimb response in the dog may involve a perceptual or insightful type of learning in the grasping of the bell-shock relationship, and also a trial-and-error type of learning in the selecting of the proper motor response for avoiding the shock. This latter may also require some degree of insight or perception depending on how the conditioning apparatus is arranged. Wide variations in both these phases of the conditioning process can be found even among simple conditioned reflexes depending on the particular details of the individual conditioning situation. The concept of the intermediary facilitatory set appears to be applicable to both phases of conditioning and to learning in general.

The particular facilitatory set pictured above in the human subject, had a good deal in it of the voluntary and

the rational. Perhaps, for purposes of illustration it might have been better had we proposed to warn our subject while he was under hypnosis, and a week or so in advance of the actual test. In performing the hand-lifting response as a posthypnotic suggestion, our subject could have been quite unaware of the underlying facilitatory set responsible for his reaction. Had we preferred a salivary response for comparison with the more classical type of conditioning, we might have suggested to our subject, again under hypnosis, that he would be extremely hungry at the appointed time and place, and that the sound of the bell would be a signal for him to receive and to eat a sizeable portion of his favorite food. These asides are mentioned merely to point out that the cerebral facilitatory sets in general may range in character from the highly voluntary and rational on the one hand to the highly involuntary and emotional on the other; and also that they exercise control over the autonomic as well as over the skeletal aspects of motor response.

For the sake of brevity we must simply state at this point, without further elaboration, that these cerebral facilitatory sets operate continually in behavior and constitute a prime factor in the control of all brain function. Thinking, perceiving, recognizing, imagining, reasoning, voluntary and reflex

reaction, as well as conditioning, learning and remembering have all been found in the laboratory to be profoundly affected by so called "mental set" (3). It is by means of differential facilitatory sets that the brain is able to function as "many machines in one," setting and resetting itself dozens of times in the course of a day, now for one type of operation, now for another. In summary, a great deal of the plasticity of vertebrate behavior, including that of learning, is to be accounted for--not by new structural associations in the fiber pathways of the brain--but by dynamic reorganization in the patterns of central facilitation.

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But this is not the whole story, for, if we put our conditioned dog into a state of deep anesthesia, or subject it to electroshock or other treatments that seemingly must wipe the brain clean of all traces of purely dynamic organization, and then set the dog aside for a four-week rest interval without any repetition of the conditioned response, we find that in spite of all this, the conditioned reflex has survived. We are forced to infer, therefore, that these dynamic readjustments we have been discussing must get reinforced in the course of time by some more permanent type of neural traces, known as the brain engrams.

In attempting to come to grips with the problem of

the patterning of the static brain engrams, it is essential that one not lose sight of the primary role of the aforementioned dynamic factors. For, even after the electroshock treatment and the four-week rest interval, the conditioned reflex is still dependent upon a preliminary rearousal of the anticipatory set. If the proper pattern of central facilitation has not been established by the time the bell sounds, the conditioned reflex fails to occur.

Once the important primary role of the dynamic facilitatory set is recognized, a number of important inferences can be drawn regarding engram patterning, some of which may be listed as follows:

a. One would not expect, on this basis, that the engrams for a CR will take the form simply of new associations between the receptor and effector centers of the brain. One is prompted to search for an entirely different type of engram pattern, namely, a pattern so designed as to facilitate, at the proper time and place, rearousal of the complex facilitatory set.

b. With much of the burden of the detailed patterning of the CR relegated to the dynamics of cerebral facilitation, the patterning of the engrams correspondingly need be much less extensive and complete than would otherwise be the case. Relatively small changes at critical points here and there in the cortical

tissues might be sufficient to reactivate a given anticipatory set in the proper dynamic background.

c. The engrams on the one hand and the facilitatory sets on the other must be regarded as functions of each other, with the CR's, habits, and memories being overall products of the combined interaction of both factors. In long-term memory and recall, the operation of the two factors becomes mutually interdependent.

d. It follows directly that the problem of engram patterning cannot be adequately handled apart from the problem of the dynamic patterning of the facilitatory sets (the insights, expectancies, attitudes, postures, and the like) with which the engrams are primarily associated.

e. Since these "insights, expectancies and the like" belong among the higher level cerebral functions, they presumably are quite complex in their physiological patterning and may involve the integration of wide-spread parts of the brain. We may expect the patterns of the reinforcing engrams to be correspondingly complex and diffused.

f. The patterning problem becomes immensely more complicated by the probability that the engrams function in large part to support the transitions or bridges between the facilitatory sets as well as the sets per se.

There are definite advantages from the engineering

standpoint in having the permanent alterations of the brain allocated to the higher level intermediary sets, instead of having them affect the sensory-motor relations directly. This makes it possible, to mention just one advantage, for different--even antagonistic--responses to be linked simultaneously to the same stimulus, as may be desirable for different situations. Such a scheme also provides much more readily for the kind of phenomena included under the terms "sensory and motor equivalence." In general, with this kind of an arrangement, the sensory and response mechanisms of the brain do not become tied down or selectively modified for specific habits, but remain free to be used in various ways and in various combinations in all categories of behavior.

The foregoing approach to the problem of conditioning and the inferences regarding engram patterning find strong support in the extensive studies by Lashley (5) and others on the effects of brain extirpation. Consider the difficulty, on the above terms, of trying to ablate even so simple a habit as the conditioned paw movement we have used for illustration. One might eliminate the CR by extirpating enough of the auditory centers of the brain to prevent the stimulus from reaching the anticipatory set. However, with a strongly organized facilitatory set, very little stimulus is needed to trigger off the response. In fact, the response may occur

spontaneously under certain conditions without any outside stimulus. Any small remnant of the primary sensory area that would permit the impulses from the bell to filter through to the central facilitatory set might be enough to set off the CR.

Similarly on the motor side, any undamaged effector mechanisms by which the animal can achieve the desired effect will be sufficient. The ability to quickly switch from one motor pattern to another to accomplish an end (motor equivalence) is already an intrinsic property of the brain well organized long before the establishment of our CR. Once the dog learns that contact with the electrode must be broken immediately after the bell sounds, any means at his disposal will automatically be called into play to accomplish this end. Extensive and widely paralyzing lesions will thus be required in the motor areas to prevent the dog from making the CR in one way or another. In some types of learning situation any residual ability to move at all may be enough to carry out the learned performance.

Finally there is the difficulty of trying to cut out the anticipatory set itself. The constellation of engrams reinforcing the facilitatory set for even the simplest CR may typically be of complex design and rather diffused through the brain, making it highly resistant to local ablation. In addition to the matter

of its complexity and diffusion, the set is supported and reinforced from all sides by a great mass of stimuli, associated not only with the conditioning chamber, but also with the situations leading to it, with the experimenter's person, even with the home cage and with various related events in the diurnal cycle. To eliminate by brain damage the pathways for all these reminders of the conditioning experience would be prohibitive.

The evidence regarding neural organization in general would lead one to expect that any anticipatory set would be sufficiently self-reinforcing and cohesive, especially following consolidation by long training, that its organization would tend to survive a considerable degree of local cortical damage. If we visualize the engrams for a given CR as microscopic changes in the neural circuits, embedded diffusely amongst a host of similar engrams for other habits, it follows that any gross lesion must necessarily affect a whole group of habits and memories, as well as whole categories of dynamic organization. Before all elements of the diffuse engram constellation for a given habit can be removed by brain lesion methods, the dynamic organization on which the habit also depends is likely first to be disrupted. In this case the whole strain of related memories dependent upon the affected dynamic pattern

will also be erased.

Spinal and decorticate conditioning seem not to be readily reconciled with this interpretation of the role of facilitatory set. The phenomena of spinal conditioning, however, may yet be accounted for on a physiological basis other than that underlying true conditioning (4). In the case of decorticate conditioning, it remains possible that the crudeness or absence of the conditioning in a decorticate mammal is correlated with the primitiveness or absence in the decorticate brain of a capacity to organize and to maintain adequate preparatory sets.

A reservation: In the foregoing discussion the existence of a distinct dichotomy is implied between the dynamic activities associated with impulse transmission, measured in terms of milliseconds, and the more lasting effects which the impulses leave behind upon the structures they traverse. The general idea of coupling new S-R or S-S relations by adjustments in facilitatory set is more readily presented by emphasizing such a dichotomy. However, neither this general idea nor the inferences drawn therefrom regarding engram patterning specifically depend on such a marked dichotomy and we may regard this latter as being probably an oversimplification of the true situation.

At present we know almost nothing about the lasting effects of impulse transmission. It is

possible a priori to conceive a whole continuum of possibilities ranging from rapidly fading physiological shifts of excitatory threshold at one extreme to the growth and maintenance of new nerve fiber connections at the other. Very possibly the more permanent engrams are not a direct product of impulse transmission itself, but arise through intermediary effects of the impulse transmission such as enduring central excitatory states, or residual potentiation (2). Since the facilitatory sets as depicted above must frequently span relatively long periods of behavior, they might well be mediated in part at least through some form of prolonged alteration of excitatory threshold instead of by continuous impulse transmission over the involved circuits. Finally, our knowledge of cerebral physiology is still too meager to rule out the possibility that a single new reaction or novel shift in the patterning of brain excitation may leave enduring physiological traces of some unknown sort that continue to influence the subsequent patterning of excitation for long periods, perhaps indefinitely until the traces are wiped out by new, incompatible discharge patterns.

Acknowledgement

In this attempt at a physiological presentation of a phase of current learning theory, I have leaned heavily on the treatment of conditioning and learning in L. E. Cole's recent text, Human Behavior (1).

References

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