

## Acquisition of Visuomotor Behavior After Neonatal Tectal Lesions in the Hamster: The Role of Visual Experience

Barbara L. Finlay, Karen Marder, and David Cordon  
Cornell University

After neonatal damage to the midbrain tectum, hamsters exhibit as adults substantially reorganized retinal projections to the thalamus and midbrain. These experiments investigated the pattern of acquisition of a range of visuomotor capacities in hamsters with neonatal tectal damage, and the role of visual experience in this acquisition, by examining the time course of visuomotor development and the effects of dark-rearing on visuomotor behavior. These hamsters acquired visual orientation and pursuit at the same age as normal hamsters, but orientation and pursuit were impaired and exhibited no improvement over time. Photophobia and edge and depth sensitivity were relatively unaffected. Dark-rearing disrupted all visuomotor behavior in the midbrain-damaged animals but had no effect on normal animals. These results are consistent with a dominant role of neocortex in the residual visuomotor capacities of animals with neonatal ablations of the midbrain tectum

The behavioral consequences of identical damage to an infant and an adult brain may often be quite different. Those cases in which children with brain damage show preservation of behavioral capacities that would be lost in an adult suffering similar damage (Lenneberg, 1967; Teuber & Rudel, 1962) have led to research on a variety of animal models for clues to mechanisms of this sparing of function. In a variety of cases, considerable neuroanatomical reorganization has been shown to accompany sparing of function (Devor & Schneider, 1975; Goldman & Galkin, 1977; Weber & Stelzner, 1977).

If, in fact, the altered connectivity demonstrated in these cases is important in sparing of function, two hypotheses, not mutually exclusive, may be entertained:

1. Altered patterns of connectivity come about by neuroembryological rules that tend to preserve adaptive function. If a retinal

neuron is prevented from terminating in its normal target area, for example, it will secondarily terminate in another visual area (Schneider, 1973), perhaps increasing the likelihood that visual information could be employed by the animal. Learning would not necessarily be of importance for the useful employment of such a pathway.

2. Animals must learn to use altered patterns of connectivity. In the case of visual orienting, for example, a learned response might consist of associating an arbitrary pattern of visual stimulation with an arbitrary head movement. Experience, in general, has been shown to be important in recovery of function after brain damage in young and old animals, in the laboratory and in the clinic (Goldman & Mendelson, 1977; Schwartz, 1964; Teuber & Rudel, 1962; Will, Rosenzweig, Bennett, Hebert, & Morimoto, 1977). In most of these studies, however, generalized effects of enrichment or practice on sparing of function were shown rather than specific effects of training in the capacity at issue.

In the Syrian hamster, the superior colliculus is important in visual orientation and pursuit (Schneider, 1969). Following neonatal lesions of the superficial layers of the superior colliculus, hamsters retain some

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Requests for reprints should be sent to Barbara L. Finlay, Department of Psychology, Cornell University, Ithaca, New York 14853.

visual orientation and pursuit (Schneider, 1973). Neuroanatomical alterations consequent to this neonatal lesion include increased retinal projections to the ventral lateral geniculate body, to the nucleus lateralis posterior of the thalamus, and to the deep layers of the residual superior colliculus (Schneider, 1973). The aberrant retinal projection to the deep layers of the superior colliculus is physiologically functional; unlike the normal projection, it is topographically disorderly and represents only part of the visual field (Finlay, 1979). Preservation of the brachium of the superior colliculus, containing the retinal and cortical afferents to the colliculus, has been shown to be necessary, though not necessarily sufficient, for the visual orientation and pursuit that these animals show (So, 1977).

In the normal hamster, the emergence of visual orientation and pursuit does not depend on visual experience (Chalupa, Morrow, & Rhoades, 1978). Thus, the hamster visuomotor system is highly suitable for investigation of the role of experience in acquisition of visuomotor behavior after brain damage. We investigated this issue in two ways. First, we examined the time course of acquisition of various visuomotor behaviors in normal hamsters and hamsters with neonatal collicular damage, predicting a protracted time course of acquisition of visuomotor behavior in the brain-damaged animals if the animals must learn to use a reorganized central nervous system. Second, we investigated the effect of dark-rearing on visuomotor behavior in the superior colliculus damaged animals, again expecting disruption of visuomotor behavior if learning plays a critical role. A preliminary report of these experiments has been published (Finlay, Cordon, & Marder, 1978).

## Method

### Subjects

Two groups of Syrian hamsters (*Mesocricetus auratus*) were tested, the first group for ontogeny of visuomotor function and the second group for the effects of dark-rearing. For the first study, 78 hamsters were used, from 11 separate litters; of these, 42 were tested from the day of birth (Day 1) to the 12th postnatal day, and 36 were tested from the 12th postnatal day to the

120th day. From birth to Day 21, litters were housed with their mothers in 28 × 33 cm plastic cages supplied with pine bedding and nesting material. Sunflower seeds, laboratory chow, and water were available ad lib. After weaning, animals were housed singly or doubly in 20 × 26 cm plastic cages for the duration of the testing period. A constant 11.5:12.5 hr light/dark cycle was maintained.

For the second study, 20 hamsters from four litters were dark-reared from Day 14 to Day 28 postnatally (eyes open on Day 15), 10 of these had neonatal collicular lesions and 10 were normal. During dark-rearing, these animals were kept in a photographic darkroom with their mothers in a light-tight box and were handled daily. At 28 days, after 6 hr of exposure to light, they were assessed on the behavioral tests described below. Animals then remained on an 11.5:12.5 hr light/dark cycle for the 1-mo testing period.

Neonatal hamsters were individually identified by injecting various patterns of india ink into the folds of skin connecting limbs and torso. On Day 11, hamsters were re-marked with ear clips.

### Surgery

Within 24 hr of birth, half of each litter received superior colliculus lesions which included all of the superficial gray layers of the colliculus and variable amounts of the intermediate and deep collicular layers, the other half of the litter received sham lesions. The litter was separated from the mother and cooled to provide anesthesia. Under a dissecting microscope, skin and connective tissue overlying the superior colliculus were slit and retracted. The superior colliculi, which are not yet covered by cortex as they are in the adult, can be seen directly through the cartilaginous cranium and were ablated directly through the cranium with an appropriately shaped heated wire. The scalp incision was then sutured, and the animal was returned to the mother. Sham operations were identical, with the heat lesion omitted.

### Behavioral Testing

Behavioral tests were administered with the experimenters blind with respect to the experimental group of the animal. The neonatal group (0–12 days) was tested each day. The juvenile group (12–120 days) was tested each day to Day 18 and thereafter at lengthening intervals. The sequence of tests never varied, though on each test, hamsters were tested in a random order. Dark-reared animals were assessed from Day 28 to Day 54 on a subset of the tests described below.

Various indexes of general maturational level were obtained. Nose-to-rump length of neonates, weight of juveniles, and date of eye opening (normally, Day 15) were recorded. Presence and vigor of rooting and orientation to tactile stimulation with a blunt probe were described, the time that each animal required to right itself after being placed on its back on a smooth surface was measured. Vestibular function and motor coordination were tested by putting each animal on a turntable and measuring the maximum speed at which the animal could counterrotate.

Activity level was measured in an open field (Plexiglas box, 28 × 33 cm) for a 3-min interval. After eye opening, this box was kept in a uniform white surround, under room lights. An identical activity test was administered in darkness, under infrared illumination and monitored by an infrared-sensitive videocamera.

Thermotaxis and photophobia were both measured on a runway on which thermal and illumination gradients were maintained, respectively. The runway was paper covered, 10 cm wide and of variable length. It was subdivided into five sections, with each section equal to three times the hamster's body length. The temperature gradient, produced by a movable 200-W bulb, was maintained at 43 °C at the section closest to the heat source and 24 °C at the section farthest from the heat source. Hamsters were placed in the section farthest from the heat source, and their position was recorded every 15 sec for 2 min. The time taken to reach the warm end of the runway was also noted. The illumination gradient was produced by a 100-W bulb, shielded by a water bath so that a uniform temperature of 24 °C was maintained in all parts of the runway. The luminance in the section closest to the light source was 18.40 cd/m<sup>2</sup>, and luminance at the dark end ranged from 12 cd/m<sup>2</sup> for the shortest length runway to .02 cd/m<sup>2</sup> for the longest length runway. Hamsters were placed in the central section, and their position recorded every 15 sec for a 3-min period; the light was then repositioned on the other side of the runway, the hamster was re-centered, and the test was repeated.

Sensitivity to the presence of an edge and differential depth judgment were assessed on a real cliff. The cliff was a movable 27 × 15 cm plywood platform positioned over a ledge covered with white contact paper. This platform could be stationed at two separate heights so that cliff heights of 5 cm and 15 cm, or 15 cm and 25 cm, could be presented to the animals. Latency to fall or jump and choice of deep or shallow side were recorded, for two trials for each hamster at each of the two pairs of platform heights. Vibrissae were clipped to eliminate one source of somatosensory stimulation, and the hamsters could not touch the deep or shallow side from the platform in either of the conditions. Although the use of a real cliff rather than a visual cliff confounds various sensory modalities, the fact that animals will cease to avoid visual cliffs after continual exposure (Seitz, Seitz, & Kaufman, 1973) led us to consider behavior on a real cliff more indicative of the real behavioral capacities of these animals.

The hamster's strong preference for sunflower seeds was used to assess visual orientation and discrimination. Recognition and approach, orientation and pursuit, and the ability to discern the seed with increasing distance were measured. The seed was presented at the end of a small metal rod and touched to the hamster's cheek, if the hamster refused the seed, the test was discontinued. Next, the seed was presented 2 cm directly in front of the hamster's nose in the horizontal plane, and approach to the seed was scored. Three tests of orientation and pursuit were done next. The seed was placed in the "approach" position and moved toward the rear of the hamster in the horizontal plane. The presence of an initial head turn (A) and pursuit of the seed through 360° (B) were scored, for both right and left movement. The seed was next held directly above the

hamster's head and moved toward the hamster's rear. Head raising was scored (C). Ability to discern the seed with increasing distance was tested by scoring approach with the seed held 12 cm (D) and 36 cm (E) away from the hamster, directly ahead.

## Histology

When all behavioral tests were completed, animals were overdosed with urethane and perfused with 10% formal-saline. Brains were cut frozen at 30 μm and stained with cresylecht violet. Animal classification into operate or sham operate was verified, and the extent of each lesion was reconstructed with the aid of a standard dorsal-view map (Finlay, Schneps, Wilson, & Schneider, 1978).

## Results

### *Extent of Lesion in the Operates*

Eighteen of the 49 animals with collicular ablations and 26 of the 49 animals with sham operations survived to the last testing day. In all these animals, reconstruction of the midbrain verified the presumed experimental group assignment. The typical lesion removed all of the identifiable superficial gray layer of the superior colliculus except a small remaining laminar zone at the most lateral margin (Figure 1). In most cases, incoming fibers of the optic tract coursed dorsally to the remaining intermediate and deep gray, in which there was variable cell loss. Lesions were deepest medially and caudally, extending to medial central gray. Only minor damage was done to the inferior colliculus, and pretectal nuclei and the nucleus of the optic tract could still be identified. A rostral, middle, and caudal section from three representative midbrains appear in Figure 1; 27.3, upper right, is the most superficial lesion observed, 19.3 shows a lesion of average extent, and 39.4, lower right, is the most extensive lesion. None of the sham operates showed any evidence of brain damage.

### *Indexes of General Maturation*

Since the purpose of this experiment was to look for differences in time course of the acquisition of visuomotor behaviors, careful determination of the relative maturational state of the early brain-damaged group and

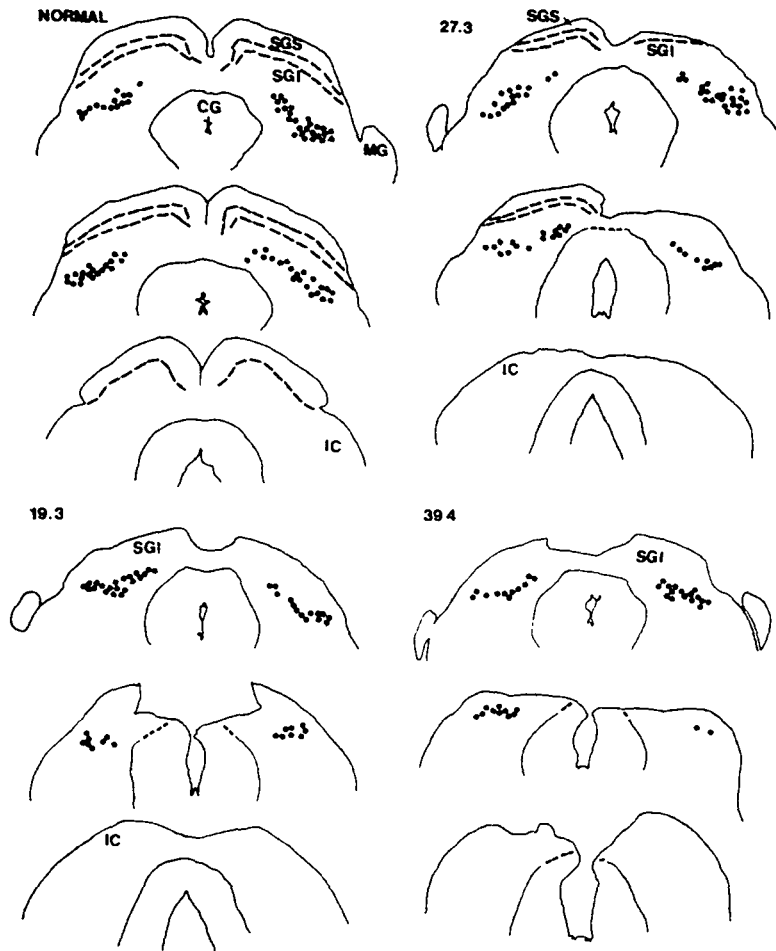


Figure 1 Coronal sections through rostral, middle, and caudal midbrain for a normal hamster (upper left) and three neonatally colliculus-ablated hamsters (upper right, lower left and right) (SGS, stratum griseum superficiale, SGI, stratum griseum intermediale, CG, central gray, MG, medial geniculate body, IC, inferior colliculus)

the sham-operated group at all postnatal ages was made. It is quite plausible that early brain damage might cause a general developmental lag due to changes in activity and nutrition or to any of a variety of secondary variables.

**Mortality** Statistically different mortality between groups was restricted to the day immediately following surgery (22 of 61 colliculus-ablated animals; 14 of 53 sham-operated animals). Sixty-eight percent of the animals survived to the second postnatal day (78 hamsters). Of these animals, 49% of the colliculus-ablated group and 67% of the sham-operated group survived to maturity; this shows a higher but not statistically sig-

nificant death rate in the colliculus-ablated group ( $\chi^2 = 4.57, p > .05$ ). Attrition was confined to the first two postnatal weeks, and no behavioral observations were eliminated because of subsequent death of the hamster. The principal cause of death was maternal cannibalism (not unusual in hamsters), which can be caused by a variety of factors including appearance of abnormality in the pups or disturbance of the mother.

**Growth and maturation.** The rump-to-crown length was never significantly different between groups (e.g., on Day 5, rump-to-crown length of colliculus-ablated animals was  $2.1 \pm .06$  cm and of sham-operated animals,  $2.2 \pm .05$  cm). After Day 20,

a consistent weight difference developed which was maintained to maturity. At Day 20, the average weight of the colliculus-ablated animals was  $19.3 \pm 2.3$  g and of the sham-operated animals,  $24.5 \pm 2.7$  g; on Day 27,  $33.9 \pm 2.4$  g versus  $40.5 \pm 1.7$  g; on Day 35,  $50.9 \pm 2.4$  g versus  $57.0 \pm 1.5$  g.

A final maturational milestone, day of eye opening, occurred on the 15th postnatal day for 53% of the operates and 53% of the shams. Of the remaining animals, 73% opened their eyes on the 16th day, and 27% on the 18th day, again equally distributed between groups.

*Reflexes and tactile orientation.* Rooting reflexes to stimulation of the side of the mouth and nose with a blunt probe were similar in the two groups. Speed and method of righting after being placed on the back were also similar (e.g., on Day 3, colliculus-ablated animals took  $6.0 \pm 2.0$  sec to right and sham-operated animals,  $7.4 \pm 1.5$ ; on Day 8, colliculus-ablated animals,  $4.5 \pm 1.6$ , sham-operated animals,  $4.3 \pm 1.1$ ). Counterrotation to rotational movement of 40 rpm was possible for 50% of the colliculus-ablated animals on Day 4 and for 50% of the sham-operated animals on the same day.

The pattern of orientation to tactile stimulation (touch with a blunt probe or a light pinch with forceps) proceeded from diffuse motor activity to localized limb withdrawal. No differences were observed between groups. Half of both the collicu-

lus-ablated and sham-operated animals were judged to produce localized limb withdrawal to tactile stimulation by Day 6. Though reactivity and orientation to tactile stimulation show a transient deficit after collicular undercuts in adult hamsters (Schneider, 1969), we could find no evidence of a deficit during development.

*Thermotaxis.* Thermotaxis in these hamsters conformed closely to a pattern described by Leonard (1974). Hamsters seek warm areas until the 10th to 12th postnatal day, when they become physiologically endothermic. The two groups never differed in the times spent at different points in the thermal gradient (Figure 2A)

*Activity.* Prior to eye opening, the activity of the colliculus-ablated animals was significantly reduced relative to controls, rising to approximately normal levels around the time of eye opening (Figure 3). Prior to eye opening, the regression equation for the change in activity in the colliculus-ablated animals relative to the sham-operated animals was  $y = 51.7 + 3.3x$ ,  $r^2 = .449$ . The variance due to the regression was significantly greater than that due to the residuals, and thus the slope was greater than zero,  $F(1, 10) = 8.14$ ,  $p < .05$ . To determine whether the observed difference in activity represented a difficulty in motor coordination, we compared the time it took the groups to reach the warm end of the thermal gradient on those days that they showed a preference for the warm end (Days 2-10; Figure 2B)

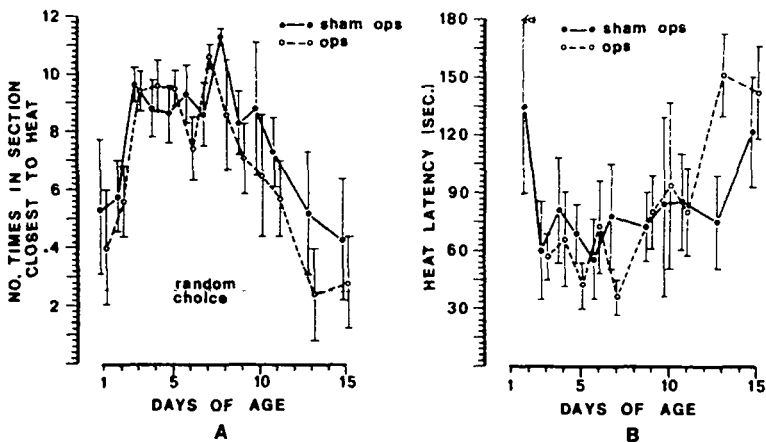


Figure 2 Mean time ( $\pm 1$  SE) spent in the warm end of a thermal gradient (A) and mean time ( $\pm 1$  SE) taken to reach the warm end from the colder end (B). (ops = colliculus ablated.)

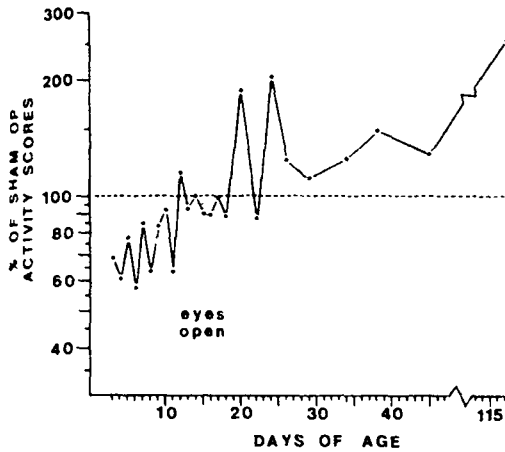


Figure 3 Open-field activity of sham-operated animals as percentage of scores for colliculus-ablated animals

Speed of locomotion and its developmental change were similar in the two groups, so the lack of activity could not be attributed to a simple motor disability.

After eye opening, spontaneous activity of the colliculus-ablated animals continued to increase relative to that of the sham-operated animals, until at 4 mo the activity level of the colliculus-ablated animals was 255% of the controls (Figure 3). The regression equation for relative activity after eye opening was  $y = 91.05 + 1.37x$ ,  $r^2 = .519$ ; this slope is significantly different from zero,  $F(1, 10) = 10.78$ ,  $p < .01$ . To determine whether this heightened activity represented some differential sensitivity to visual stimulation, we tested the relative activity of the two groups in the dark, monitored by an infrared-sensitive videocamera under infrared illumination. Both groups increased their activity markedly in the dark. However, the activity difference between the two groups persisted ( $t = -4.9$ ,  $p < .001$ ), and we conclude that the difference in activity level is unrelated to visual stimulation. Qualitatively, our impression of the difference between the groups was that the colliculus-ablated group ran continuously, nose to the ground, without the frequent stopping and rearing characteristic of normal hamsters.

#### Visuomotor Behavior After Eye Opening

For all the following data, effective mat-

uration was measured in days after eye opening rather than in postnatal age, since the critical variable is onset of visual sensitivity. Day of eye opening was taken as Day 15, and other days are corrected to this day, for all measures of visuomotor behavior.

**Photophobia** Both groups showed evidence of photophobia throughout the testing period, particularly pronounced up to Day 25, as has been demonstrated for numerous rodent species (Gottlieb, 1971; Figure 4). Prior to eye opening, neither group showed a preference for the light or dark side of the runway under these conditions of illumination.

**Sensitivity to edges and heights.** Upon eye opening, sham-operated animals showed an increased latency to fall or jump from the edge of the cliff (Figure 5). We compared the latency of individual sham-operated hamsters on Day 14 to the latency on Day 16 with the Wilcoxon signed-ranks test for matched pairs, and the increase in latency over those two dates was significant ( $p < .018$ ). The sham-operated animals showed a preference for the shallow side of the cliff considerably later (Days 25–30, Figure 6). After Day 38, latency again began to decrease; the cliff heights used were small, considering the body size of a mature hamster. In summary, normal hamsters changed their locomotor behavior in the presence of a cliff coincident with eye opening and showed sensitivity to the relative height of the cliff somewhat later.

By Day 22 and thereafter, colliculus-ablated animals showed latencies indistinguishable from those of sham-operated animals on the cliff edge. Their latency to fall or jump between Day 14 and Day 16, while increasing, did not reach statistical significance (Wilcoxon signed-ranks test for matched pairs,  $p > .14$ ), and it appeared that they were acquiring sensitivity to the presence of the edge at a slower rate than the normal animals. To test this, we computed a rate of change function, for each group separately, by subtracting the scores on consecutive days between Day 14 and Day 25. Sham-operated animals showed the largest increases in latency early in this period; colliculus-ablated animals showed the most increase at the end of this period.

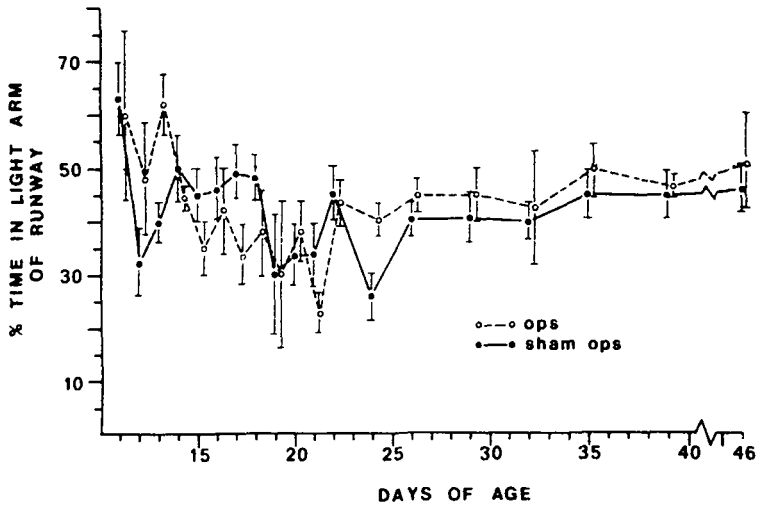


Figure 4 Percentage of time ( $\pm 1$  SE) spent in the lighter half of a runway with an illumination gradient (ops = colliculus ablated)

Thus, the regression equation fitting the changing latency for the sham-operated animals has a negative slope ( $y = 14.52 - .55x$ ,  $r^2 = .10$ ), and the regression equation for the colliculus-ablated animals has a positive slope ( $y = 19.85 + 1.34x$ ,  $r^2 = .534$ ). These two slopes are significantly different ( $p < .05$ ). In summary, by two measures, colliculus-ablated animals show less change in locomotor activity in the presence of an edge than normal hamsters do shortly after eye opening, but later in development the two

groups are indistinguishable. Some evidence of a similar slight retardation may be seen in the appearance of a preference for the shallow edge by the colliculus-ablated animals on Days 23 and 27 (Figure 6). We confirm the observation of Keselica and Rosinski (1976) that collicular lesions do not impair depth judgments in mature hamsters, but we do show evidence of a developmental lag in this capacity consequent to colliculus lesions.

*Visual approach and orienting.* Figure

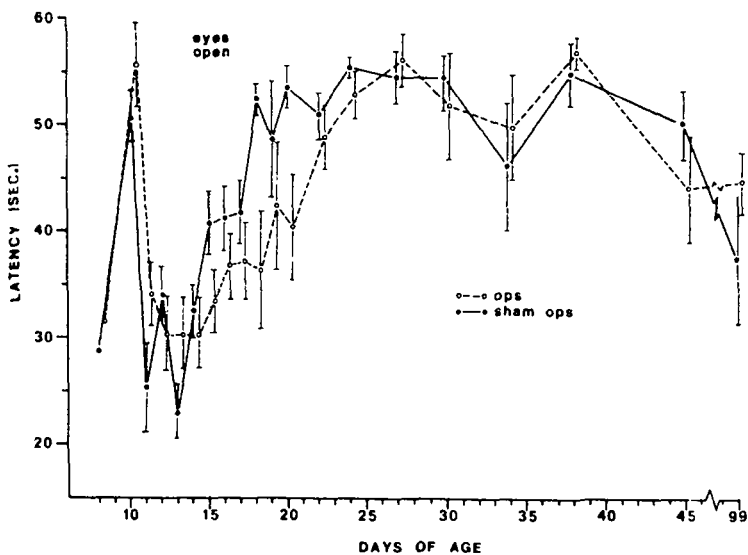


Figure 5 Mean latency to fall or jump from a cliff edge ( $\pm 1$  SE) (ops = colliculus ablated.)

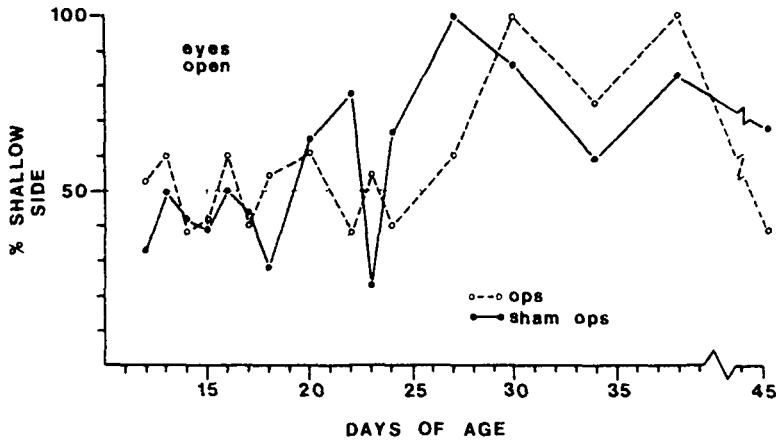


Figure 6 Choice of side for fall or jump on a cliff with two depths (number shallow/number shallow + deep) (ops = colliculus ablated.)

7 shows the pattern of acquisition of visual orientation and approach in sham-operated and colliculus-ablated groups. Only those hamsters that both would accept seeds and would approach seeds 2 cm away are included in this analysis (95% of shams, 81% of colliculus-ablated animals). Since this test depends on the hamster's motivation to get sunflower seeds and its ability to recognize them, in addition to its orienting ability, this test must be considered a probable under-

estimation of the actual orienting capacities of these hamsters. Even with these difficulties, visual orientation as measured by this method appears early in development and reaches mature capability only 5 days after eye opening.

In Figure 7, a square is darkened when 50% of the animals in a group show the particular behavior. Measures A-C measure orientation and pursuit (head turn to the side, pursuit to the side, upward head turn).

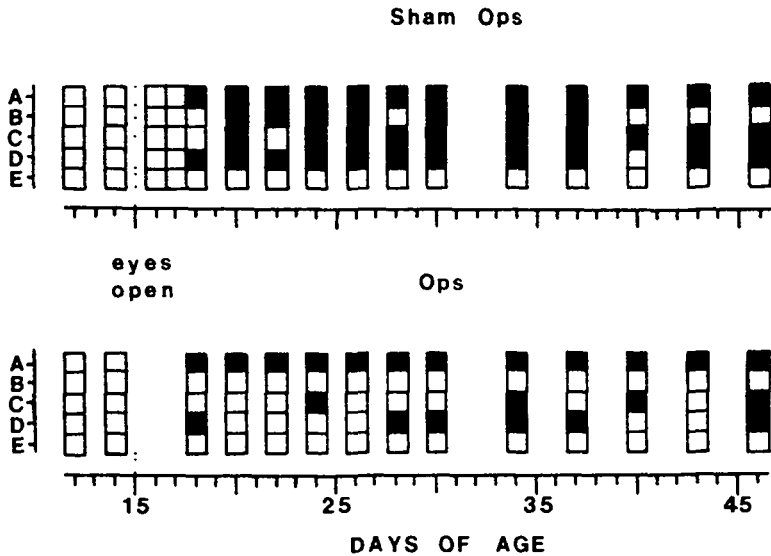


Figure 7 Frequency of positive responses to five measures of ability to orient to sunflower seeds (A, initial head turn following a seed moved in a circular path at nose height; B, 360° turn following a seed moved as in A, C, looking upward at a seed presented above the hamster's head, D, approach to a seed 12 cm ahead; E, approach to a seed 36 cm ahead. Dark squares indicate positive responses by 50% or more of hamsters tested. ops = colliculus ablated)



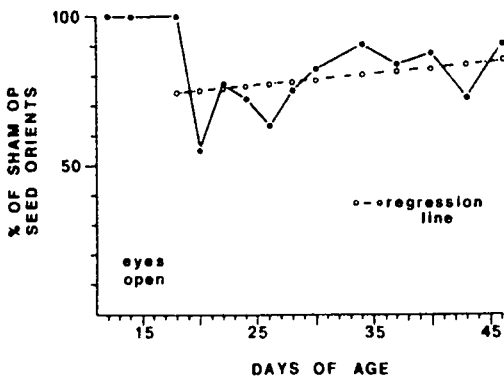


Figure 8. Orients to seeds by colliculus-ablated hamsters as the percentage of sham-operate scores for a composite score of six tests

Colliculus-ablated animals can make an initial head turn toward a seed but consistently fail to pursue it, and they only rarely make upward head turns. Normal animals perform these tasks with fair reliability from Day 20 on.

Measures D and E show the number of times hamsters approached seeds at 12 cm away and directly in front, and at 36 cm away. Thirty-three percent of the sham-operated animals approached seeds at 36 cm.

As Figure 7 shows, colliculus-ablated animals show no evidence of improvement in visual orientation with experience. They show the first evidence of visually elicited approach and orienting at the same time as sham-operated animals, but with a relative disability that is maintained to maturity. In Figure 8 is the relative capability in approach and orienting of colliculus-ablated animals compared with sham-operated animals, with the use of a score combining all the approach and orienting measures described above. The regression equation to fit this data is  $y = 67.31 + .38x$ , not significantly different from a slope of zero,  $F(1, 10) = .84, p > .05$ . None of the subtests of orienting and approach show evidence of differential improvement by the colliculus-ablated animals over time.

#### *Visuomotor Behavior of Dark-Reared Hamsters*

Twenty hamsters, half colliculus-ablated

and half normal, were deprived of light stimulation from 2 days prior to eye opening until 2 wk after eye opening; this duration of deprivation was chosen because hamsters perform at approximately mature levels 2 wk after eye opening on all visuomotor tasks of interest. We investigated all those behaviors showing some evidence of collicular involvement: activity, edge and depth sensitivity, and approach and orienting. In general, colliculus-ablated animals showed a major effect of dark-rearing, but normal animals did not.

The activity score of dark-reared colliculus-ablated animals ( $40 \pm 5.1$ ) was not significantly different from that of dark-reared normal hamsters ( $34 \pm 7.1$ ), light-reared colliculus-ablated hamsters ( $46 \pm 10.0$ ), or light-reared normal hamsters ( $41 \pm 6.7$ ) on the first day of testing, Day 28 (Kruskal-Wallis one-way analysis of variance,  $\chi^2 = .39$ ). Thereafter, from Day 30 to Day 46, the activity of the dark-reared colliculus-ablated animals increased faster than that of any other group. On Day 30, the dark-reared colliculus-ablated group had an activity score of  $81 \pm 9.3$ , contrasted with the score of the light-reared operates of  $40 \pm 7.8$ . This difference is significant (Mann-Whitney rank-sum test,  $p < .005$ ). By the last testing day, the activity rate of the light- and dark-reared colliculus-ablated groups had again converged, both groups remaining markedly more active than either the dark- or the light-reared normal hamsters. The fact that the relative activity of the dark-reared operates on testing Days 30–46 was markedly higher than that of the other experimental groups should be kept in mind in the interpretation of the tests of visuomotor activity.

Figure 9 (top) shows the effect of dark-rearing on latency to fall or jump off the cliff edge, averaged over all four heights. All light-reared animals and dark-reared normal animals show essentially maximum latency to leave the cliff edge; dark-reared colliculus-ablated hamsters fall off the cliff at latencies that average below those exhibited by normal hamsters prior to eye opening. Kruskal-Wallis one-way analyses of variance were computed for Days 28, 30, and 46 between the four tested groups, and each

showed a major between-groups difference (Day 28,  $\chi^2 = 5.60$ ,  $p < .001$ ; Day 30,  $\chi^2 = 6.93$ ,  $p < .0005$ ; Day 46,  $\chi^2 = 8.24$ ,  $p < .0005$ ). Over time, the dark-reared colliculus-ablated animals improve to normal levels. Increased activity cannot account for the poor performance of the dark-reared operates since they perform at their worst levels when their activity rate is identical to that of the other groups (Day 28) and perform best when their activity rate has reached its relatively highest point (Day 54). The impression these animals give is not of increased interest in or exploration of the edge, or misjudgment of its depth, but rather complete inattention to the presence of the edge.

Choice of deep or shallow side of the cliff parallels the latency data. Dark-reared operates perform at chance on all testing days. Both light-reared groups choose the shallow side almost 100% of the time on these

testing days (Figure 6); the dark-reared normal animals also choose the shallow side after the first trial day (17% on Day 28, 17% on Day 29, 72% on Day 30).

Dark-reared operates, in contrast to all other groups, show a major deficit in visual orienting capacity on first exposure to light, which improves over time. Shown in Figure 9 (bottom) is the performance of all four groups on a composite score of the three easiest visual orienting tasks (approach A, B). The behavior of the dark-reared normal animals is indistinguishable from that of the light-reared normal animals, as has been reported by Rhoades and Chalupa (1978) and Chalupa et al. (1978). Light-reared colliculus-ablated hamsters perform at a consistently lower level. Dark-reared colliculus-ablated animals on the first testing day show no evidence of any sensitivity to visual stimulation whatever. On Day 28, the light-reared colliculus-ablated animals are significantly different from the dark-reared colliculus-ablated animals on this score (Mann-Whitney rank-sum test,  $p < .009$ ); the same is true on Day 30 (Mann-Whitney rank-sum test,  $p < .005$ ). By Day 44, after 16 days of light exposure, the two groups are no longer significantly different.

## Discussion

### Extent of Lesions

The lesions described in these animals, removal of all the superficial gray layer of the superior colliculus and variable amounts of the intermediate and deep layers and sparing of the pretectal nuclei and accessory optic tract in the large majority of cases, are quite comparable with those described by Schneider (1973). It is thus likely that the same anatomical reorganizations and physiological reorganizations described previously (Finlay, 1979) occurred in the animals presented here.

### General Maturation of Nonvisuomotor Capacities

No evidence of a general developmental lag in the early brain-damaged group. Only two of the indexes of general maturation

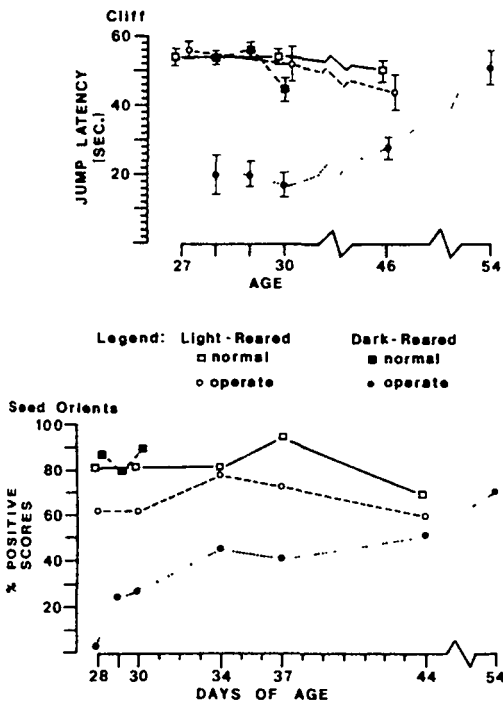


Figure 9. Effect of dark-rearing on latency to fall or jump from a cliff edge (top) and ability to orient to sunflower seeds (bottom). (Jump latency [in seconds] is presented as mean  $\pm 1$  SE; seed orients are presented as percentage of positive responses on the three easiest tasks.)

tion, weight gain and activity level, showed any evidence of lag in the colliculus-ablated group. Size, date of eye opening, rooting, righting, tactile orientation, counterrotation, onset and cessation of thermotaxis, and speed of locomotion were all indistinguishable in the colliculus-ablated and normal groups. Since we could show no evidence of behavioral depression on any of these measures, we believe that the lowered activity rate observed in operated animals prior to eye opening reflects a direct effect of the superior colliculus on activity level prior to eye opening rather than a general effect of surgical trauma. Why animals with collicular lesions then become hyperactive later in development is not clear; however, paradoxical effects of surgical or neurochemical treatments on the activity of immature and mature animals have often been observed (Snyder & Meyerhoff, 1973). We propose that the change in weight gain in these animals is secondary to their rather dramatically increased activity.

*A changing role of the superior colliculus during normal development?* Since the superior colliculus receives input from several sensory modalities (Dräger & Hubel, 1975; Finlay et al., 1978; Stein & Arigbede, 1972) and since cells in the superior colliculus become responsive to somatosensory and auditory stimulation before they are sensitive to visual stimulation (Stein, 1978), several investigators have suggested that the superior colliculus might be responsible for the orientation to thermal, tactile, or auditory stimulation that animals show before eye opening (Leonard, 1974; Stein, 1978). We were able to find no hint of a deficit in orientation to either tactile or thermal stimuli during development, even though the majority of the collicular lesions included substantial removal of the deep and intermediate gray layers of the superior colliculus, where somatosensory innervation is found. Of course, the hypothesis that the superior colliculus is one of many structures that subserve this generalized orienting function is not ruled out by this observation.

Routtenberg, Strop, and Jerdan (1978) presented evidence that the negative phototaxis exhibited by rats prior to eye opening is mediated by the dorsal midbrain, princi-

pally superior colliculus. We found no evidence for this in our animals and suggest that either (a) damage to some other structure than the superior colliculus, perhaps habenula or pretectum, is responsible for the lack of negative phototaxis shown by the neonatal rats or (b) the aberrant retinal projections formed in the hamster after early tectal damage somehow spare this behavior.

Whereas damage to the superior colliculus in an adult hamster does not affect sensitivity to the presence of an edge, or differential depth judgment (Keselica & Rosinski, 1976), we observed minor retardation in these capacities in hamsters with early colliculus damage. Animals with either neonatal or adult colliculus damage show considerably fewer exploratory or scanning head movements under a variety of conditions (Finlay, Mort, Berg, Hersch, & Falino, 1979) than do normal hamsters. This response mode may enable the hamster to direct its attention to discontinuities, such as edges, and appropriately modify its behavior during early stages of visual exploration, as well as to provide additional parallax and surface occlusion cues to depth.

#### *Acquisition of Orientation and Pursuit After Early Midbrain Damage*

In the adult hamster, removal of the superficial layers of the superior colliculus leads to a deficit in visual orienting in the upper and peripheral visual field and spares orienting in the central visual field (Finlay et al., 1979); total undercuts of superficial and deep superior colliculus totally abolish orienting (Finlay et al., 1979; Schneider, 1969).

Animals with neonatal damage, in which deep colliculus is partially spared, show the pattern of animals with removal of the superficial layers only: severe orienting deficits in upper and peripheral visual field and preserved orienting in central visual field. So (1977) showed that damage to the brachium of the superior colliculus, which contains retinal and cortical afferents to the tectum, prevents the sparing of central field orienting. Thus, it appears that deep col-

liculus and aberrant retinal and cortical innervation to it must remain to preserve central visual field orienting.

We hypothesized that if learning new visual-to-motor associations were essential to acquire visuomotor function in brain-damaged animals, two observations would be made: (a) The time course of acquisition of visuomotor behavior should be protracted or abnormal in brain-damaged animals, and (b) visual deprivation should severely disrupt the visuomotor behavior of brain-damaged animals. Experiments designed to test these two hypotheses have produced contradictory results. Animals with neonatal lesions of the superior colliculus show onset of visual orienting at the same time as normal animals, and little change occurs in this behavior over time that would be indicative of a role for learning in the refinement of visual orienting. Paradoxically, however, all the visuomotor behavior we tested was profoundly disrupted by dark-rearing in the colliculus-ablated animals, but intact dark-reared animals were not distinguishable from intact light-reared animals on the same tests on their first exposure to light. We suggest that in accord with the results of the first experiment, learning is not of critical importance in the sparing of visual orienting and that the general deficit caused by dark-rearing is due to a functional lesion of the visual cortex. Other hypotheses can also explain these data; the aberrant projections to the brain stem may be more sensitive to disruption by dark-rearing, for example.

Several lines of evidence, however, suggest the first hypothesis. Alterations in visual cortex physiology due to dark-rearing have been reported in several species (Baker, Grigg, & Von Noorden, 1974; Wiesel & Hubel, 1965). Chalupa et al. (1978) found no change in the responses of neurons in the superior colliculus of hamster consequent to dark-rearing, with the exception of those properties demonstrated to be dependent on the integrity of visual cortex; the same type of result has been reported for the cat (Hoffman & Sherman, 1975). As stated before, the cortical and retinal afferents to the tectum must be preserved to spare visual orienting in hamsters. No investigator has found profound deficits in behavior on the

visual cliff consequent to a tectal lesion (Keselica & Rosinski, 1976), whereas several investigators have implicated posterior cortex in this capacity.

In sum, we propose that the preservation of orienting and approach capabilities in the Syrian hamster subjected to early midbrain damage depends on the preservation of the deep layers of the residual superior colliculus and its cortical and retinal afferents (So, 1977) and also on the functional integrity of visual cortex. In an adult animal with an intact tectum, a major lesion of the posterior cortex does not produce deficits in approach and orienting (Schneider, 1969), possibly because the intact tectum can also support this function. The early tectal lesion may serve to unmask the normal contribution of visual cortex to orienting in central visual field.

This experiment demonstrates the extreme fragility of a neuronal system after brain damage. The results of this study and others (Goldman & Mendelson, 1977; Schwartz, 1964; Will et al., 1977) underscore the importance of close attention to experience and environment after damage to an infant brain.

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