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Superior Colliculus Lesions and Environmental Experience: Nonvisual Effects on Problem Solving and Locomotor Activity[1]

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WELDON, D. A. AND C. J. SMITH. *Superior colliculus lesions and environmental experience: Nonvisual effects on problem solving and locomotor activity.* PHYSIOL. BEHAV. **23**(1) 159–165, 1979.—Bilateral lesions of the superior colliculus were produced in rats reared in either a restricted or complex environment. Problem solving ability in a Hebb-Williams closed field and activity in an open field were subsequently observed in conditions of either bright or dim illumination. Animals with superior colliculus lesions were deficient in problem solving ability and were hyperactive in the open field. Complex environment exposure during development increased problem solving ability and initial ambulation scores in all groups. Extent of pretectal damage and behavioral measures were significantly related for animals reared in the complex, but not in the restricted environment. There were no interactions with illumination level, suggesting that the deficits resulting from collicular lesions are not dependent upon the availability of visual cues.

Visual system Superior colliculus Environmental enrichment Problem solving Locomotor activity
Open-field test Closed-field test Developmental psychobiology

CURRENT theory has pointed to the existence of 2 visual systems, one (the geniculo-striate system) mediating discriminative functions, and another (the superior collicular system) mediating visual attentional functions [42]. Superior colliculus lesions produce deficits in attention on tasks requiring visually guided behavior in rodents, carnivores and primates [46]. Schneider [42] demonstrated that hamsters with bilateral collicular lesions committed more alley entrance errors in a T-maze but were not deficient in performing visual discriminations, and therefore suggested that the colliculus is involved in orientation. In similar studies, more alley entrance errors have been observed for colliculectomized cats [57], although not for rats [15]. Rats with collicular lesions are not deficient in orientation per se [23], but are less responsive to the introduction of novel stimuli [21-23], lending support to the attentional hypothesis of colliculus function. These attentional deficits are probably responsible for the impairment of the rat's problem solving, as measured by closed-field performance, and in jumping from a platform to the correct stimulus box [2,44].

Although the superior colliculus has been discussed in terms of its visual function [47], there is an accumulating literature on the multimodal nature of that area with studies indicating a convergence of visual, auditory and somesthetic input and processing there [11, 12, 15, 21-23, 28, 29, 30, 34, 48, 49]. It is possible that the maze performance deficits following colliculus lesions are due to nonvisual effects of the manipulations. On the other hand, animals with colliculus lesions might be impaired in maze performance because they do not use visual cues as well as controls. The present experiment attempted to address these possibilities by testing animals with colliculus lesions in a maze task when visual cues were either readily available (i.e., in bright illumination) or obscured (i.e., in very dim illumination). If the effects of superior colliculus lesions are dependent upon visual information, an illumination × lesion interaction was expected.

Literature on recovery of function has shown that the effects of brain damage can vary as a function of preoperative experience. In particular, animals which have been

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TABLE 1
NUMBER OF ANIMALS PER GROUP, TESTED IN BRIGHT AND DIM ILLUMINATION

Rearing Environment	Testing Condition	Control	Superior Colliculus
Restricted	Bright	2,3,3	1,3,5
	Dim	2,3,3	3,1,6
Complex	Bright	3,2,2	2,3,6
	Dim	3,2,3	5,2,5

Note: The numbers separated by commas refer to the number of animals in replications 1, 2 and 3, respectively.

reared in a complex environment are less affected by hippocampal lesions than are animals with more "impoverished" early experience [25]. Interactions between lesions and preoperative experience have also been observed in studies on the septal nuclei and the neocortex [9, 10, 43]. Preoperative experience was included as a variable in the present experiment, therefore, to see if similar interactions would occur when brainstem lesions were made and to observe if the effects of superior colliculus lesions seen previously would generalize across animals with different developmental histories.

Previous experiments have indicated that superior colliculus lesions produce hyperactivity in the open field [17,44] and in other measures [1,27]. To investigate this effect further, the present experiment also included open-field tests at two different times (before and after closed-field testing).

METHOD

Animals

Male, 21–25 day old, hooded rats of the Long Evans strain were obtained from Charles River Breeding Laboratories (MA). Temperature in the vivarium was maintained at 21±1°C and the lighting was on a 12:12 light-dark cycle with lights on at 0600 hr.

Design

The factors of the 2×2×2 design were: lesion (superior colliculus and operated controls), developmental experience (rearing in either a complex or restricted environment), and illumination during testing (bright and dim illumination). Because of the magnitude of this study, the data were collected in three replications, and Table 1 indicates the number of animals contributing to the data from each replication. In replications 1 and 2, animals tested in the "dim" conditions were run in the closed-field test with the illumination of only one 7.5 W red light. To be more certain that the "dim" condition was in fact reducing the availability of visual cues, animals in replication 3 were tested with additional procedures to reduce both extramaze and intramaze cues (see Procedure below). As will be described below, the results did not vary as a function of the procedure employed.

Apparatus

Environments. For the complex environment conditon, a 48×61×122 cm free environment was constructed of a metal frame surrounded by hardware cloth. A metal incline provided access to 2 wooden shelves suspended 34 cm above the main floor. Playthings consisted of tin cans of various sizes, an acrylic plastic swing, a wooden see-saw, and a metal object dangling from the roof via a cable. Cages for animals in the restricted condition were ordinary rat cages of dimensions 20×24×19 cm high.

Closed-field test. The 75×75×10 cm closed field used in a previous study [44] was modified slightly. Briefly, the apparatus was a wooden maze with an acrylic plastic floor and ceiling. The apparatus enabled an animal to run from the start box to the goal box, consume its reward, and return to the start box via an outside alley, thereby eliminating any need for intertrial handling. Two clear plastic doors, one placed at the entrance from the alley to the start box and another placed at the entrance to the goal box from the maze area, opened sideways with a push by the animal and could be pulled closed by the experimenter via attached nylon lines. The barriers were suspended from the maze ceiling in the configuration used by Rabinovitch and Rosvold [40]. The walls and barriers were painted black and the floor was painted gray and outlined with black lines into 36 thirteen-cm squares.

Illumination for both the open- and closed-field tests was provided by either ceiling fluorescent lights (the bright condition) or by a 7.5 W red light suspended 1.12 m above the floor of the closed field and 1.9 m above the floor of the open field (the dim condition). The luminance levels were measured to be 5.95 and 0.05 Lux, respectively, using a Norwood Model C light meter.

A second procedure for the dim condition reduced the availability of visual cues further by using a homogeneous white sheet attached to a wire frame to form a cylinder 1 m high and 1 m in diameter. The cylinder was attached to a pulley system from the ceiling of the experimental room so that it could be lowered around the maze to prevent the use of extramaze room cues. A wooden platform 75×75×0.5 cm was painted black and placed over the gray floor of the maze to reduce the availability of intramaze cues by minimizing the contrast between the barriers and the floor.

Open-field test. The 1×1×0.45 m wooden field had a floor which was painted gray, divided by black lines into 16 equal squares, and covered with tinted acrylic. Illumination for the dim and bright conditions was provided as described above.

Procedure

Upon arrival at the laboratory, all animals were placed in either the complex environment or in individual standard rat cages. Food and water were presented ad lib. For the complex environment condition, the location and nature of the playthings were changed every 2 weeks. The number of animals in the complex environment was 36, 18 and 25 for the three replications.

Open-field test. Open field testing occurred both before and after the Hebb-Williams test. For the before condition, animals were tested 16–17 days after operation. For the observations after the Hebb-Williams test, animals were run 66, 57 and 62 days after operation. Beginning 2 days before experimentation, animals were maintained on 23 hr food deprivation with 1 hr exposure to rat pellets per day. Animals were placed in a corner of the open field and the number of squares entered with at least 2 paws was measured for 2 min on each of 2 successive days. Animals were run between

2000 and 2300 hr, without the experimenter's knowledge of their group designations.

Closed-field test. On the 18–20th day following surgery, training and testing in the Hebb-Williams closed field began according to the procedure used by Rabinovitch and Rosvold [36]. The 12 days of testing (5 trials/day) began after all animals had met a criterion of 5 start box to goal box runs in 30 sec. Reinforcement was 0.07 ml of condensed milk with sucrose. Animals were fed wet mash for 40–50 min after each day's training. Length of pretraining required was 35, 25 and 31 days for the three respective replications. Animals that had not reached criterion by these dates were dropped for nonperformance. The animals were tested between 1900 and 0100 hr, and the experimenter was unaware of group designations. In replications 1 and 2 animals in the dim lighting condition were tested with the illumination provided by the red light bulb. In replication 3 additional efforts were made to reduce the availability of visual cues. In particular, a homogeneous cylinder was lowered around the maze to prevent animals from using extramaze room cues, and a black platform was inserted in the maze to minimize the discriminability of the barriers from the floor (thus reducing intramaze cues).

Surgery

At 90 days of age the animals were anesthetized with 3 ml/kg Equithesin (Jensen-Salsbery Laboratories) and surgery was performed. After the head was shaved and placed in the stereotaxic instrument, 4 holes were drilled in the skull at the appropriate locations and a stainless steel electrode, insulated except for 1 mm at the tip, was lowered to the coordinates A 1.1, L 1.5, V 2.0 and A 0.2, L 1.5, V 1.5. Four 15-mA radiofrequency lesions were made with reference to an anal electrode with a Radionics lesion maker (Model RFG-4). Sulfathiazole powder was applied to the area and the wound was closed with interrupted silk sutures. Control animals received treatment identical to that of the superior colliculus animals, except that the electrode was lowered only 1.5 mm and current was not passed.

Histology

At the conclusion of the experiment the animals were deeply anesthetized and perfused intracardially with 0.9% saline followed by a 10% Formalin-saline solution. After the brains were blocked and embedded in celloidin, 40 μm sections were cut and stained with cresyl violet. Slides were inspected microscopically, and lesions were drawn onto diagrams modified after those in the Pellegrino and Cushman [37] atlas. The five diagrams used were equally distributed throughout the extent of the superior colliculus. Sizes of lesions were then quantified by determining the area of the lesions on the diagrams by superimposing graph paper (0.25 cm squares) and counting the number of squares in the designated areas.

Data Analysis

Data were analyzed with an unweighted means analysis for unequal cell sizes [56]. Lesion-performance correlations were obtained using Pearson correlation coefficients.

RESULTS

Analyses of variance determined that the effects of lesions, environment and illumination conditions did not vary as a function of the procedure used to decrease visual cues. The following data and analyses, therefore, are reported for both procedures combined.

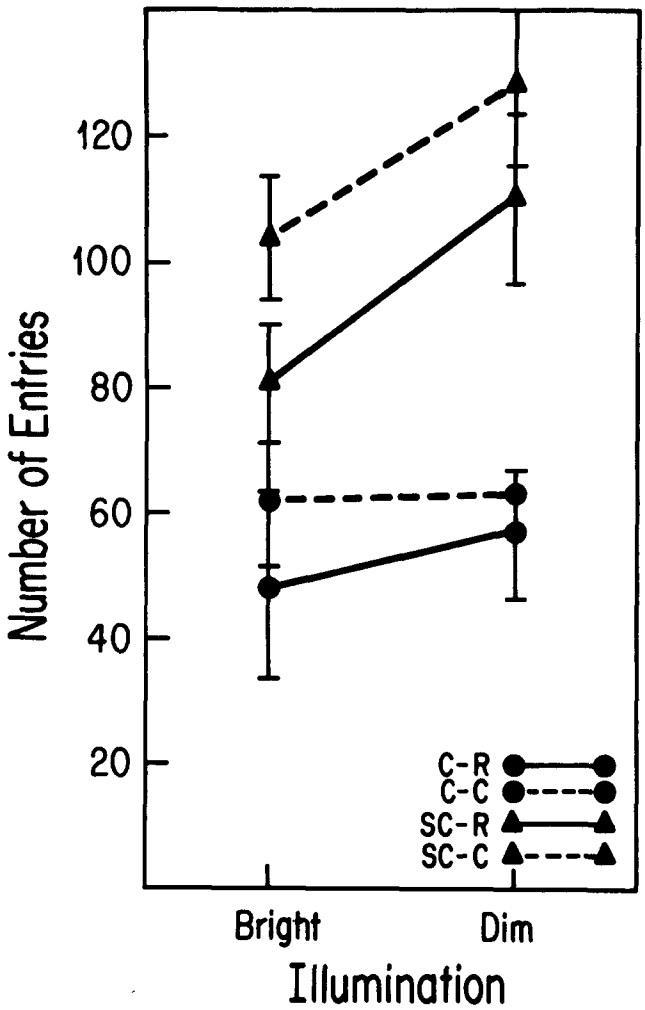

FIG. 1. Mean number of squares entered in the open field prior to closed-field testing under conditions of either bright or dim illumination. Standard error of the mean is indicated for each point. Groups represented are: controls, restricted environment (C-R), controls, complex environment (C-C), superior colliculus, restricted environment (SC-R), and superior colliculus, complex environment (SC-C).

Initial Open-Field Test

Data from open-field tests were summed across minutes and days. The results of the first open field measure are shown in Fig. 1. Animals with SC lesions were more active than controls, $F(1,65)=35.34$, $p<0.001$. Animals reared in the complex environment were significantly more active than those reared in the restricted environment, $F(1,65)=4.92$, $p<0.05$. Animals tested in dim illumination were more active than those tested in bright illumination, but this effect only approached statistical significance, $F(1,65)=3.59$, $p=0.06$.

Closed-Field Test

Figure 2 shows the mean total number of errors for the

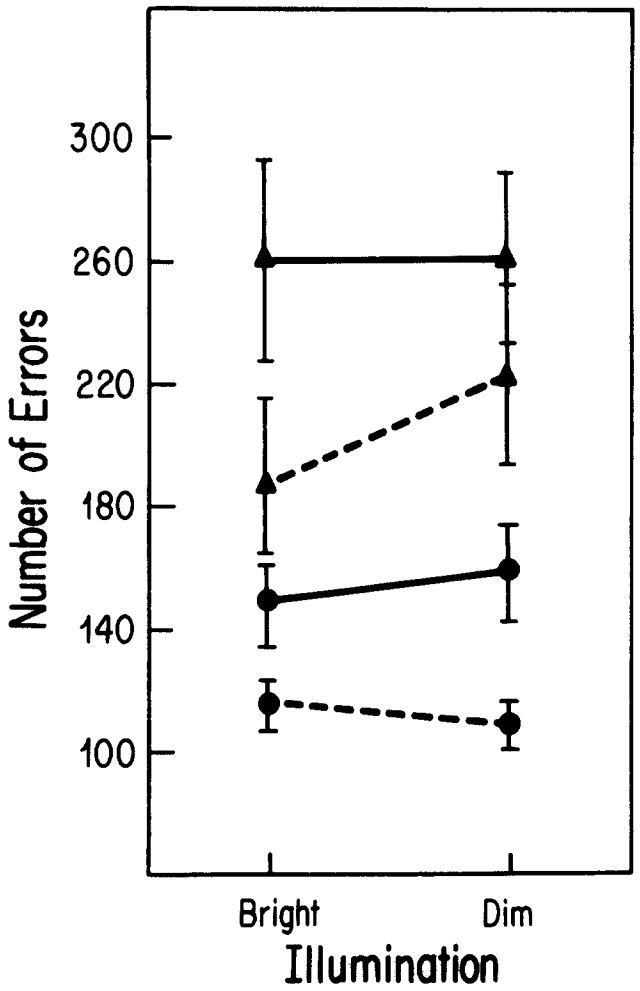

FIG. 2. Mean total number of errors in the Hebb-Williams closed-field test. Key as in Fig. 1.

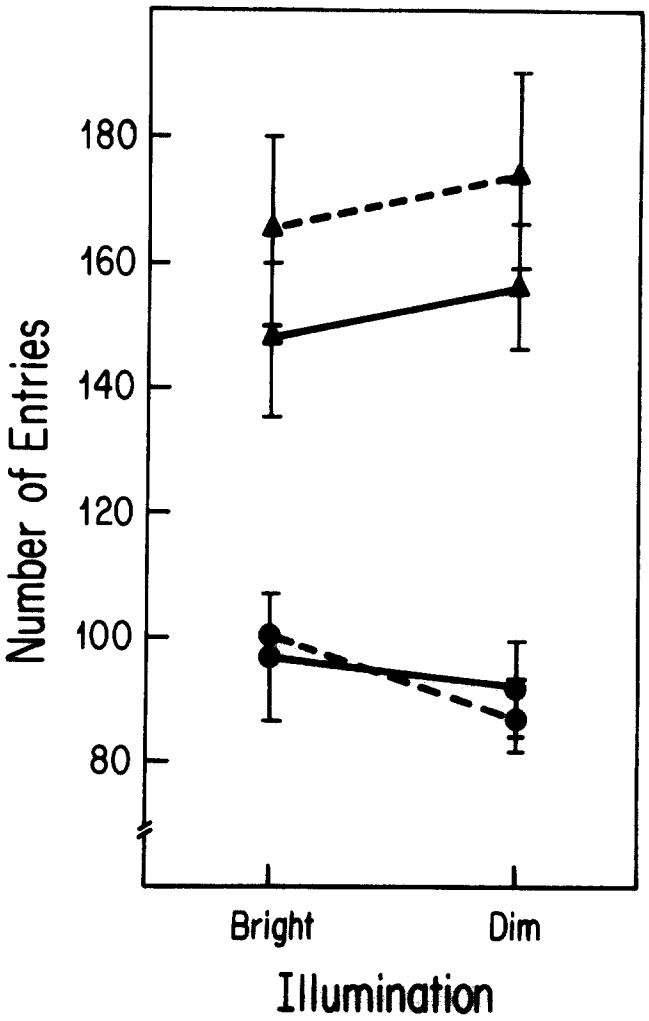

FIG. 3. Mean number of squares entered in the open field after closed-field testing. Key as in Fig. 1.

four groups. Animals with SC lesions produced more errors than controls, $F(1,65)=34.12$, $p<0.001$, and animals reared in the complex environment produced fewer errors than animals reared in the restricted environment, $F(1,65)=8.06$, $p<0.01$. Neither the illumination main effect nor the interactions approached statistical significance.

Second Open-Field Test

Figure 3 illustrates the mean ambulation scores for the four groups for the open-field test administered after the closed-field test. Again animals with superior colliculus lesions were significantly more active than controls, $F(1,65)=54.50$, $p<0.001$. The illumination main effect, environment main effect and interaction effects did not approach statistical significance. The relationship between the total ambulation scores of animals before and after closed-field testing was quite high (Pearson $r=.75$, $N=73$, $p<0.01$).

Histological Findings

Figure 4 illustrates the largest and smallest lesions in each of the four groups with superior colliculus lesions. Lesions were centered in the superior colliculi and damage to other areas was very slight. Damage extended into the overlying cortex (39 animals), pretectal areas (18 animals), central gray (24 animals), tegmentum (12 animals) and inferior colliculus (7 animals). Despite the impression given by Fig. 4, hippocampal damage was rare (3 animals). Damage to the overlying cortex, superior colliculi, central gray, and pretectal areas was quantified as described in the Method section, and correlation coefficients were computed between the resulting estimates and the behavioral data. The results of these computations are presented in Table 2. The results indicate a negligible relationship between the amount of central gray damage and the behavioral measures. Pretectal and cortical lesion sizes were significantly related to ambulation measures in animals reared in the complex environment but not for animals reared in the restricted environment. For closed-field test performance, there was a significant relationship between colliculus damage and performance for the restricted animals, but not for animals reared in the complex environment.

DISCUSSION

The present results confirm previous findings of deficits in problem solving in animals with superior colliculus lesions [44]. Most importantly, they indicate that the effects of colliculus lesions do not vary as a function of illumination, suggesting that the deficits are not explained solely by dis-

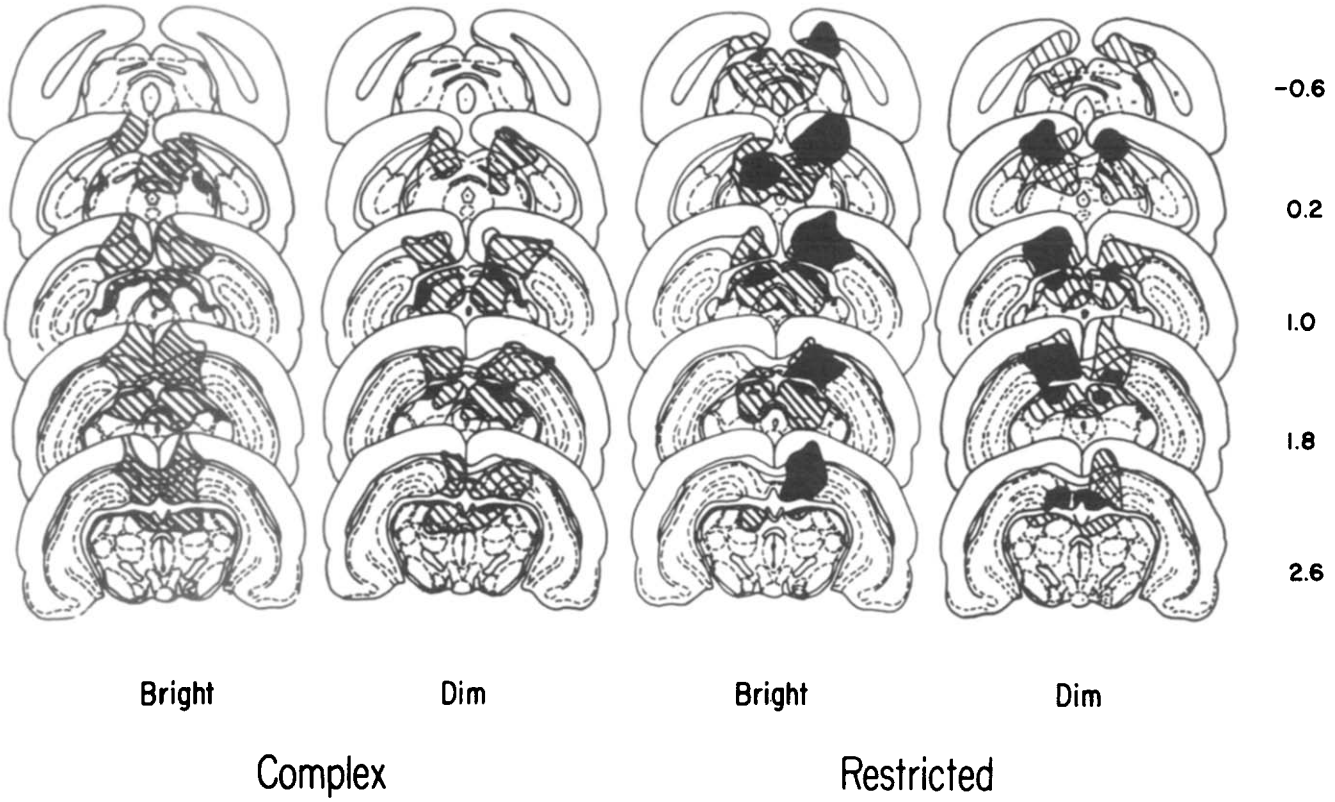

FIG. 4. Largest (hatched areas) and smallest (darkened areas) superior colliculus lesions in the four groups. Anterior-posterior coordinates (relative to interaural line) appear to the right of each level. Diagrams after Pellegrino and Cushman [37].

TABLE 2

PEARSON PRODUCT MOMENT CORRELATION COEFFICIENTS BETWEEN EXTENT OF LESIONS AND PERFORMANCES ON OPEN- AND CLOSED-FIELD TESTS

Brain Area	Closed-field Test		First Open-field Test		Second Open-field Test	
	Complex‡	Restricted§	Complex	Restricted	Complex	Restricted
Superior Colliculus	.21	.70†	.35	−.02	.25	−.08
Pretectum	.58†	.43	.68†	−.10	.65†	−.28
Central Gray	.25	.38	.21	.01	.01	−.02
Cortex	.27	.43	.50*	.17	.54*	−.03

*$p<0.05$
†$p<0.01$
‡N = 23
§N = 19

ruption in visual function. Consistent with electrophysiological evidence for the superior colliculus as an area of sensory integration [11, 12, 16, 48, 49, 51], disruption of this location impairs solution of problems in which visual, auditory and somesthetic stimuli change constantly. These results support the accumulating evidence that colliculus lesions produce a deficit in attention [21-23]. An animal which does not respond appropriately to novel stimuli would understandably be handicapped in closed-field performance. Nonvisual functions have also been found for the visual cortex in animals performing maze and avoidance tasks [14, 30, 32, 35, 36, 38, 52, 53].

A second important contribution of the present research is that it provides behavioral evidence of a deficit in spatial processing following lesions of the superior colliculus. This observation is consistent with electrophysiological findings that the superior colliculus in at least two rodent species is spatiotopically organized [11, 12, 16, 51]. On the other hand, superior colliculus lesions have not been observed to produce deficits in the acquisition and retention of other maze tasks [4,50]. A critical difference between the closed-field test and other maze tasks might be the demand in the former case for flexibility of an animal's responding. In the closed-field test, rats must face a novel pattern every day. Consis-

tent with this line of reasoning is the fact that Hebb-Williams performance and reversal learning performance are related [41]. In addition, both cats and rats with superior colliculus lesions are deficient in reversal performance ([58] and Weldon, unpublished results).

In support of many previous studies, animals in the present experiments which were reared in complex environments were better in problem solving than were animals reared in restricted environments [3, 5, 18, 19, 34, 45, 59]. In contrast with at least some previous findings, however, were the results indicating that lesion effects did not change as a function of experience before operation [9, 10, 25, 43]. One reason for the difference in results might be that brain stem areas such as the superior colliculus are not as affected by environmental experience as are other neural structures like the limbic system and neocortex. It should be noted, however, that animals with visual cortex lesions which have been tested in the present experiments did not show lesion × experience interactions (Weldon and Smith, unpublished observations).

The present study demonstrates that rats not using visual cues perform as well as do those animals using visual cues on the Hebb-Williams closed-field test. Rats do not require visual cues for solution of enclosed mazes [39, 52, 53]. Our results do not imply, however, that rats given the opportunity to use visual cues in enclosed mazes will not do so: alteration of extramaze cues during testing has been shown to impair problem solution ([3, 18, 26] and Smith, unpublished data).

The results reported here have shown that rats with superior colliculus lesions are hyperactive in the open field up to 69 days postoperatively, regardless of developmental experience or conditions of illumination. Hyperactivity has now been demonstrated for a variety of measures including the open field ([17,44] and the present study), a field test for light aversion [1], and a jiggle cage [27]. Other studies, however, have not found hyperactivity following superior colliculus lesions [20,22], perhaps due to more superficial lesions [17].

Although the effects of lesions on activity existed at both initial and second open-field tests, the facilitative effects of environmental enrichment during development were only found during the first test. Perhaps the effects of early environment on activity are mediated by differences in timidity and emotionality. According to this explanation, animals that have been handled and/or have become habituated to an experimental situation might not show effects that were apparent when tested for the first time. A closer look at these variables might help to explain why some investigations have reported increases in activity following environmental enrichment [6, 8, 13, 19, 24], but others have not [3, 7, 45, 59, 60]. A similar explanation can be used with respect to the results of the illumination variable. Although the results in the initial test indicated a greater ambulation level in those animals tested in dim light vs those tested in bright light, the pattern did not exist in the second test session. Even though the first trend did not attain statistical significance, the pattern was similar to that seen previously in rats tested in dim illumination [54,55].

Since lesions of the superior colliculus produce both hyperactivity and deficits in problem solving, it was of interest to determine whether the two dependent measures were related. Pearson correlation coefficients between the number of errors in the closed-field test and ambulation scores on the first and second open-field tests were .42 and .50, respectively ($N=73$, $p<0.01$). Although these data could be suggested to imply that the deficits in problem solving can be attributed to hyperactivity, we choose to point out, as we have previously [44], that the proportion of variance in error scores accounted for by activity levels is quite incomplete (.25). An interesting result of the lesion size–behavior correlations was that the relationships between the extent of pretectal damage and behavioral measures were statistically significant for animals reared in the complex environment but not for animals reared in the restricted environment. Similarly, the correlations between Hebb-Williams errors and superior collicular lesion size varied as a function of developmental experience, with animals reared in the restricted environment exhibiting a higher relationship than those reared in the complex environment. Further evidence is required to determine whether these differences reflect real differences in brain function due to early experience, or if they simply represent trivial patterns which are specific to the particular lesion configurations. It should be noted, however, that Layman [31] also observed that animals with lesions in the anterior superior colliculus and pretectal areas were more impaired in discrimination learning than were animals with lesions in the superior colliculus alone.

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