Neural basis of the Conditioned Reflex

On the Role of Cerebral Facilatory Set in Learning and Memory[1]

R. W. Sperry[2]

Division of Biology, California Institute of Technology

National Institute of Neurological Diseases and Blindness

[Let us] Consider the brain of the dog recently [conditioned] 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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[2]After 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, "<u>In what kind of pattern are the neural engrams of a conditioned reflex laid down?</u>"

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 rises ~~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 this 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

~~dynamic readjustment in the intermediary patterns of central facilitation.~~

As yet our knowledge hardly touches the physiology of these central facilatory 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) is ~~becomes~~ a problem essentially of the dynamic organization of the facilatory 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 facilatory set appears to be applicable to both phases of conditioning and to learning in general.

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

Spence — Hebb

Learning theories differ on intervening variable (I), + necessary cond. = II

I { a) perception or SS (sign significate) theories
vs
b) S-R (stimulus-response)

a) law of effect — Thorndike, Hull,
b) contiguity — independent of reinforcement (Tolman, Lewin, Guthrie, Rexroad)
c) 2-factor — 2 diff. learning processes a & b
(Thorndike, Skinner, Kogan, Maier & Schneirla, Stephens, Nuttle, Mowrer,)

a) Percept'l — Kohler, Koffka, Lewin, Tolman, Adams, Zener
b) modif'n of S-R tendencies — Gates, Guthrie, Thorndike (?) Hull?

"retroactive strengthening of a R" [in our view there's nothing retroactive about the strengthening — of the antic. expectancy set]

[The R's hv effect, good or bad, only in terms of the prevailing motivation, drive, set, need,]

Hull attempted to apply law of effect to classical condit'g.
reward, escape, & avoidance = common situat.

learned R = instrumental in achieving goal.

"relatively simple & highly controlled nature of the CR makes it, Hull believes, the ideal place to look for fundamental mechanisms and principles underly'g b'hr modification."

Skinner & others distinguish carefully classical & instrumental
instrumental R's = largely skeletal vs ~ = autonomic
contiguity learning vs effect learning Schlosberg 1937
Mowrer 1st that all learning = law of effect, but now thinks condit'g of autonomic R's = by contiguity
emotional conditioning vs problem solving learning
[maybe expectancy = the common denominator underlying both]

Spence – Habit cont – 2 –

Resolve contiguity vs effect issue by showing that in both have the expectancy that is really learned & then act accordingly, automatically

Expect shock after bell

" " if don't lift paw, paw lifting to avoid shock

The effect is always relative to the problem, the need, the goal, the answer sought. Maybe if expect a given R to achieve goal, will use it — but have to expect it, to be aware of the beneficial character or it isn't learned.

Probably the beneficial R is not learned unless the beneficial effect registers in awareness? so expect it it to work again?

an expectation can be reinforced as well as bodily needs, aims, problems, etc.

Effect in terms of relief from drive

None of these boys – Hull, Spence, Skinner, etc. speculate on the nature of the physiological mechanisms.

" and in the human subjects it is not entirely clear whether the responses occur as a result of complex voluntary sets established in the subject"

Spence refers to intermittent reinforcement as not supportg law of effect. ~~as law of~~

So, even in a simple motor conditg, shock to paw & findg correct paw movt, it is not the beneficial effect per se that is important, but rather the expectation that it will work. Three expectancy's, dynam. cereb. sets control everything.

Extinction may go faster w. massed trials whereas conditioning does better with spaced trials, so Spence thinks they're not fundamentally the same.

"Just as Tolman does not conceive of conditioning as the strengthening of a response but as the acquiring of a cognitive structure concerning the sequence of psychological events, so he does not conceive of extinction as the weakening of a R, a new diff't cognition develops when reinforcement stops & reinforces another R."

Extinction = a reversal of a previously learned expectation & thus differs from positive conditioning. Can see how the two might differ & massed trials be more effective in extinction

Discovery by insight vs trial-&-error
Spence vs insight [= a good supporting factor]
"Response tendencies" or "hypotheses"
The S-S or ppn theorists (Woodworth, Tolman, Leeper, etc.)

Gestalt psychology believes learning is merely a part of the larger prob. of pperceptual organizatn. but they fail to relate pres ppn to past & memory

Tolman's theory = free of physiological expln.

Hull refers to receptor-effector connections being strengthened by reinforcement. Thorndike thinks of strengthening S-R bonds by changing synaptic conductn.

So far as the expt'l evidence is concerned there is little data bearing on the question whether the functional tie-up is between sensory-motor events or between successive sensory events will also be erased.

Spinal and decorticate conditioning seem not to be readily reconciled with this interpretation of the role of facilatory 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.

omit

<u>A reservation</u>: 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 facilatory 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 over-simplification 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 facilatory 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

1. Cole, L. E. Human Behavior, 1953, World Book Co., New York.

2. Eccles, J. C. and McIntyre, A. K., 1951, Plasticity of mammalian monosynaptic reflexes. Nature, 167: 466-468.

3. Gibson, J. J. A critical review of the concept of set in contemporary experimental psychology. Psych. Bull., 1941, 38:781-817.

4. Kellogg, W. N. Is "spinal conditioning" conditioning? J. exp. Psychol., 1947, 37:264-265.

5. Lashley, K. S. In search of the engram. Symp. Soc. Exp. Biol., 1950, 4:454-482.

6. Spence, K. W. Theoretical interpretations of learning. In S. S. Stevens (Ed.) Handbook of Experimental Psychology. New York: Wiley, 1951, pp. 690-729.