

**RESPONSES OF VISUAL,
SOMATOSENSORY, AND AUDITORY NEURONES IN THE
GOLDEN HAMSTER'S SUPERIOR COLLICULUS**

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SUMMARY

1. The response characteristics of visual, somatosensory, and auditory neurones in the golden hamster's superior colliculus were investigated.

2. As has been noted for other mammalian species, a distinct difference between the functional organizations of the superficial and deeper layers of the superior colliculus was observed.

3. Neurones in the superficial layers were exclusively visual, with small receptive-fields, and generally did not show response decrements with repeated stimulation. The sizes of the receptive-fields did not vary appreciably as a function of retinal eccentricity.

4. In the deeper layers, visual receptive-fields were large, or could not be accurately delimited, and response habituation was often evident. In addition, many cells in the deeper layers of the colliculus responded only to somatosensory stimuli. Far fewer cells, which appeared to be confined to the caudal portions of the colliculus, responded to auditory stimuli. Polymodal cells were also encountered.

5. Selectivity to opposing directions of movement was tested for ninety-four visual cells. Using a 'null' criterion, 27.7% of these cells were judged to be directionally selective. A distribution of the preferred directions of these cells showed a significant preference for movement with an upper-nasal component. With a statistical criterion, 60.6% of these cells were considered to show a significant asymmetry in responding to movement in opposing directions.

6. Directional selectivity was also tested for ninety-two cells following acute, unilateral, lesions of the visual cortex. For the eighty cells recorded, homolateral to the ablated cortex, 27.5% were judged as directionally selective using the statistical criterion, while 12.5% were selective with the 'null' criterion. Of the twelve cells isolated in the colliculus, contralateral

to the lesions, seven were judged as directionally selective with the statistical, and three with the 'null' criterion.

7. The effects of visual cortical lesions upon directional selectivity appeared to be confined to cells in the superficial layers of the colliculus. It was suggested that directional selectivity of many cells in the superficial layers of the tectum of the hamster is organized cortically.

8. A clear spatial correspondence was observed for the receptive-fields of visual, somatosensory, and auditory neurones.

9. As has been suggested for other species, the hamster's superior colliculus appears to play an important role in orienting the animal toward visual, somatosensory, and auditory stimuli.

INTRODUCTION

Results of single cell studies in a variety of mammalian species (Dräger & Hubel, 1975; Goldberg & Wurtz, 1972; Gordon, 1973; Masland, Chow & Stewart, 1971; Michael, 1972; Schiller & Koerner, 1971; Stein, Magalhaes-Castro & Kruger, 1976) have suggested that the superior colliculus is involved in the orienting of an animal towards stimuli in its environment. This hypothesis has, in general, been supported by the types of behavioural deficits which have been observed following tectal lesions (Schneider, 1967, 1969; Sprague & Meikle, 1965; Raczkowski, Casagrande & Diamond, 1976).

In spite of the impressive communality of functional organization which is apparent across species with regard to the superior colliculus, there are also some noteworthy species differences. For example, receptive-field studies in the cat (Sterling & Wickelgren, 1969; Rosenquist & Palmer, 1971), and ground squirrel (Michael, 1972), have revealed that the majority of visually responsive tectal units exhibit directional selectivity. On the other hand, the incidence of directionally selective units in the tectum of the mouse (Dräger & Hubel, 1975), and the rabbit (Masland *et al.* 1971) has been reported to be considerably lower. In the monkey, directionally selective units have been rarely observed (Cynader & Berman, 1972; Schiller & Koerner, 1971), and such cells are apparently absent in the tectum of the rat (Humphrey, 1968).

The severity and persistence of behavioural deficits following tectal lesions also appears to differ across species. In the cat, Sprague and his co-workers (Sprague, 1972) have demonstrated a marked inattention to (and poor localization of) visual, auditory, and somaesthetic stimuli following large lesions of the superior colliculus. Sensory neglect has also been recently observed in the tree shrew (Raczkowski *et al.* 1976) after

interruption of the descending projections of the deep superior colliculus. On the other hand, in the monkey only subtle deficits have been reported following tectal lesions (Anderson & Symmes, 1969; Wurtz & Goldberg, 1972).

Perhaps the most striking impairments following lesions of the superior colliculus have been noted in the golden hamster (Schneider, 1967, 1969). In this animal, complete bilateral undercutting of the colliculus abolishes visual following and orientation to both visual and acoustic stimuli. Furthermore, in contrast to the cat (Sprague, 1972), where considerable recovery of function is evident 1 month post-operatively, the orientation deficits observed in the hamster are apparently permanent.

More recently, Schneider (1975) has noted that unilateral lesions of the hamster's visual cortex cause a transient but striking deficit in orienting behaviour. This finding was interpreted as suggesting that unilateral cortical lesions produce a depression of function in the homolateral tectum. Such an interpretation is consistent with Sprague's (1972) proposal regarding the interdependence of cortical and mid-brain visual functions, which has been supported by both behavioural (Sprague, 1966; Sherman, 1974) and neurophysiological studies (Wickelgren & Sterling, 1969; Rosenquist & Palmer, 1971) in the cat. Although corticotectal projections have been demonstrated in the hamster anatomically (Schneider & Jhaveri, 1974), the possible significance of these inputs upon the functional organization of collicular neurones is, as yet, unknown.

In the present study, we investigated the neuronal response properties of the hamster's superior colliculus. In particular, we sought to determine the following: (1) the incidence of directionally selective cells; (2) the effects of lesions of visual cortex upon directional selectivity; and (3) the correspondence of visual receptive-fields with the receptive-fields of the somatosensory and auditory neurones recorded from the deeper layers of the colliculus. Following the completion of these experiments, a study dealing with the functional organization of the superior colliculus of the hamster was published by Tiao & Blakemore (1976c).

METHODS

Twenty-five adult (6 month), male hamsters, each weighing between 150–225 g were used in this study. Following anaesthesia with sodium pentobarbital (53 mg/kg), in eighteen animals, an opening was made in the skull over the left superior colliculus, and the eyelids were cut away bilaterally. In the other seven animals, a bilateral opening was made in the skull, the dura was removed unilaterally, and most of visual cortex was aspirated away down to the level of the white matter. Two stainless steel screws were threaded into the nasal bone and a single inverted bolt was cemented between them. The bolt was securely fastened to an aluminium bracket which fitted onto the stereotaxic frame. In all experiments, the nasal bone was

maintained in a horizontal position; thus the animal's head was elevated at an angle of approximately 10° .

During the experimental session, the animal was maintained on supplemental doses of sodium pentobarbital and chlorprothixene. As noted by Dräger & Hubel (1975), for the mouse, this combination of drugs results in a light anaesthetic state where the animal sits motionless, but reacts vigorously to noxious stimuli. The pupils were dilated with homatropine hydrobromide, and the corneas were protected with clear silicone fluid (Dow Corning Medical Fluid, 500 s.c.). Corrective lenses were not employed, since rodents with small eyes have a very large depth of focus, and attempts at retinoscopy lead to systematic errors of hypermetropia (Glickstein & Millodot, 1970). Rectal temperature was continuously monitored and maintained at about 36.5°C with a circulating hot-water pad. The exposed dura was kept moist with repeated applications of mineral oil.

The animal faced a tangent screen, set in most experiments at a 65° angle to the long axis of the animal's body. The screen was 28 cm from the right eye of the hamster. In most experiments, the background illumination level was 4.0 cd/m^2 . Upon this, stimuli were superimposed, having an intensity of $1.5\log u$ above background or $1.0\log u$ below background.

Single-cell recordings were carried out in the conventional manner, using lacquer-coated tungsten micro-electrodes. In the initial experiments, electrodes with impedances of 8–12 $\text{M}\Omega$ (measured at 1 kHz) were employed. Since it was difficult to isolate single units in the superficial layers with electrodes in this impedance range, micro-electrodes measuring above 20 $\text{M}\Omega$ were used in all subsequent experiments. Electrodes were oriented perpendicular to the surface of the brain. Preceding each electrode penetration, the right optic disk was projected and marked on the tangent screen. A net drift in eye position of about 2° of visual angle was typically noted over an approximately 6 h period when appropriate levels of light anaesthesia and sedation were maintained. The fact that large shifts in receptive-field position during the mapping and subsequent testing of individual visual cells were not observed is also indicative of the stability of eye position obtained with this preparation.

Auditory stimuli consisted of white noise bursts (Belton Masking Generator) or pure tones (Hewlett-Packard, 200AB Audio Oscillator), which were amplified and then gated by an interval cycler (Hunter, 124S). These were delivered by a small shielded speaker whose position was systematically varied in a circular fashion around the animal's head in the horizontal plane. The most effective method, however, for activating auditory units was usually through the use of crude complex stimuli, such as finger snaps, key jangling and hissing sounds. Somatosensory stimuli were delivered with a blunt probe, or with fine-tipped camel's hair brushes. Joint rotation was also tested. In one experiment, quantitative data were obtained regarding somatosensory receptive-field organization using an electromechanical stimulator of the type described by LaMotte & Mountcastle (1975).

Visual receptive-fields were plotted with hand-held stimuli, including spots and slits produced by an ophthalmoscope, as well as with the edge of a black square. The borders of the receptive-fields were marked with pencil directly on the tangent screen. Receptive-field positions were referenced to the optic disk. Subsequently, all receptive-fields were transferred to a spherical polar co-ordinate grid with its origin touching a tangent plane forming a 65° angle with the long axis of the animal's body. In each experiment, the zero point of the grid corresponded to a point 14° down and 12° nasal from the projection of the optic disk. This point of origin was chosen for the grid system, since, in preliminary experiments, it was observed to correspond to the shortest projection point from the animal's contralateral eye. Although an effort was made in each experiment to maintain a constant head position, it should be

clear that the use of the procedure described above for referencing the loci of the receptive-fields to the optic disk compensated for any small deviations in the angle of eye elevation from one experiment to another. In those few instances where receptive-fields were plotted using a screen, either perpendicular or parallel to the animal's body, the loci and extent of the receptive-fields were transferred, and adjusted to the grid co-ordinate system described above.

In testing for directional selectivity, two photosensitive diodes were attached to the screen approx. 1 cm from the borders of the receptive-field. A visual stimulus moving across the field produced a pulse (Schmidt trigger) when crossing each photodiode. The first pulse triggered a timer, while the second pulse stopped the timer, thereby permitting a measure of the average speed of the moving stimulus. The first pulse also triggered a storage oscilloscope whose upper beam displayed the unit's activity, while the lower beam indicated the offset of the first pulse and the occurrence of the second pulse. A spike count for each stimulus presentation was obtained directly off the oscilloscope screen. In addition, the unit's activity was fed through a spike discriminator into a counter with a digital display. Directional selectivity was tested vertically and horizontally, as well as for the two oblique axes bisecting these quadrants. Each stimulus direction was tested at least 5 times with a tolerated speed variance of 5% above or below the designated speed. An inter-trial interval of at least 10 s was employed. Typically, only that speed which was qualitatively judged to yield the most vigorous discharges was employed to determine directional selectivity. For some units, however, up to 3 different speeds were used. For thirty cells, directional selectivity tests were repeated following intervals of 15 min–2 h, and in all instances, repeat determinations were consistent with initial judgments regarding the presence or absence of directional selectivity, as well as the direction of the preferred stimulus movement.

Electrolytic lesions were made at one or more loci in each penetration (35 μ A, 2 s). Generally, no more than three electrode tracks were made in a single animal. Following termination of the last penetration, the animal was given a lethal dose of barbiturate, and then perfused through the heart with saline, followed by 10% buffered Formalin. After storage of the head in Formalin for several weeks, the brain was removed, imbedded in liquid paraffin, and the portion containing the superior colliculus was sectioned at 10 μ m. Every tenth section was stained with cresyl violet for reconstruction of the electrode tracks. To facilitate the identification of the various laminae, several brains were stained by the method of Klüver & Barrera (1953).

The dorsal surface of the brains of the seven animals with lesions of visual cortex were photographed, following removal of the dura. The extent of each lesion was subsequently outlined directly on the photographs. These brains were then sectioned, as described above, for reconstruction of the electrode tracks, as well as the extent of the cortical lesions. In no instance did the lesion extend through the white matter to the collicular surface.

RESULTS

Four hundred and thirty-seven single units were isolated in fifty-five electrode penetrations through the hamster's superior colliculus. The data to be presented are based on the 411 units which were judged to be neurones using conventional criteria (Hubel, 1960). Of these, 137 were recorded in hamsters with unilateral ablations of visual cortex. Table 1 summarizes the classifications of all the cells recorded in intact animals.

Before describing the response characteristics of neurones encountered in the hamster's superior colliculus, a general description of the sequence of responses observed in a typical electrode penetration will be provided.

When the micro-electrode entered the most superficial layer of the superior colliculus, multiple unit activity, responsive only to visual stimulation, was observed. Little or no spontaneous activity was evident in any of the three superficial layers (stratum zonale, stratum griseum superficiale, stratum opticum). A small moving spot of light, or the leading edge of a black square, defined the receptive-zone of the background

Table 1. Receptive-field types

<i>a. Exclusively visual</i>	154
Small fields	124
Directional	44
Non-directional	28
Large fields	30
Directional	13
Non-directional	9
<i>b. Exclusively somatosensory</i>	98
Body	78
Vibrissae only	20
<i>c. Exclusively auditory</i>	14
<i>d. Bimodal</i>	6
Visual-somatosensory	1
Visual-auditory	3
Auditory-somatosensory	2
<i>e. Trimodal</i>	3
<i>f. Unresponsive</i>	12
Total	287

activity. This area was stimulated continuously with moving stimuli as the electrode was slowly advanced, in order to isolate the responses of a single unit. Cells isolated in the superficial layers typically showed poor signal to background ratios (2 or 3:1), even with electrode impedances over 20 M Ω .

In the intermediate and deeper layers of the colliculus (stratum griseum intermediale, stratum album intermediale, stratum griseum profundum, stratum album profundum), the receptive-fields of isolated visual neurones were larger, and the intensity of visual background activity decreased considerably. In addition, the signal to background ratios improved markedly, so that ratios of 10:1 were not uncommon. For most visual neurones isolated below the stratum opticum, rapid response habituation was evident, and in some cases the borders of the receptive-fields could not be accurately delimited. The large receptive-fields usually overlapped the

smaller fields obtained from neurones in the superficial layers.

Just below the depth from which neurones with large fields were found, and to a certain extent intermixed with these, the first cells responsive to extra-visual stimulation were encountered. The vast majority of these were responsive to somatosensory stimulation. As will be discussed below, for a single electrode penetration, there was a good correspondence between the loci of the somatosensory receptive-fields on the surface of the body and those obtained for the visual neurones in visual space. Exclusively auditory and polymodal cells were found only in the deeper layers, but these were encountered rather infrequently.

Visual response properties

As shown in Table 1, 154 (53.6%) of the cells isolated in the superior colliculus of the hamster responded only to visual stimulation. Only one cell gave evidence of a clear response to stimulation of either eye; the rest of the neurones were responsive only to contralateral eye stimulation. However, only 3 penetrations were made through the most anteromedial quadrant of the colliculus which has been shown (Leonard, 1974) to receive a sparse projection from the ipsilateral eye. Following the completion of our experiments, Tiao & Blakemore (1976c) reported a significant proportion of binocular cells in the anterior portion of the hamster's colliculus.

In the hamster's superior colliculus, as in that of other species (Sprague, Berlucchi & Rizzolatti, 1973), the vast majority of visual units yielded much more vigorous discharges to stimuli that were moved across the receptive-field than to stationary flashing lights. For cells in the superficial layers which did respond to stationary stimuli, only phasic responses were observed. These were predominately on-off in nature, but a number of cells exhibited only on or off responses. Light spots much smaller than the dimensions of the receptive-field in all cases yielded responses which were typical of the field as a whole, suggesting a homogeneity of organization within a given receptive-field.

Directional selectivity was tested in ninety-four cells. Two separate criteria were used in determining whether or not a cell was directionally selective. In the first instance, a reliable asymmetry of responses to movement in opposing directions was determined by a statistical method (Rhoades & Chalupa, 1976). With this quantitative procedure, 60.6% of the cells were judged to be directionally selective. Fig. 1A shows the distribution of preferred directions of these cells. While an over-all tendency for cells to prefer movement with an upward and nasal component is apparent, this preference was not found to be statistically significant ($\chi^2 = 11.63$, $P > 0.05$). The second criterion employed for

judging selectivity in these cells was that of Barlow & Levick (1965). In this instance, a cell was considered directionally selective only if it exhibited a preferred and an opposing 'null' direction. With this criterion, 27.7% of the cells were directionally selective. Fig. 1*B* shows the distribution of preferred directions of these twenty-six cells. A clear preference ($\chi^2 = 16.46$, $P < 0.05$) is evident for the upward and upper nasal directions. For all cells determined to be directionally selective with either criterion, the preferred direction was unchanged by reversing the contrast of the moving stimulus.

The centre of a crude area centralis in the hamster has been shown to be 39° directly temporal on the retina to the optic disk (Tiao & Blakemore, 1976*a*). Using this estimate, the preferred directions of the twenty-six cells, judged to be selective by the 'null' criterion, were examined in relation to the position of the area centralis. Fourteen of these cells showed a preference for movement which contained no centripetal component, while in the other twelve cells at least one vector of the preferred direction was centripetal.

Fig. 2 shows the visual receptive-fields plotted for cells recorded during one electrode penetration through the hamster's superior colliculus. Small receptive-fields ($< 200 \text{ deg}^2$) were obtained for cells recorded from the superficial layers, while markedly larger fields were plotted for cells 5-10, which were located in the intermediate and deeper tectal layers. The borders of the fields are denoted with straight lines, but this resulted from the method used to plot the fields, which was with the leading edge of a hand-held wand. Polar diagrams for the cells which were directionally selective, as determined by the statistical measure, are also shown. In some instances, the polar diagrams show a substantial difference in the total spike count for two opposing directions, but the direction is not considered to be preferred due to large response variability.

Receptive-field sizes of all visual cells are shown as a function of depth in the tectum in Fig. 3. While it was not possible for a number of cells to be assigned to specific layers on the basis of histological reconstruction of electrode tracks, it is clear that small receptive-fields predominate in the superficial layers. Large fields and visual cells with indeterminate receptive-field borders become much more common with increasing depth in the tectum.

As has been noted above, another major difference between the response properties of the visual cells in the superficial layers and those in the deeper layers was the tendency for the latter to demonstrate rapid response decrements with repeated stimulation. This was rarely observed for cells found in the superficial layers. Fig. 4 shows the responses (spike number) of two cells, recorded in the same experiment, as a function of number of

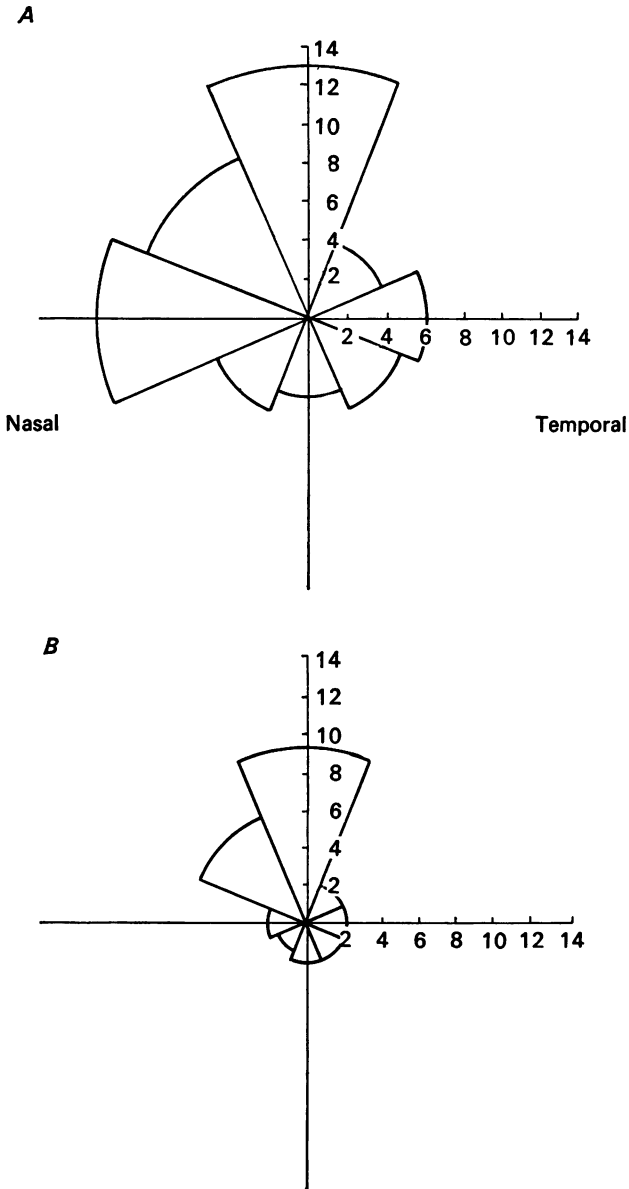


Fig. 1. In *A*, is shown a distribution of the preferred directions of cells, judged to be directionally selective using the statistical criterion. Where a cell was found to be selective for more than one direction, that direction which accounted for the most variance in its *t* test is represented. In *B*, is shown a distribution of the preferred directions of the cells judged to be directional using the 'null' criterion.

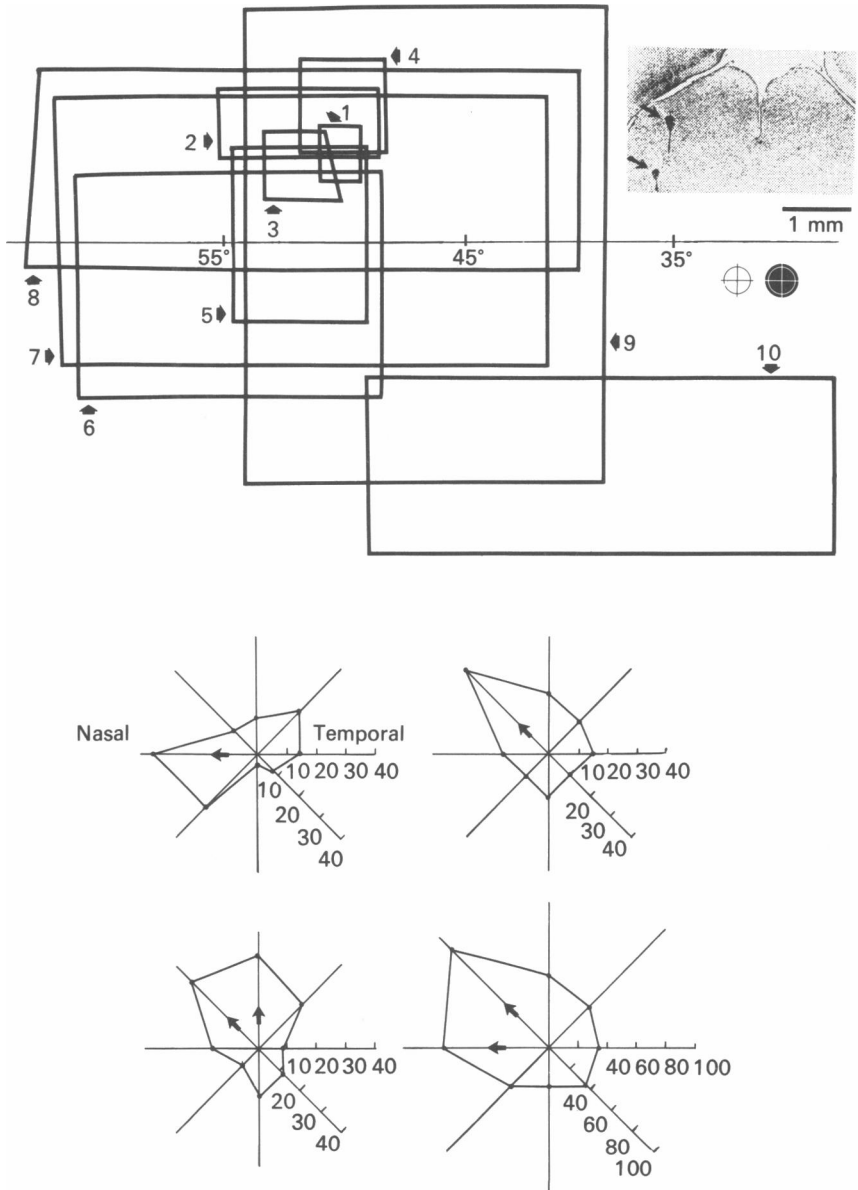


Fig. 2. The sizes and loci of 10 visual receptive-fields plotted during 1 penetration through the hamster's superior colliculus. The degrees of visual angle are referenced to the point on the tangent screen, which was closest to the animal's eye. The horizontal line is the mid line of the polar coordinate grid system. Cell 1 was recorded *ca.* 100 μ m above the first identifying lesion, while cell 10 was isolated *ca.* 250 μ m below that lesion. The

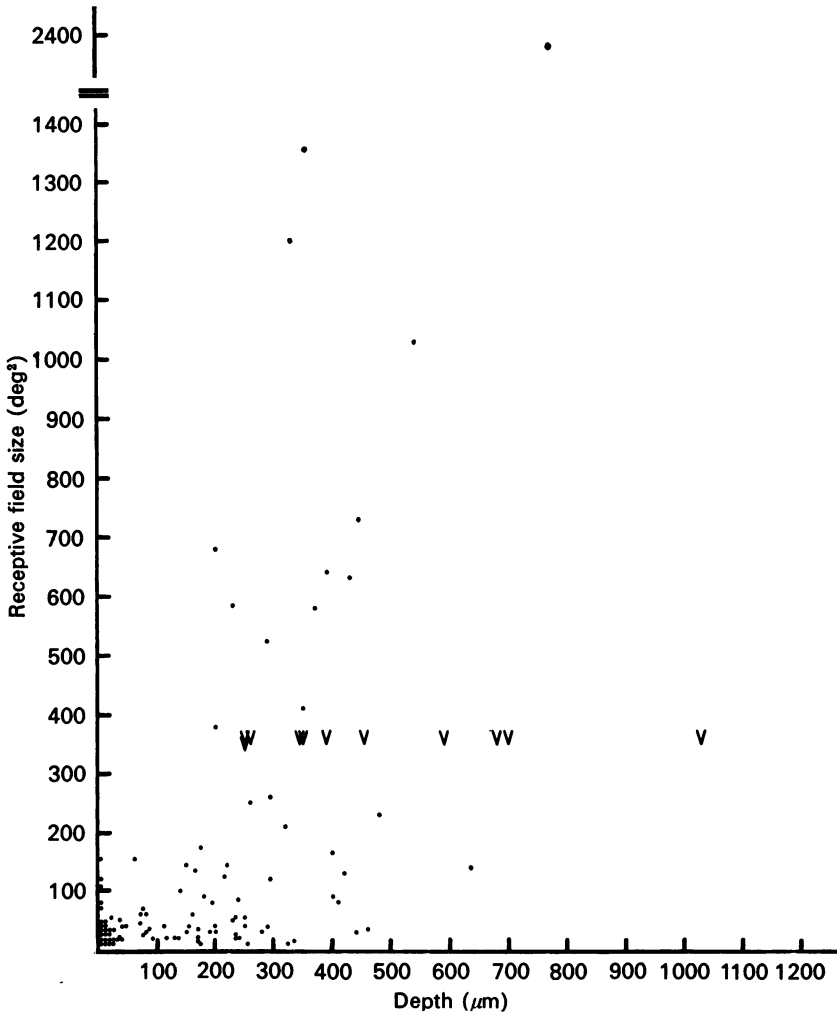


Fig. 3. Receptive-field areas as a function of recording depth in the superior colliculus. The depth of visual cells for which the borders of the visual field could not be accurately delimited are indicated with V's.

ventral lesion was made at the first somatosensory cell encountered in this penetration. At the bottom are 4 polar histograms, showing the spike counts for different directions of movement for the four cells which were determined to be directionally selective with the statistical criterion. In each instance, the stimulus was a 5° light spot moved at about 20 deg/s. The preferred directions are denoted by arrows.

trials, at 3 different stimulation rates. On the left side of Fig. 4 are the data obtained from a cell in the deeper layers. A comparison of the 3 stimulation rates (2, 10, and 20 s, inter-trial intervals) indicates that, even with an inter-trial interval of 10 s, an over-all response decrement is still apparent. In contrast, are the data for a cell recorded in the superficial layers (right side of Fig. 4), which showed no changes with repeated stimulation at any

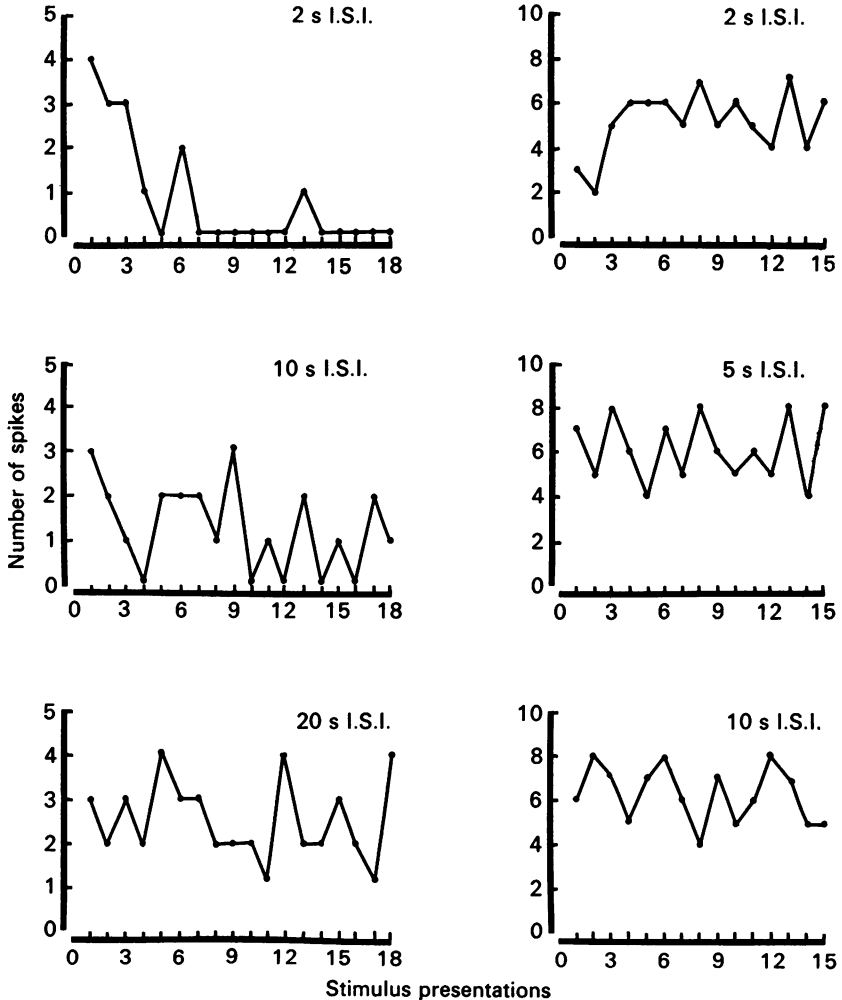


Fig. 4. The number of spikes obtained in response to stimuli moving across receptive-fields as a function of the number of stimulus presentations for two cells. In *A*, the cell was located about 520 μm from the tectal surface while in *B*, the cell was in the superficial layers, about 10 μm from the surface. The inter-stimulus interval in each instance is denoted by the I.S.I.

of the 3 rates tested. In view of the above findings, we employed inter-stimulus intervals of at least 10 s when testing for directional selectivity of all visual cells. Where there was any indication of response decrements with repeated stimulation, the responses of the cell were re-tested at even longer inter-trial intervals.

While the present experiments were not designed to investigate topographic representation, in general, we observed a topographic arrangement of the hamster's tectum similar to that which has been reported in other species (Kruger, 1970). Temporal fields projected posteriorly in the colliculus, nasal fields anteriorly, upper fields medially, and lower fields laterally. Within the limits of the loci in the tectum from which we recorded, there was no indication that receptive-field sizes changed as a function of retinal position. Fig. 5 shows the sizes and loci of the receptive-fields for the first cells isolated in each of twenty-three penetrations. All of these cells were within 150 μm of the tectal surface. All of the fields depicted in Fig. 5 were plotted in experiments where the tangent screen formed a 65° angle with the long axis of the animal's body. Four other penetrations were made when the screen was parallel to the animal's body, and three when the screen was perpendicular to the animal. The first receptive-fields of these penetrations are not shown in Fig. 5. These were between 70–110° from the zero point of the grid. In all cases, the fields were no larger ($< 150 \text{ deg}^2$) than the average size of field shown in Fig. 5.

For most visual cells, only a qualitative estimate of speed sensitivity was obtained. With few exceptions, most cells preferred speeds of less than 50 deg/s, and most of these showed maximal discharges between 10–20 deg/s. The effects of stimulus speed for three cells are shown in Fig. 6. In testing for directional selectivity, we typically employed speeds which were close to the optimal speed for a given unit. Most cells were tested for directional selectivity at only 1 stimulus speed. However, for eight cells, directional selectivity was tested at two speeds, and for two cells at 3 different speeds. The maximum range of speeds tested for a given cell was 20–80 deg/s. In none of these cells did we observe that directional selectivity was dependent on the speed of the moving stimulus. However, the size of our sample in this case was quite small, and the cells were tested only over a rather restricted range of speeds.

Effects of visual cortical lesions on directional selectivity

In the cat (Wickelgren & Sterling, 1969; Rosenquist & Palmer, 1971), it has been demonstrated that the directional selectivity of cells in the superficial layers of the superior colliculus is dependent on corticotectal inputs. It was of considerable interest, therefore, to determine whether or

not lesions of the visual cortex had any effect on the incidence of directionally selective cells in the tectum of the hamster.

Lesions encompassing all but the most posterior portion of V_1 , most of V_m , and extending into V_2 , as defined by Tiao & Blakemore (1976*b*), were

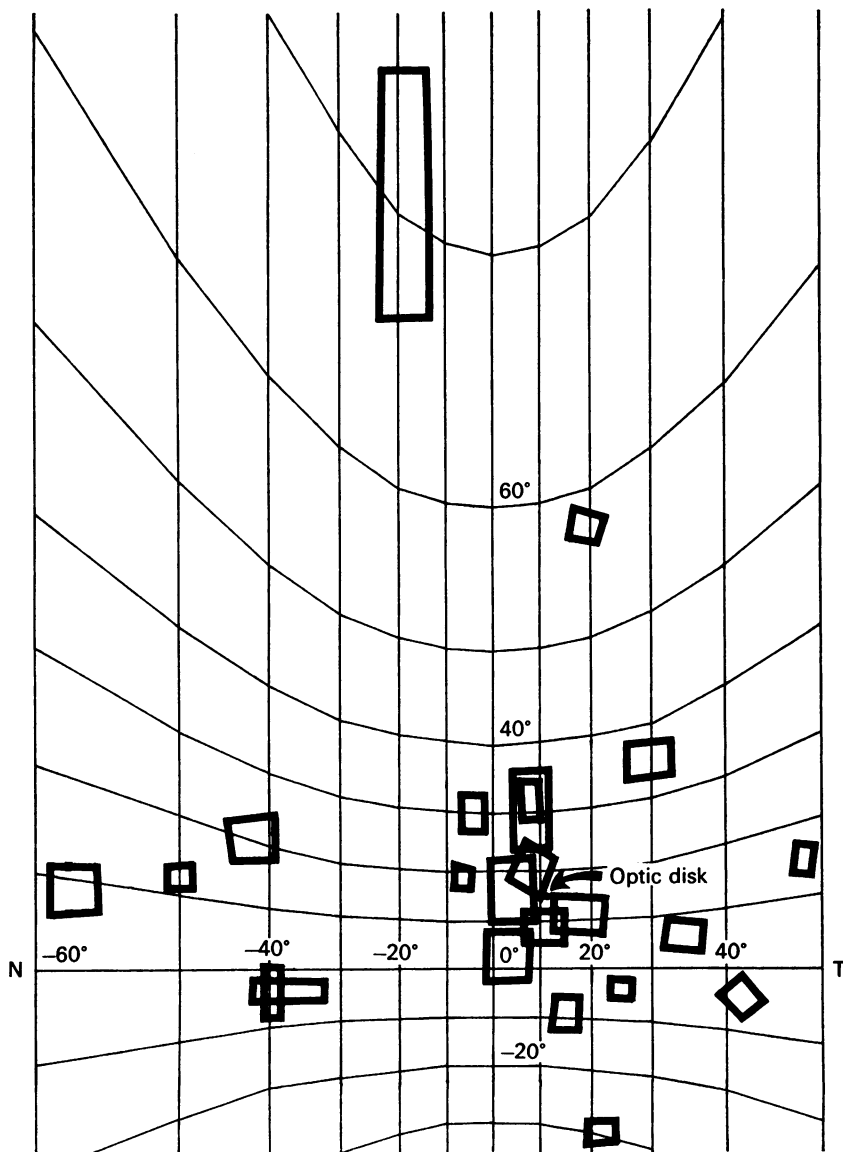


Fig. 5. The sizes and loci of the receptive-fields plotted for the first visual cell encountered in each of 23 electrode penetrations through the colliculus. All cells were within 150 μm of the tectal surface.

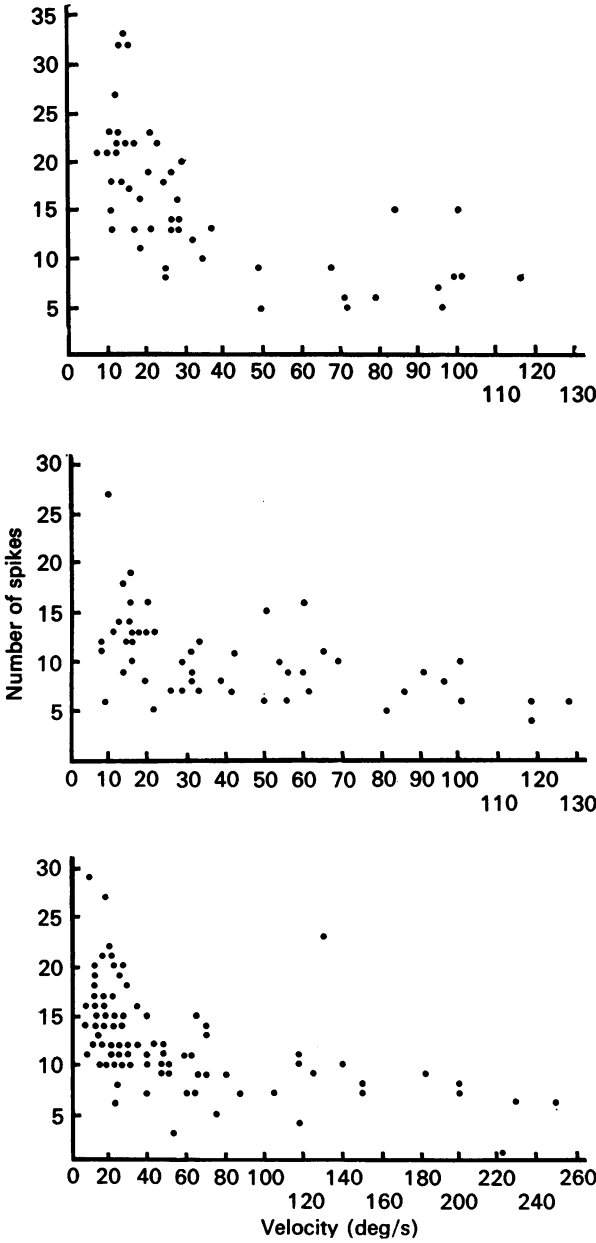


Fig. 6. The no. of spikes obtained as a function of the velocity of a stimulus moving across the receptive-field is shown for three cells. Each point represents the response to one stimulus presentation.

made in seven hamsters. The locus and extent of the cortical lesion for each animal is shown in Fig. 7. The drawings shown are tracings of photographs taken of the dorsal surface of the perfused brains. About 90% of V_1 was ablated with some sparing of the most posterior portion subserving superior visual fields. In addition, some portion of V_2 was also damaged, although the correspondence of the lateral extent of the lesions and V_2 cannot be accurately ascertained, due both to tissue shrinkage and to the great difficulty in determining the lateral limit of this representation electrophysiologically (Tiao & Blakemore, 1976*b*). Fig. 8 shows representative sections from one animal (L-1) which were used to reconstruct the cortical ablation. In all animals the lesions invaded the white matter, but did not infringe upon the superior colliculus.

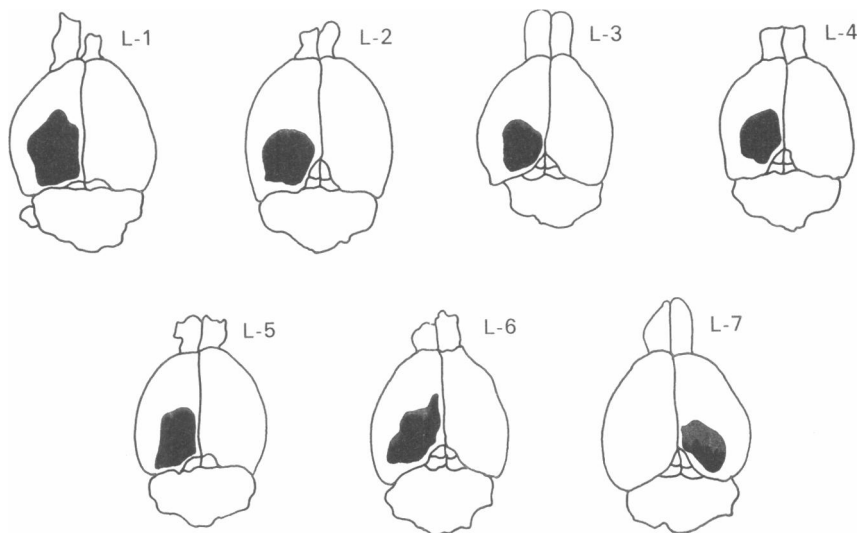


Fig. 7. Dorsal reconstructions of cortical lesions made in seven hamsters. The drawings are tracings of photographs taken of each brain. Shaded areas indicate the extent of lesions.

Using these preparations, 124 single neurones were isolated in 15 penetrations through the colliculus homolateral to the cortical ablation and thirteen cells were recorded in two penetrations through the contralateral tectum. Eighty cells on the homolateral side, and twelve on the contralateral side, were tested for directional selectivity using both the statistical and 'null' criteria. In all instances, the receptive-fields plotted for these cells were well within the portion of the visual field encompassed by the V_1 lesion. Employing the statistical criterion, 27.5% of the cells tested on the lesioned side exhibited selectivity. A similar reduction in the

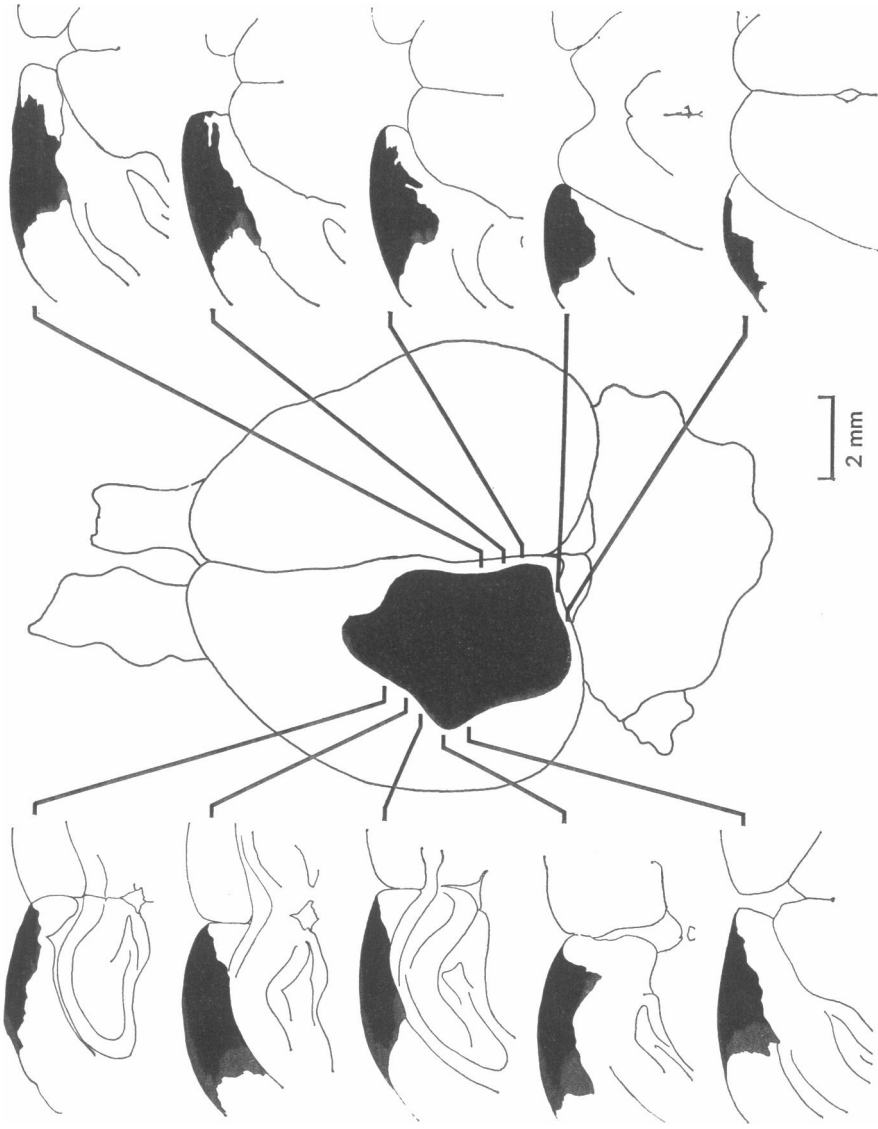


Fig. 8. Selected coronal sections showing extent of lesion in one animal (L-1). The correspondence of the coronal sections to the dorsal reconstruction is indicated by connecting lines. Shaded areas represent the portion of cortex and white matter which was removed by aspiration.

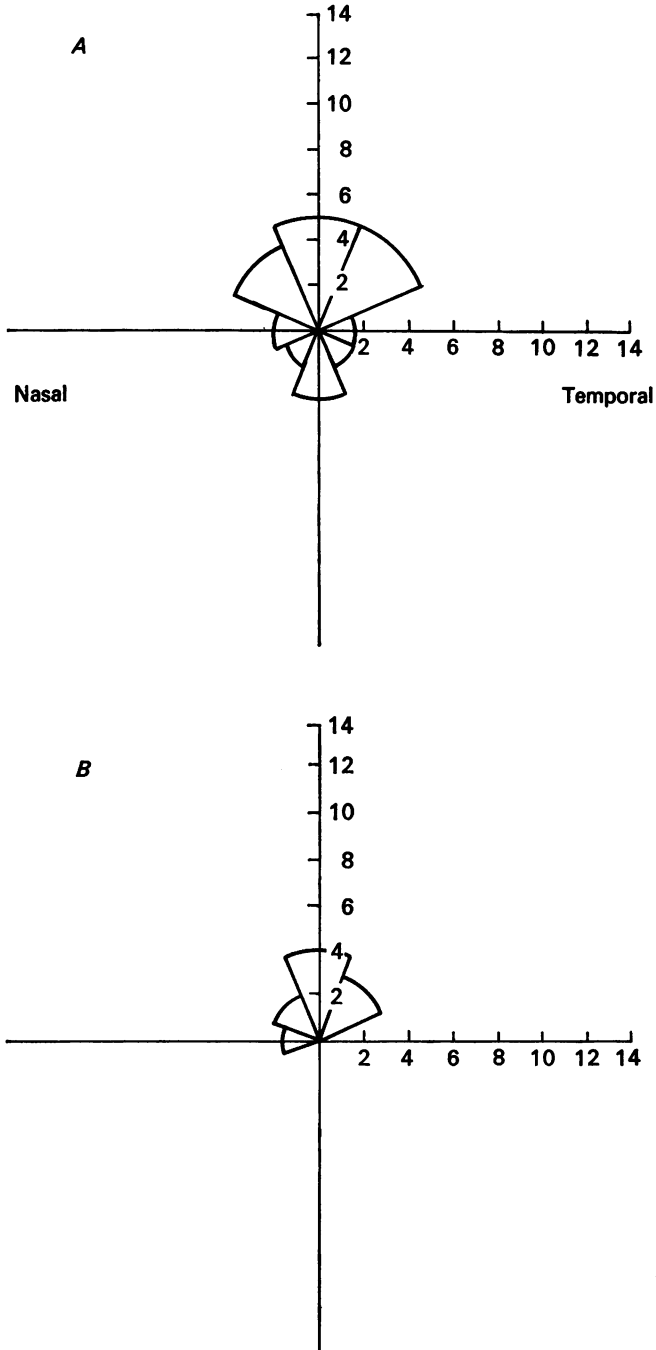


Fig. 9. The preferred directions of cells recorded from the superior colliculus of hamsters with lesions of visual cortex. In *A*, selectivity was judged by the statistical criterion, while in *B* the 'null' criterion was employed.

number of directionally selective neurones was also observed when the 'null' criterion was used. With this definition, only 12.5% of the cells were considered to be directionally selective. Of the twelve cells isolated in the contralateral colliculus, seven were judged as directionally selective according to the statistical criterion. Three of these exhibited selectivity, as defined by the 'null' criterion.

Fig. 9 summarizes, both for the statistical and 'null' criteria, the preferred directions of the cells judged to be selective in the colliculus ipsilateral to the cortical lesions. Although the proportion of cells showing directional selectivity, following cortical ablations, was reduced by more than 50%, the distribution of preferred directions did not appear to be appreciably altered.

In the cat, there is some suggestion (Mize & Murphy, 1976; Rizzolatti, Tradardi & Camarda, 1970), that the effects of visual cortical lesions upon directional selectivity of collicular cells may be restricted primarily to the superficial layers. Fig. 10 compares the % of directionally selective cells in the superficial and deep layers of intact and lesioned hamsters. While it is difficult, as previously mentioned, to assign cells to specific tectal laminae, we are confident that all cells considered as deep were isolated in the layers ventral to the stratum opticum. It is readily apparent, from Fig. 10, that the effects of visual cortical lesions are limited to the cells of the superficial layers. It should be noted, however, that the number of cells in the deep layers of both the intact and lesioned animals, for which parametric tests were carried out, was relatively small.

Apart from the effect described above on directional selectivity, no other obvious changes in receptive-field organization or general responsiveness were observed for cells in the colliculus ipsilateral to the damaged cortex. Furthermore, while only a small number of extra-visual cells were investigated in the lesioned animals, no changes were observed in the response properties of these neurones.

Somatosensory response properties

In the deeper layers, the first extra-visually responsive cells were encountered. With relatively few exceptions, these were only responsive to somatosensory stimulation. Of particular interest was the close correspondence obtained in a given electrode penetration between somatosensory receptive-fields on the body surface and the visual fields recorded from cells in more dorsal layers of the colliculus. Since the micro-electrode penetrations, in most cases, were not normal to the tectal surface, our information regarding this correspondence is, for the most part, limited to the rostro-caudal axis of the colliculus. The visual receptive-fields, as well as the somatosensory fields obtained in three electrode penetrations in one

experiment, are shown in Fig. 11. The 4 somatosensory fields encountered in the first electrode penetration were all localized to the two longest vibrassae. These two vibrassae appeared to cross the visual receptive-fields plotted for the cells isolated in the upper portions of this penetration.

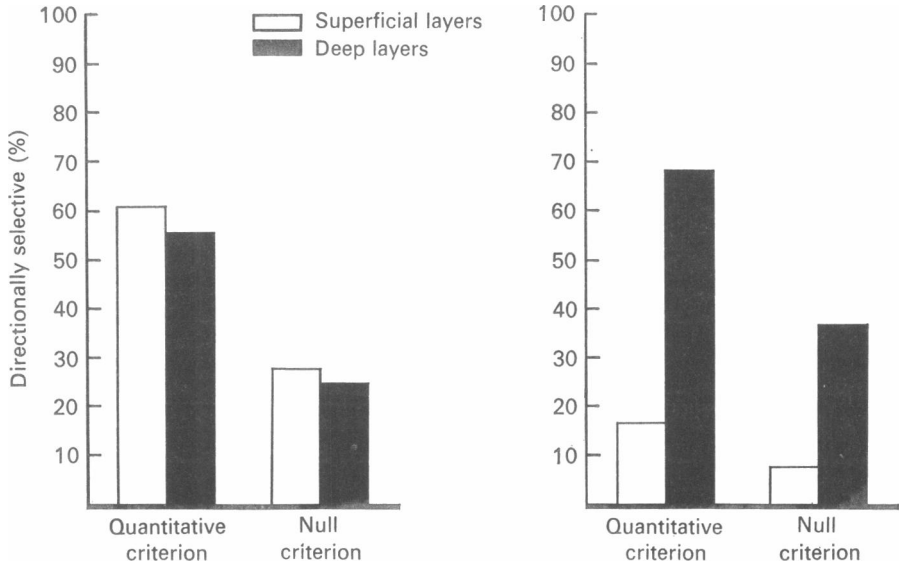


Fig. 10. The % of directionally selective cells recorded from the superficial and deeper layers of the superior colliculus as determined by the statistical and 'null' criteria. On the left are the results obtained from intact hamsters, while on the right are the data obtained from animals with lesions of visual cortex.

A correspondence between the responsive whiskers and the visual receptive-fields has been previously documented in the superior colliculus of the mouse (Dräger & Hubel, 1975, 1976). For the mouse, it was reported that by far the most common somatosensory responses were evoked by stimulation of the animal's vibrassae. In the hamster, however, only twenty of the ninety-eight somatosensory cells recorded responded exclusively to stimulation of one or more whiskers. In all instances, the responsive vibrassae showed a correspondence with the visual receptive-fields of the cells recorded dorsally in the penetration, in that, the shorter and more anterior whiskers were associated with the most nasal visual fields and the longer more posterior vibrassae were isolated ventral to visual cells having more temporal receptive-fields. This relationship was observed by sighting the receptive-fields from behind the animal through the responsive vibrassae, and also by sighting from the visual receptive-field to the eye of the animal. Typically, vibrassae-responsive neurones

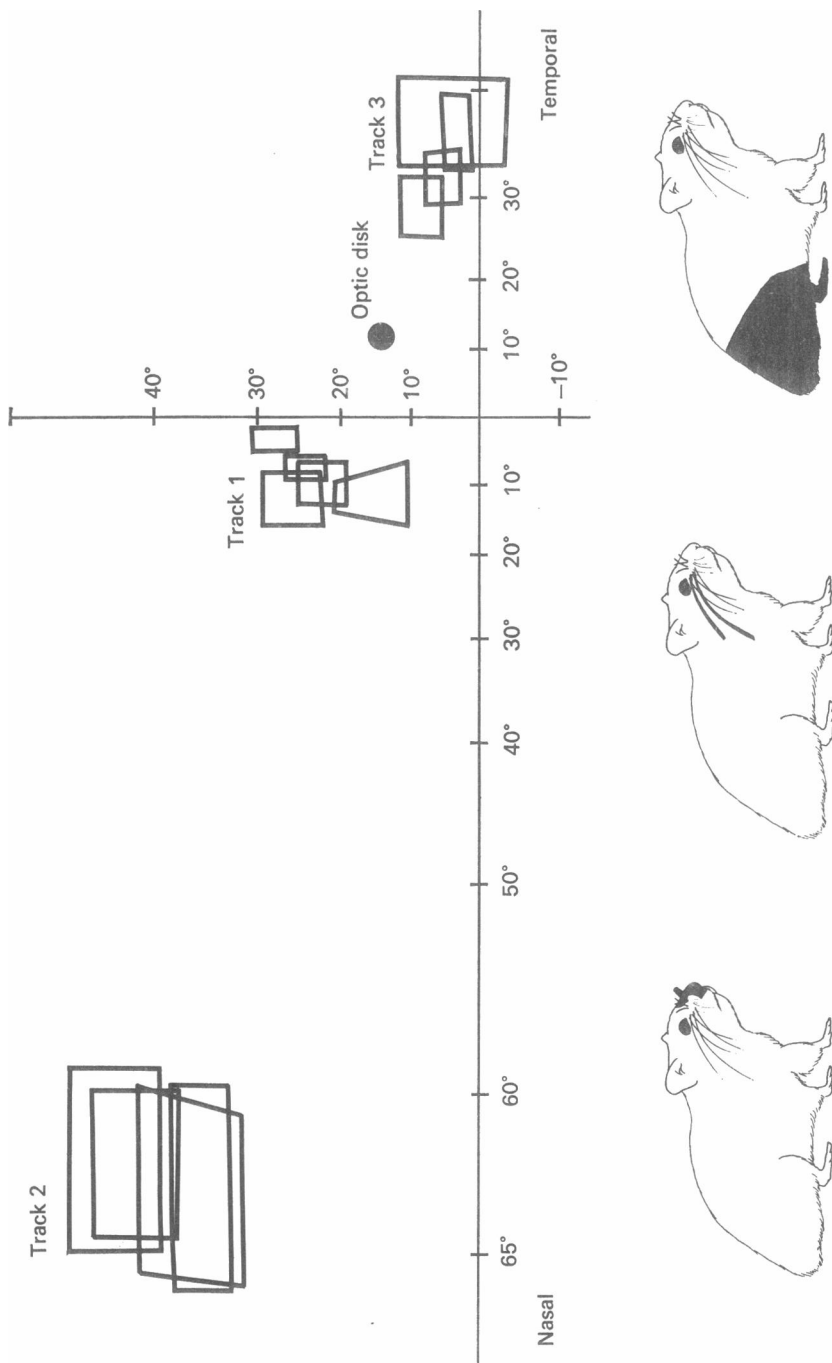


Fig. 11. The spatial correspondence between visual and somatosensory receptive-fields obtained in 3 electrode penetrations in one experiment. The dark portion of the animal's body indicates the somatosensory receptive-fields. The intersection of the vertical and horizontal lines denotes the origin of the polar co-ordinate grid system.

tended to be aggregated in a single penetration through the tectum, as indicated by track 1 of Fig. 11. However, there were some exceptions to this generalization. See for example, track 2 of Fig. 11 which had one cell responsive solely to displacement of vibrassae, and several cells responsive to touching of the animal's skin. In most instances where the somatosensory fields were localized to the animal's face, they were confined to the contralateral side. In three cells, a slight but definite extension of the receptive-fields across the mid line was observed. These neurones were encountered in penetrations where cells having the most nasal visual fields were isolated.

In track 3, the visual receptive-fields were located temporally and the somatosensory fields were on the posterior portion of the animal's body. Fields of the posterior body were always quite large, when compared to those of the animal's face. In addition, posterior fields were often found to extend well over the mid line on to the ipsilateral side of the body. These posterior fields were typically asymmetrical, in that, they extended less ipsilaterally than contralaterally on the animal's body. In one penetration through the most posteromedial portion of the colliculus, all somatosensory cells isolated had receptive-fields which were confined, for the most part, to the ipsilateral side of the body. Each of these fields extended only slightly on to the contralateral side.

Almost all somatosensory cells could be activated by light taps with a blunt probe. Four cells were encountered which appeared to respond only to slight displacement of the lower jaw, but not to touch of the body surface. Two other cells, with high rates of spontaneous activity, were completely suppressed for at least 30 s by the application of light pressure to their receptive-fields.

Using the blunt probe and camel's hair brushes, it was found that different portions of somatosensory receptive-fields responded in the same fashion, indicating a relatively homogenous organization. These observations were documented quantitatively through the use of an electro-mechanical stimulator, which permitted the application of stimuli having constant intensity and duration to discrete loci within the receptive-field. The results of these tests are shown for three cells in Fig. 12. The somatosensory field for each of these cells is shown, as well as the number of action-potentials evoked by a displacement (2.5 mm) of a probe tip (diam. 3 mm, one-third surface), placed directly on the animal's skin at different points within the receptive-fields. The latency to the first spike for each locus stimulated is shown to the right. In the cell shown in Fig. 12c, a clear but less vigorous off-set discharge was observed, in addition to the normal on-set response.

In most penetrations through the lateral portions of the superior

colliculus, systematic shifts of the somatosensory receptive-fields on the body were observed as a function of depth of the electrode (Figs. 13a, b). These shifts in receptive-field positions from upper to lower portions of the body most likely reflect the lateral deviations of the electrode with increasing depth in the tectum. However, there were other penetrations (Fig. 13c), in which the fields shifted from higher to lower, and back to

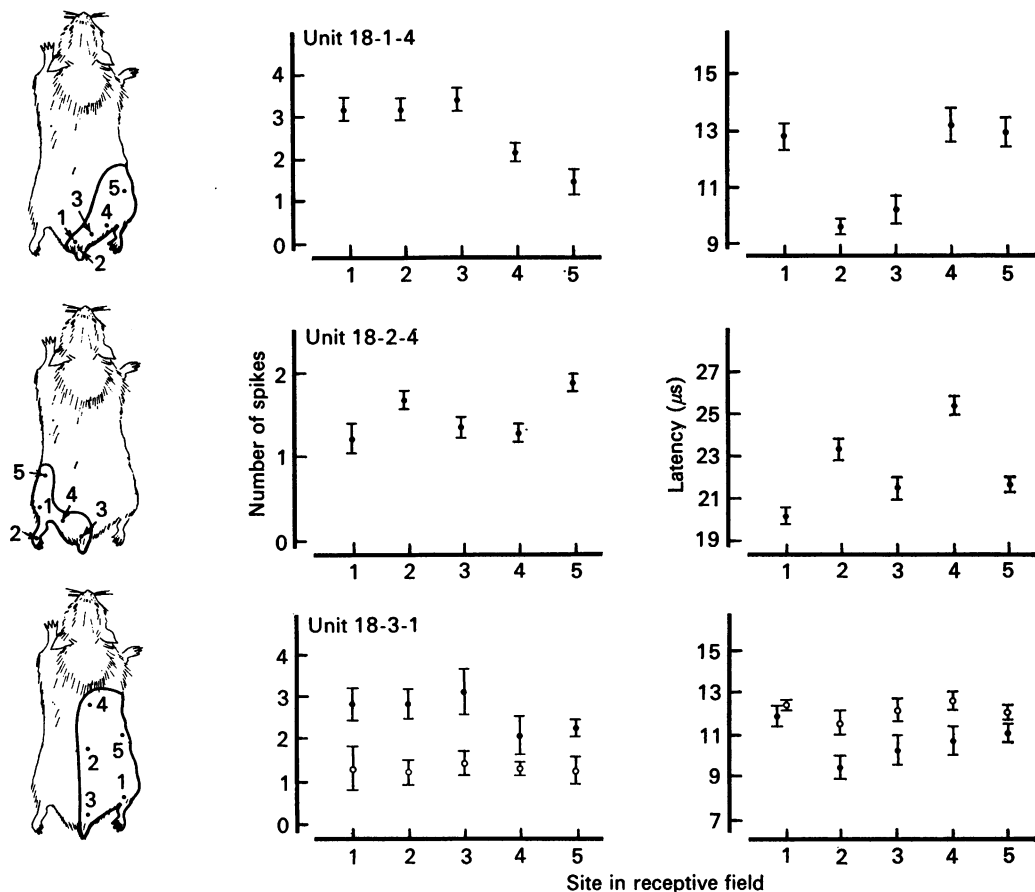
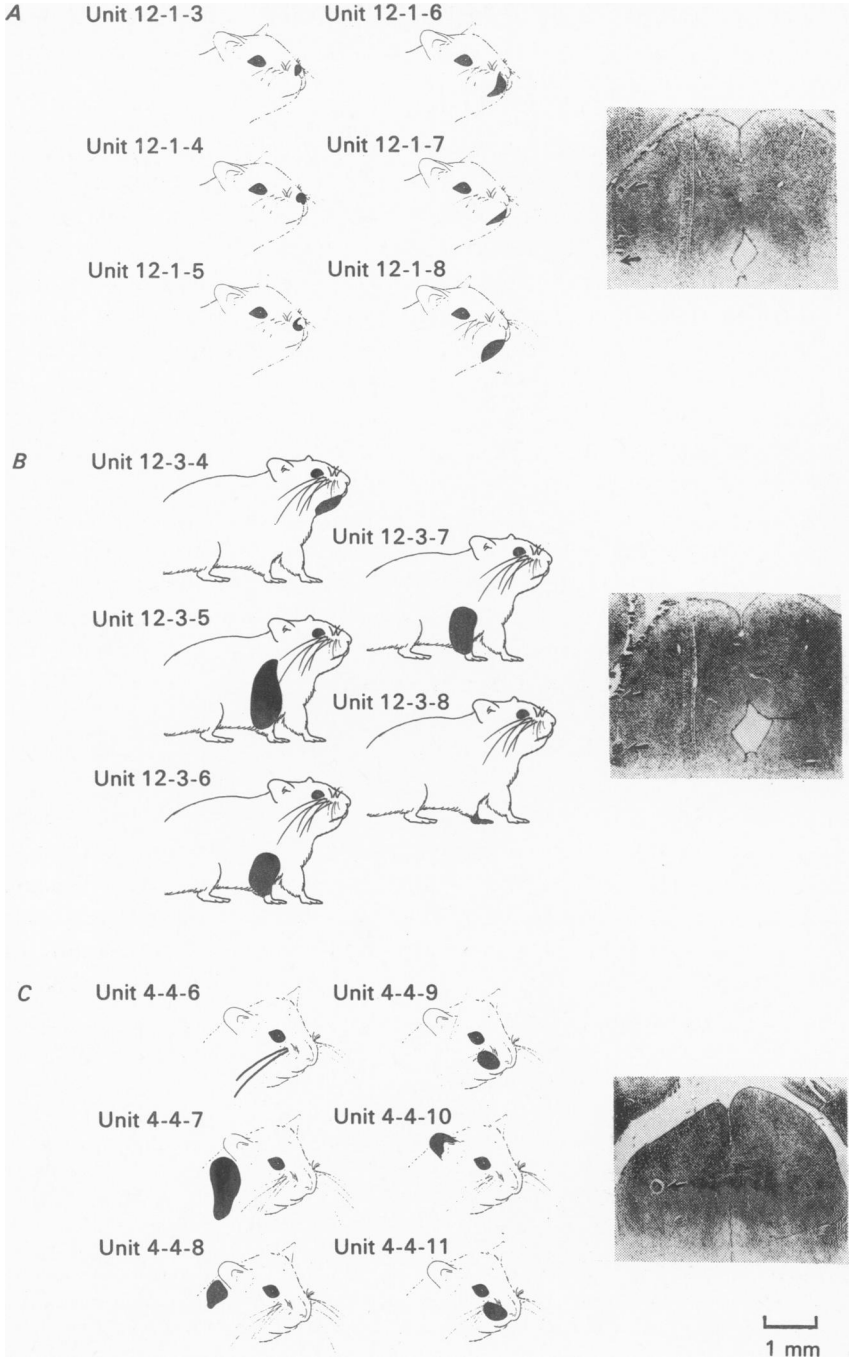


Fig. 12. Response magnitudes and latencies for 5 loci in each of 3 somatosensory receptive-fields. In the graphs to the left, each point represents the mean number of spikes evoked over 10 stimulus presentations. The s.e. of mean is indicated above and below each mean. To the right, is shown the mean latencies to the first action potential for each response. The loci stimulated and the area of the receptive-fields are indicated in the left portion of the fig. The open circles in C refer to the off response. The stimuli were 2.5 mm displacements of a 3 mm probe tip with a stimulus duration of 200 ms. At each point, the probe tip was placed just touching the surface of the skin.



higher portions of the face or upper body. It is unclear why some penetrations showed this apparently random scatter, since in all cases the angle of the electrode did not vary appreciably.

Auditory response properties

Only fourteen cells were found to respond exclusively to auditory stimulation. All of these were located in the posterior portions of the colliculus, and thus corresponded to temporal visual fields. Most of the auditory cells preferred complex stimuli, such as key jangling, finger snaps, and hissing sounds to pure tones. An attempt was made for most cells to get an indication of their tuning functions by using pure tones of different frequencies. In all instances, it was found that the cells responded over a broad range, although most of them showed some preference for higher frequencies. However, the small number of auditory cells which responded reliably to pure tones, and our inability to equate stimulus energy at different frequencies, precluded a detailed investigation of frequency tuning. Of greater interest was the horizontal extent of the auditory receptive-fields, and their correspondence with the visual fields of cells recorded in the same penetration. This correspondence is shown for three cells in Fig. 14. There was, however, one cell which responded with an approximately equal number of spikes to a stimulus whose position was varied over 120° in the horizontal plane.

DISCUSSION

As has been reported for a number of other mammalian species (Albano, Humphry & Norton, 1975; Dräger & Hubel, 1975; Cynader & Berman, 1972; Gordon, 1973; Humphrey, 1968; Masland *et al.* 1971; Michael, 1972), the superior colliculus of the golden hamster showed a distinct difference in the functional organization of the superficial (as compared to the deeper) layers. Neurones in the superficial layers were exclusively

Fig. 13. The shifts in somatosensory receptive-fields obtained with increasing depth in the colliculus for 3 electrode penetrations. In each case, the electrode was oriented perpendicular to the cortical surface. In *A* and *B*, a systematic descent of receptive-fields on the body surface is evident. In *C*, however, fields shift from upper to lower and back to upper portions of the body. To the right are photomicrographs showing the corresponding electrode penetrations through the superior colliculus. In *A*, the first somatosensory cell was recorded about $750 \mu\text{m}$ above the lower lesion, the last somatosensory cell was recorded at the lesion. In *B*, the first somatosensory cell was isolated about $350 \mu\text{m}$ above the lower lesion, the last cell at the lesion. In *C*, the first cell was at the lesion and the last cell $320 \mu\text{m}$ below the lesion.

visual, had smaller receptive-fields, and generally showed no evidence of response habituation, even with relatively short inter-trial intervals. In contrast, the receptive-fields of visual cells in the deeper layers were typically large, and responses often showed rapid habituation. The majority of cells in the deeper layers responded to somatosensory stimulation. Auditory cells appeared to be confined to the posterior portions of the tectum, underlying temporal visual fields. Polymodal cells were also encountered in the deeper layers, but these were quite rare.

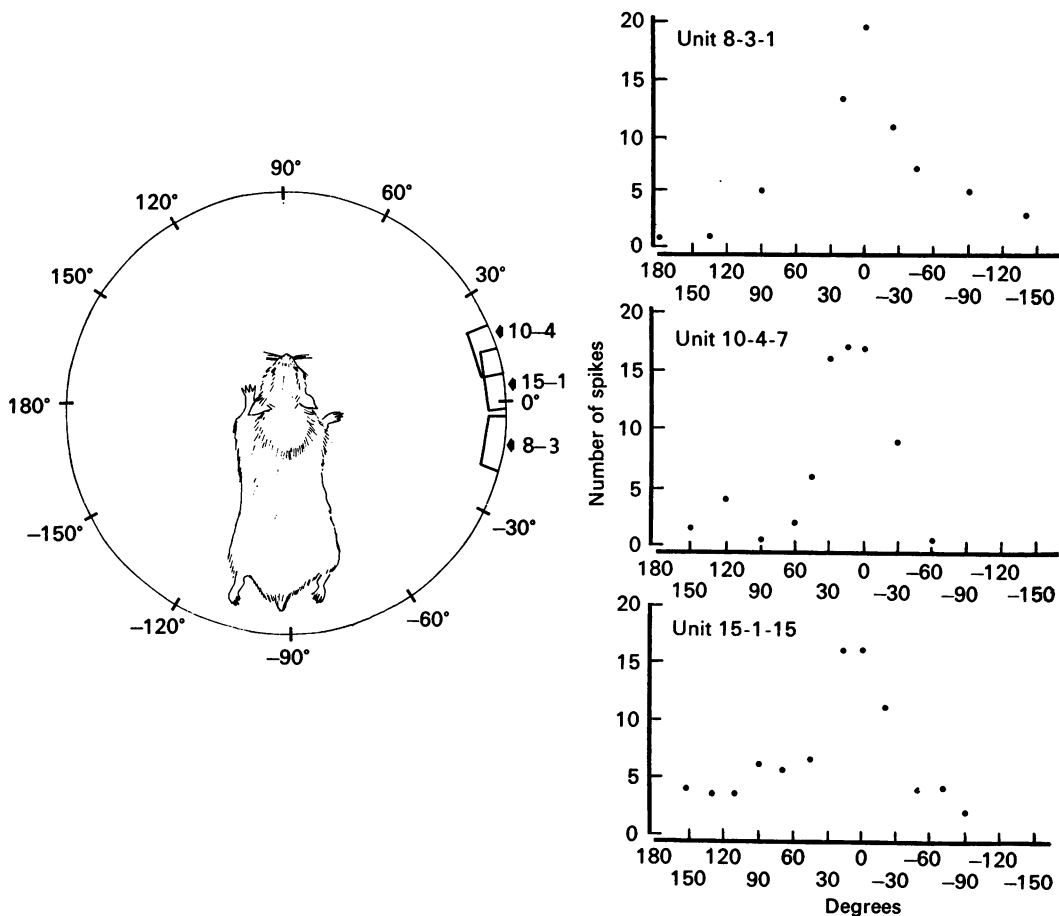


Fig. 14. The correspondence between visual and auditory receptive-fields. At the left, the locus of the visual receptive-fields plotted during 3 electrode penetrations through the posterior portions of the colliculus. At the right, for three auditory cells the number of spikes obtained for 5 stimulus presentations at different positions of the sound source around the animal's head. In all cases, the sound was a white noise burst (100 ms duration).

A prominent feature of visual cells, both in the superficial and deeper layers, was their preference for moving stimuli rather than stationary flashing lights. While cells in the superficial layers typically yielded weak responses to flashing stimuli, most cells in the deeper layers responded only to movement. For many cells in the superficial and deeper layers, there were distinct differences in responses to opposing directions of movement. Various investigators studying the properties of tectal cells in different species have employed different definitions of directional selectivity. The standard definition of directional selectivity was provided by Barlow & Levick (1965), in their classic investigation of directional selectivity in the retina of the rabbit. This criterion was utilized by Sterling & Wickelgren (1969), in their investigation of the superior colliculus of the cat. Using this criterion in the hamster, 27.7% of the ninety-four cells tested were judged to be directionally selective. A distribution of the preferred directions of these cells showed a clear preference for movement with an upper-nasal component. A similar preference has been found for directionally selective cells of the tectum of the mouse (Dräger & Hubel, 1975).

Other investigators have specified directional selectivity in the tectum as a difference (2:1) in spike counts between opposing directions of stimulus movement (Dreher & Hoffmann, 1973; Hoffmann, 1973; Hoffmann & Sherman, 1974). Directional selectivity has also been defined as a 'clear and consistent asymmetry in directional response' (Rosenquist & Palmer, 1971, p. 634). The statistical measure which we employed, in addition to the 'null' criterion, provided a quantifiable means for judging the asymmetry of the responses of a cell to opposing directions of movement. In addition to considering the magnitude of the responses to opposing directions, this measure also takes into account the variability of those responses. With this criterion, 60.6% of the cells in the colliculus of the hamster were considered directionally selective. With the statistical criterion, no single direction was found to be preferred significantly more than others. This agrees with our earlier conclusion (Rhoades & Chalupa, 1976), which was based on a smaller sample of cells. However, with the present somewhat larger sample, a greater number of cells were found to prefer movement in the upward direction.

The difference in the estimates provided by these two measures is largely the result of the fact that, using the 'null' criterion as defined by Barlow & Levick (1965), any cell which showed an appreciable response (that is, activity exceeding the spontaneous level of the cell) in the non-preferred direction was not considered to be directionally selective. In contrast, the statistical measure judged cells as selective when there was a reliable difference in the responses to opposing directions of movement, even when movement in the non-preferred direction yielded a considerable

number of discharges. The fact that the 'null' criterion yielded a sample of cells with a significantly asymmetrical distribution of preferred directions, while the statistical measure did not suggest that the definition of Barlow & Levick (1965) for directional selectivity results in a more homogeneous sample of directionally selective cells.

Tiao & Blakemore (1976*c*), using the criterion of Barlow & Levick (1965), found that about 12% of the cells in the superior colliculus of the hamster were directionally selective. It is unclear why our estimate of directionally selective cells, using the 'null' criterion, in the intact hamster is considerably higher than that provided by Tiao & Blakemore (1976*c*). Possible sources of this discrepancy may include differences in the anaesthetic employed and/or differences in the sampling characteristics of the electrodes utilized. However, in both studies a preference for movement with an upward component was observed for directionally selective cells.

In the cat, it has been well established that directional selectivity of tectal neurones in the superficial layers is organized by inputs from visual cortex (Berman & Cynader, 1972, 1975; Rosenquist & Palmer, 1971; Wickelgren & Sterling, 1969). Projections to the superior colliculus from visual cortex have been demonstrated in several species (Garey, Jones & Powell, 1968; Giolli & Guthrie, 1967; Harting & Noback, 1971; Wilson & Toyne, 1970), including the hamster (Schneider & Jhaveri, 1974), where the corticotectal terminals appear to be confined to the superficial grey and optic layers. The results of the present study indicate that the cortical inputs to the tectum of the hamster play an important role in the organization of directional selectivity of many cells in the superficial layers. The fact that directional selectivity of cells in the superficial layers was not completely abolished by our cortical lesions may have been due to the sparing of some portions of the cortical input to the colliculus. In particular, the area designated as V_2 by Tiao & Blakemore (1976*b*), was only partially damaged by our lesions. Alternatively, it is also possible that directional selectivity of some tectal neurones may be organized intrinsically, or by inputs other than those from visual cortex. The latter possibilities seem especially likely for the directionally selective neurones encountered in the hamster's deeper tectal laminae, since the % of directionally selective cells isolated in the deeper layers appeared to be unaltered after cortical ablations.

In contrast to the cat (Berman & Cynader, 1972), and the monkey (Cynader & Berman, 1972; Schiller, Stryker, Cynader & Berman, 1974), the size of receptive-fields in the superior colliculus of the hamster was not observed to increase with retinal eccentricity. In an anatomical investigation of the retina of the hamster, Tiao & Blakemore (1976*a*), found a

six-fold increase in ganglion cell density from the periphery of the retina to an area slightly temporal on the retina to the optic disk, and concluded that the hamster has a crude area centralis. In an accompanying paper, these investigators (Tiao & Blakemore, 1976*b*), reported that visual cortical receptive-fields tended to increase in size with retinal eccentricity. With regard to collicular receptive-fields however, Tiao & Blakemore (1976*c*), also noted that receptive-field size did not vary appreciably with eccentricity. We did observe a pronounced increase in somatosensory receptive-field size when recording in the caudal portion of the colliculus. These somatosensory fields corresponded to temporal visual fields. This suggests that, in the superior colliculus of the hamster, there may be an increased convergence of peripheral inputs to somatosensory neurones, but not to visual neurones in the superficial layers.

In all penetrations through the superior colliculus, a clear spatial correspondence was observed between visual and somatosensory receptive-fields. This finding has also been observed by Schneps & Finlay (1976), as well as Tiao & Blakemore (1976*c*). Such correspondence may be a general feature of mammalian superior collicular organization, since similar findings have been reported recently for the mouse (Dräger & Hubel, 1975, 1976), and the cat (Stein *et al.* 1976). Somatosensory neurones have also been encountered in the deeper layers of tectum in the monkey (Cynader & Berman, 1972), and the rabbit (Masland *et al.* 1971), but the visual-somatotopic correspondence in these species remains to be documented.

Auditory units in the hamster were confined to the posterior portions of the colliculus underlying temporal visual fields. The receptive-fields for most of the auditory units were fairly restricted, and corresponded rather well to the visual fields recorded in a given penetration. One cell, however, was encountered which yielded responses to auditory stimuli positioned over a wide area around the head of the animal. In the mouse, Dräger & Hubel (1975), also observed that auditory cells were localized to the posterior portion of the superior colliculus. In the cat, on the other hand, Gordon (1973) found that auditory-visual correspondence of receptive-fields was evident throughout the deep layers of the colliculus. It appears, therefore, that a major difference exists regarding auditory functional organization in the superior colliculus of rodents, as compared to that of cat.

A possible explanation for this difference may be provided by the limited sound localization cues which are available to animals with a small inter-aural distance. Such animals might be expected to have considerable difficulty localizing sources of very brief sounds restricted to frontal areas, since intensity, phase and latency differences would be minimal. These cues would, however, be available when sources of sound were

located in the periphery of the animal. The hypothesis we are advancing may be stated as follows: since small rodents cannot effectively utilize inter-aural differences for orienting to frontal sound sources, there would be no apparent reason for restricted auditory receptive-fields representing frontal areas in the superior colliculus. This speculation, of course, assumes that the auditory input to the colliculus is, in fact, involved with orienting behaviour. In this regard, it may be worthwhile to investigate behaviourally the ability of hamsters to localize sources of sound.

As has been noted by other workers (Dräger & Hubel, 1975; Gordon, 1973; Stein *et al.* 1976), the close correspondence of diverse sensory inputs to the superior colliculus lends further support to the view that one of the functions subserved by this structure is the orientation of the animal to stimuli in its environment. Schneider (1967, 1969), in his behavioural studies, found marked impairments in orienting toward both visual and auditory stimuli, following undercutting of the superior colliculus of the hamster. Only transitory deficits, however, were observed in the animal's ability to orient toward tactile stimuli. The neurophysiological findings of the present study would seem to predict that lesions of the superior colliculus of the hamster should result in orientation deficits to visual, auditory and somatosensory stimuli. The apparent discrepancy between the deficits predicted by our neurophysiological findings and the behavioural data actually obtained by Schneider (1967, 1969), could be explained by the possible involvement of other brain structures in somatosensory localization function.

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