the liver within the critical postnatal hours. Furthermore, any treatment may adversely affect the delicate metabolic balance of the newborn, whereas fetal rats may tolerate artificial interference better, since their metabolism is buffered by that of the mother.

The foregoing results (Fig. 5) demonstrate the possibility of producing newborns with a "precocious" enzyme pattern. Injection of fetuses with a combination of appropriate hormones that may extensively enhance biochemical differentiation could be looked upon as a way to shorten the necessary period of gestation. Such enhancement by the prenatally initiated formation of enzymes necessary for important liver functions may be of particular benefit to prematurely born animals.

Summary

The course of enzymic differentiation in liver can be altered in a positive, biologically meaningful direction by the administration of glucagon, epinephrine, and thyroxine to fetal rats *in utero*. The premature accumulations of specific enzymes occur within hours after such administration, are inhibited by actinomycin, and provide a suitable system for studying the mechanism of gene expression. Glucagon and epinephrine are probably the natural stimuli for the formation of enzymes that accumulate precipitously during the hours immediately following birth. Their action may be mediated through cyclic AMP; dibutyryl cyclic AMP can evoke the appearance of tyrosine aminotransferase in fetal livers too young to respond to glucagon. Thyroxine is important in promoting aspects of enzymic differentiation that occur during late fetal life.

Rats injected prenatally with thyroxine were born with precociously elevated levels of liver enzymes. Such artificial stimulation of the course of enzyme differentiation during the fetal stage may facilitate the metabolic adjustment of newborn or prematurely born animals to extrauterine existence.

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Two Visual Systems

Brain mechanisms for localization and discrimination are dissociated by tectal and cortical lesions.

Gerald E. Schneider

The term *vision* subsumes a complex variety of processes, thus, for fruitful scientific discussion, a reference to "vision" usually requires further specification. Likewise the term *blindness* is not self-defining. An animal or patient showing what appears to be total blindness under one set of conditions may reveal considerable visual capacity in a different situation. Such phenomena have led to discrepant conclusions in the literature on the neurological bases of vision, particularly on visual defects following various types of brain damage. The discrepancies have often been resolved through careful attention to *stimulus* conditions: variations in level of illumination, movement of stimuli, and type of pattern have led to the definition of particular types of partial blindness. However, the nature of the *response* has received less attention in studies of visual processes: an anopia found in a test requiring one type of response may vanish or turn out to be an amblyopia in tests requiring a different response.

For example, after preliminary neurological testing of golden hamsters with total ablations of the superior colliculi of the midbrain, I concluded that they were essentially blind (though their pupils still reacted to light). Unlike normal animals, they could find food only by touch and olfaction. I initially assumed that an inability to localize a stimulus in visual space (that is, to make orienting movements of the head or body in the direction of a stimulus within the field of vision) implied an inability to identify shapes and patterns visually, since shapes and patterns are defined by the spatial arrangement of their parts. But subsequent experiments (*1*) which required different responses have forced me to drop this assumption, for the "blindness" appeared only when orienting movements were required. Study of other hamsters after ablations of visual areas of the cerebral cortex showed that a related assumption—the assumption that the ability to localize objects

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in space by means of vision implies pattern vision—is also false. These animals were found to be "pattern blind" in tests of learned visual discriminative responses, yet they showed considerable ability to localize objects in space by means of vision.

This evident dissociation between two kinds of effects—those following ablation of the superior colliculi and those following ablation of "visual cortex" (*2*)—had not been made clear by previous investigations of animals with brain lesions, even though the brain-lesion method has long been used in attempts to distinguish between the functions of these two areas, which represent older and newer structures in the evolution of visual integrating mechanisms. In this article I deal with two aspects of this distinction: (i) the manner in which both the stimulus conditions and the response requirements must be varied to define differences in the effects of lesions, and (ii) the interpretation of the differences thus found, from the standpoint of comparative neurology. The methodological considerations appear to resolve some contradictions in the literature. The interpretation is based in part on a review of work on other species which indicates discrepancies that cannot be resolved from methodological considerations alone.

Past Agreements and Disagreements

Early neurological investigations based on clinical tests of visual responsiveness led to the conclusion that blindness could result from ablation of the superior colliculi in the rabbit, rat, and dog (*3*) even though the anatomical pathway from the retina to the lateral geniculate nucleus of the thalamus, and thence to the visual cortex, was intact. A similar blindness was reported to result, at least in cats, dogs, and monkeys (*4*), from ablation of posterior neocortical areas, even though connections between retina and midbrain were intact. In later investigations undertaken to test visual discrimination ability it was found that removal of the posterior neocortex, including at least the striate cortex, caused pattern blindness (*5, 6*), although animals with this lesion could still discriminate differences in total luminous flux (*6, 7*). But in similar investigations of rats with considerable damage to the superior colliculi, no such pattern blindness was found (*8*), and these studies led to conclusions that were contrary to those of the early studies of colliculus lesions.

Similar discrepancies have appeared in the more recent reports on studies of cats with ablations of the superior colliculi. Such animals show a severe disturbance of the ability to orient head and eyes toward visual stimuli (*9, 10*), and some deficits (below-normal performance) in auditory and tactile localization (*10*). In one study, Blake (*9*) found, in addition, that the ability to discriminate visual patterns was lost following such surgery, while a brightness discrimination, tested by a different method, was undisturbed. However, the deficit in visual-pattern discrimination was not confirmed by other investigators (*11*).

The dissociation I have found for the hamster—which, I believe, resolves such differences—was not brought out by the earlier experimental studies, apparently because they relied on variation of stimulus properties and omitted any variation of the required response (*12*).

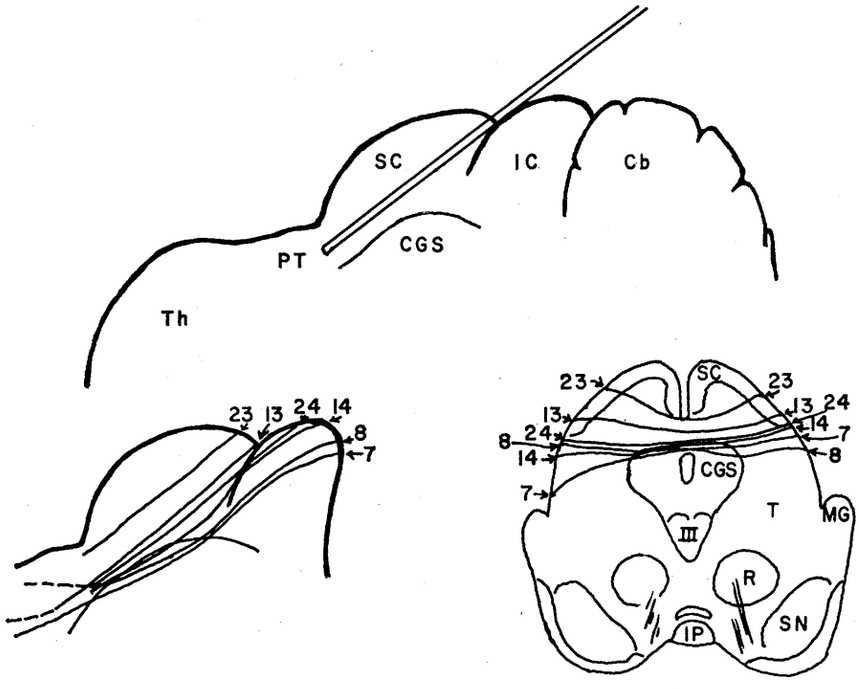

Fig. 1. (Top) Schematic side view of the surface of the brain stem of the hamster, showing the intended route of the surgical knife over the cerebellum (*Cb*) and inferior colliculus (*IC*), under the superior colliculus (*SC*), above the central gray substance (*CGS*), and into the caudal pretectum (*PT*), well behind the thalamus (*TH*). (Bottom left) Reconstructed actual pathways of the surgical knife in six hamsters tested for visual discrimination abilities (dashed lines indicate unilateral damage). The lesion of case 7 is inadequately illustrated because of the asymmetrical tilt of the knife: on the left, the lesion resulted in nearly total destruction of pretectal nucleus, nuclei of the optic tract, habenula, and nucleus lateralis posterior of the thalamus; on the right, the cut reached the surface in the pretectum, severing the brachium of the superior colliculus. (Bottom right) Frontal section through the middle of the superior colliculi, showing the appearance of the knife cuts in the cases of the drawing at left. At the surface of the superior colliculi, the superficial gray layer, where the retinal fibers terminate, is outlined. (*IP*) Interpeduncular nucleus; (*MG*) medial geniculate body; (*R*) red nucleus; (*SN*) substantia nigra; (*T*) midbrain tegmentum (reticular formation); (*III*) oculomotor nucleus.

Hamsters Allow a New Approach

The Syrian golden hamster has two distinct advantages as a subject for an investigator who wishes to compare the behavioral effects of cortical and tectal lesions. First, informal neurological examination is greatly facilitated by the usually insatiable propensity of this animal to search for sunflower seeds, one after another in quick succession, and to put them in its cheek pouches. Second, a direct surgical approach to the superior colliculi is possible because the caudal pole of this region is not covered by cerebral cortex, as it is in rats and cats.

Most of the lesions of the superior colliculi were made by undercutting this structure with a specially designed

surgical knife, consisting of a steel blade (2.5 millimeters long, 2 millimeters wide) attached to a needle shaft. With the shaft held in the electrode carrier of a stereotaxic machine and vibrated transversely by a massage vibrator to achieve better cutting, the knife was inserted beneath the medial superior colliculi after being passed over the cerebellum and the inferior colliculi. Then it was moved to either side of the midbrain as vibration was continued. Histological results for the animals tested on visual discrimination problems are illustrated in Fig. 1.

Lesions of the visual cortex were produced by suction removal of the pial surface of areas 17 and 18 in many cases of bilateral lesion, or of a wider area in several cases of unilateral lesion. Inspection of cell-stained serial sections from the brains of the animals with bilateral lesions revealed degenerative changes throughout most of the dorsal lateral geniculate nucleus and, to a lesser extent, in the lateral nucleus of the thalamus. Cell loss in degenerated areas was not complete, in contrast to reported effects of such lesions in rats and monkeys. The histological results are illustrated in Fig. 2, where the additional degeneration produced by the larger lesions in some cases of unilateral lesion is also presented.

The experiments reviewed here involved 38 brain-damaged hamsters, 13 normal controls that had undergone sham operations, and numerous additional normal animals used in supplementary observations.

"Clinical" Tests: Tectal Blindness

A simple perimetry technique enables an observer to demonstrate a hamster's capacity for locating a stimulus—usually a hand-held sunflower seed—placed at various locations near the animal's head. A normal animal accustomed to contact with humans will move its head in various directions—to the right, to the left, or upward—in order to obtain a seed, often before the hand-held seed touches its whiskers. If the animal's eyes have been removed, no such movements occur until the whiskers are touched, at which time the animal moves its head in the direction of the food and takes it in its mouth. Systematic application of this technique, involving

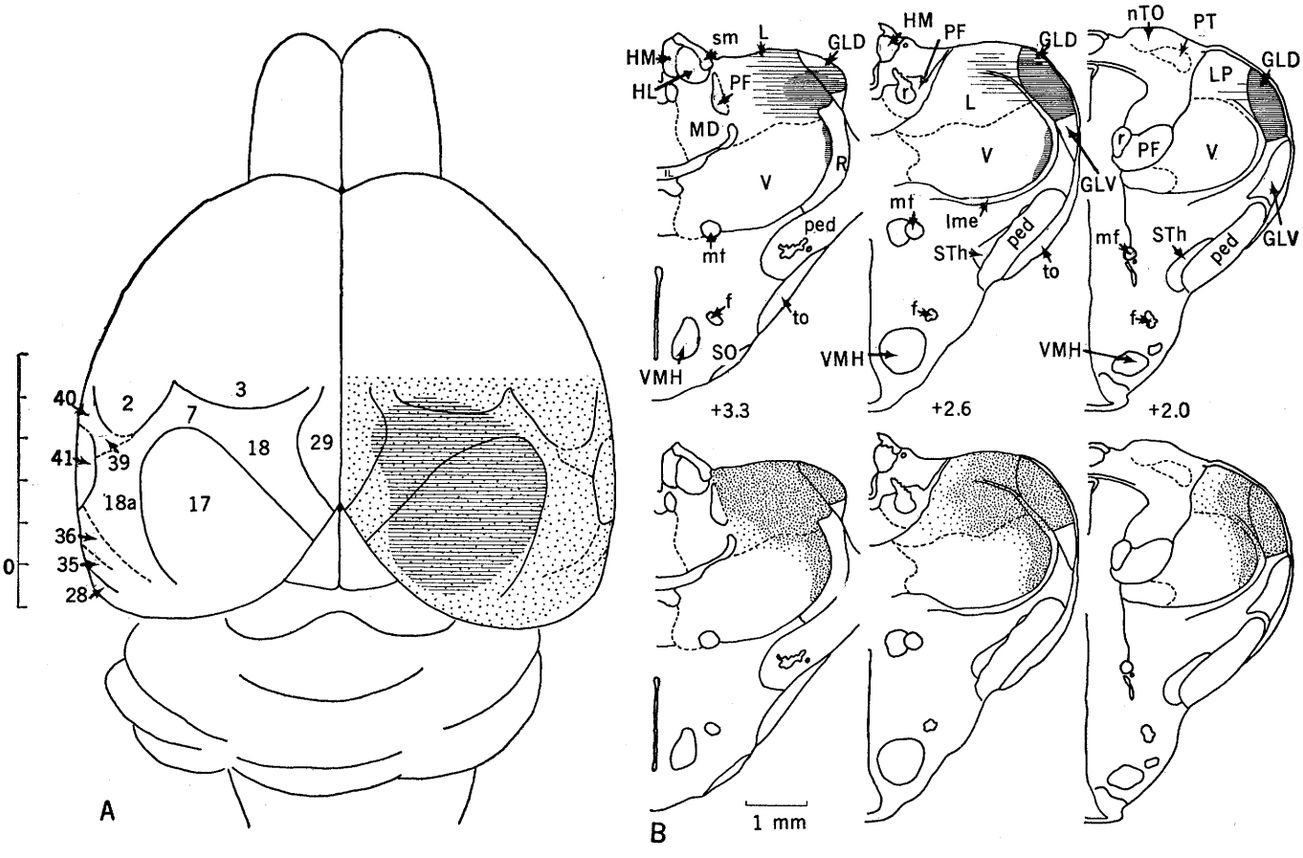

Fig. 2. (A) Dorsal view of hamster brain drawn to scale. (Left side) Fiber-architectonic map of visual areas (*31*); the numbering is Krieg's for the rat (*32*). Dashed lines indicate difficulty in consistent delineation; absence of border, as between areas 7 and 18, indicates that there were no sharp changes in histological appearance in the 25-micron frontal sections used. (Right side) Outlines of largest and smallest neocortical lesions. The horizontal bars cover the lesion of most of areas 17 and 18; the placement of the lesion was based on an early mapping of visual cortex by cytoarchitecture (appearance and organization of cell bodies). The scale is in millimeters; the lambda point serves as the zero reference in the anterior-posterior plane. The brain is correctly aligned when the skull is leveled by placing the bregma and the occipitointerparietal suture at equal elevations. (B) Drawings of frontal sections through the thalamus below a cortical lesion showing typical patterns of partial retrograde degeneration following the smallest type (top) and largest type of lesion. Density of stippling or lines corresponds to severity of degeneration. Not shown is the partial degeneration usually found in the anteroventral nucleus and, in the case of the largest type of lesion, in the medial geniculate nucleus. Dashed lines indicate divisions difficult to delineate. (*HL*) Lateral habenular nucleus; (*HM*) medial habenular nucleus; (*f*) fornix; (*GLD*) dorsal lateral geniculate nucleus; (*GLV*) ventral lateral geniculate nucleus; (*IL*) intralaminar nuclei; (*L*) lateral nucleus; (*lme*) external medullary lamina; (*LP*) lateral posterior nucleus; (*MD*) medial dorsal nucleus; (*mt*) mamillothalamic tract; (*nTO*) nucleus of the optic tract; (*ped*) cerebral peduncle; (*PF*) parafascicular nucleus; (*PT*) pretectal nucleus; (*r*) fasciculus retroflexus; (*R*) reticular nucleus; (*sm*) stria medullaris; (*SO*) supraoptic nucleus; (*STh*) subthalamic nucleus; (*to*) optic tract; (*V*) ventral nucleus; (*VMH*) ventromedial nucleus of the hypothalamus.

presentation of hundreds of seeds to each of many animals, yielded valuable data which guided the planning of further experiments.

After the superior colliculi had been totally undercut, the hamsters acted, on such a test, as though they were completely blind, and they failed to recover visual orienting capabilities. Such lesions were found in the brains of three animals which survived for 3, 3½, and 8 months, respectively, after surgery. Although no visually guided responses were seen during tests of the orienting capacities of these hamsters, the animals showed vigorous localization movements once their whiskers were touched, except during the first few days following surgery. The only observed lasting deficit in tactual localization was the animal's reluctance to turn its head sharply upward to get a seed touching the vertical whiskers; the animals preferred to rear on their hind legs to get the seed. Even this could not be attributed to an ordinary paralysis since the full range of normal head movements was observed during stereotyped actions such as digging and grooming.

In cases where the surgical knife failed to reach the rostral end of the superior colliculi or where it passed above the collicular tissue along the lateral edge of the brain stem, partial recovery of the ability to make visually guided localization movements occurred (there were 11 such cases). The recovered ability was limited to orientation to stimuli in the lower part of the visual field, except in the few cases where the lesions were very shallow, where the only lasting deficit was a failure to locate seeds directly overhead. Such shallow lesions damaged principally the medial tectal areas, which are known to receive projections from the lower parts of the retinas (*13*).

In one hamster the tectum was not undercut, but most of the fibers carrying the visual input to this structure were interrupted by severing the brachium of the superior colliculus. A resulting deficit in visual-localization ability (unchanged after 7 months) was quite like that of animals in which the tectum had been undercut and rostral or lateral tissue only slightly spared. The animal could make visually guided movements toward seeds only when they were presented in the lower nasal fields.

Ablation of the visual cortex, including ablation of most of the striate cortex and a medial parastriate area, caused no defects, after the first postoperative week, in visual-localization ability, except for slightly subnormal performance in following a seed moving back and forth in the lower visual fields. In 13 animals with this lesion, no other neurological deficit could be detected by means of informal testing procedures.

Unilateral lesions led to results in essential agreement with the effects of the bilateral lesions. Thus, in four cases of incomplete undercutting of the right superior colliculus, the animals initially showed no localization ability of any kind when seeds were presented on the left side. The ability to make tactually guided responses was quickly recovered, while the ability to make visually guided responses to objects presented in the lower left quadrant was slowly recovered; responses to objects presented to the animal's right remained stronger. These animals also showed, in light or in darkness, a tendency to circle to the right, a symptom which gradually decreased until only a preference for right turns remained. In two subjects the fibers carrying the visual input to the superior colliculus (the brachium of the superior colliculus) were partially severed on one side. These animals showed no circling movements or tactual-localization deficits but did show visual-localization deficits similar to those of animals with unilateral undercutting of the colliculus.

Unilateral ablation of the visual cortex, even if the lesion was large and included both medial and lateral parastriate areas, together with ablation of the posterior parietal cortex and most of the auditory cortex (Fig. 2), caused (in four animals studied) only a transient loss of ability to orient toward seeds presented in the half-field opposite the lesion; recovery was almost complete, and only a slight preference for responding to the side ipsilateral to the lesion remained.

Variations of Response and Stimulus

The informal methods which yielded these results could not readily be used to answer questions such as the following: Is the unresponsiveness of animals with tectal lesions limited to the visual modality? Most of these animals showed normal pupillary light reflexes, but do any other responses to visual stimuli remain intact? Could the apparently normal orienting to overhead cues in animals with cortical lesions be corroborated if one used a more quantitative technique, especially if any possible influence of subtle nonvisual cues were eliminated?

To obtain answers to such questions, 24 animals (eight with cortical and eight with tectal lesions and eight control animals that had undergone surgery which did not cause brain damage) were tested with apparatus in which the frequency of untrained and unrewarded head-raising responses and of freezing (or arrest) responses to overhead visual movement or sudden sounds could be measured (see *14*). The experimenter did not know, during the tests, whether or not the subject had a brain lesion.

The results were in good agreement with those of the more informal tests. Frequent head-raising responses were made both by the animals with cortical lesions and by those that had undergone sham operations; the overlap in scores obscured any group difference in responsiveness that may have existed. Very few head-raising responses were made by subjects with tectal lesions; none at all were made by those animals that were later found to have the most complete damage to the superior colliculi. Furthermore, results for head-raising in response to the auditory stimuli paralleled those for the visual stimuli. Thus, the lesions of the superior colliculi were as effective in abolishing orientation to overhead sounds as in abolishing orientation to overhead visual movements (though not orientation to tactile stimulation)—a result which is in agreement with observations on cats with such lesions (*10*).

When the less frequently occurring freezing responses of the same animals were compared, it became evident that the differences described above were not simply differences in ability to detect the stimuli. The ordering of group scores for freezing was exactly the reverse of the ordering of the head-raising scores. Subjects with lesions of the superior colliculi showed significantly more freezing than animals in the other groups did. Here was a first indication that the unresponsiveness of the animals with tectal lesions was not a matter of blindness or deafness in the usual sense of these terms.

The experiment just described made use of naturally occurring responses of hamsters; the head-raising and freezing responses to the stimuli presented occur without any special training. Would similar group differences be found if

the learning of visual discriminative responses were required—for example, if the animal had to learn to approach one visual pattern and not to approach a different one in order to obtain a reward? If the hamsters with undercutting of the superior colliculi suffer from defective attention mechanisms—as their lack of spatial orientation might indicate (see *10*)—they could be expected to have special difficulty in solving problems requiring discrimination of visual cues, particularly if these cues consisted of patterns differing in spatial arrangement and not in average luminosity. However, a similar argument might lead one to predict that the hamsters with visual-cortex ablations, with nearly normal spatial orientation abilities, would solve such problems with comparative ease—an expectation quite contrary to results obtained with rats with such cortical lesions (*5*) and with monkeys and other animals. But the prediction required experimental test, since the hamster should not be assumed to be a rat, much less a monkey.

A series of visual discrimination problems was presented to each of 16 hamsters (six with tectal lesions, five with cortical lesions, and five normal), interspersed with some tests of transfer of training to different stimulus pairs, in order to compare the cues used to solve the problems (*1*). In these tests, which began 7 weeks after surgery, a thirsty animal was required to walk down an elevated alleyway toward two adjacent doors made of transparent Plexiglas. The doors, whose upper sections were hinged at the top, were made visually distinct by means of cards attached to the back sides. If the hamster pushed the door which presented the negative-stimulus card, it found the door locked, an error was recorded, and it could then push through the other door and obtain water. If it pushed only the door which presented the positive stimulus it made no error on that trial (even if it had approached—but not pushed—the incorrect door). In either case, the hamster found a water spout after passing through the correct door, and was allowed a 2- to 3-second drink before being placed in a holding cage for 15 seconds, then placed back at the starting point.

A summary of the results on three problems will serve to make the principal point. These problems consisted of a discrimination between (i) white and black, (ii) horizontal and vertical stripes [¼ inch (0.6 centimeter) wide, alternating black and white], and (iii) a speckled pattern and diagonal stripes (of equivalent average reflectance).

The hamsters with lesions of the superior colliculi demonstrated excellent learning of all these problems, even when no residual ability to make visually guided localization movements could be detected. Slightly subnormal performance on the initial white-black discrimination test did not recur in later relearning tests.

The performances of the animals with visual-cortex lesions showed that a hamster is indeed like a rat in that the occipital cortex contains mechanisms essential in the learning of pattern discrimination. Of the five subjects, two failed to discriminate white from black, four failed to discriminate horizontal from vertical stripes, and all five failed to discriminate the speckled pattern from stripes. The one cortically damaged animal that solved the second problem was found to be the one with the largest normal areas in the lateral geniculate nuclei; however, these nuclei in the brains of the other four animals showed small normal areas presumably compatible with a slight amount of intact cortex in area 17 (*15* and Fig. 2).

Some type of progressive deterioration during the three problems cannot be conclusively ruled out. However, in later tests there were two problems which all of the cortically damaged animals solved. The first was discrimination of a bright, transluminated door from a black door. The second was discrimination of the speckled pattern from a gray of equivalent average reflectance; solution of this problem indicated a type of residual discrimination ability also found in the monkey without striate cortex (*16*).

Variation of the Required Response

The surprisingly normal performance of the hamsters with surgically undercut superior colliculi seems to indicate a basic disagreement with Blake's (*9*) results on cats with superior-colliculi ablations. These cats showed severe deficits in both visual orientation ability and pattern discrimination ability, while my hamsters showed only the former. However, Blake's testing method differed from mine in certain essential respects. For the hamster, the only decision requiring vision was that of whether to push or not push a door; even when the hamster approached the incorrect door repeatedly, no error was recorded so long as it did not push the door against the lock. In the experiment with cats, a barrier separated the approaches to the doors, so that, once the animal reached a certain point, it had to guide its motion toward the correct door by entering one of the two approach alleys (12 inches long). Merely approaching the incorrect door by entering the wrong alley constituted an error and ended the trial. To make the hamster apparatus more comparable to this apparatus, a small barrier was constructed to fit between the approaches to the doors, to form approach alleys 2½ inches long leading to the two doors. After this alteration the hamsters with lesions of the superior colliculi and the normal hamsters were tested to determine their ability to relearn a discrimination between light and dark and between horizontal and vertical stripes (*14*). Two types of errors were recorded. If, in approaching the doors, a hamster failed to orient his motion toward the correct door and entered the alley leading to the incorrect door, an "orienting error" (or "approach error") was recorded. If he then actually pushed against the incorrect door, a "door-push error" was also recorded.

The results for one type of error were very different from the results for the other type. In agreement with our previous finding, the animals with tectal lesions had "door-push-error" scores like those of normal animals. However, in contrast to the normal animals, they made a great many "orienting errors"; this was especially true in the case of the two animals with the largest lesions (*17*). These animals found it difficult or impossible to orient their motion toward the correct door before passing the short barrier. Thus, subject M-7, with the superior colliculi totally undercut, was soon performing at a level of 100 percent correct responses on the discrimination of horizontal from vertical stripes when only door-push errors were considered, yet continued at chance levels of performance for 200 trials when orienting errors were considered. The poor performance could not be attributed to myopia, since, when the barrier was removed and the stimuli were moved to various distances behind the transparent doors, performance remained high up to a door-to-stimulus distance of 7 inches.

These results appear to resolve the discrepancy between results of the study in which ablation of the superior colliculi in cats abolished the ability to

discriminate patterns (*9*) and the results of studies with hamsters in which such lesions seemed to be compatible with normal or nearly normal visual discrimination abilities. The discrepancy is resolved when, in the light of results of the tests with the modified apparatus, we modify our earlier conclusion and conclude that animals with lesions of the superior colliculi are capable of normal or near-normal visual discrimination so long as they are not required to make visually guided orienting movements toward the positive stimulus.

Overview

The results of the hamster experiments are summarized in Fig. 3. Supplementary experiments (*1*), in which responses to novel visual, auditory, somesthetic, or olfactory cues were measured, yielded results which were compatible with those presented above. Ablation of the superior colliculi had little effect on *detection* of a novel stimulus, as revealed by arrest of movement or by locomotor approach responses; however, such lesions severely disrupted *spatial orientation* toward the source of a novel auditory or visual stimulus.

Implications for Comparative Neurology

One may conclude that, once the newer cortical visual structures have evolved, to subserve at least conditional responding to shapes and patterns, the older tectal structure still functions as an area where neural impulses converge to affect orienting movements. In species like the hamster, and probably in other animals with a relatively large tectum, these orienting movements depend upon movements of the head. Eye movements appear to be of little or no importance for spatial orientation in this animal, although compensatory ocular movements and transitory convergence movements are seen. The view that the tectum is important for the control of head movements is compatible with the connections of a major anatomical pathway originating there. The most direct pathway from the superior colliculi to motor neurons is by way of the tectospinal tracts, which descend as far as the interneuronal pool of the ventral horn of the cervical cord, close to the motor neurons that control the neck musculature.

A major output of the visual cortex is to the superior colliculi [each part of area 17 projects to a topographically corresponding part of the tectum (*18*)], a fact which indicates that ablation of this midbrain structure should destroy an important function of the cortical system. The results reported above suggest the hypothesis that such a function involves a "higher" control over spatial orientation mechanisms (at least over orientation by head motions), and may have led to the evolution of striate cortex. This cortical structure has clearly become essential for more than control over orientation, as attested by the severe disturbances of pattern discrimination learning that, in many species, are caused by its removal. Lesion studies have indicated that projections from striate cortex to circumstriate areas are of great importance for such discriminative functions, at least in monkeys (*19*). However, this extrastriate cortex receives visual input other than that coming from the striate area, thus there is a possibility that information critical for visual discrimination learning could, in species where this route is particularly well developed, bypass the striate cortex. This probably accounts for a recent surprising result in experiments with the tree shrew. In this creature, which represents a form that is in many respects transitional between insectivores and lower primates, ablation of striate cortex alone is not sufficient to disrupt pattern discrimination habits (*20, 21*). To obtain such a disruption, one must remove much of the surrounding cortex as well (*21*). The critical route for transmission of visual information from the retina is apparently a pathway, by way of this animal's huge superior colliculus, to the nucleus lateralis posterior of the thalamus, and thence to the circumstriate cortex (*21, 22*). Thus, an attempt to follow the relevant pathways for the "two visual systems" in the tree shrew might lead through the optic tectum in the case of either visual localization or visual discrimination; this would make the dissociation described for the hamster much harder to obtain in the tree shrew.

Is the considerable dissociation between two visual systems in the golden hamster of any help in understanding visual processes in monkey and man? Much evidence has been adduced to support the notion that, in these primates, the striate cortex is essential for visual control of both spatial orientation and discrimination of patterns. For example, careful analysis of the visual capacities of monkeys subjected to occipital lobectomy led Klüver to conclude (*6*) that such animals had lost all ability to respond to spatial cues by means of vision (while retaining an ability to react to differences in total luminous flux). Since these monkeys retained an intact anatomical pathway from retina to superior colliculus, why was the latter structure unable to mediate some spatial orientation responses? Some recent evidence supports the idea that lesions of the visual cortex, because they remove a massive input to the tectum, can result in a functional depression of the tectal mechanism; that is, a cortical lesion, if it removes a critical amount of input to the superior colliculi, can produce a functional lesion of the tectum. In Sprague's studies of cats (*23*), unilateral removal of area 17 or areas 17, 18, and 19 caused only a transient depression of the ability to orient to objects in the opposite visual field, but removal of most of the posterior neocortex—most or all of which projects to the superior colliculus—led to a lasting hemianopia in the orienting tests. Yet if the opposite superior colliculus was then destroyed, much orienting ability returned on the previously blind side. It seems that a depressed optic tectal mechanism can be made functional again by such a procedure.

But the effects of visual-cortex removal now appear to have been exaggerated even for the higher primates, and this has led to some overrating of the role of striate cortex. Denny-Brown and Chambers (*24*) found that bilateral destruction of area 17 in rhesus monkeys, a procedure which led to retrograde degeneration of the lateral geniculate nuclei, did not abolish the ability to localize moving objects, especially under conditions of low illumination, as discovered by clever informal testing. Such a result has been confirmed and amplified by Humphrey and Weiskrantz (*25*) in more systematic investigations of monkeys whose striate cortex has been removed. The residual orienting ability in the absence of area 17 in the monkey may be similar to the orienting ability of hamsters with the visual cortex ablated and retinotectal connections intact, although such hamsters could also localize stationary objects. The amblyopic eye of humans with strabismus can mediate nearly normal spatial orientation, whereas visual acuity is considerably subnormal—a condition which may be comparable to that of animals lacking striate cortex (*26*).

Correspondingly, the role of the superior colliculi has been underrated for

mammals. This is most evident in the recent studies of tectal lesions in cats and hamsters, but it may be true even for monkeys and man. One laboratory (*27*) has reported that ablations of the superior colliculi in monkeys resulted in profound disturbances of visual responsiveness, interpreted as "a severe loss in visual attention." Attention is commonly assumed to be manifested by orienting movements, or even to be directly dependent upon such movements. My hamsters certainly lost the ability to make orienting movements, although independent measures of arrest responses and of visual discrimination learning proved them to be in other respects quite capable of paying attention. Experiments leading to contrary interpretations are not hard to find. From a second laboratory (*28*) come reports that ablations of the superior colliculi in monkeys led to no more than transitory effects in tests which concentrated on measures of eye movements. From a third laboratory (*29*), from an experiment not originally directed at solving this problem, comes an account of findings intermediate between no effects at all and general losses of attention. Large lesions in the superior colliculi of rhesus monkeys resulted in what was described as a "peripheral field defect." It may be that only in the periphery of the visual fields of the monkey are the demands on orienting mechanisms similar to those in the entire visual field of the hamster. In the peripheral field of higher primates, head movements may well play a proportionately greater role in shifts of gaze than eye movements do. If the superior colliculus is more important for head movements, the study of eye movements alone after superior-colliculus ablation may not reveal a defect. Again my suggestion is that various *responses* as well as various stimuli must be investigated.

Thus, some of the contradictions in the literature are beginning to be explained. In animals such as monkey or man, the exquisite cortical mechanisms for detailed discrimination and for plastic motor control can mask the functions of the ancient tectal mechanism. However, the degree of this masking may depend on the point of view of the investigator. We may perhaps gain some direct notion of tectal control when we experience an abrupt, involuntary orientation of the head toward a suddenly moving or otherwise compelling stimulus in the periphery of our field of vision, or toward an unexpected or ominous sound. In the hamster, this kind of orientation is the principal type.

How general is the dissociation between visuomotor mechanisms for localization and identification? A recent symposium (*30*) has dealt with this question. Different approaches to problems of understanding visually guided behavior in fish, hamster, monkey, and man indicate that the distinction between localizing and identifying may be useful in attempting to interpret quite diverse results of comparative anatomical, physiological, and behavioral studies. An answer to the question "Where is it?," when put to the visual systems of mammals like the hamster, requires the optic tectum, if the answer is to be given in terms of visuomotor localizing responses. By contrast, an answer to the question "What is it?" requires forebrain mechanisms (the visual cortical areas in mammals), at least if the answer is to be in the form of a learned response. Different systems for visual localization may be important in some species, and the learning of visual discriminations may not always demand mediation by cortical structures. However, a good case can be made for the notion that a dissociation of the two mechanisms—for localization and for identification—can be considered basically similar in the central-nervous-system control of vision in all higher vertebrates.

Summary

Fundamentally different types of relative blindness are produced by ablation of cortical or tectal visual areas of the hamster's brain. Undercutting the superior colliculus abolishes the ability to orient toward an object, but not the ability to identify it, according to tests of pattern discrimination learning. Ablating visual cortical areas has reciprocally opposite effects.

Such results, obtainable only by varying the required response as well as the stimulus in tests of visually guided behavior, may be interpreted as a dissociation between mechanisms for two types of visuomotor control which are maintained throughout vertebrate evolution, although the possibility that the

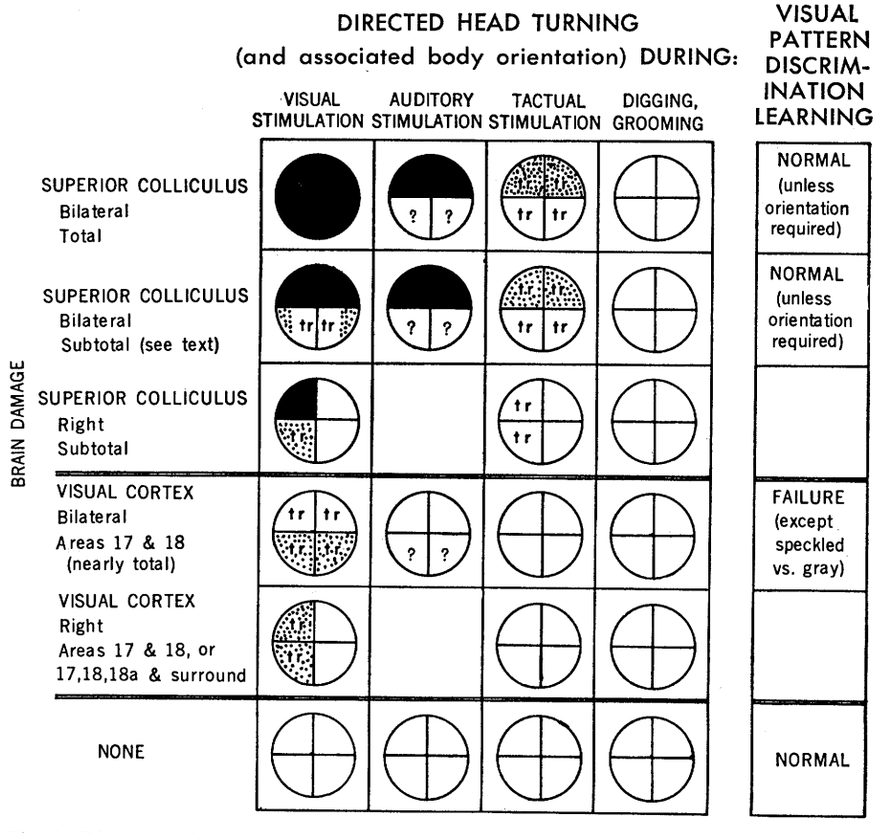

Fig. 3. Diagrams showing the abilities of hamsters with various types of brain damage to turn the head toward the left or right (lower quadrants of circles), or raise the head (upper quadrants) in response to the type of stimulation indicated at top of column: (black quadrant) failure to turn; (stippling) turns, but fewer than normal; (*tr*) transient deficit or failure; (?) not tested. At the far right, results on the visual discrimination tests are summarized.

hamster is a particularly simple case should be borne in mind. One mechanism is concerned with the locating of objects, at least insofar as orientation of the head and body toward a stimulus source is involved. The other mechanism is concerned with the specific identification of objects, and with actions directed toward or away from them.

References and Notes

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12. Response variation is also emphasized by R. A. McCleary [see, for example, *J. Comp. Physiol. Psychol.* **53**, 311 (1960)] and others investigating transfer of information from one brain half to the other, and by N. Geschwind [*Brain* **88**, 237 (1965); *ibid.*, p. 585] in analyzing effects of cortical lesions in man. My approach resulted also from H. L. Teuber's emphasis [*Ann. Rev. Psychol.* **6**, 267 (1955)] on the need for "double dissociation" as a minimum requirement for distinguishing effects of manipulating two brain regions: If lesion *A* leads to effect *a* and not *b*, while lesion *B* leads to effect *b* and not *a*, then a functional distinction between the two brain regions is indicated.
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15. The degenerated areas contained many normal or nearly normal neurons, indicating that the lateral geniculate nucleus may project to cortex outside area 17. This finding is similar to results obtained for the hedgehog by W. C. Hall and I. T. Diamond [*Brain, Behav. Evolut.* **1**, 181 (1968)].
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17. A warning to those who may wish to replicate this result is in order: it is of critical importance that the normal animals perform well in terms of either type of error recording. I have observed that, in apparatus of slightly different design, normal animals may fail in terms of "orienting errors."
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31. The stain, for visualizing normal axons and cell nuclei, was a modified Nauta technique developed with the collaboration of Robert Fink at M.I.T. Unmounted sections 25 microns thick, cut frozen, are washed thoroughly and put overnight in a solution of 2.5-percent silver nitrate (8 parts) and pyridine (1 part); after washing, one follows steps 5 through 7 of procedure I of R. P. Fink and L. Heimer [*Brain Res.* **4**, 369 (1967)].
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33. Aid and encouragement throughout this work came especially from Professors H. L. Teuber and W. J. H. Nauta, and from Patricia D. Schneider. The development of the interpretations was aided particularly by discussions with the workers cited in (*30*) and with Dr. W. A. Richards. Ann Graybiel helped with the microscopic analysis that led to the preparation of the cortical map of Fig. 2. Janet Stuart helped with some of the histology. Initial support for the work came from a Public Health Service predoctoral fellowship and a training grant in psychobiology to M.I.T. from the National Institute of General Medical Sciences. Subsequent support came from PHS grant NB 06542 to Dr. W. J. H. Nauta and from NASA grant NsG 496 to Dr. H. L. Teuber.

Science and the City: The Question of Authority

The research and development activities of the Department of Housing and Urban Development are analyzed.

James D. Carroll

In his speech (*1*) accepting the first Mellon Institute Award, delivered at the Carnegie-Mellon University on 10 May 1968, D. F. Hornig asked, "Is there a crisis in science?" He answered this question with the observation that, in an immediate sense, there is a crisis in financial support. In a long-term sense, however, he argued that there is a crisis rooted in the fact that members of Congress and of the public see "a scientific community which, insisting on its purity, will not deign to communicate with the public and justify itself, but prefers to believe that its virtues are so self-evident that a right-minded society must necessarily support it on its own terms." He concluded that the scientific community through its pride and aloofness "has done much to alienate itself from the society which supports it."

Authority and Relevance of Science to Society

As Hornig's remarks indicate, the social authority and social relevance of public science and technology today are in question. While there are many reasons for this, one basic reason is that science and technology only partially meet and relate to the expectations and values of metropolitan America, particularly the expectation that some form of decent urban life can be maintained in the United States and that progress can be made in resolving the inextricable

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