

A NEUROETHOLOGICAL APPROACH TO HAMSTER VISION

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SUMMARY

The contributions of the midbrain optic tectum to visuomotor behaviors likely to be important to hamsters in the wild were studied, including aperture detection, insect catching, and barrier avoidance. Following tectal undercuts, hamsters ceased to make direct approaches to apertures in the posterior 180° of the visual field; this appeared to be mediated by a loss of exploratory or scanning head movements. Reorientation to and pursuit of crickets jumping out of grasp into the visual periphery was impaired, though initial approach to them was not. Barrier avoidance was unaffected by tectal undercuts. This pattern is similar to the contribution of the frog and toad optic tectum to analogous visuomotor tasks. The contribution of the tectum to searching and scanning in the hamster is an extension of the basic orienting capabilities dependent on optic tectum in anurans.

INTRODUCTION

Both neuroethologists and physiological psychologists studying the vertebrate visual system propose to give a complete account of its functional neuroanatomy. To date, however, these accounts are rather disparate, due to two factors: basic theoretical approach, i.e. whether an evolutionary or mechanistic explanation is to be given; and choice of species, principally amphibians and fish for neuroethologists, and mammals and some birds for physiological psychologists. Due to the relative difficulty of extracting operant responses from amphibians and some reptiles, and the stereotypy of these animals' behavioral repertoires, neuroethologists working with these animals not only

choose to, but must work with natural categories of behavior. Physiological psychologists, typically working with mammals which can more easily be induced to press bars, open doors and run mazes, have worked with unnatural behaviors in unnatural settings, but have produced well-controlled analyses of defined perceptual tasks. This consistent correlation of species and experimental approach has led to an unfortunate discontinuity in our understanding of brain evolution and behavior: the visual world of non-mammals is apparently replete with the meanings of surface and barrier, prey and threat, mate and rival, while mammals appear to concern themselves with the more abstract dimensions of flux, spatial frequency, wavelength, pattern and place.

The functions of the midbrain tectum have been approached from both of these perspectives. In the mammal, deficits in attention and inability to orient, particularly to stimuli in the visual periphery, have been reported consequent to tectal damage, while flux, brightness and pattern discriminations are in general less impaired [1, 2, 16, 19, 24].

The functions of the anuran optic tectum (principally the frog, *Rana pipiens* and the toad, *Bufo bufo*) have been described from a neuroethological point of view: the recognition and capture of prey, and successful escape from visual threat depend on the integrity of optic tectum [5, 11], while the recognition and negotiation of surfaces and stationary barriers are not affected by tectal lesions [11, 13], but do depend upon the integrity of pretectal pathways [14].

We have asked neuroethological questions of a mammal, the hamster, one studied in some detail from the perspective of physiological psychology [6, 19, 20, 23]. The hamster is a solitary, nocturnal, burrowing animal, and is both granivorous and insectivorous. We have chosen to investigate those behaviors natural to hamsters similar to those that have been studied in anurans. Deficits caused by damage to the nervous system will be considered in regard to their effect on adaptive behavior. These behaviors are aperture detection and barrier avoidance [13] and prey recognition and capture [4, 11]. With this approach we hope to demonstrate the continuities of the functions of the midbrain tectum across species, as well as the changes in the contribution of the midbrain tectum to changing visuomotor requirements of new behavioral niches.

METHODS

Subjects

Thirty-eight Syrian hamsters (*Mesocricetus auratus*) were used in this study. Twenty-four male hamsters were used in the barrier avoidance study; a subset of 8 of these, and 4 additional males, were used for the cricket-catching study. A separate group of 6 females was used for the aperture detection study. Animals were housed individually in clear plastic cages on pine bedding, with

water, chow and sunflower seeds available ad libitum for the duration of the study, except where noted.

Surgery

In adult hamsters, the superior colliculi were undercut stereotaxically using a method slightly modified from the one described by Schneider [23]. Animals were anesthetized with thiopental (Nembutal, 0.08 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 thinned scalpel blade, 1 mm wide, was inserted 6 mm at an angle 55° from the vertical and drawn back and forth to isolate the superficial and intermediate layers of the colliculus from the brain stem bilaterally. In some animals, the scalpel was then raised, moved 0.5 mm more caudally, reinserted to the same depth and the procedure repeated.

Neonatal collicular lesions were performed in the manner described by Schneider [24]. Within 24 h of birth, a litter of hamsters was removed from the mother. Each hamster was cooled before surgery, to reduce mobility and blood flow, and provide anesthesia. An incision was made in the scalp overlying the colliculi, visible through the cartilagenous cranium. The superficial layers of the colliculi were destroyed directly through the cranium with an appropriately shaped heated wire. The scalp incision was then closed, the hamster warmed, returned to the mother and allowed to mature normally.

Ablations of posterior neocortex in adult animals was done by aspiration, the extent of the aspiration determined by skull coordinates. This preparation was used only in the barrier avoidance task.

Sham operations were not included because a previous study in this laboratory, also using videotape analysis, indicated no effect of sham surgery on the types of head movements studied here [19].

Behavioral tests

(A) *Aperture detection.* The apparatus for this experiment is diagrammed in Fig. 1, and consisted of a circular chamber, 76 cm in diameter, with 6 evenly-spaced doors around the perimeter. A white barrier, continuous with the perimeter wall, blocked 5 of the 6 doors, while the door that opened was inset and black. Hamsters started from the center hole, found the open door by any route, pushed the door open, descended under the apparatus, arrived back at the center opening where a sunflower seed could be found, and re-emerged from the center to begin another trial. While the hamster was under the arena, the open door was changed on a random schedule. Thus, the initial position of the hamster's head, relative to the open door, on emerging from the center hole was not controlled and repetitions were run until a satisfactory distribution of all possible head position/door position combinations was reached.

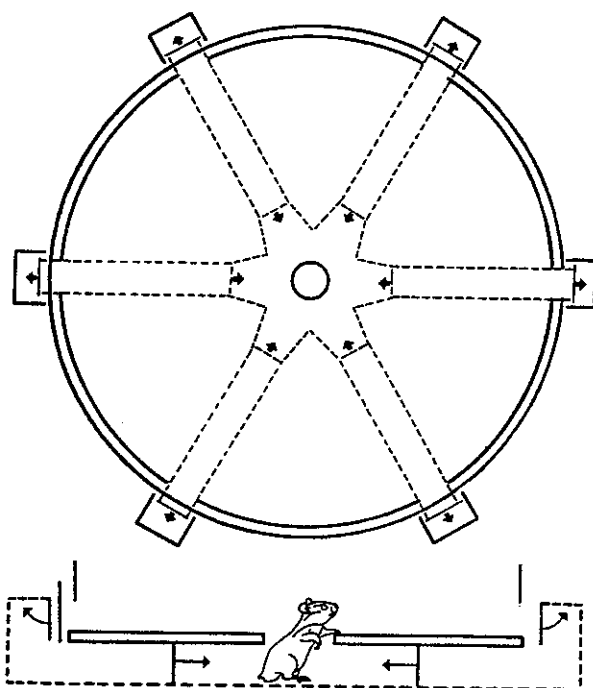


Fig. 1. Top view (above) and side view (below) of the aperture detection apparatus. Runways under the surface of the apparatus are indicated with dotted lines. Arrows indicate direction of opening of one-way doors. A hamster entered the arena from the center hole, found the one open door (inset and black) by any route, and pushed it open to descend under the apparatus. On return to the area under the center hole the hamster received a sunflower seed, and when the seed was eaten or pouched, it exited the center hole to initiate another trial. In the interim the hamster was under the arena, the open door was changed on a random schedule.

After initial habituation and training, hamsters ran rapidly in this apparatus, performing about 30 trials a day in 7–12 min. When performance was stable, the hamster was videotaped with a camera mounted directly overhead until approximately 10 trials were recorded at each of the 6 possible classes of initial head position relative to door position (straight ahead, 60° left and right, 120° left and right, directly behind). Then a tectal undercut was made, and the animal was given 4 days of postoperative recovery. Initial post-lesion behavior was videotaped for at least 3 weeks or until performance had stabilized. Stabilized performance was defined as no increase or decrease in total percentage of direct approaches over a period of a week.

Two animals with presumed neonatal tectal ablations were also trained in the apparatus beginning at 2 months of age.

Trials were scored by a frame by frame analysis of videotaped recordings. The angular orientation of the hamster's initial head position relative to the door was taken from midline of the hamster's head when its nose had emerged from the center hole and its eyes were in line with the edge of the hole. The

sequence of head movements made before a door choice was analyzed by advancing the tape 10 frames at a time (160 msec intervals) and recording the new head position relative to the initial one. A head turn was judged continuous until the hamster either reversed direction or paused for 160 msec. The final run to the target door was scored as 'direct' when the path to the target door, from a distance of one body length from the center hole, was approximately straight and the animal did not contact the side wall of the apparatus; otherwise the run was classed 'indirect'. The classification of 'direct' and 'indirect' runs by angle from the open door is taken from initial head position only.

(B) *Cricket catching*. The animals in this study were deprived of food until their weights were reduced to 85% of ad libitum weight. During testing, the animals were maintained at this weight and fed standard laboratory chow on a 23 h deprivation schedule.

Testing was carried out in a rectangular arena which measured 68 × 49 × 28 cm. The floor and sides of the arena were white and were covered with clear contact paper. A Sony videocamera was positioned 150 cm directly above the arena and each trial was videotaped. Each animal was given two habituation trials to acquaint him with the arena and with eating crickets (*Acheta domesticus*), which all hamsters did readily after a few attempts. The hamsters were then tested individually for 3 days, each test lasting 5 min. At the start of each trial, the hamsters were weighed, their vibrissae were clipped, and they were then placed in the center of the arena which had a cricket in each of its 4 corners. The hamster was allowed to roam and prey at will until all the crickets were consumed or until 5 min had elapsed.

After the 3 days, animals were randomly assigned to either of two groups, with 4 animals receiving collicular undercuts and 4 others bilateral enucleations. In a second experiment, because the enucleated animals did unexpectedly well, an additional attempt to determine the important modality for this task was made. The hearing of an additional group of 4 animals tested was temporarily impaired by blocking their ears with a silicone rubber gel. All animals were retested 7 days after surgery, or immediately after the ear blockage using the same procedure as above, for 3 days.

The videotapes were scored for each of 22 separable events, in 4 general categories: initial approach and search, reorientation and pursuit after cricket escape, consummatory behavior, and non-prey related behavior such as sitting, grooming and so forth. Each tape was scored once by the experimenter and once by a second observer unaware of the experimental group of animals with the occasional exception of the enucleates. The correlation between the ratings of the two observers was $r = 0.93$. Because of the distance and overhead angle of the videocamera and the black eyelid fringe of the hamster, enucleation was not always possible to discern.

(C) *Barrier avoidance*. Barrier avoidance was tested in an arena

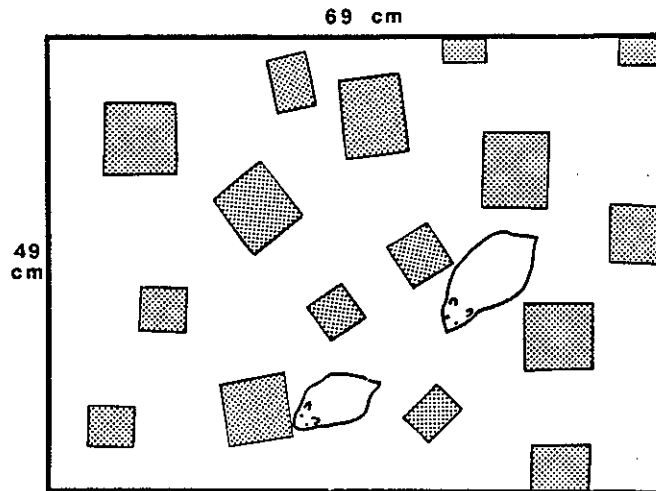


Fig. 2. Top view of the barrier avoidance apparatus. Hatched rectangles indicate solid wooden blocks attached to the floor as indicated.

59 cm \times 48 cm filled with 4.8 \times 4.8 cm and 7.2 \times 7.2 cm wooden blocks (Fig. 2). Young (between 3 and 4 months of age) and comparatively small male hamsters were chosen as experimental subjects. They were induced to run rapidly through this apparatus by one of a second set of 4 hamsters chosen for their large size and aggressive tendencies (the chasers). Each chaser was given 5–10 min to mark the box as his territory before the experimental hamster was introduced. Each experimental animal was run only once for 5–10 min. The chasers were apportioned as evenly as possible across experimental groups though complete counterbalancing was not possible due to the occasional and unpredictable disinclination of the chaser to chase. There was no overall effect of particular chaser on the experimental subject's velocity (4 tests, one per treatment type, largest $F = 3.25$; $df = 2,21$; $P > 0.05$).

Surgery (enucleation, 6 animals; superior colliculus undercut, 6 animals; posterior neocortex aspiration, 6 animals) was performed at least 10 days prior to experimental test. All experimental runs were videotaped and all scoring of videotapes was done by two scorers, one unaware of the experimental group of the hamster (with the exception of the occasionally visible enucleation).

Three performance measures were made: average velocity; relative percentage of time spent in run, walk or pause; and numbers of direct collisions with barriers or walls taken from two ten second samples of continuous running where the average velocity was between 18 and 20 cm/sec. the highest velocity range that included all groups. The choice of 10 sec samples was highly constrained by availability of running bouts of this length and velocity. Choices, when necessary, were dictated by uniformity of velocity throughout the run. Two second samples were chosen for uniform velocity.

Histology

After all behavioral tests were completed, animals with lesions were sacrificed with an overdose of anesthetic and perfused with 10% formal saline. Brains were removed, embedded and sectioned, stained with cresylecht violet and reconstructed with the aid of standard dorsal and lateral views of the hamster brain [7, 23].

RESULTS

Aperture detection

All 4 normal hamsters trained on the apparatus shown in Fig. 1 behaved quite similarly after their first few days of habituation. If a hamster chanced to emerge from the center hole such that the open door was in the 180° of the visual field directly in front of him, he would go directly to that door the great majority of the time (average, 93%). If the open door was behind the hamster, direct approaches were somewhat less frequent, but still occurred more than half the time (average, 62%).

Performance on this task after superior colliculus undercut is shown in Fig. 3 as the pre-operative to post-operative difference in direct approach to doors to the front and to the rear. All animals show a similar pattern. Direct approach is unchanged for the doors in the anterior 180° of visual field, and is considerably diminished for doors in the posterior 180°. For the 3 anterior doors there was no significant change over groups pre- to postoperatively (Wilcoxon signed-rank test, $T = -24$, $P > 0.05$). For the 3 posterior doors, the decrement in direct approach is highly significant ($T = -1$, $P < 0.001$). The two animals with the largest lesions showed the largest effect. Animal 51.2 had an essentially complete undercut, and animal 71.5 had a bilateral and complete transection of the brachium of the superior colliculus, which contains all retinal and cortical afferent fibers. Animals with lesser, but still large lesions show a major effect.

A change in strategy of executing this task for all hamsters with collicular undercuts may be seen in Fig. 4A and B. In A, trials where animal 51.2 made direct approaches to doors directly ahead, 60°L, 120°L and 180° pre-operatively (left) and post-operatively (right) are reproduced. The animal's head position is plotted each 160 msec and changes in head direction are indicated by a cross on the bar and a change from open to filled bars. Fig. 4B shows the same sequence for cases when the same hamster made indirect approaches to the door. These runs were not chosen to be unusually illustrative; they were simply the first instance of each class of run encountered on the videotape. The change in postoperative performance is clear. Animals spend little time scanning the arena and exit from the center hole directly. This lowered rate of head movements

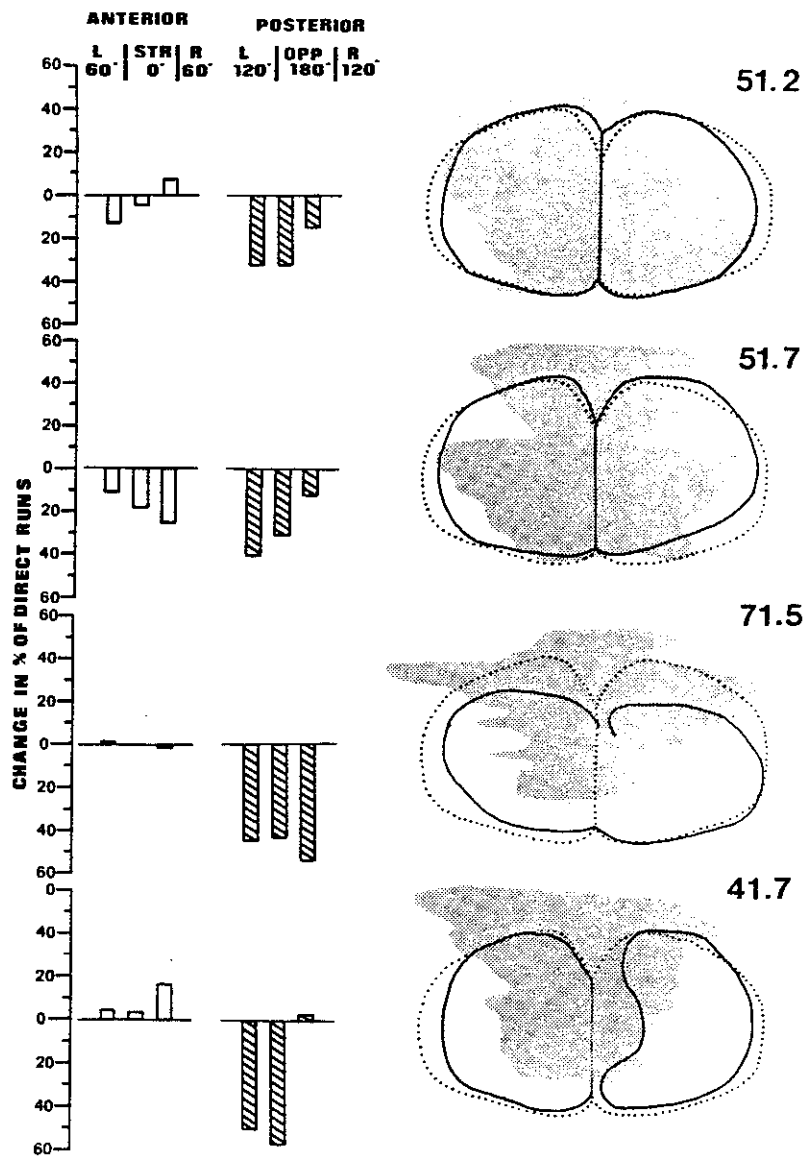


Fig. 3. Left: change in the percentage of direct runs pre-operatively to post-operatively for each hamster receiving a tectal undercut, for all initial head positions relative to the open door. White bars, anterior doors; hatched bars, posterior doors. Right: reconstruction of the extent of tectal undercut for each hamster. Dotted lines, normal extent of the superficial gray layer of the superior colliculus in dorsal view; solid lines, reconstructed size of the remaining superficial gray layer in each hamster; hatched area, extent of complete undercut of the superficial gray layer of the superior colliculus.

occurred in every hamster, including the hamster with the neonatal colliculus ablation (discussed below).

Prior to surgery, the hamster's initial head movement on exit from the

center hole was only partially predictable from the location of the open door relative to initial head position. If the door was in the anterior 100° of visual field, the hamster's first head turn was toward the door (76% direct turns, $\chi^2 = 38.31$, $P < 0.0005$) though subsequent head turns routinely were made away from the door before the hamster finally began an approach to the door (as in Fig. 4). Fifty degrees to the left and right of the midline was chosen to amply include all of the hamster's binocular visual field and the most acute sector of the hamster's visual field with the greatest visual acuity (the peak of receptor density for each eye is approximately 20° to the left and right of midline; the peaks of the two eyes do not coincide [7, 25]). In the posterior 260° of the visual field, the initial head turn did not relate to door position (56% of initial turns were toward the door, $\chi^2 = 3.77$, $P > 0.05$).

Post-operatively, all initial head turns were significantly predicted by door location (anterior 100°; 78% of turns were toward the open door, $\chi^2 = 42.75$, $P < 0.0005$; posterior 260°, 65% turns toward door, $\chi^2 = 23.48$, $P < 0.001$). This effect can be explained by the deletion of exploratory head movements in the colliculus ablated animals; the animal's first head turn usually marked the beginning of his door approach (as in Fig. 4); however, a significant amount (35%) of these approaches were in error.

The animal with the most complete undercut, 51.2, was selected for detailed analysis of 25 pre-operative and 25 post-operative trials. His performance showed that there was not an across-the-board loss of all head movements, but selective loss of large amplitude head movements (Fig. 5) corresponding to the selective deficit in peripheral visual field approach ($\chi^2 = 13.94$, $P < 0.05$).

Two animals with presumed neonatal collicular ablations were also trained on the task. On reconstruction, only one proved to have a collicular lesion, which included all of the superficial gray bilaterally, but spared some intermediate and deep gray on the lateral brainstem margins. The animal which proved to have received no lesion of any kind had behavior quite similar to all other normal hamsters in frequency of direct approach (0°, 86%; 60°R, 90%; 60°L, 100%; 180°, 50%; 60°L rear, 75%; 60°R rear 71%). The performance of the hamster with the collicular ablation was markedly different; although he approached doors in front directly more than half the time (0°, 89%; 60°L, 54%; 60°R, 86%), he rarely approached doors to the rear directly (180°, 10%; 60°L rear, 7%; 60°R rear, 36%). In general, his performance was quite similar in pattern and worse overall than the performance of animals given collicular undercuts as adults.

A prior study of a similar door-choice problem in our laboratory [19] showed that sham operations had no effect on scanning head movements. The fact that the one hamster with neonatal tectal damage shows the same pattern supports the observation that tectal damage and not acute surgery per se affects head movements.

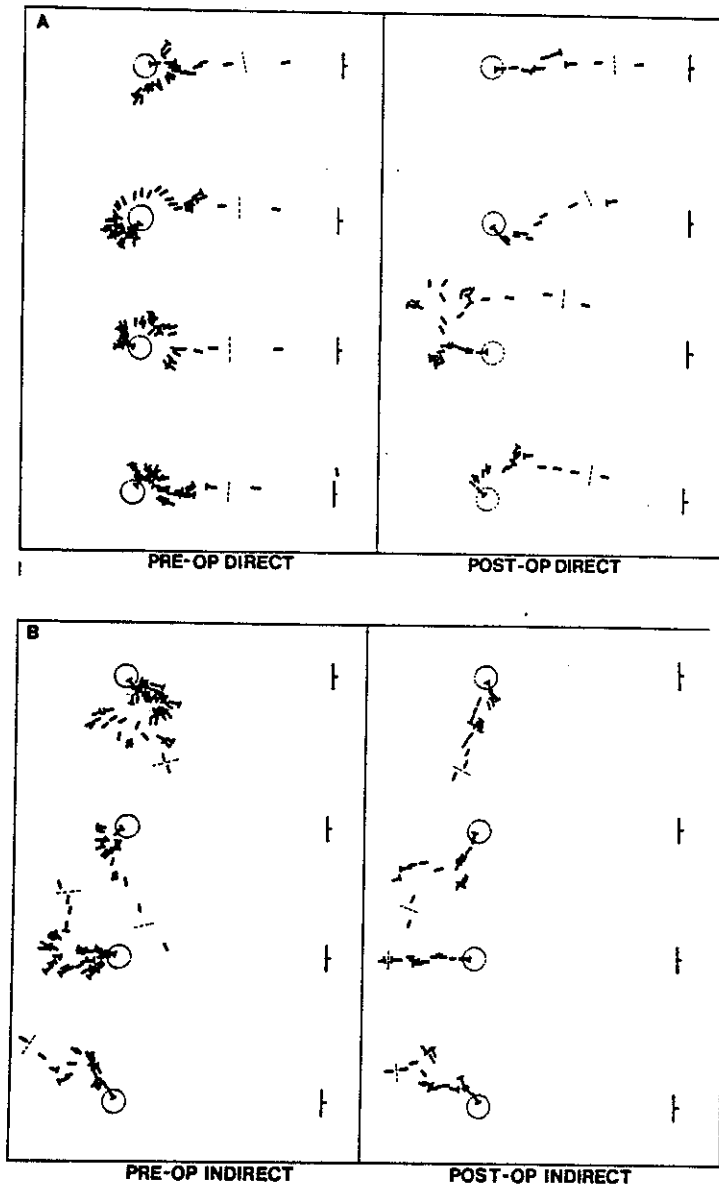


Fig. 4. Successive positions of a hamster's head (51.2) taken from videotape, on exit from the center hole of the aperture detection apparatus for 4 classes of door approach. A, left: direct approaches to door, pre-operatively, for 4 initial head/door positions. A, right: post-operative direct approaches. B, left: pre-operative indirect approaches. B, right: post-operative indirect approaches. Dotted circle shows center hole. Dotted line, one hamster-body length from center hole; solid bar to right, position of open door; lines, position of hamster's head each 160 msec. Change in direction of head movement is marked with a bar on the line.

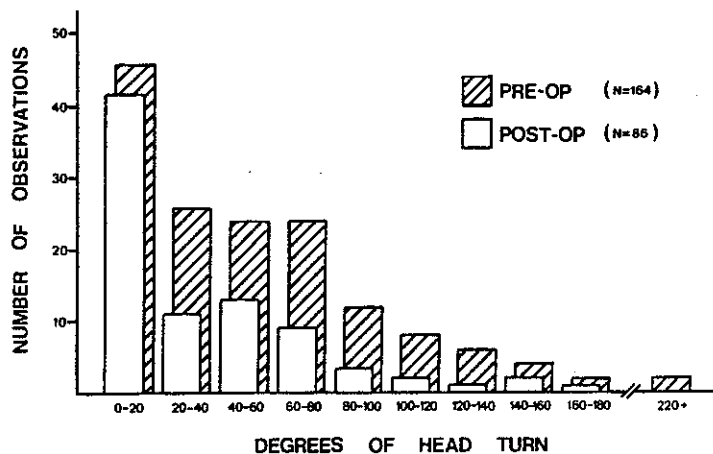


Fig. 5. Amplitude, in degrees, of continuous head turns by hamster 51.2 for 25 pre-operative and 25 post-operative aperture detection trials.

Cricket catching

Qualitative observations of prey catching in the normal hamster revealed evidence of both a systematic search procedure, and quick reactivity to cricket movement during a chase. Since the hamsters and crickets were both free to move about the arena, encounters between the two could occur at all possible locations. Since many crickets remained in their initial corner, however, hamsters appeared to incorporate this fact into a search strategy and approached corners first as they began their search. Hamsters became quicker and moved more efficiently until it became rare that they would advance in any direction but toward a cricket.

A normal hamster would begin a search by first turning his head from side to side several times, and then moving toward a cricket, usually one of those that chanced to be in front of him. When close enough, the hamster would stretch out his neck and attempt to capture the cricket with his mouth. If successful, the hamster would consume the cricket; if unsuccessful, the hamster would pursue the cricket by twisting his head or moving his body, depending on how far the cricket had moved and attempt again, until the cricket was caught and consumed. The hamster would then approach a new victim and repeat the sequence. At first videotaping the average time taken for a normal hamster to catch and consume 4 crickets was 104 sec.

Animals with collicular lesions turned their heads somewhat less frequently on initial search (normals, $\bar{x} = 5.16$, undercuts, $\bar{x} = 3.83$). As in the aperture detection task, although initial approach and orientation did not appear abnormal, when a cricket jumped behind or to the side of the hamster, it would

often not pursue the cricket, but rather move off after the next closest cricket. Consummatory behavior was normal in appearance.

Normal hamsters with ears temporarily plugged with silicone resembled animals with collicular undercuts; their initial approach to a cricket did not appear to be qualitatively or quantitatively abnormal, but they quite often failed to pursue crickets that jumped to the rear or out of their visual field.

Enucleated animals did not appear to search out or directly approach stationary crickets, and would often walk by one apparently unaware of its presence. If the cricket moved, or the hamster collided with it, the hamster would immediately orient and approach, then attempt to maintain contact and capture it. If the cricket jumped away, the hamster would sometimes move in the proper direction, but if contact was not quickly re-established, the hamster would cease pursuit.

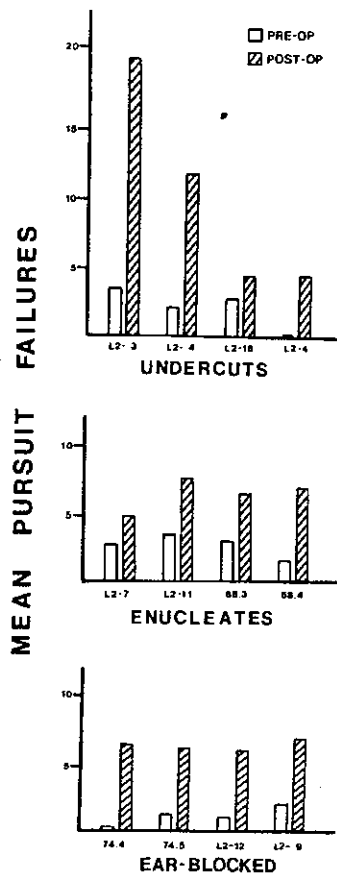


Fig. 6. Pursuit failures for individual hamsters before and after either superior colliculus undercut, enucleation or ear blockage during attempts to capture 4 crickets. A 'pursuit failure' is either a failure to pursue a cricket, or a mis-orientation after a cricket was contacted, escaped, and jumped out of reach. White bars, pre-operative pursuit failure rate; hatched bars, post-operative pursuit failure rate.

The quantitative results for cricket pursuit after an unsuccessful capture attempt for all 4 groups are shown in Fig. 6. When an animal oriented inappropriately after a cricket escape, or did not pursue it, it was scored as a pursuit failure. All groups showed a significant increase in pursuit failures post-operatively. The colliculus undercuts as a group had a pre-operative mean of 1.9 pursuit failures as compared to a post-operative mean of 9.2 ($t = 2.39$, $df = 3$, $P < 0.05$), the enucleates, 2.6 pre-operatively compared with 5.7 post-operatively ($t = 3.97$, $df = 3$, $P < 0.02$), and ear-blocked, 1.5 versus 6.83 ($t = 11$, $df = 3$, $P < 0.01$). These results are consistent with both an auditory and visual contribution to the re-orientation and pursuit process, and a major contribution of the superior colliculus, perhaps reflecting the integration of the auditory and visual information in the superior colliculus.

Lesion extent paralleled the extent of the pursuit failure deficit. Animal L2-13 had a deep and complete bilateral lesion, undercutting all of deep and intermediate gray from the surrounding midbrain, as well as the most dorsal part of central gray. L2-14 had a lesion of similar bilateral extent, though not as deep; all of superficial gray was isolated or damaged. L2-18 and L2-4 had primarily unilateral lesions.

No significant differences appeared in measures of initial approach to crickets, which appeared qualitatively abnormal only in the enucleate group. All post-manipulation groups took somewhat longer to locate and contact crickets, the enucleates taking by far the longest: enucleates, 109.2 sec pre-operative, 142.4 post-operative; ear-blocked, 99.2 sec pre-operative, 121.1 post-operative; colliculus undercut 103.9 pre-operative, 127.2 post-operative. For the ear-blocked and superior colliculus undercut animals, the fact that approach and search time was not markedly different serves as an indication that motivation to gather crickets was not substantially altered by the manipulation.

Threat and barrier avoidance

The extent of the visual cortical lesions is shown in Fig. 7. The same animals given collicular undercuts in the cricket-catching study were used in the barrier avoidance study.

Stringent criteria were used to define a collision with a barrier in this naturalistic condition: only direct, nose-on collisions with barriers were scored as collisions. For each hamster, 20 sec of chase was scored, this chosen with a narrow velocity window (between 18 and 20 cm/sec, a good run, but not a maximum-speed scramble for a hamster).

Animals with undercuts of the superior colliculus were not different from normal in their collision rate (normal collision rate = $2.3 + 0.46$, superior colliculus undercuts $2.44 + 0.35$, $t = -0.32$, $df = 8$, $P > 0.05$). Enucleates (collision rate = $3.8 + 0.37$) collided with barriers more significantly than both normals

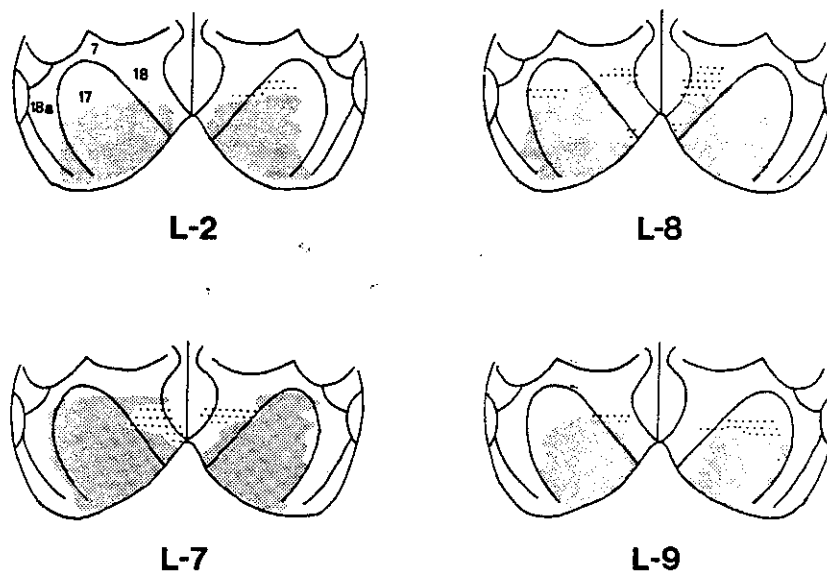


Fig. 7. Extent of cortical damage in animals used in the barrier avoidance task. Stippling indicates complete cortical ablation, and small dots partial damage.

and superior colliculus undercuts (enucleates vs normals: $t = -25$, $df = 8$, $P < 0.025$). Animals with striate lesions had a collision rate similar to the enucleates (3.2 ± 0.52), but the comparison with normals did not reach statistical significance ($t = -1.3$, $df = 9$, $P < 0.21$).

Average velocity over the entire behavioral sample showed again only a difference for enucleates. The average velocity of enucleates was significantly reduced by loss of the upper velocity range. Enucleates never exceeded a velocity

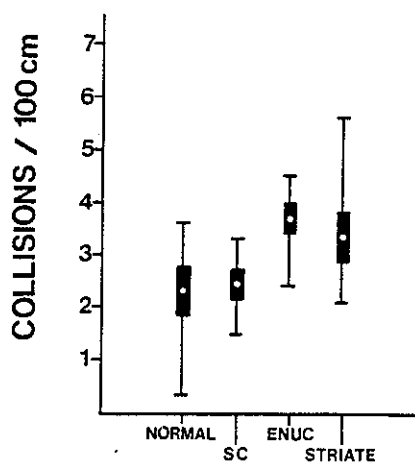


Fig. 8. Numbers of direct collisions with barriers per 100 cm run in the barrier avoidance experiment for each experimental group. Dark bars, one standard error of the mean; bar, range of all observations.

of 26.4 cm/sec, while 34% of the normals exceeded this rate. Neither the superior colliculus undercuts nor the posterior cortex-damaged animals were significantly different from normal in average velocity or velocity range.

DISCUSSION

Nature of the functions dependent on the superior colliculus in hamster

Hamsters with collicular lesions show a consistent pattern of deficits that manifest themselves in a variety of tasks where the visual direction of behavior plays a role. Orienting head movements of at least two kinds are involved: (1) orientation to particular objects in the visual periphery, such as sunflower seeds or crickets, where the goal is often grasp of the object by mouth, and (2) exploratory or investigatory head movements where acquisition or inspection of a designated target does not appear to be the goal of the behavior. Consequent to these losses, a variety of behaviors likely to be important in natural settings are altered. Hamsters fail to locate apertures in the visual periphery, lose track of prey, and show inefficient seed-gathering strategies [17]. Spared is approach to a variety of visual targets in ventral visual field, including seeds, crickets and apertures, as well as the ability to avoid stationary barriers while moving.

The orientation deficit might either be perceptual or motor in nature; the animal may either be failing to detect peripheral stimulation, or may simply have lost the ability to make an orienting movement. Since single neurons of the superior colliculus are often both 'sensory' and 'motor' in their response, it is likely the behavioral deficit is dual in nature [21, 26]. Several investigators have been able to show a deficit in reaction to visual stimuli in the visual periphery in animals with collicular lesions [9, 16], and this interpretation is consistent with the hamster data for stimulus-elicited orienting to seeds, crickets and apertures.

In the hamster, there also appears to be a dissociable class of exploratory, scanning head movements for which there is no evidence of a specific visual trigger. For example, in the aperture detection task, the initial head turn of the normal hamster is only partially biased by target door position, and the hamster almost invariably spends some time scanning the arena before proceeding forward. Animals who have collicular undercuts demonstrate that it is not necessary to scan with normal frequency to perform the task; in a sense, their behavior is more efficient in that their initial head turn is highly related to door position. Scanning is characteristic of hamsters on entrance to any open arena [19]. Such a stereotypic exploratory pattern would have a variety of uses for a foraging animal, in route selection, food localization and predator detection.

Phylogeny of visuomotor behavior

How are rather widely varying behavioral repertoires mapped onto neural structures that appear rather stable over evolution in their fundamental organization? Comparisons of the uses of vision in the hamster (*Mesocricetus auratus*) and anurans (principally *Rana pipiens* and *Bufo bufo*) may give some first clues.

The frogs and toads that have been most extensively studied [4, 5, 11–13] are predators of live prey. There is no evidence for exploratory scanning, though toads will take account of a variety of obstacles in moving toward prey [18] and show stereotyped rooting on smelling prey odor [10]. The frog avoids predators, and thus has a mechanism for predator detection and for plotting appropriate escape routes [12]. Of these behaviors, to date, avoidance of predator and pursuit of prey appears to depend heavily on the optic tectum [4, 5, 11], while negotiation of barriers is not influenced by tectal lesions [11, 13], but depends on pretectal [14] and, possibly, thalamic structures.

The hamster shares many of these uses of vision and adds several. The hamster's food sources are more varied than frogs', including both seeds and insects. The hamster must then forage for seeds and grains that form a major part of its diet. This animal has developed active searching strategies, as well as the simple ability to orient toward and approach a food source, once recognized. Both this study and the study of Keselica and Rosinski [17] have shown evidence of quickly learned, efficient search patterns for food, and evidence of tectal involvement in some facet of this search procedure. Hamsters with collicular lesions took longer to collect crickets in this study, and in Keselica and Rosinski's study [17], did not gather a matrix of presented seeds by the most efficient path. In food-getting in the hamster there is thus both a contribution of tectum to direct frog-style orientation, and an additional contribution, possibly using the same basic orienting mechanism, to more complex search strategies. Interestingly, the contribution of the tectum to direct orientation is not as complete as it is in the frog. Frogs with tectal ablation show a complete lack of ability to orient throughout the entire visual field, while in hamsters with ablations or undercuts of the upper collicular layers this deficit is confined to the visual periphery [6]. In the gerbil, Ingle et al. [15] have shown that additional removal of visual cortex abolished the residual orientation to seeds and suggest that cortical projections to remaining deep tectum mediates this ability. Schiller et al. [22] have demonstrated a similar effect in monkeys; eye movement range is restricted only by combined tectal and frontal cortex lesion.

Both the hamster and frog must recognize barriers during locomotion, and in neither does this capacity appear to involve the optic tectum. We have in this study some evidence that some part of this function depends on the integrity of the thalamocortical pathway in the hamster, i.e. animals with cortical lesions collided with barriers at a rate close to the enucleate rate. Our data are closely comparable to those of Goodale and Milner [8] who found that

cortical, but not tectal lesions impaired the ability of gerbils to detour around a barrier to reach a more distant aperture. In frogs, the ability to locate and jump through an aperture in a barrier is similarly undisturbed by tectal lesions [13]. This aperture detection sparing in frogs should not be confused with the aperture detection deficit in the visual periphery in hamsters: in the case of the frog a deficit is defined by the collision with the aperture walls, while in hamster the deficit is an apparent loss of ability to notice or orient directly toward a distant peripheral aperture and at no time does the hamster collide with any surface or barrier in this task.

Comparative neuroanatomy attempts to understand the evolution of neural structure by the description of homologies and divergences in neural connectivity in extant species representing diverse evolutionary paths. Detailed behavioral descriptions, and knowledge of basic functional neuroanatomy, would add much to the study of comparative neuroanatomy. Neural homologies are clearly more convincing when behavioral continuities can also be demonstrated, and this behavior is best described in terms of the animal's survival requirements. Thus far the similarities in tectal function among diverse vertebrate species (especially using ethological criteria) are impressive, and should encourage an extension of this comparative approach.

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