Lateral cerebral peduncle lesions: Amnestic effects on a visual habit in the rat*

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Discrete bilateral electrolytic lesions destroying the lateral half of the cerebral peduncle and the overlying lateral nucleus of the substantia nigra (which disconnect a pathway from the occipital cortex to the brainstem reticular formation) in the rat produced profound losses in retention of a horizontal-vertical discrimination habit. Similarly placed lesions had a significantly smaller amnestic effect on a nonvisual (kinesthetic) discrimination habit. These results, in conjunction with others, suggest that a direct occipitoreticular pathway may be involved in the performance of visual discrimination habits, possibly serving in visuomotor integration, attention to visual cues, and/or formation of visual engrams.

It has repeatedly been found in the rat that bilateral removal of the visual cortical areas abolish retention of brightness as well as pattern discrimination habits, whereas bilateral destruction of the more anterior portions of the cerebrum (including the motor cortex) has little or no effect (Horel, Bettinger, Royce, & Meyer, 1966; Lashley, 1929, 1931; Thompson, 1969). These results, coupled with others (Myers, Sperry, & McCurdy, 1962), strongly suggest that optic impulses, once they reach the striate cortex (and/or adjacent visual "association" cortex) are channeled either directly or indirectly to some portion of the brainstem motor system responsible for the appearance of discriminative responses to visual cues.

In the current study, the hypothesis (see Thompson, 1965) that occipitoreticular pathways provide an important functional link between the neocortical visual areas and the brainstem motor areas is examined. Provisional support for this hypothesis comes from three different sources: (1) stimulation or destruction of different regions of the brainstem reticular formation has profound influences on motor performance (Magoun, 1963); (2) lesions damaging either the nucleus cuneiformis of the mesencephalic reticular formation (Thompson, 1965) or the nucleus reticularis pontis oralis (Thompson & Henderson, 1971) produce significant losses in retention of a visual pattern discrimination habit; and (3) one contingent of occipitofugal fibers takes a descending course through the lateral half of the cerebral peduncle and, at approximately the level of the substantia nigra, leaves the peduncle at right angles to terminate in the nucleus cuneiformis and the nucleus reticularis pontis oralis (Valverde, 1962). Further

support for this hypothesis would be realized if discrete lesions destroying the lateral half of the cerebral peduncle at nigral levels were found to seriously impair retention of a visual pattern discrimination habit.

METHOD

Adult male albino rats of the Wistar strain were trained to approach a horizontal black and white striped card (positive) and to avoid an adjacent vertical black and white striped card (negative) in a Thompson-Bryant (1955) discrimination apparatus. Under the motive of escape from footshock, a response to the unlocked positive card admitted S to the goalbox, whereas a response to the locked negative card was automatically punished by mild shock to the feet. The positive card was switched from the left to the right window in a strict double-alternation sequence. Eight trials were given daily with an intertrial interval of 60 sec. The criterion of learning consisted of no more than one error in 2 successive days. Following learning, the majority of Ss sustained one-stage bilateral electrolytic lesions in the vicinity of the lateral half of the cerebral peduncle at nigral levels (Group LCP), four received more dorsally placed lesions damaging the region of the medial geniculate nuclei (these Ss served as the operated control group—Group OC), and seven Ss constituted the normal control group (Group NC). After a recovery (or rest) period of 7 to 14 days, the Ss were given a retention test which consisted of relearning the visual pattern problem. Retention was measured in percentage error savings scores.

Additional rats were used to determine the effects of lateral peduncular lesions on retention of a nonvisual discrimination habit. They were initially subjected to enucleation of the eyes under deep chloral hydrate anesthesia. After a 2-day recovery period, they were trained on an incline

box (kinesthetic) problem under the motive of escape from footshock to choose the arm that was inclined upward and avoid the arm that was inclined downward. Eight trials were given daily with an intertrial interval of 60 sec. Specific details of the apparatus and training procedures may be found elsewhere (Thompson, Lukaszewska, Schweigerdt, & McNew, 1967). Following learning (at least 15 correct responses within 2 successive days), the majority of Ss sustained bilateral electrolytic lesions in the vicinity of the lateral half of the cerebral peduncle at nigral levels and four served as the normal control group. The retention test was given 7 to 14 days later and consisted of relearning the kinesthetic habit.

Upon completion of the retention test, each brain-damaged S was anesthetized, its vascular system perfused with 10% Formalin, and the brain removed and stored in 10% Formalin for 2 days. The brain was then blocked, frozen, and sectioned frontally at 90 microns. Every third section through the lesion was photographed at 14X with a Leitz enlarger. These photographs of unstained sections yield differentiation of the brain field similar to that obtained with a fiber stain (see Thompson, 1969) and permit ready identification of the three major zones of the lesion—the vacuolated area, the narrow rim of severely coagulated tissue, and the surrounding gliosis.

Of the 39 Ss in this study receiving lesions in the lateral peduncular area, 29 were discarded because their lesions encroached upon the optic tract or lateral geniculate bodies, produced necrosis of the hippocampus due to vascular damage, or failed to destroy bilaterally at least the lateral one-third of the cerebral peduncle at nigral levels. The remaining 10 Ss sustained lateral peduncular lesions which, in most cases, extended dorsally, destroying the entire lateral nucleus of the substantia nigra and partially damaging the medial geniculate nucleus. Thus, the experimental groups are most aptly described as having lesions to the lateral pedunculo-nigral area.

RESULTS

Despite the moderate size of the lesions [see Fig. 1(A), (B), and (C)], the majority of Ss suffering lateral pedunculo-nigral lesions showed no obvious evidence of brain damage by the end of the second postoperative day, nor did they exhibit any belated symptomatology. Eating and drinking habits were unimpaired, and there were no signs of motor dysfunction. The only notable behavioral change involved a heightening of startle reflexes to auditory and tactile

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Fig. 1. Photographs of unstained sections showing lesions of the lateral pedunculo-nigral area in two rats (A and B) tested on the visual habit (savings scores were 10% and -82%) and one rat (C) tested on the kinesthetic habit (savings score = 60%) and a lesion of the medial geniculate nucleus (D) in one rat tested on the visual habit (savings score = 67%).

stimulation. The Ss sustaining damage to the medial geniculate nucleus and adjacent midbrain tegmentum (Group OC) recovered rapidly from surgery and appeared "normal" by the second postoperative day.

With respect to the visual habit, the seven Ss of Group NC earned error savings scores ranging from 83% to 100% (mean = 94.7%). Three of the four Ss of Group OC earned savings scores in excess of 82%, but the remaining S achieved a savings score of 67% (mean = 86.3%). In contrast, the five Ss of Group LCP earned savings scores of -200%, -82%, 7%, 9%, and 10%. The Mann-Whitney test disclosed that Group LCP was inferior to Groups NC and OC in retention of the pattern problem ($p < .01$). No significant difference was found between the latter two groups.

Concerning the kinesthetic habit, the four normal control Ss earned perfect savings scores (100%). The five Ss with lateral pedunculo-nigral lesions earned savings scores of 40%, 57%, 60%, 76%, and 85% (mean = 63.5%). Statistically, the Ss with pedunculo-nigral lesions were significantly inferior to the control group in retention scores ($p < .01$).

Of particular interest was the finding that lateral pedunculo-nigral damage produced greater amnesic effects on the visual discrimination habit than on the kinesthetic discrimination habit—the difference

between the means was significant beyond the .01 level. It is important to point out that this comparison is reasonably valid to the extent that (1) the kinesthetic habit was virtually of equal difficulty to the horizontal-vertical habit (the former was learned with an average of 18.1 errors and the latter with an average of 18.3 errors); (2) no significant difference in mean savings scores occurred between the kinesthetic normal control group and the visual normal control group; and (3) the lateral pedunculo-nigral lesions received by the kinesthetic Ss were comparable in both locus and size to those received by the visual Ss.

DISCUSSION

The dramatic amnesic effect observed on the pattern habit is quite remarkable when it is considered that the rats with lateral pedunculo-nigral lesions not only appeared normal by the second postoperative day, but were excellent runners in the apparatus during the entire retention test. Since these lesions produced considerably larger deficits on the visual habit than on the kinesthetic habit (there was no overlap between the two groups), explanations of the visual discrimination impairment cannot readily be ascribed to motivational, emotional, motorial, or intellectual disorders. As mentioned earlier, these lesions did not encroach upon the classical retino-geniculo-

striate system, nor did they damage the ventral lateral geniculate nuclei or any other area of the brainstem previously found to be critical for normal retention of visual discrimination habits (see Thompson, 1969). In all cases, however, the lateral pedunculo-nigral lesions extended into the area of the lateral terminal nucleus of the accessory optic system. This damage does not appear to contribute to the amnesic effects observed on the visual habit, since the Ss of Group OC suffered substantially larger lesions of this area (Fig. 1D) and yet performed as well as the normal control group. Although other possible explanations cannot be totally dismissed, we prefer to interpret the visual deficits as a result of disconnection of direct occipitoreticular fibers which pass through the lateral pedunculo-nigral area. Further support for this interpretation is found in the succeeding paper (Howze & Thompson, 1972).

The finding that the kinesthetic habit was less susceptible to interference by lateral pedunculo-nigral lesions than the visual habit was not surprising. Since previous work has shown that the kinesthetic habit is more dependent upon the sensory-motor cortex than upon the occipital cortex (Lashley, 1929; Thompson, Malin, & Hawkins, 1961) and since the sensory-motor cortex sends its fibers through the more medial portions of the cerebral peduncle and nigra en route to the reticular formation (Valverde, 1962), it might be expected that damage to the lateral pedunculo-nigral area would have considerably less effect on retention of the kinesthetic discrimination habit.

Finally, the overall results of these experiments support the notion advanced at the outset of this paper that an occipitoreticular pathway is involved in visual discrimination performance in the albino rat. The functional significance of this pathway, however, remains to be explicated. Possibilities include visuo-motor integration, attention to visual cues, and the formation of visual engrams.

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