

The role of the superior colliculus in visually guided locomotion and visual orienting in the hamster

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Visually guided locomotion toward goal doors designated by various cues was assessed in normal hamsters, hamsters with undercuts of the superior colliculus, and hamsters with neonatal lesions of the superior colliculus. Scanning of visual arrays, orientation to novel stimuli, and orientation to sunflower seeds were assessed in the same animals. Collicular lesions produced no deficit in accuracy of choice of goal door, type of route taken, or speed of locomotion. By contrast, the same hamsters showed major deficits in spontaneous scanning and orientation to stimuli in the visual periphery. Hamsters with neonatal and adult collicular lesions performed identically on every task except orientation to sunflower seeds presented at various locations in the visual field; adult operates were somewhat more variable in their performance. The implications of these results for the concept of encephalization of function and the phylogeny of the optic tectum are discussed.

In every vertebrate that has been studied, the mid-brain tectum plays some role in visuomotor behavior (Ingle & Sprague, 1975). In highly visual animals with marked retinal specializations for pattern vision, the superior colliculus has been implicated in acquisition of visual targets, particularly peripheral ones (Butter, Weinstein, Bender, & Gross, 1978; Keating, 1974) mediating movement of the fovea or area centralis to a target. In nonmammalian predatory species both with and without retinal specializations (Ewert, 1970; Ingle, 1973), the tectum has been implicated principally in prey acquisition, mediating a ballistic movement of body midline and mouth to a prey object. In addition, the tectum has also been implicated in a variety of other visual functions, including optomotor responses (Springer, Easter, & Agranoff, 1977), visually guided locomotion (Schneider, 1969), and pattern vision (Casagrande & Diamond, 1947). Construction of the phylogeny of the optic tectum requires understanding of these divergences in tectal function as well as commonalities in species with diverse visuomotor behavior.

Foraging animals without marked retinal specializations, such as rodents and herbivores, would add an interesting piece of information to understanding of tectal evolution, and some information has been gathered. However, a coherent account of tectal function in rodents has been unavailable, due to the conflicting reports of the visuomotor deficit produced by collicular lesions. In the hamster, Schneider (1967,

1969, 1970) has shown a deficit both in visual orienting, as measured by head turns to sunflower seeds, and in visually guided locomotion consequent to a collicular undercut, and has characterized these symptoms as indicative of a general disability in spatial localization, knowing where things are. In the rat, Dyer, Marino, Johnson, and Kruggel (1976) and Goodale and Murison (1975) find no evidence of such a general deficit in spatial localization consequent to tectal ablation, finding only a disability in attention and the "orienting reflex," defined as cessation of locomotion, rearing, and head turning toward a novel stimulus. Since these studies differ on at least three important dimensions—type of lesion, species of animal, and behavioral assessment—accounting for the difference has been problematic.

In this study, we have undertaken to replicate the experimental paradigm of Goodale and Murison (1975), in which animals must locate and find their way to a goal door designated by brightness in an array of doors, using hamsters in which the colliculi had been undercut by the method of Schneider (1969). Particular attention was paid to the way the animals learned and performed the task, using videotape analysis. In addition, the orienting capacities of these same animals to novel stimuli and sunflower seeds were studied.

Schneider has also presented evidence that hamsters given collicular ablations on the day of birth do not show as profound a deficit in general visuomotor capacity as do animals receiving collicular undercuts at maturity (1970). We have assessed a group of animals receiving collicular ablations at birth on the various visuomotor tasks described above, with par-

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ticular attention to whether classes of visuomotor behavior may be dissociated by their differential impairment or sparing with adult vs. neonatal lesions. A preliminary report has been published (Finlay, Mort, Berg, Hersch, & Falino, 1979).

METHODS

Subjects

Twenty golden hamsters of both sexes were used in this study; in any testing situation, males and females were run in separate but identical apparatus to minimize olfactory distractions. Animals were housed in individual clear plastic cages with pine bedding and hamster chow available ad lib. During testing, the animals were maintained on a 24-h water-deprivation schedule. Of the 20 animals, 6 normal animals were trained to criterion on a brightness discrimination problem, whereupon 3 received collicular undercuts and 3 had sham operations. Another 12 animals were run as normal/neonatal operate pairs. Each pair received identical handling, and the experimenter was not aware which animal was normal and which was the neonatal operate. When both members of the pair reached criterion, they were identified, and the normal animal then received a collicular undercut. These animals were also assessed for distractibility and orientation to sunflower seeds.

The remaining two normal animals were trained to do a pattern discrimination and then were given collicular undercuts. The visual orienting capacities of these two animals were assessed in detail by videotape analysis.

Surgery

Neonatal collicular lesions were performed in the manner described by Schneider (1970). Within 24 h of birth, a litter of hamsters was removed from the mother and cooled to provide anesthesia and reduce mobility. A slit was made in the scalp overlying the colliculi, which are visible through the cartilaginous cranium and whose boundaries are marked by the transverse sinuses and the occipitointerparietal suture. The colliculi were destroyed by heat lesion directly through the cranium, using an appropriately shaped heated wire. The scalp incision was then closed with one or two sutures. Upon completion of surgery, the animals were returned to the mother and allowed to mature normally.

In adult hamsters, the superior colliculi were undercut stereotaxically by the method described by Schneider (1967). The animals were anesthetized with thiopental (Nembutal, .08 mg/100 g). A slit, 7 mm wide, was made in the cranium 1.8 mm posterior to the lambda point. Into this slit, a specially formed scapel blade was introduced at an angle 55 deg from the vertical, and drawn back and forth to undercut the superior colliculi bilaterally. Sham operations were identical, but without the scalpel insertion.

Apparatus and Training Procedures for the Brightness and Pattern Discrimination

The apparatus, shown in top view in Figure 1, consisted of an open box with a floor space of 45 × 90 cm with walls 28 cm high. The floor and three walls were painted white. Three 8 × 8 cm rectangular openings were evenly spaced, 30 cm apart, on the fourth wall; this wall was painted black. An indicator light (Sylvania No. 120 MB) was mounted over each opening. The hamsters entered the arena from an enclosed startbox, through a door centered on the opposite wall.

Background lighting was provided by a shaded 100-W bulb approximately 2 m from the apparatus. Luminance of the dark wall was .20 cd/m²; the indicator lights produced a local illumination of 58.93 cd/m². Trials were videotaped with a Model 1610x Sanyo videocamera mounted above the apparatus.

The brightness discrimination task consisted of choosing the illuminated opening. The hamster was given 15 sec after entering the arena to make a choice. Correct choices were rewarded by

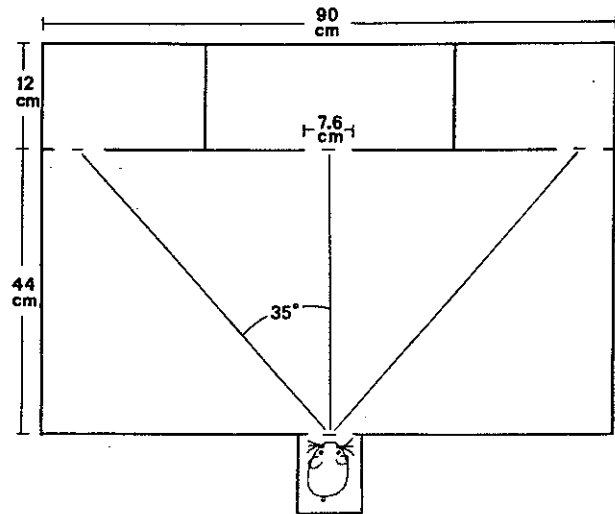


Figure 1. Overhead view of apparatus design used to train and test all subjects. The arena was uncovered, whereas the startbox was enclosed. The three lines (not present in the actual box) represent direct approach routes to the open doors. Each door was 8 × 8 cm and directly beneath an indicator light. Removable clear plastic doors were used to cover incorrect doors. The water reward was behind each door at all times.

access to two drops of water on a glass slide behind the goal opening and a 10-sec reinforcement period; incorrect choices resulted in a firm nose bump against the clear plastic barrier to the two other openings and termination of the trial. Water was always present behind all three doors. The position of the illuminated door was changed in a pseudorandom sequence so that no door was designated correct for more than three consecutive trials. Each animal was run through 30 trials a day for 5 days a week until a criterion of 80% correct choices was achieved.

For each trial during training the following were recorded: time to door (from when the hamster's rear legs left the startbox to the time its vibrissae touched the plastic of the incorrect door or its head entered the correct opening), method of approach (classified as "direct," "edge" if by way of the box perimeter, or "indirect"), scanning (as defined by the hamster directing its nose toward at least two different openings, before traveling more than one body-length from the startbox), and door of choice. A choice was judged incorrect and the trial terminated if the animal came within vibrissae-length of the incorrect doors. A quantitative analysis of these same parameters was made from the videotapes of criterion and postlesion runs. All results presented for time to door, approach, path length, and scanning during training were taken from the 12 normal/neonatal operate pairs. The data from the remaining three adult operates and three sham operates were added only to the results for scanning at criterion and accuracy of the postoperative brightness discrimination.

Since two possible cues to correct door were available—the indicator light and the clear plastic barriers on the incorrect doors—animals that had reached criterion were run on 2 separate days either without lights or without plastic barriers for 15 of the 30 trials, to determine which cue was critical to the task. The same procedure was done postlesion to determine if the cue had changed. A reliability measure was made of the videotape scoring of scanning. A randomly selected series of 30 trials was rescored by the same scorer with 90% reliability.

After normal hamsters reached criterion and other orienting data were collected, the superior colliculi were undercut. All animals survived, and they were given 3 days for postoperative recovery. Postoperative training continued until criterion was reached for at least 2 consecutive days.

Pattern discrimination and visually guided locomotion were assessed in an identical fashion. A card, 7.4 × 7.4 cm, with either wide or narrow stripes, was mounted over the correct door in the same position that the indicator lights had been. Wide stripes (subtending 4.7 deg per cycle from the startbox door) were always the positive stimuli; narrow stripes (.6 deg per cycle) were mounted over the negative doors. Contrast of the wide and the narrow stripes was the same (approximately 1 log unit) and the average luminance was 4.45 cd/m². This task, a difficult one for hamsters, was chosen in order to maximize the utility of scanning. The hamsters were able to reach only 60% accuracy on this task.

Tests of Visual Orienting

Orienting to novel stimuli was assessed during the brightness discrimination test in a manner analogous to that of Goodale and Murison (1975), but using louder and brighter distractors. Distracting stimuli—a flashing 200-W light bulb located to the rear left of the arena and synchronized with the sharp clang of a wooden dowel on a metal trash can—were added to Trials 9, 14, 19, and 24 in a series of 25 trials on the day following the criterion run. This series of runs was videotaped. For the animals trained in the pattern discrimination, a less massive distracting stimulus was employed—two flashing indicator bulbs without additional auditory distraction.

Orientation to sunflower seeds was assessed by the method of Schneider (1969). The 12 normal/neonatal operate pairs were tested informally for orienting to sunflower seeds 60, 90, and 120 deg from the midline (0 deg) in the hamster's horizontal plane. Seed pursuit was also scored. The orienting of the two animals trained in the pattern discrimination was assessed quantitatively with videotape analysis (Finlay et al., 1979).

Histology

Lesioned animals were perfused with 10% formol saline. Brains were removed, embedded, and cut frozen in 30- μ m coronal sections. Every fifth section was stained with cresyl violet and reconstructed with the aid of standard dorsal and lateral view reconstructions of the midbrain (Finlay, Schneps, Wilson, & Schneider, 1978; Schneider, 1969).

RESULTS

Extent of Lesion

Of the nine animals that received collicular lesions, on reconstruction all showed evidence of collicular damage, though of markedly varying amounts. Four had essentially complete collicular undercuts, as demonstrated in Figures 2 and 3 (animals 93, 42, 35.9, and 35.8). A series of three coronal sections for animal 42 is shown in Figure 4, to demonstrate the extent of the undercut with respect to collicular laminae. These lesions isolated the superficial and a variable amount of the intermediate gray layers from the deeper layers of the superior colliculus bilaterally. A minor amount of tectum was not undercut at the farthest lateral margins, which would represent the extreme lower and temporal visual field. At the most rostral levels, the undercut was deep to the stratum opticum and superficial gray, which might serve to spare ascending tectal projections; however, this was also characteristic of the undercuts made by Schneider (1969, 1970). There was some invasion of caudal diencephalon bilaterally, deep to the pretectal nuclei and optic tract; it is not clear what fibers of passage

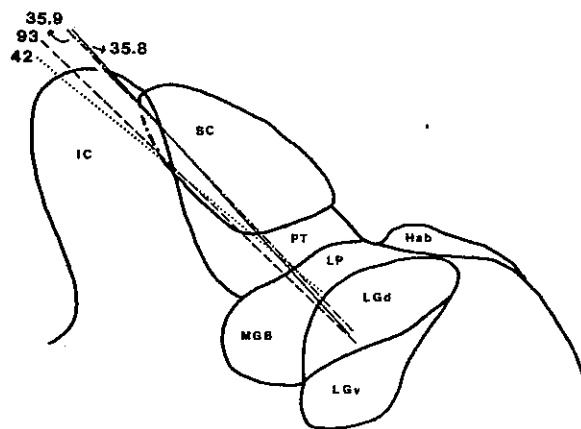


Figure 2. Lateral view outline drawing of adult hamster mid-brain showing angle and depth of scalpel penetration for operates receiving superior colliculus undercuts: 35.9, 35.8, 93, and 42. Abbreviations used: IC, inferior colliculus; SC, superior colliculus; PT, pretectal area; MGB, medial geniculate body; LP, lateral posterior nucleus; LGd, dorsal lateral geniculate nucleus; LGv, ventral lateral geniculate nucleus; Hab, habenula.

such a transverse section would interrupt in posterior thalamic nuclei. Minimal damage to inferior colliculus occurred.

Of the remaining five animals, three received complete unilateral undercutting of the superior colliculus and moderate damage to the remaining side. One had marked damage to rostral superior colliculus, and also damage to pretectal nuclei and nucleus lateralis posterior of the thalamus. A final animal had only minimal damage to medial and most superficial tectum. For any data representing average group performance, data from all animals with major collicular undercuts are pooled, eliminating the one animal with minor medial damage. When individual differences did occur that reflected amount of collicular damage, individual performance is presented.

Lesion extent in the animals subjected to heat lesion of the superficial layers of the superior colliculus at birth was remarkably uniform and similar to lesions reported previously by Finlay (1979), Finlay, Marder, and Cordon (1980), and Schneider (1970). The entire superficial gray layer of the superior colliculus was removed, with the exception of minor sparing at the most lateral margin. Lesions were deepest medially, extending to approximately the surface of the central gray; laterally, about half of the normal volume of the intermediate gray was removed, as computed from subsurface landmarks. Pretectal nuclei could still be identified, as could the inferior colliculus, which intruded into the space vacated by the superior colliculus. This extent of lesion has been shown in electrophysiological studies to be associated with a spared representation of nasal and lower nasal visual

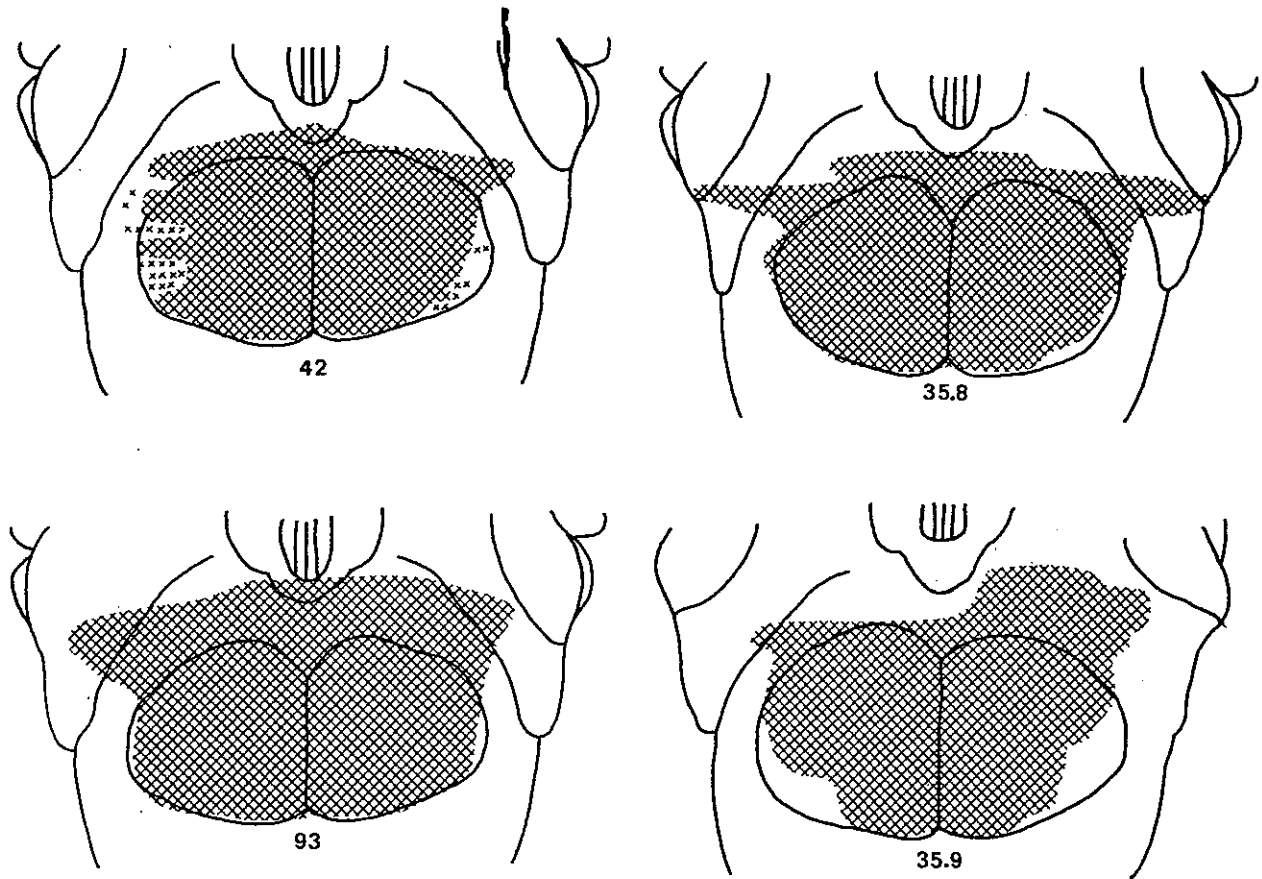


Figure 3. Dorsal view outline drawing of adult hamster superior colliculus. Cross-hatched areas indicate extent of lesion as determined from reconstructions of four operates: 42, 35.8, 93, and 35.9. Xs indicate superficial damage.

field in the deep layers of the remaining intermediate gray (Finlay, 1979).

Effects of Collicular Lesions on Visually Guided Locomotion

Shown in Figure 5 is the rate at which the normal and neonatally operated hamster groups learned the brightness discrimination task. It is clear that the performance of the two groups is nearly identical. Mean number of trials to criterion for normals was 480.8 ± 46.3 and for neonatal operates was 465.8 ± 83 ($t = -.161, p < .88$).

The cue that the animals used to perform this discrimination was the brightness difference. Since water was present behind every door, it could not supply a differential cue. When the cue lights were not present, both the normal and neonatally operated animals' performance fell to chance (average for normals was $37\% \pm 4.4\%$; for neonatal operates, it was $45\% \pm 5.7\%$). Conversely, when the clear plastic barriers to the incorrect doors were removed, but the light cue was maintained, the animals in both groups remained at criterion (normals, $76\% \pm 3.7\%$; operates, $84\% \pm 3.8\%$). The same dependence on the light cue was true after surgery for the adult operates.

The postoperative performance of the nine hamsters receiving a collicular undercut and the three sham operates is shown in Figure 6. All of the sham operates were back to criterion performance within 3 days of postoperative testing, as was the hamster with minimal collicular damage. However, two of the animals receiving complete collicular undercuts were also performing at criterion within 3 days, and the remaining two (42 and 93) reached criterion at 8 and 11 days, respectively. The animals showing the longest recovery period were 91, the hamster with extensive damage to the pretectal nuclei and posterior thalamus, and 93, whose lesion also invaded posterior thalamus (Figure 3).

Scanning

No difference emerged between groups in type of route taken to the goal door, all groups taking the most direct route preferentially (normal animals, 75% ; neonatal operates, 69% ; adult operates, 72%). We measured directly from videotapes the precise path length to goal door at criterion for a set of 9 trials for 3 animals from each of three groups. When Door 1 was the correct choice, the average path length for normals was 58.2 ± 2.3 cm; for adult operates,

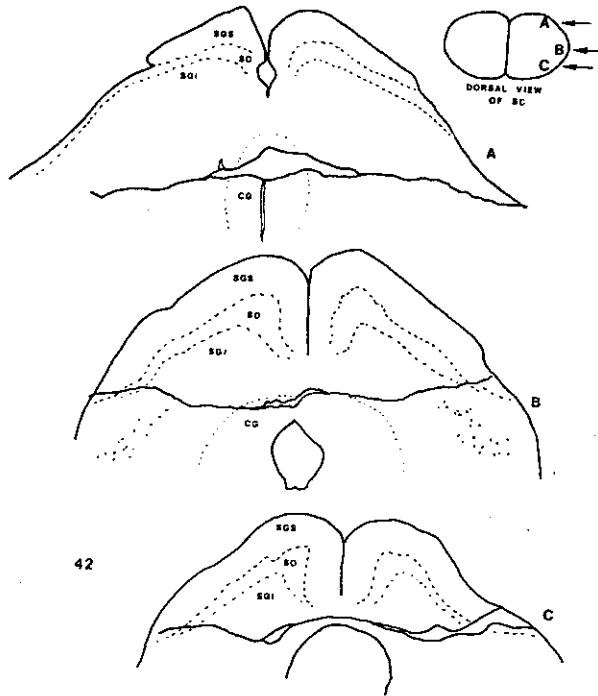


Figure 4. Drawings of cresyl-violet-stained coronal sections from the brain of adult operate 42, showing degree of superior colliculus undercut. Drawings A to C represent rostral to caudal sections, respectively. Abbreviations used: SGS, stratum griseum superficiale; SO, stratum opticum; SGI, stratum griseum intermediale; CG, central gray area (stratum griseum centrale).

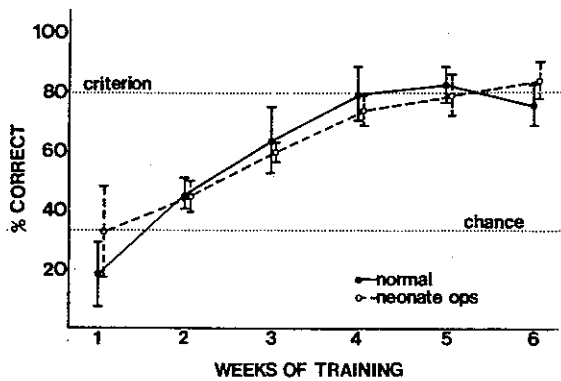


Figure 5. Learning curves for normal, N=6, and neonate operate, N=6, hamsters. Performance was measured by percent correct out of 30 trials per day averaged over a 5-day week for 6 weeks. Trials in which no door was approached were not averaged. Bars represent two standard errors from the mean.

it was 60.3 ± 3.6 cm; and for neonatal operates, $55.2 \pm .6$ cm.

Time to door was also measured from the videotaped criterion runs. Normals averaged 3.25 ± 1.75 sec, adult operates 3.0 ± 1.2 sec, and neonatal operates, $1.4 \pm .4$ sec. In this case, although neonatal operates

run somewhat faster than normals, the difference is not significant ($t = -1.25, p < .26$). What is striking is the much greater variability in time to the goal door of the normals.

Two additional hamsters were trained on discrimination of low- and high-frequency stripes of equal contrast, and then given collicular undercuts. Both lesions were large. One hamster had a complete unilateral undercut through the ventral margin of the stratum griseum profundum on the left side and major damage to the right side sparing the rostralateral quadrant of the colliculus; the other had an undercut deep to the superficial gray on the left extending to the lateral margin of the midbrain, and a very deep, but not laterally extensive, lesion on the left, coterminous with the dorsal aspect of the central gray. One performed at preoperative levels within 2 training days, the other within 11 training days.

Careful observation of the strategy employed by the normal hamsters and neonatal and adult colliculus-ablated hamsters in execution of the brightness discrimination task did disclose a major difference in the behavior of the animals at trial initiation. Upon leaving the startbox, the normal hamsters would briefly pause or rear and look toward (as taken from head position on videotape) two or more doors in the array confronting them. They performed this scanning motion approximately three-quarters of the time (Figure 7). Neonatal operates and adult operates rarely showed this pattern; both groups are highly different from the normal hamsters [one-way ANOVA, $F(2,14) = 90.60$], but not different from each other (Newman-Keuls test on pairwise comparisons, $p > .05$). Pair 6 includes an inadvertant control animal, the

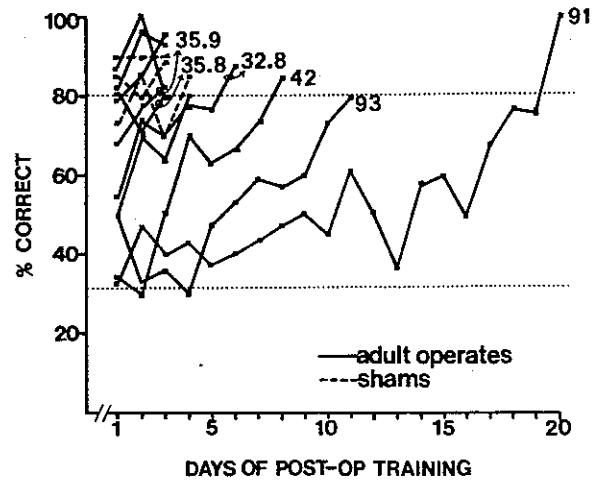


Figure 6. Post-operative performance for adult operates, N=9, and sham operates, N=3. Performance was measured by percent correct out of 30 trials per day until criterion level was achieved. Trials in which no door was approached were not averaged. Bars represent two standard errors from the mean. Animals discussed individually in the text are labeled.

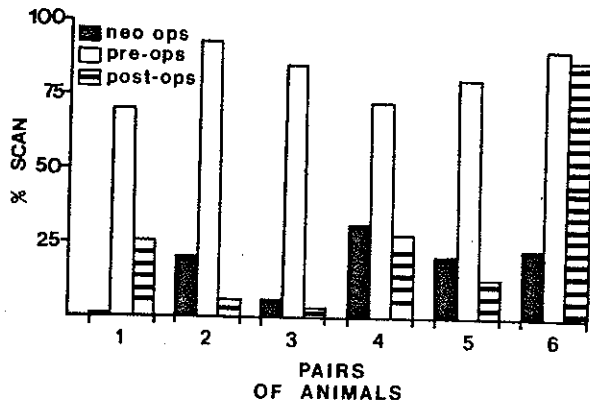


Figure 7. Percent of trials in which scanning was observed for normals, $N=6$, and neonatal operates, $N=6$, as measured from 30 trials per day over a 5-day week for 6 weeks of training. Scanning was defined as the animals' midline directed towards at least two doors within one body-length from the startbox. The right side of the graph shows the percentage of trials during criterion performances in which scanning was observed. Criterion scanning was also assessed from videotaped trials for normals, $N=12$, neonatal operates, $N=6$, and adult operates, $N=8$. In all cases, trials in which no approach was made were not averaged. All bars represent two standard errors from the mean.

animal that received only minor midline damage. Since we were unaware of the inadequacy of the lesion when scoring this animal, it serves as a control for the fact that the experimenters were not blind to the condition of the adult postoperative animals. It is interesting both that the adult collicular undercut need not be total to produce a major deficit in scanning (pairs 1, 4, 5), and that these three pairs also show relatively, though not significantly, more scanning than the two complete undercuts, pairs 2 and 3.

Since hamsters could clearly perform this task with the normal amount of error and the same evidence of visual guidance without "scanning," one might question whether this behavior was, in fact, related to the visual aspects of the task at all. Evidence that scanning is related to the visual demands of the task comes from the changing behavior of the hamsters during training (Figure 8). Neonatal operates started at a low level of scanning and did not increase their scanning rate over training; normal hamsters started at a significantly higher base rate ($t = -3.31, p < .01$) and increased markedly in their rate as they learned the task.

Orienting to Novel Stimuli and Food

Disruption of ongoing activity and orientation to a distracting stimuli was measured for all groups during performance of the brightness discrimination. Shown in Figure 9 is the increased time of all groups to reach the goal door on those trials where distraction was introduced. All groups' performances, in terms of increased time, were equally disrupted by this distraction.

All groups show orientation to the distractor, though not at a high rate: normals on 23% of the trials, neonatal operates on 23% and adult operates on 15%. Cessation or slowing of activity without a head turn was more common.

The two animals trained on the pattern discrimination were distracted by the flashing of an additional indicator light only. Although, with this number of animals, these data must be regarded as tentative, prior to surgery the animals showed an average increase of 222% in time to door on distraction trials, and following surgery, time was 98% of normal.

Orientation and pursuit of sunflower seeds was tested in all adult hamsters pre- and postoperatively, and for all neonatal operates. Preoperatively, all hamsters turned toward seeds presented at 60, 90, and 120 deg from midline in the horizontal plane. For the four animals with complete collicular undercuts, taking right and left visual field presentations

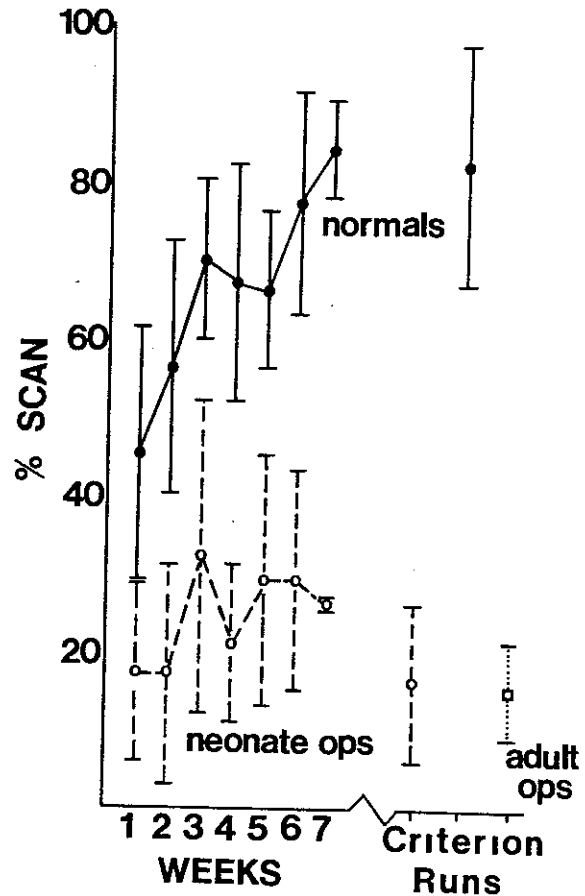


Figure 8. Percent of videotaped trials at criterion in which scanning was observed. Six pairs of hamsters are shown including scores of the neonatal operate, normal adult, and the same adult postoperatively for each pair. The pairs, from 1 to 6, were (1) 35.6 and 35.10, (2) 35.7 and 35.9, (3) 35.11 and 35.8, (4) 32.3 and 32.6, (5) 32.9 and 32.5, and (6) 32.4 and 32.8.

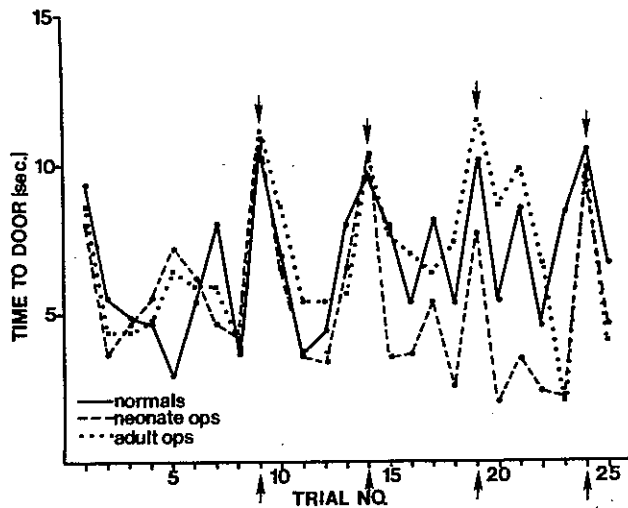


Figure 9. Time latencies, as measured by time of door approach during 25 trials for normal, $N=6$, neonatal operate, $N=6$, and adult operate, $N=5$, hamsters at criterion. Added to Trials 9, 14, 19, and 24 (indicated by arrows) was a massive auditory and visual distraction.

as separate observations 5 of 8 observations were positive at 60 deg, 7 of 8 were positive at 90 deg, and 1 of 8 was positive at 120 deg. No neonatal operate failed to orient at 60 deg. At 90 deg, of five neonatal operates tested, 6 of 10 observations were positive at 90 deg; at 120 deg, only 1 out of 10 observations was positive. Pursuit of a moving sunflower seed was subnormal in both the adult and neonatal operate groups.

A more detailed quantitative analysis by videotape of sunflower-seed-evoked orienting movements was done on the two animals trained on the pattern discrimination whose collicular undercuts were described previously. The first animal had a deep and complete undercut of the superior colliculus on the left side; the lesion isolated all of the colliculus, including the deep gray layers, from more ventral midbrain. This animal showed no orienting movements of any kind in any location in its right visual field. By contrast, on the left side, where the lesion was also deep but did not extend to the lateral margin in the rostral part of the colliculus, visual orienting could still be elicited in the lower nasal visual field, the sector of superior colliculus spared by the undercut. This corresponds directly to the observations of Schneider (1969).

The other hamster whose undercut was complete on the left side, though much more superficial, undercutting only the superficial gray and stratum opticum, showed a performance characteristic of the other animals tested informally for orienting. It showed reliable, though slow, orientation to seeds presented in the right central and the lower nasal

visual field. This hamster had an incomplete undercut on the right side, and showed turning to seeds presented in the lower left visual field.

In summary, the only type of lesion completely abolishing all orienting in the visual field was one including the isolation of deep and intermediate gray from surrounding midbrain. Isolations of only superficial gray spared orientation to stimuli presented to central and nasal visual field, but produced a marked deficit in the periphery.

DISCUSSION

Nature of the Deficit Produced by a Collicular Lesion in Hamster

Hamsters with collicular lesions presented a uniform and limited pattern of deficits in the battery of behavioral tests described here. When presented with a visual discrimination, they failed to spontaneously produce the scanning movements regularly shown by normal hamsters. When presented with sunflower seeds, they showed a pronounced deficit in ability to direct the head and body toward the seed, which was variable with the depth of the colliculus undercut. This disability varied with the position of the seed in the visual field; hamsters with isolated superficial gray and stratum opticum were often able to turn toward seeds in the anterior visual field, but showed a near total disability in the peripheral and upper visual fields. They could be distracted by and showed orienting movements toward striking novel stimuli that contained both visual and auditory components, but were less distracted than normal by visual stimuli alone.

By contrast, hamsters with collicular undercuts or neonatal lesions showed no evidence of a deficit in visual guidance to goals marked by brightness or pattern cues. There is other evidence of visually guided locomotion in hamsters with collicular damage: hamsters with collicular undercuts can note the edge of a visual cliff and choose the shallow side with normal accuracy (Finlay et al., 1980; Keselica & Rosinski, 1976), and they can locomote around stationary barriers with a speed and accuracy that is comparable to that of normal hamsters (Finlay et al., 1979).

This deficit may be described as the loss of a response mode, the ability to make head and eye movements to visual stimuli, which has implications for various types of orienting behavior. Although this deficit could be characterized as a deficit in attention, not a great deal is gained by such a description. For example, in the brightness discrimination task, the hamsters had demonstrably attended to the visual cue in order to perform the task, but did not show the motor pattern of spontaneous scanning. This response mode allows the hamster to acquire food

and investigate novel objects, as has been described for anurans (Ewert, 1970; Ingle, 1973). Keselica and Rosinski (1976) have shown that hamsters with collicular undercuts fail to use appropriate search and gathering strategies when presented with an array of sunflower seeds. A second use for this response mode might also be possible: animals with retinal specializations successively orient their eyes so that the area of interest falls on the area of greatest receptor density, improving discrimination. While the hamster does not have an area of marked retinal specialization, there is enough difference in receptor density between central and peripheral retina to suggest that this type of behavior might also prove useful to the hamster for some discriminations (Finlay et al., 1978; Tiao & Blakemore, 1976). We were unable to demonstrate this, however, in our pattern discrimination task.

Studies of the Function of the Superior Colliculus in Rodents

Like several other investigators (Dyer et al., 1976; Goodale & Murison, 1975; Keselica & Rosinski, 1976), we have failed to find evidence of a deficit in visually guided locomotion in rodents after collicular lesions, in contrast to the findings reported by Schneider (1969). Schneider's formulation is so compelling, however, that it is necessary to account for the discrepancy between laboratories in some detail. Three possibilities suggest themselves. First, since we did have two animals with rather profound, though not permanent, deficits in visual guidance whose undercuts included part of posterior thalamus and pretectum, it may be that some subsector of this complex is critical for visually guided locomotion and was consistently interrupted in Schneider's undercuts and not in those presented here. Second, some detail of the training procedure may be critical. In particular, two of our animals required a rather lengthy error correction period postsurgically in our procedure. Since approach errors were permitted in the paradigm reported by Schneider, hamsters may have been insufficiently motivated to change their behavior after a passing disability. Third, it may be that the discriminanda used by Schneider required that the animals scan the array in order to acquire enough information for a choice. If this is the case, approach to the discriminanda would be a plausible way of acquiring information if scanning were not possible.

Recovery of Function

Our evidence for recovery of orienting movements to sunflower seeds for neonatal operates vs. adult operates is not compelling, in contrast to Schneider (1970). As reported by Schneider (1970), neonatal operates showed consistent and reliable turning to stimuli presented in the central and lower visual fields, and failed in the upper and temporal visual

fields. Adult operates were somewhat more variable in performance: Adult operates whose lesions undercut deep gray as well as superficial gray showed no visually elicited orienting, while those with more superficial lesions performed in a manner similar to the neonatal operates. Since all neonatal operates showed some sparing of the intermediate and deep gray layers of the tectum, it is not clear whether the presence of an aberrant retinal projection to the remaining deep layers is critical (Schneider, 1970), or whether the sparing of some tectal tissue per se is the determining factor in the preservation of orienting capability.

Phylogeny of the Optic Tectum

As contradictions are resolved concerning tectal function for a variety of species, one is struck with the commonality of the deficits described as consequent to tectal ablation independent of the amount of neocortex.

The deficits shown by animals with large amounts of neocortex are, after tectal ablation, very similar to those shown by hamsters. Atectal hamsters, when confronted with a visual array, fail to make spontaneous scanning movements; atectal monkeys show little spontaneous ocular motility (Pasik & Pasik, 1964). Both hamsters and monkeys show a generalized loss of attentiveness, but both can continue to make orienting movements to stimuli in central visual fields and fail to attend to stimuli in peripheral visual fields. Localization of stationary targets by reaching is largely spared in monkeys and in cats after collicular lesion (Butter et al., 1978; Winterkorn & Meikle, 1977); in hamsters, the deficit in localization by whole-body movement is, if anything, less profound than that seen in monkeys and cats. Given the radical alteration in the amount of cortex devoted to representations of the visual field over two species, it is remarkable that the tectum remains so consistent in function.

For nonmammalian species, a complementary pattern has emerged. Although the optic tectum is the major projection zone of the retina, numerous visual capacities are maintained after tectal lesions. Cartilaginous fishes deprived of optic tectum can still do pattern discriminations and show visually guided locomotion (Graeber, Ebbeson, & Jane, 1973). Bony fish, though they cease to strike at food, show optokinetic nystagmus and various light reflexes (Springer et al., 1977). Turtles without tecta navigate normally on visual cliffs and show optokinetic nystagmus (Hertzler, 1972). Anurans, while ceasing to strike at food, retain other visually guided behaviors such as barrier avoidance (Ingle, 1973). In spite of massive alterations in size and complexity of neuroanatomical substrates, species as diverse as hamsters, dogfish, toads, and rhesus monkeys retain some very fundamental similarities in visual organization.

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