# Learning and the Associative Pathways of the Human Cerebral Cortex[1]

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THE NATURE OF THE CHANGE that occurs in the brain when the individual learns is recognized today as one of the most significant problems of physiological psychology. Many theories, some with limited, but most with no, experimental foundation, have been proposed to account for this change. The critical physiological aftereffects of learning in mammals have been assumed in all such theories to occur in the cortex of the cerebral hemispheres, inasmuch as this part of the brain appears to be the most complex of all nerve structures and most affected by evolutionary development.

Accounts of numerous experiments have been published that purport to prove the very old idea that the cerebral cortex is the primary part of the nervous system concerned in learning (*1*). These experiments have involved surgical destruction of massive areas of the cortex and the observation that such ablations reduce the ability of animals to learn and to retain what has been learned. It is now recognized that these studies contained a weakness or fault in design, which precludes concrete conclusions from them concerning the physiology of learning functions. From results of the experiments it is impossible to tell whether the observed deficiencies in learning were the result of some integrative or learning disturbance itself or the outcome of motor and sensory defects that invariably appear when the visual, somesthetic, motor, and frontal areas of the brain are removed.

A new experimental approach has been made in recent years to this problem of the controlled study of learning and the cerebral cortex. This work has involved the study of the associative connections between different areas of the cortex. Through proper surgical operations and tests of learning it has been possible to investigate the role of the cortex in learning functions without producing in the animal subjects motor and sensory defects that complicate the observations of learning and retention.

Wing and the writer (*2*) performed a first study of this sort, whereby it was shown that generalization and second-order derivation of conditioned visual reactions in dogs with respect to auditory stimuli do not depend upon associative connections between the visual and auditory areas of the cortex. Lashley (*3*) has performed a somewhat more general experiment along the same lines, in which it was proved that extensive destruction of the associative neurones within and between areas of the rat's cortex has no observable effect upon learning and retention of the maze habit.

Through an opportunity afforded by a special project primarily oriented toward the neurosurgical control of epilepsy (*4*), it has been possible to extend, in a limited way, this controlled study of the role of the associative mechanism of the cortex in learning. An investigation was made of the effects of cutting most of the associative connections between the two cerebral cortices upon learning and transfer of learned responses from one side of the body to the other.

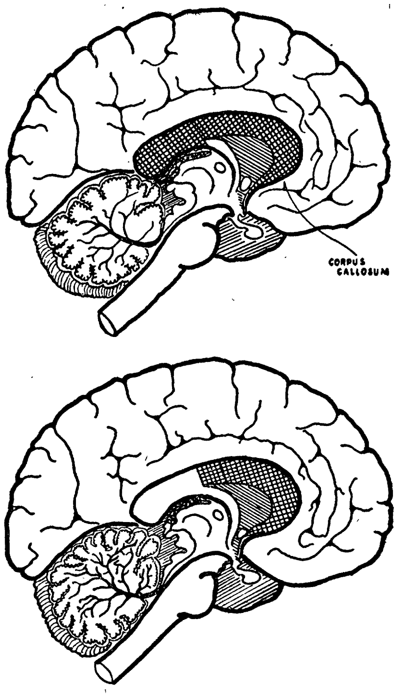

FIG. 1. The extent to which the fibers of the corpus callosum were cut in cases with complete section (top) and in the case with the least extensive lesion (bottom).

The neurosurgical operation involved consisted of cutting the pathways of the corpus callosum (Fig. 1) completely or in part. This body, the most extensive single band of fibers in the nervous system, contains all the interconnecting neurones between the two cerebral cortices, except for the very limited interconnections of a small tract called the anterior commissure.

In all, nine patients were selected for study. The

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[1] The cooperation of William P. Van Wagenen and Andrew Akelaitis, whose help made these studies possible, has been greatly appreciated.

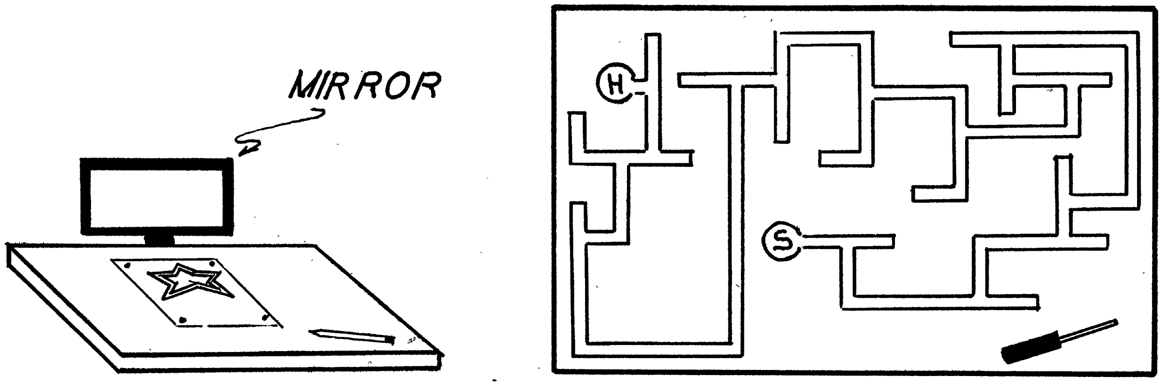

FIG. 2. Diagrams of the general nature of the mirror-drawing and the maze tasks. When in operation, a screen prevents a direct view of the star in the mirror-drawing situation. Time of performance is used as a measure of reaction. In the maze task the learning and transfer of learning are measured in terms of the number of trials required to trace the maze without error.

neurosurgeon's[2] notes, taken at the time of operation, described six of these patients as having complete section of the corpus callosum. In two patients all the commissure was cut except for the posterior tip. One patient had two thirds of the whole tract sectioned. The effect of the most extensive section is to isolate neurally to a more or less complete degree the cortex or covering of each of the two cerebral hemispheres.

Two types of learned performances were studied—mirror-drawing learning and nonvisual stylus maze learning (Fig. 2). Subjects learned these two tasks with the preferred hand and were thereafter tested to determine the degree to which this learning improved performance by the subordinate hand. For example, before operation subjects learned to trace the maze with the preferred hand while blindfolded, and the number of trials required to learn the habit without error was recorded. The subjects were then tested to determine how many trials were required to relearn to trace the same maze with the nonpreferred hand without error. After the neurosurgical operations, the same subjects were required to learn, using the preferred hand, a maze of a level of difficulty equal to the one learned before operation but with different blind alleys. Again they were tested for the number of trials to relearn the maze with the subordinate hand. The effect of the operation upon both learning of the maze, as well as upon the degree to which the learning by the preferred hand was transferred to the nonpreferred hand, could thus be determined. By alternating the order of mazes used before and after operation among different subjects, secondary effects of maze difficulty were controlled.

Because the learning of the mirror-drawing performance involves learning of new general perceptual relations, rather than specific responses of turning a particular direction, as in the maze habit, postoperative observations only were made with this task. In this case the time required by the subject to trace the star after a set number of trials was measured. The transfer score in this task was obtained by determining the difference in time required to trace the star with the nonpreferred hand before and after training in tracing the star with the preferred hand.

Results showed that there was no discernible effect of the operations upon the mirror-drawing learning and mirror-drawing transfer. After operation, the mean performance time of the patients in this task, during both learning and transfer, was almost identical with that of a group of twenty-three control subjects.

The experiments on maze-learning and maze-transfer permitted comparison of preoperative and postoperative performance. In one set of observations the comparison was made between paired scores on the same five subjects before and after operation. Additional observations made possible comparison of results on seven epileptic subjects trained and tested preoperatively, and on nine subjects trained and tested postoperatively.

Table 1 summarizes the results of the first set of observations. It will be noted that no significant differences in preoperative and postoperative scores were found for the paired scores. The difference in transfer trials is significant at the 10 per cent level.

TABLE 1

DIFFERENCES IN PAIRED PREOPERATIVE AND POSTOPERATIVE LEARNING AND BILATERAL TRANSFER SCORES*

| Score | $M_1$ (Preoperative) $N=5$ | $M_2$ (Postoperative) $N=5$ | $\sigma_1$ (Preoperative) | $\sigma_2$ (Postoperative) | $t$ |
|---|---|---|---|---|---|
| Learning trials | 42.0 | 66.0 | 22.1 | 34.9 | 1.14 |
| Transfer trials | 7.4 | 26.4 | 4.8 | 12.7 | 2.59 |
| Percentage transfer | 82.2 | 52.2 | 10.2 | 33.8 | 1.54 |

* Learning trials refer to the number of trials required to learn the maze with the preferred hand. Transfer trials mean the number required to relearn the maze without error with the nonpreferred hand. The percentage transfer score is the transfer-trial score weighted in terms of the learning-trial score.

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[2] William P. Van Wagenen.

In keeping with accepted statistical criteria, this difference is judged to represent no significance at all.

Similar comparisons made between the unpaired preoperative and postoperative scores based on nine operated cases and seven unoperated epileptic subjects give difference results. It should be noted that the five subjects on whom paired preoperative and postoperative scores were obtained were also common to the two groups in these observations. These data are given in Table 2. With these unpaired scores, significant differences are found for transfer trials. When these transfer trials are weighted relative to the number of trials required to learn (percentage transfer score), this weighted transfer score is also found to change significantly as a result of the operation.

TABLE 2

DIFFERENCES BETWEEN PREOPERATIVE AND POSTOPERATIVE LEARNING AND BILATERAL TRANSFER SCORES IN THE MAZE

| Score | Mean preoperative $N=7$ | Mean postoperative $N=9$ | $\sigma$ preoperative | $\sigma$ postoperative | $t$ |
|---|---|---|---|---|---|
| Learning trials | 39.9 | 69.4 | 15.7 | 33.2 | 2.00 |
| Transfer trials | 7.0 | 25.3 | 4.1 | 11.6 | 3.74* |
| Percentage transfer | 82.1 | 55.8 | 8.8 | 10.5 | 2.14† |

* Significant at the 1% level.
† Significant at 5% level.

Over-all results of the experiment seem to show that there may be some, but a limited and inconsistent, relation between the neural activities of the intercortical association pathways and the bilateral transfer of learned response that has been assumed to depend upon crossed connections between the two cerebral cortices. In all observations, except those concerned with the unpaired subjects in the maze study, the hypothesis that the differences found may arise from chance cannot be rejected. The functional dependence of bilateral transfer upon intercortical connections is possibly greater for the transfer of the maze habit than for mirror-drawing performance, inasmuch as some significant changes were noted for the maze transfer as a result of the cutting of the fibers of the corpus callosum. This difference in the effects of the operation upon transfer of the two performances may possibly be accounted for in part by the fact that the primary projection areas of the somesthetic system, the critical sensory mechanism for the maze performance, receive mainly nerve pathways from the contralateral side of the body, whereas the visual system, used primarily in the mirror-drawing performance, is equally represented in the two cerebral cortices.

The inconsistent data obtained on the maze habit may be clarified somewhat by observations taken on the subjects' performance after operation. None of the subjects had lost his memory for general orientation in the maze. The errors made by the operated subjects, among those few who showed an increase in errors postoperatively, consisted of an inability to eliminate finally and consistently entrance in one or two blind alleys. Any postoperative increase in trial scores required to reach the criterion of learning in these subjects is best described as an inconsistent performance at or near the level of perfect running of the maze. All operated subjects were able to produce more or less accurately a pencil diagram of the pattern of correct paths of the maze upon completion of the experiment.

The present experiment represents one of the very few attempts that have been made to investigate by controlled experiment the factors of neurone conduction in the human brain in the development and maintenance of learned habits. The results may be interpreted in several ways, especially if one seeks to support unfounded speculative ideas about the neural trace in learning. For example, it may be proposed that, because of the multiplicity of sensory projection in different areas of the cortex, a variety of specific synaptic channels is provided in the brain, and that the corpus callosum is not essential for any of the crossed relations between the two sides of the body in learning and bilateral transfer of learned habits. Inasmuch as the experiment lacked rigid anatomical controls, it may also be asserted that some commissure fibers, left intact, could maintain the crossed functional relations between the two sides of the body.

If a priori considerations of the present experimental results are set aside, possibly significant conclusions may be derived from this study and from similar work already reported on infrahuman animals.

In one sense, the results are inconsistent in meaning. It has been found that section of the corpus callosum produces no discernible effect upon mirror-drawing transfer. In the case of two different sets of observations on the maze habit, however, the data are consistent with alternative hypotheses that some change and no change occurred in bilateral transfer as a result of the operation. Generally, the results would seem to be interpreted most correctly at this time, especially if the nature of the actual behavior of operated subjects in performing in the maze is considered, by the statement that extensive destruction of most of, if not all, the neural connections between the two cerebral cortices produces either no diminution—or at least an inconsistent diminution—of the ability of human subjects to transfer to the opposite side of the body motor habits learned by use of the preferred side.

If the above general statement of the present results is accepted, and if this finding is considered in relation to data from infrahuman animal studies, in which functions of the intracortical association pathways in learning have been investigated, certain ideas about the rôle of the cortex in learning may be suggested. Taken together, all these studies seem to point to two main conclusions: (1) there is no specific or generalized integrative neural mechanism of the cortex explicitly essential for learning and related functions, which may be rendered seriously inoperative by injury to intracortical and intercortical association pathways; and (2) the neural integrative functions of the cortex in learning are therefore closely bound to the specific reactive and psychophysical mechanisms of the sensory and motor projection areas of the brain and are apparently inseparable from the processes underlying reactive and psychophysical aspects of behavior. These tentative conclusions suggest the necessity of new approaches to both the psychology of learning and the understanding of the physiology of the cortex. The concepts of generalized cortical mechanisms for learning, which act to link or prime, so to speak, synaptic neural chains for integrating different sensory-motor mechanisms in behavior, or which are defined in terms of equipotential masses of cortex functioning (*5*), are to be questioned particularly as a result of the cited experimental data. Taken literally, the available experimental results would seem to stress especially the possibilities that the cortex, in contrast to traditional thinking, is primarily a reaction system and that, physiologically, learning consists of alterations within components of this reaction system, whether involving changes within the neurone or between neurones. If these possibilities are found to be true in fact, the problem of analyzing the nature of learning changes within the brain may turn out to be far more difficult than it is now conceived to be.

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# *Technical Papers*

## Photolabile Pigments in Invertebrates[1]

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The basic mechanism of vertebrate sensitivity to light is the presence of a photolabile pigment that bleaches upon exposure to light and regenerates in the dark. These pigments have long been associated with vertebrate photoreceptor systems and, except for very low concentrations in a few rodless retinas, have been uniformly demonstrated in all vertebrate retinas. The photic responses of invertebrates are closely analogous to those of vertebrates in both behavioral and kinetic aspects (*1*). It is to be expected that a similar photochemical receptor mechanism would be present in the invertebrates as well as in the vertebrates, particularly a light-absorbing pigment which initiates the primary step in the visual process, that of absorbing the incident radiant energy and initiating a physiological response in consequence.

Invertebrates, with few exceptions, have not yielded photolabile pigments. Bliss (*2, 3*) has demonstrated pigments which become photolabile after treatment with formalin, and St. George and Wald (*4*) demonstrated a photolabile pigment in the retina of the squid which bleaches under illumination, releasing the carotenoids that have been associated with the vertebrate visual cycle.

Several additional invertebrate species were examined to determine the occurrence of directly photolabile pigments. The two species reported here are *Nereis* and the starfish *Asterias rubrens.* These were chosen because of their representative position in their respective phyla and their taxonomic position relative to other phyla.

All operations were carried out at 10° C in very dim red light, from which the animals were completely shielded except for a few moments during processing. The animals were kept in complete darkness for 48 hr before extraction. The eye tissue was dissected away as free as possible from the surrounding structures. The dissected tissue was rinsed in sea water and drained on filter paper, and ground for 6–8 hr until a fine uniform paste resulted. The thick paste was then extracted with solvents that are effective for the extraction of visual purple. It was then centrifuged at high speed and stored at low temperature. The solutions were measured within a few hours of the completion of the extraction. At no time, until the measurements were made, did the temperature of the animals or solutions exceed 10° C.

The two species used yielded a pigment photosensitive to digitonin solutions and none to purified bile salt preparations. The photosensitivity was determined by measurement of the absorption spectrum of the solution before exposure to light, exposing the solution for short periods to the light of a 100-w lamp filtered through a 3-in. water layer, and again determining the absorption spectrum. The difference between the unexposed and exposed solutions represents the pigment that disappeared during illumination.

In Fig. 1 is plotted the absorption spectrum of the digitonin extract of the *Nereis* extract. The absorption decreases regularly from the blue to the red end of the spectrum. The difference between the unilluminated

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