Responses to Visual Stimulation and Relationship Between Visual, Auditory, and Somatosensory Inputs in Mouse Superior Colliculus

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SINGLE-CELL STUDIES of responses to natural stimulation have been made in the superior colliculus of many vertebrate species (6, 11, 12, 14, 20, 22, 25, 32–36, 41, 43, 50). While a number of differences have been noted, the general picture is a surprisingly uniform one. Most of the reports have stressed such features as the responsiveness of cells to moving objects regardless of precise shape, a marked increase in field size with increasing depth in the tectum, and in the deep layers the presence of somatosensory and auditory input as well as visual, with a tendency for many cells to habituate to repeated stimulation.

These studies, together with ablation experiments (40) and the analysis of eye movements in response to local tectal stimulation, have made it evident that one important function of the superior colliculus is concerned with the orienting of an animal's head, ears, and eyes toward a stimulus in the environment (29, 33, 36) or, in a more general interpretation, with shift of attention (54). In the monkey, for example, the superior colliculus seems to be the site of a mechanism whereby a stimulus in some part of the visual field produces eye movements that bring that part of the field onto the foveas (29, 34–36).

The presence of auditory and somatosensory input to the tectum suggests that these modalities also play a part in orienting the animal to stimuli in the environment. In support of this are the findings of Wickelgren/Gordon (12, 50) that the optimum position of a sound source relative to a cat's head, for producing responses from a particular part of the colliculus, was highly correlated with the positions of visual receptive fields of cells in the same part of the colliculus. The optimum directions of stimulus movement were also usually the same for the two modalities. For cells responding to tactile stimulation the correlation was far less clear, but cells with tactile fields on the animal's face did tend to occur in the anterior part of the tectum, where the visual field input is from the midline, whereas cells with fields on the paws or trunk were located more posteriorly, where temporal visual fields are represented. A similar correlation has also recently been observed by Stein et al. (42).

In an animal like the cat, whose eye movements and particularly head movements are well developed, no part of the body bears any constant relationship to the visual fields, and hence no very close relationship would be expected between the tectal representations of the somatosensory and visual systems. The mouse, however, moves its eyes very little (5) and tends to orient its whole body toward an interesting stimulus rather than turning its head or eyes. Furthermore, one richly innervated organ, the vibrissae, crosses in front of a large part of the mouse's visual fields, as shown in Fig. 1. In investigating the mouse superior colliculus it is obviously important to look closely at the relationship between the topographic representations of these two sensory systems. The following study was undertaken to examine the responses of tectal cells to visual, somatosensory, and auditory stimuli, with particular attention to a correlation between their topographic projections.

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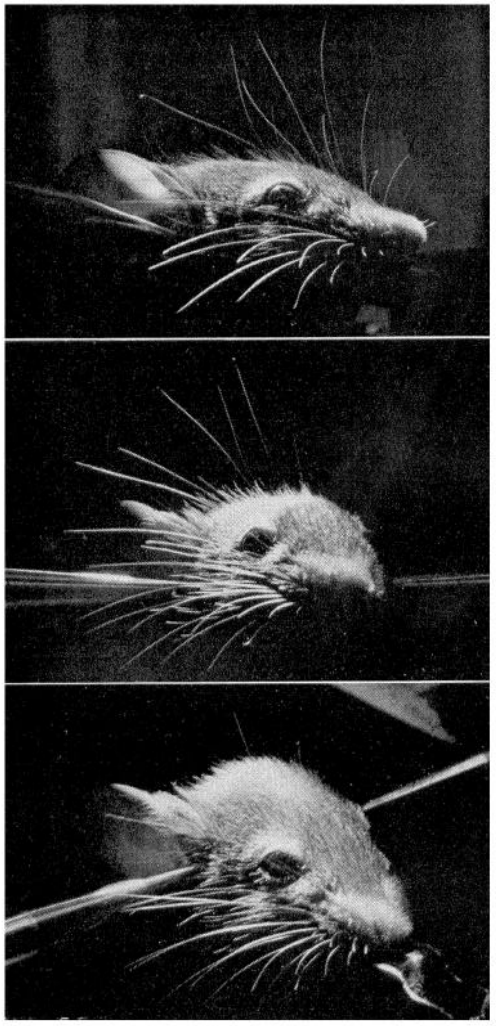

FIG. 1. Three photographs of a mouse to show whiskers crossing in front of visual field.

METHODS

The 14 mice used in the present experiments were of the C57BL/6J strain (breeding stock obtained from the Jackson Laboratories, Bar Harbor, Maine). The mice were 2–4 mo old and weighed 20–28 g. Detailed procedures for stimulating and recording from mouse visual system have already been published (7). Mice were anesthetized with pentobarbital (60 mg/kg initial dose, supplemented as required with 0.02-mg doses) and chlorprothixene (Truxal), a tranquilizer (single dose, 0.12 mg). Atropine (0.3 mg) was given to counteract the vagotonic effects of the anesthetics and prednisolone (2 mg) to prevent brain edema. No significant eye movements were observed, either directly or in recording receptive fields, and it was, therefore, not felt necessary to paralyze the eye muscles. Artificial respiration was consequently not necessary, but the trachea was cannulated. A temperature of 36–37°C was maintained by a manually controlled heating pad.

The eyes were covered with contact lenses. A conical mask over either eye permitted stimulation of separate eyes or of whiskers while blocking off vision. The mouse faced a back-illuminated translucent tangent screen set at right angles to the long body axis, 10.5 cm away. The screen was marked off in 10° circles centered about the projected body axis. In two of the experiments, in which the temporal visual fields were explored, the screen was turned at right angles to its usual position, i.e., parallel to the long axis of the mouse, and degree circles were centered on a line running through the two eyes. The screen was lit diffusely by a 0.4 cd/m^2 background on which were superimposed stimuli about 0.8 log units brighter. Light stimuli or shadows of various shapes, moving or stationary, were generated by a hand-held slide projector or a Zeiss hand lamp.

For stimulating the whiskers or the fur we used a small hand-held blunt-ended probe, working with the aid of a Zeiss operating microscope. For permanent records a small mechanical transducer (Pitran, a pressure-sensitive transistor) was mounted on the end of the probe and brought sharply against the end of the hair to stimulate it, while triggering the sweep of a storage oscilloscope. We tested only for light touch and occasionally joint sensation; noxious stimuli were impractical in these lightly anesthetized mice. Auditory stimuli consisted of clicks or tones with controlled rise-fall times, as well as more complex stimuli: by far the most effective were clicks produced by fingernails, and these were used to estimate the regions over which responses could be evoked. In recording auditory responses, the Pitran was used as a microphone to trigger the oscilloscope sweep.

The mouse was supported in a head holder by a short bar of metal glued to the skull. No ear bars were used, but the head was held in roughly the same position as that obtained with a standard stereotaxic instrument, i.e., the snout was somewhat higher than that of a normal standing mouse (26). The cortex overlying the tectum on one side was exposed by removing about 4 mm^2 of bone. The dura was left intact and stability was obtained with a shallow well of agar. Electrodes were electropolished tungsten coated with lacquer to within 2–10 μm of the tip. Penetrations were generally made in the coronal plane at an angle of 15–20° to the vertical, so that the electrode entered roughly per-

pendicular to the tectal surface. In one experiment (Figs. 14 and 15) the penetrations were all vertical and consequently traversed the tectum obliquely.

The responses of cells were recorded on a spot plotter (49) using a storage oscilloscope triggered from a photoelectric cell driven by the visual stimulus or, in the case of auditory or whisker stimuli, from the Pitran.

For electrode-track reconstructions, several electrolytic lesions (2 μA × 2 s, electrode negative) were made in most penetrations, including one at the tectal surface and one at the end of the penetration. The mice were perfused with 10% formalin; brains were embedded in celloidin and sectioned at 25 μm, and the sections stained for Nissl substance with cresyl violet.

The tectal layers are poorly demarcated in Nissl stain but conspicuous in fiber stain. In one experiment lesions were, therefore, made at the first recordings of somatosensory or auditory responses, in each of nine penetrations; the brain was cut in frozen sections at 30 μm and stained for normal fibers with the Schneider modification of the Fink Heimer stain (38) (see Fig. 9).

For the autoradiograph shown in Fig. 7, one eye of a mouse of the same strain was injected with 10 μCi of methionine-^{35}S by pressure injection (specific activity 160 Ci/mmol; New England Nuclear Corp.). Seventeen hours later the mouse was perfused with 10% formalin; the brain was cut in frozen sections 30 μm thick, and the sections were mounted on subbed slides and coated with Kodak nuclear track emulsion type NTB2. The section shown in Fig. 7 was exposed in the cold for 6 days before it was developed in Dektol and counterstained with Thionine.

RESULTS

In all the 59 penetrations through the mouse superior colliculus a consistent sequence of events was observed. The moment of entry of the electrode was marked by a sudden increase in background activity, which responded vigorously over a small, compact visual-field region. Single cells resolved out of this background had fields in the same region. As the electrode penetrated deeper, passing through the superficial gray layer and into the intermediate layers, visual receptive fields became larger and showed more scatter; cells responded less securely and frequently showed marked habituation to repeated stimulation. Cells responding to auditory or somatosensory stimuli were first seen intermixed with visual cells in the intermediate layers; here we also found bimodal and trimodal cells. With increasing depth these other modalities assumed more importance and the visual less until, in the deep layers, cells responding to visual stimuli became rare. The most striking feature of this study was the constant topographical relationship between the somatosensory fields, especially those involving the whiskers, and the visual receptive fields of the overlying cells. There was also a relationship, though a looser one, between visual receptive fields and the direction relative to the animal's head from which auditory responses could be evoked.

In the paragraphs that follow we begin by outlining the properties of visual units in the upper and intermediate layers. We then give a rough description of the retinotopic projection onto the tectum and finally describe responses in the intermediate and deeper layers, with particular reference to the interrelationship between somatosensory, visual, and auditory responses.

A total of 385 recordings were made in 14 mice. Of the total of 66 penetrations, 7 were for retinotopic mapping purposes and were restricted to superficial tectal layers. As judged from waveshape criteria (15), 165 of the records were probably from tectal cells and 11 from terminals of retinal ganglion cells. Two hundred and nine were from unit clusters or poorly resolved units: these were useful for certain purposes, such as topographic mapping of the tectal surface and for continuous assessment of the relative contributions of the different modalities during long electrode tracks. The distribution of cells into the main functional groups is given in Table 1.

Superficial layers

As soon as the electrode entered the tectum, dense multiunit activity was recorded. This responded over a small compact region averaging 9° in diameter (4–15°). The size of the region did not seem to vary in any systematic way with position in the visual field. The initial tectal multiunit activity showed very little response to diffuse illumination. A small slowly moving dark or light spot was by far the most effective stim-

TABLE 1. *Classification of 165 tectal cells*

Cell Type	Numbers
Exclusively visual	88 (53)
Small field	
Nondirectional	35 (21)
Directional	11 (7)
Large field*	
Novelty	30 (18)
Other	12 (7)
Exclusively somatosensory	33 (20)
Exclusively auditory	14 (8)
Bimodal	15 (9)
Visual-somatosensory	10 (6)
Visual-auditory	2(1)
Auditory-somatosensory	3 (2)
Trimodal	4 (2)
Unresponsive	11 (7)

Values in parentheses are percentages. * Diameter 20° or over.

ulus, producing a roar of activity. Turning on or off a stationary light spot was also very effective.

In all, 47 cells were studied in the stratum zonale and stratum griseum superficiale. With fine electrodes single units could be resolved from the multiunit background activity within a few microns of the surface. The uppermost units usually had receptive fields in almost precisely the same area as the fields of the massed background activity, and of almost the same size, suggesting that the fields of neighboring cells had remarkably uniform size and very little scatter in their position. The fields at this superficial level were smaller than at any other depth in the tectum. The only exceptions, at deeper levels, were a few small-field units, which we believe were retinal axon terminals. In Fig. 5, which is a plot of receptive-field diameter versus depth, the receptive fields of the superficial units and of the massed surface activity are all crowded into the lower-left corner of the diagram.

The spontaneous activity in the upper-layer cells was quite low under these anesthetic conditions, especially when compared with the vigorous responses to visual stimuli. Spontaneous rates were generally less than about 3 impulses/s. Both cells and the multiunit background responded best to a small spot ranging in size from a few degrees up to the diameter of the field center itself, moved at slow rates of about 5–30°/s. The exact shape and size were unimportant. For a given cell a dark spot might be preferred over a light, or the reverse; cells favoring one or the other were seen with about equal frequency. In cells that responded to both black and white stimuli, the receptive-field maps were the same, whichever stimulus was used. For mouse cortical cells, light stimuli are, on the whole, far more effective than dark ones (7), suggesting that the tectal and geniculocortical pathways may be fed by different populations of retinal cells (9, 25). In marked contrast to most deeper-layer visual cells, those in the superficial layers continued to fire without decline in rate as long as the stimulus was moved over the receptive field, and there was no hint of any habituation to repeated stimulation. In these movement-sensitive cells no response could be evoked by stimulation of areas outside the activating regions, but the absence or weakness of the responses to diffuse light suggested that there was some suppressive contribution from the surround. Moreover, about half of the cells responded weakly or not at all to a slit, edge, or spot that was larger than the diameter of the activating region. Turning a small spot on or off within the field, while less effective than a moving spot, nevertheless evoked very brisk responses, which were most often on-off in type, but could be off, or occasionally, on. Three cells showed well-sustained responses, but the rest responded in a very transient way. The upper part of Fig. 2 shows a dot diagram of the responses of a typical superficial cell to a light spot turned on and off. The lower half shows responses of the same cell to a slowly moving short slit; a slit longer than the receptive-field center was ineffective.

Although most upper-layer cells showed no directional preference to moving spots, 11 of the 46 were clearly directional, with a gradual decline in response as the direction of movement deviated from the optimum and little or no response to the direction opposite to the optimum. This is in contrast to the orientation-specific responses seen in the mouse cortex, where movement opposite to the optimum may evoke a response, and movement at 90° usually evokes none (7). In Fig. 3*A* a diagram of response

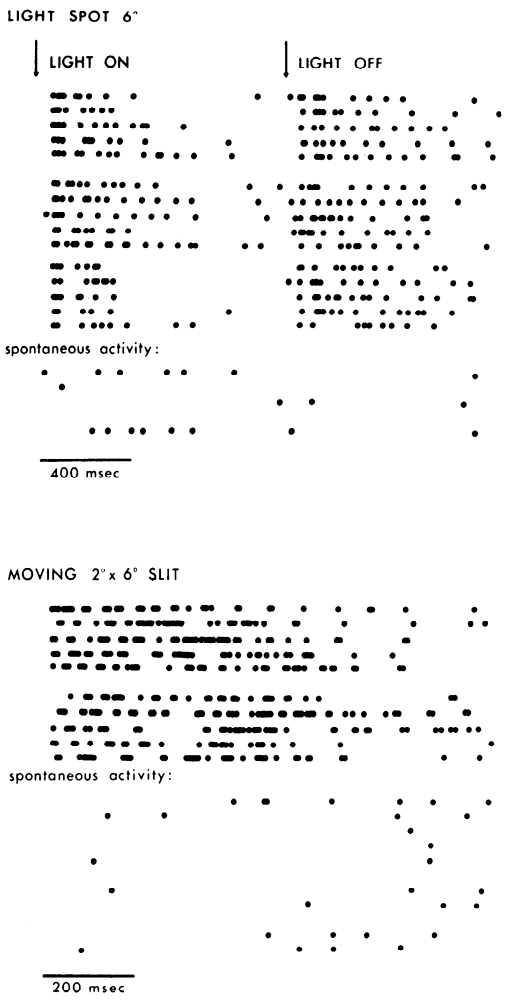

FIG. 2. Responses of an upper-layer cell whose receptive field was round, 9° in diameter, located 15° temporal to the midline on the contralateral side, 27° above the horizontal. Upper dot diagram shows on-off responses to a 6° spot confined to the field center. A large spot was almost ineffective. Lower diagram shows response to a 2° x 6° slit swept across the field at a rate of 13°/s in a direction perpendicular to its long axis. This stimulus was much more effective than a stationary spot (note faster sweep in lower diagram).

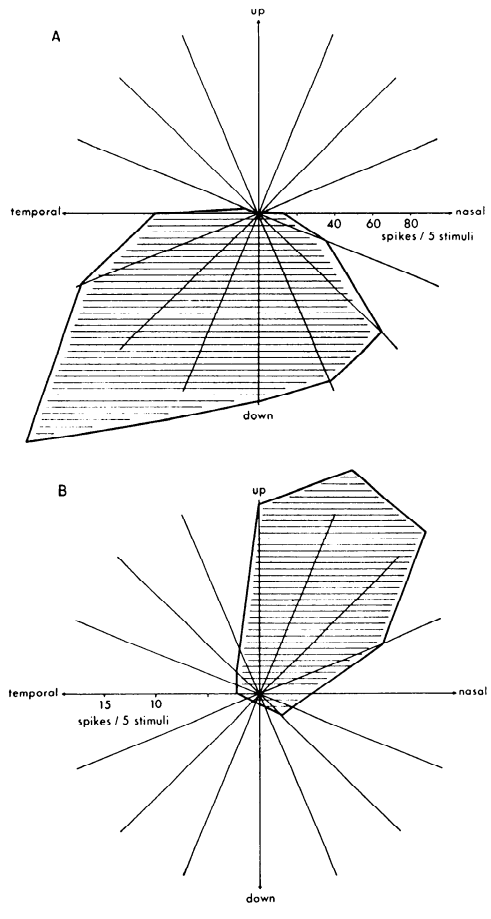

FIG. 3. *A:* polar histogram of direction-specific responses of an upper-layer cell to a slit 8° x 3° swept across the 10°-diameter receptive field in various directions. Distance of each point from origin represents size of response, in spikes per five stimuli. Field located 70° temporal to midline, 20° below the horizontal. *B:* polar histogram of an intermediate-layer directional cell. Receptive-field diameter 25° in its horizontal extent, spot diameter 8°. Between each sweep there was a pause of 10 s.

magnitude (number of spikes/5 stimuli) is plotted in polar coordinates for one of these upper-layer cells. The optimum direction of movement for the majority (although not all) of these cells was roughly upward, the cell of Fig. 3*A* being somewhat unusual in this respect. The question of preferred directions is discussed further in the section on intermediate and deep layers.

As the electrode penetrated deeper into the superficial gray layer the field centers of successive cells gradually became larger, roughly doubling over the first 150 μm, but the general response characteristics remained about the same. This progressive increase in field size with depth is illustrated in Figs. 14, 15, and 17. In each track the numbers beside the fields mark the order in which they were recorded; 1 referring to the fields of the first-encountered multiunit activity.

Eleven units from the upper layers had properties very different from those just described. Fields were small (3–10° in diameter) and mostly sustained off-center in

type, with varying degrees of antagonism from the surround. Spontaneous firing rates were very high, and spikes were small and brief in duration. Figure 4 shows a dot diagram from one such unit, with responses to flashing a small spot of light in the field center. We suspect that these units were retinal afferents, i.e., the axons or terminal arborizations of retinal-ganglion cells.

Intermediate and deep layers

As the electrode neared the bottom of the superficial gray layer and entered the middle layers (stratum opticum and intermediate gray layer), there was a change in the physiology. The background became less noisy, the cells were more easily resolved and had even larger receptive fields. Initially these large field cells were intermixed with upper-layer-type cells; deeper they strongly predominated. In the region where small and large field cells were intermixed (probably the stratum opticum), a large field could often be mapped with a simultaneously recorded small field, usually surrounding it but occasionally completely separate from it. Thus, at this depth the scatter in field size and position was much larger than in the upper layers. This variation in scatter and increase in field size with depth are illustrated in Fig. 5 (see also Figs. 14 and 17).

The dominant visual-cell type (30 of 42) in the intermediate and deep layers had a number of characteristics in common. As in the upper layers, the best stimulus was a small spot of any shape moved slowly through the visual field; darker spots were usually more effective than light ones, and diffuse light and spots larger than about 15° were virtually ineffective. Deeper cells were very different, however, in responding inconstantly and often relatively poorly even to these stimuli. They especially differed in showing a marked falloff in response when the same stimulus was repeated and a revival in responsiveness when the stimulus was changed—for example, by moving it to a new part of the receptive field or by simply waiting a short time. Responses to movement were not well sustained, and a cell would respond only fleetingly as a spot entered the receptive field. In all of these respects the cells were very similar to the prevailing deep tectal cells described in other species (6, 12, 14, 16, 20, 32, 43, 44) and often referred to as newness or novelty units. The remaining 10 units in these layers also had relatively large fields (i.e., >20°) but differed from the other 30 in a variety of ways. Some showed no habituation; some gave sustained on- or off-responses; one responded to a large edge moved in any direction; one gave prolonged afterdischarges to light.

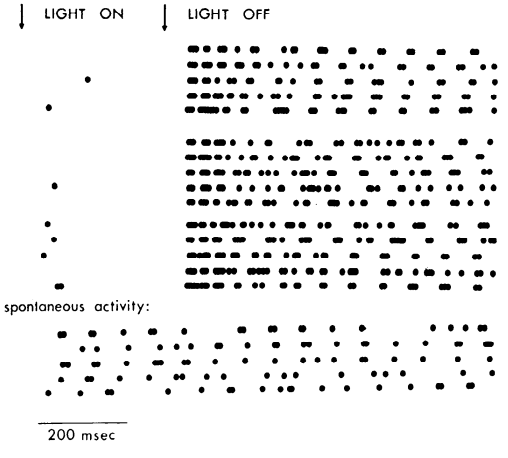

FIG. 4. Responses from an upper-layer off-center unit, recorded 230 μm from the tectal surface, probably from the axon or axon terminals of a retinal ganglion cell. Receptive-field center 5° in diameter; spot size 4°.

In contrast to upper-layer cells, where directional preference was seen in less than one-fourth of all cells, many visual units in the intermediate layers preferred one direction of movement. The diagram of Fig. 3*B* shows a polar histogram of an intermediate-layer directional cell, a novelty unit, which responded with unusual vigor to upward movement but hardly at all to downward. This cell showed moderate habituation, so that only by waiting 10 s between stimuli was it possible to compare different directions. The directionality of other novelty units was not always as marked as for this one; most cells, though preferring one direction of movement, gave some response to all directions, and 5 of the 30 cells showed no discrimination at all. The proportion of cells exhibiting directional preference was nevertheless higher than in the upper layers.

As mentioned above, in the mouse tectum

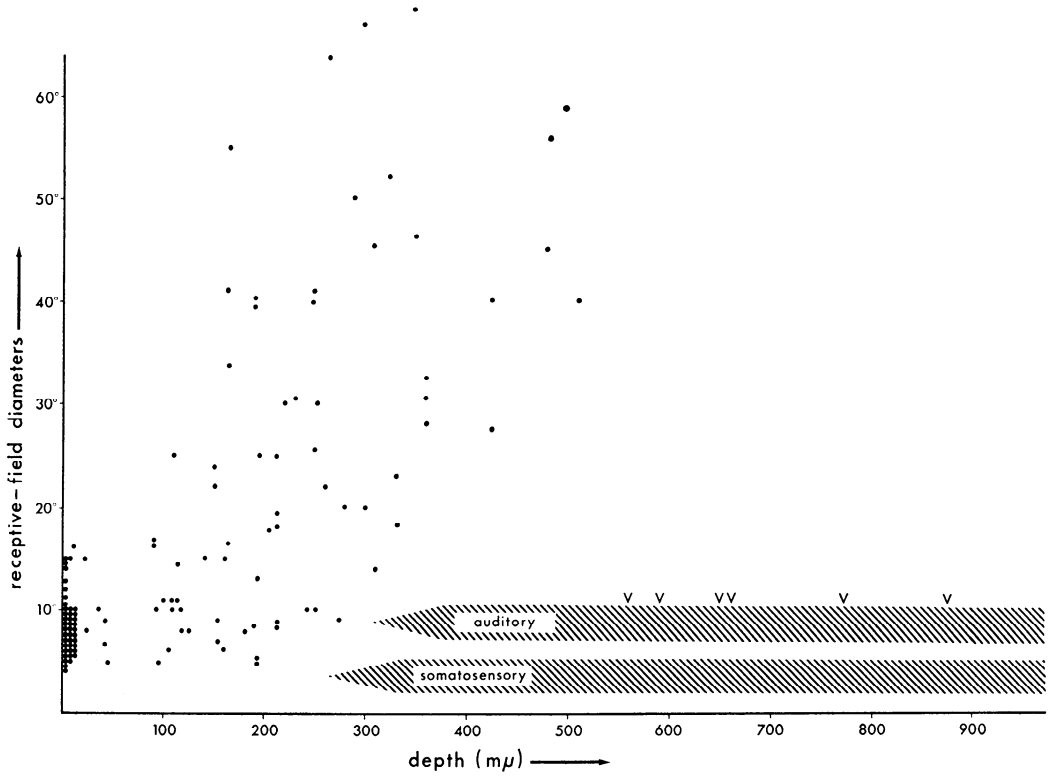

FIG. 5. Receptive-field diameters of visual cells plotted against depth in the tectum. Dots in uppermost 15 μm represent fields of initial multiunit recordings in 41 penetrations. Other dots represent visual receptive fields of single cells. Depths at which auditory and somatosensory cells were recorded are indicated by shaded bars. V, depths at which visual responses were obtained, but fields were too vague for size to be assessed. These deep visual fields were all large.

almost all of the directional cells showed a preference for upward movement. Figure 6 indicates the preferred directions of all 38 of the directional cells observed, including 11 directional cells from the upper layers. Three of these upper-layer cells responded to down-and-temporal movement, but all of the deeper layer directional cells preferred upward movement. There was a clear tendency for cells with more nasally located fields to prefer upward movement with a nasal component, and for cells with temporal fields to prefer movement up and temporal. The preferred directions were thus upward with a centrifugal component, in the head position used in these experiments. If one corrects the observations for the more flexed head position in the normal standing mouse, the optimal movement directions for the temporal fields become upward and perhaps slightly nasal (depending on the head flexion), and the nasal fields remain unchanged. Thus, normally the preferred movement directions are probably up and nasal. There was also a tendency for the large receptive fields to be elongated, with the long axis oriented in a direction

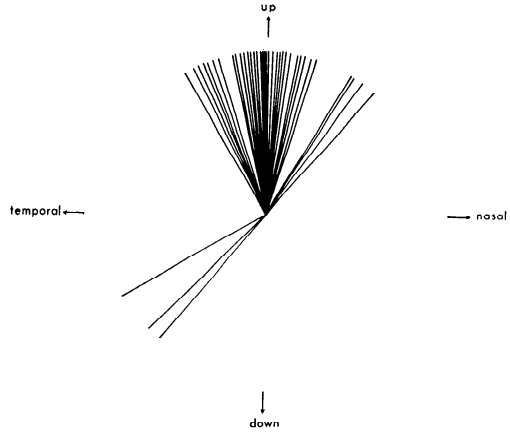

FIG. 6. Optimal movement directions for all 38 directionally sensitive units. Eleven were recorded from upper layers; these include the three that responded best to movement down and temporal.

perpendicular to the optimum movement direction.

Binocular interaction

Binocular interaction was rarely seen. The ipsilateral eye was tested whenever fields were in the region of binocular overlap, but gave responses in only four penetrations, all of which were in the anteromedial tectum. Fields were close to the midline and above the horizon. In two penetrations binocular cells were recorded just below the tectal surface; the receptive fields through both eyes were about equal in size, and they projected onto the screen side by side, 13–20° apart. This is roughly the separation of receptive fields of cortical binocular units under similar anesthetic conditions (7), and we assume that the fields in the two retinas were in corresponding areas.

In the other two penetrations, binocular units were recorded deeper in the tectum, probably in the stratum opticum. Fields through the two eyes differed in size and in relative position, but here we could not be sure that the recordings were from single units. It is possible that these two penetrations passed through the clusters of ipsilateral input described in the next paragraph, but at present we cannot be certain of this.

Histologically there is a considerable projection from the ipsilateral eye to the anterior and medial part of the tectum, which is easy to miss in recordings because of its distribution. Figure 7 shows an autoradiograph of a coronal section through the anterior part of a mouse superior colliculus. One eye was injected with 10 μCi of methionine-^{35}S and the mouse was perfused 17 h later in order to show the primary optic projections (13, 52). In contrast to the cortical ipsilateral projection, which seems to be evenly distributed in layer IV (8), the ipsilateral fibers to the tectum mainly terminated in several discrete clusters and, in contrast to the tectal fibers from the contralateral eye, which terminate in all three upper tectal layers (21, 47), the majority of the fibers from the ipsilateral eye ended more deeply, probably in the stratum opticum

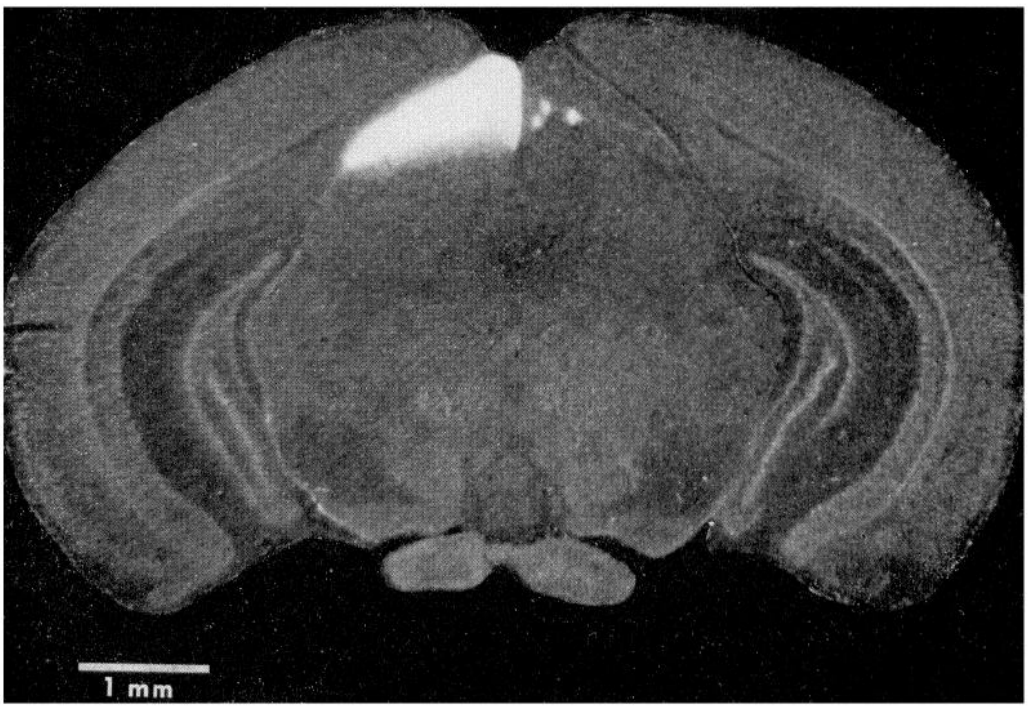

FIG. 7. Dark-field photomicrograph of autoradiograph in coronal section, through anterior third of superior colliculus. Right eye injected with 10 μCi of methionine-^{35}S; survival time 17 h. Dense label can be seen in upper layers of contralateral (left) superior colliculus. On the ipsilateral side, three small clusters of silver grains are visible in the intermediate layers; these are cross-sections of long slender aggregations; the most medial cluster is the longest, extending for almost 1 mm in the rostrocaudal direction.

and the lowest part of the stratum griseum superficiale. Only some faint label could be seen in the stratum zonale in this and other sections. The particular pattern of ipsilateral projection seen in this section, a termination in discrete clusters located medially and anteriorly, was also observed in three other eye-injected mice which are not included in this series. Thus, it seems to be a constant feature. That the ipsilateral projection to the tectum ends more deeply than the contralateral has been described for a primate (46).

Topographic representation of visual field

The topographic arrangement of the visual field on the mouse tectum was generally similar to that found in other vertebrates (for review see ref 19). The plan is shown in the diagram of Fig. 8. The contralateral temporal visual field projected posteriorly and slightly medially, and the superior field medially and slightly anteriorly. The obliquity of this map may be less marked in a normal standing mouse, in which the head is more flexed compared with the position in our head holder. Medially the tectum dips down into a midline groove that separates the two colliculi. As the electrode descended along this medial bank, the fields continued to move up and temporally. Nasally the projection through the contralateral eye extended over

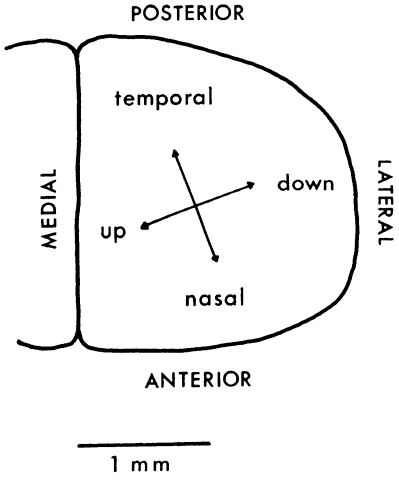

FIG. 8. Diagram showing general plan of projection of visual field onto superior colliculus.

to the ipsilateral side of the animal's long axis. At an elevation of 20–30° above the horizontal, for example, the receptive fields extended across the midline for 35°, which at this level is roughly as far as the contralateral eye can see (see Fig. 16*B;* for comparison with other mammals, see ref 18).

Deeper layers: visual and somatosensory responses

Just below the depth at which the small-object, habituating large-field cells were found, and to some extent intermixed with them, cells were first encountered that responded to somatosensory or auditory stimuli. Still deeper these other modalities tended to take over completely, so that visual responses were only rarely found below the intermediate gray. Of the 19 cells that responded to visual stimuli as well as to either auditory or somatosensory (i.e., vision plus sound and vision plus touch), three had the visual properties of the newness cells described above. All 19 had large receptive fields. Most were relatively sluggish, giving at best only transient off-responses or responses to movement. They were often difficult to map precisely.

It seemed important to determine the exact tectal layer in which the somatosensory and auditory responses first appeared. Although the majority of penetrations were reconstructed histologically, it proved difficult, using the Nissl stain, to be sure of precise layer boundaries. We therefore did an experiment specifically to answer this question: in one mouse nine penetrations were made, and a lesion was placed at the earliest sign of somatosensory or auditory responses. Histologic sections were stained for normal fibers (38). All nine lesions, two of which are shown in Fig. 9, were in the stratum griseum mediale.

Responses to somatosensory stimuli were similar in most of the tectal units, whether unimodal somatosensory or bi- or trimodal. By far the commonest somatosensory responses were evoked by whisker stimulation. Cells responded best to tapping a whisker gently from any direction, giving a short burst of 2–5 spikes, with no obvious difference in response for different directions and no obvious habituation. Tonic discharges to whisker deflection were never

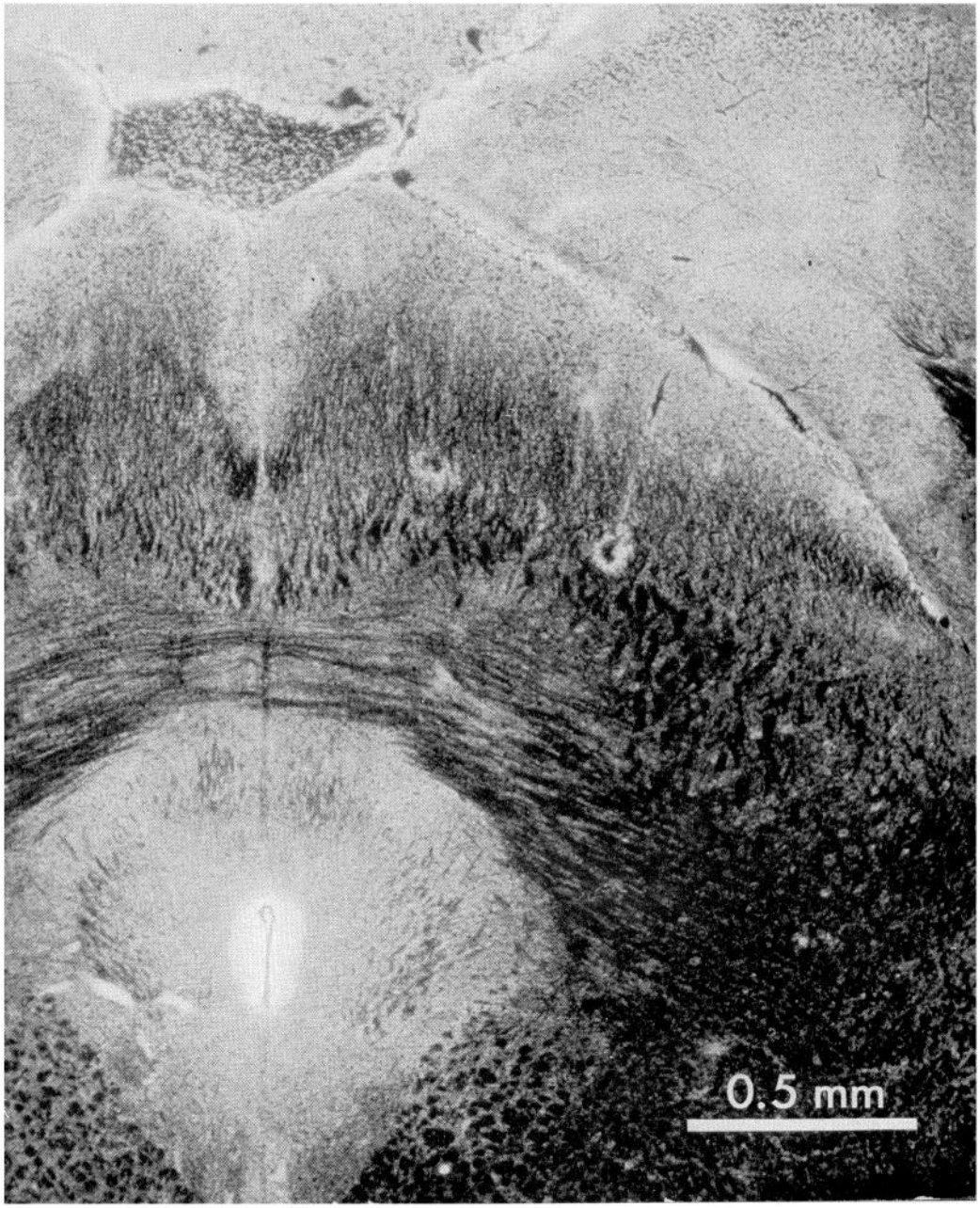

FIG. 9. Coronal section through superior colliculus showing two lesions in the stratum griseum mediale, made at the first appearance of auditory (left lesion) or somatosensory (right) responses. Schneider modification of Fink-Heimer stain, for normal fibers (38). (For tectal layers, see ref 39.)

seen, at least under these anesthetic conditions, but a few spikes sometimes occurred when a whisker was released from its bent position. A given somatosensory cell could usually be driven by more than one whisker and sometimes by up to six separate ones, the responses being best to one or two of them and fainter to the surrounding ones. The degree of convergence of whiskers onto single cells was quite limited: no cells responded to more than about six whiskers and, in particular, none responded to all

the whiskers or anything approaching half of them. Neighboring cells likewise all favored roughly the same group of whiskers, so that for unit clusters the maximum number of whiskers from which responses could be evoked was likewise less than about seven. There was usually some spatial summation in that displacing all of the responding whiskers at the same time or in sequence, for example by blowing, was more effective than moving one alone.

A typical visual-somatosensory unit is illustrated in Fig. 10. This bimodal cell was situated 600 μm below the tectal surface. To visual stimulation it was strongly directional, responding with separate bursts to both the leading and trailing edge of an upward-moving light square, as shown in the upper part of the figure. The lower part shows the response of the same cell to touching a whisker, with 2–4 spikes following each deflection, and an occasional spike or two on release. As with most of these cells, there was very little spontaneous activity.

The most striking feature of the somatosensory input was its topographic organization and, in particular, the relationship between somatosensory and visual receptive fields, either in the same (bimodal) cell or in cells beneath the same point on the tectal surface. A major part of the mouse's visual field is crossed by whiskers. Whenever visual receptive fields of the superficial tectal cells were located in regions crossed by whiskers, any somatosensory responses seen in the same track were evoked only from whiskers or immediately adjacent fur, but never from more distant parts of the body. The whisker terminology used in Figs. 12–14 and 16 is shown in Fig. 11 and is taken from Van der Loos and Woolsey (48).

In any penetration perpendicular to the tectal surface the parts of the body or the whiskers from which one could evoke somatosensory responses were closely correlated with the receptive-field coordinates of the overlying or intermixed visual cells. This is illustrated for four experiments, in Figs. 12–14 and 17. In the experiment of Fig. 12 three penetrations were made in a sequence, the points of entry into the tectum proceeding in an anteromedial-to-posterolateral direction. As expected from the topography, the three visual-field regions from which

FIG. 10. Responses of a visual-somatosensory bimodal cell. Upper set of dots represents responses to moving a light square 15° x 15° over receptive field in the preferred direction (upward). Stimulus velocity about 30°/s. Responses are seen for both leading and trailing edges. Receptive field about 50° temporal and 20° above horizon. Lower dots represent responses to displacing whisker A1. Note the very low spontaneous activity; dots at right-hand end of diagram were evoked by release of the whisker.

upper-layer cells were driven were one below the other, about 20° from the midline. Somatosensory responses in all three penetrations involved the more anterior whiskers. The three sets of whiskers were likewise one below the other, ending with some of the most anterior and inferior ones (D4 and D5) together with some of the skin of the inferolateral snout. In the experiment of Fig. 13 three sets of visual receptive fields proceeded from up and temporal to down

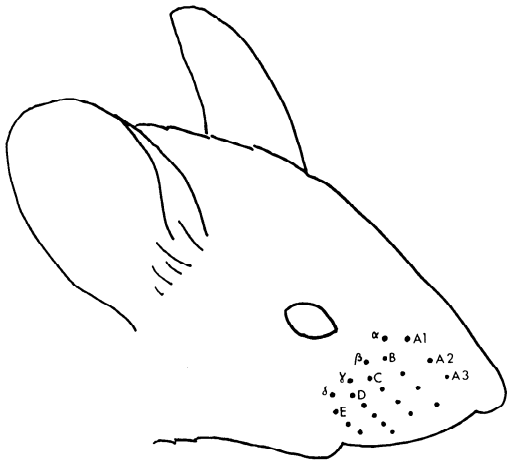

FIG. 11. System for numbering mouse whiskers (taken from Van der Loos and Woolsey, ref 48).

and medial, ending up, in track 3, 20° in the ipsilateral field of vision. The associated whiskers again progressed from posterior to anterior, ending with a group that included the upper member of the pair of tiny hairs on the tip of the nose (upper nose whisker), conspicuous in the top photograph of Fig. 1. Finally, in Fig. 14, penetrations 1–3, a visual sequence from down and lateral to up and medial was again associated with a corresponding shift in whisker fields. The track reconstructions for this experiment are given in Fig. 15. (Penetration 4 is discussed below.)

The correlation was so orderly that one could construct a map of the whiskers in relation to the visual-field positions of the overlying cells (Fig. 16*A*).

We first assembled the information from all the penetrations perpendicular to the tectal surface, determining for each penetration the center whisker of the group of whiskers evoking responses, or the most effective whisker in the group, and plotting for this whisker the position of the receptive fields at the point of entry into the tectum. The receptive-field positions for a given

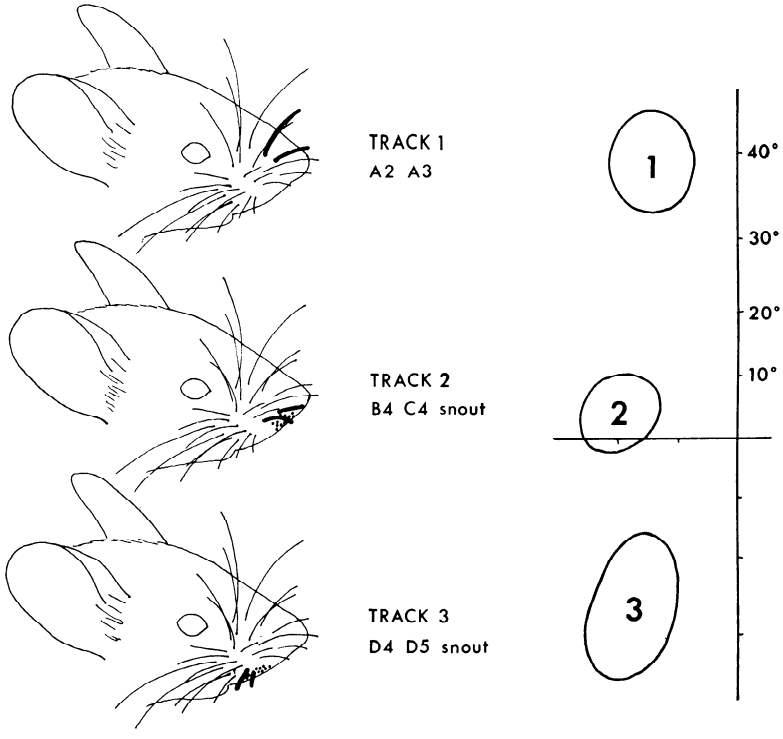

FIG. 12. Diagram showing visual field regions and whiskers from which responses could be evoked in three successive electrode tracks perpendicular to surface of left superior colliculus. The mouse faces the tangent screen, which is illuminated from behind, at right angles; to the right of the figure, the axes cross at the projected longitudinal axis of the mouse. To the left, whiskers from which maximum responses could be evoked are drawn more thickly; for whisker-numbering system see Fig. 11. Responsive regions of fur on anterolateral snout are indicated with dots.

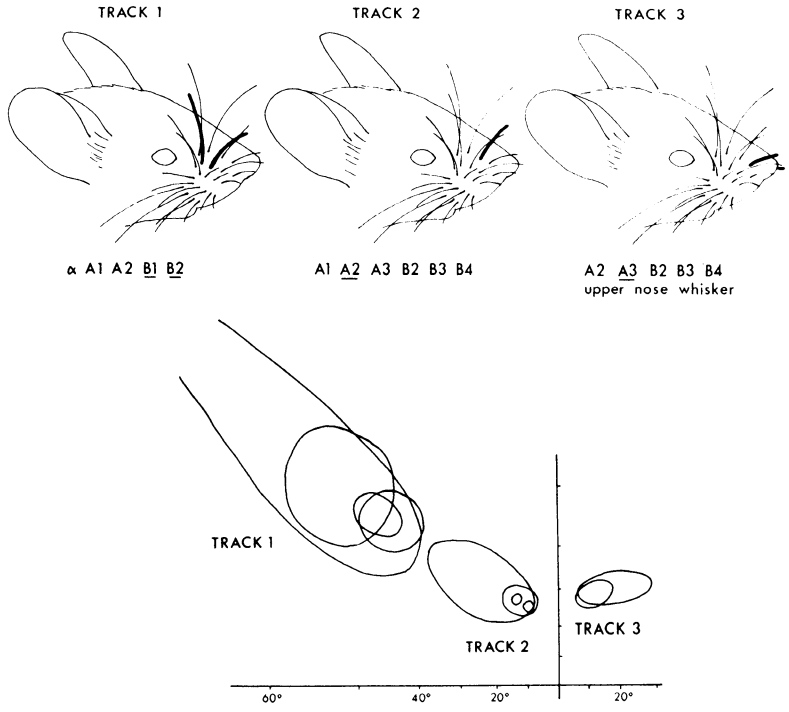

FIG. 13. Visual-field regions and whiskers from which responses were evoked in three successive penetrations. Here all whiskers evoking responses are indicated, with the most sensitive ones underlined.

whisker, obtained in the different experiments, were averaged by eye and their center estimated, and the process was repeated for each whisker, giving the map of Fig. 16*A*. The map is only approximate, first, since the position of each whisker number represents the average of several visual-field positions obtained at the surface in several experiments, and second, each whisker number refers to the central, or most effective, whisker in a small cluster. For example, in Fig. 14, track 1, whisker C2 was the most effective of a group of five. For this penetration, the number C2 was placed just below the horizontal, 53° out. In other penetrations, made in different experiments, the positions corresponding to whisker C2 were slightly higher, so that the average, in Fig. 16*A*, came to lie just above the horizontal meridian. While relatively crude, this map nevertheless at once suggests that the whiskers associated in the tectum with a given region of visual field are the ones crossing that part of the field. To prove this we outlined on the screen the positions of each whisker as projected from the homolateral eye (Fig. 16*B*). The agreement between the two maps is good, except that the A row projects somewhat higher on the visual fields, and the D row lower, compared with the physiologically ascertained correlation shown in Fig. 16*A*. This is possibly because in the anesthetized mouse the whiskers are angulated back slightly from their normal position, and hence are closer to the eye, causing the A row to project higher and the D row lower on the screen.

Figures 14 and 17 illustrate two experiments in which mouse fur was represented. In Fig. 14 the fourth track began with a visual representation far down in the visual field, located on the heating pad on which the animal lay. The somatosensory fields of the underlying cells were on the paw, with responses to touch on the dorsal surface but not the plantar. Joint movement was ineffective. In another penetration far lateral in the tectum and also associated with inferotemporal visual receptive fields (not illustrated), cells deep in the tectum could be driven by light touch over the entire paw.

Figure 17 illustrates the results of three penetrations made posteriorly in the tectum, where the temporal fields are represented.

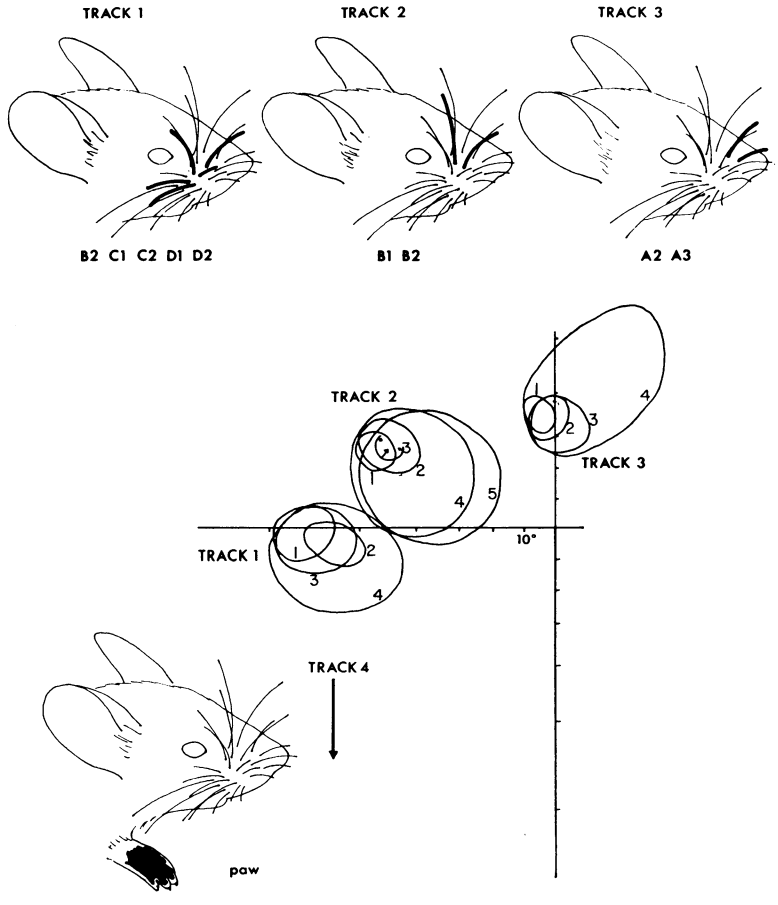

FIG. 14. Somatosensory and visual-field correlations for four successive penetrations. For each track, successively recorded visual receptive fields are numbered. In track 4 the visual receptive field was in the far inferotemporal part of the visual field and could not be mapped on the screen. The somatosensory field in this track was on the dorsum of the paw. In these four tracks the electrode penetrated in the true vertical, and therefore obliquely, from medial to lateral in the tectum. There was in each penetration, a corresponding drift of visual receptive fields down and nasally, as expected from the topographic map. Histological reconstructions of these four penetrations are given in Fig. 15.

Here the screen was set parallel to the mouse's long axis so that the vertical and horizontal axes of the diagram crossed at 90° temporal in the visual field. The visual receptive fields of the first track (solid lines) were roughly on the horizon; the associated somatosensory fields were quite large, including the fur below the eye and ear, the posteroinferior edge of the pinna, the shoulder, and the anterior two-thirds of the flank. In the next track the visual receptive fields were higher (dotted lines), and somatosensory fields were restricted to fur behind the eye extending back to the anterior edge of the ear. In the third penetration the visual fields were still higher (solid lines), and the somatosensory fields were limited to the upper edge of the ear. In a final penetration in this animal, not illustrated, the fields moved even higher and more temporal, ending up on the ceiling. Here the electrode went down the medial slope of the colliculus and never reached the deep layers.

Distribution of somatosensory and auditory modalities

Auditory responses were obtained in 25 of 45 deep tectal penetrations, somatosensory responses in 41 of 50. (In 5 penetrations in which ear bars were used, auditory stimulation could not be tested.) The two modalities appeared at about the same depth in

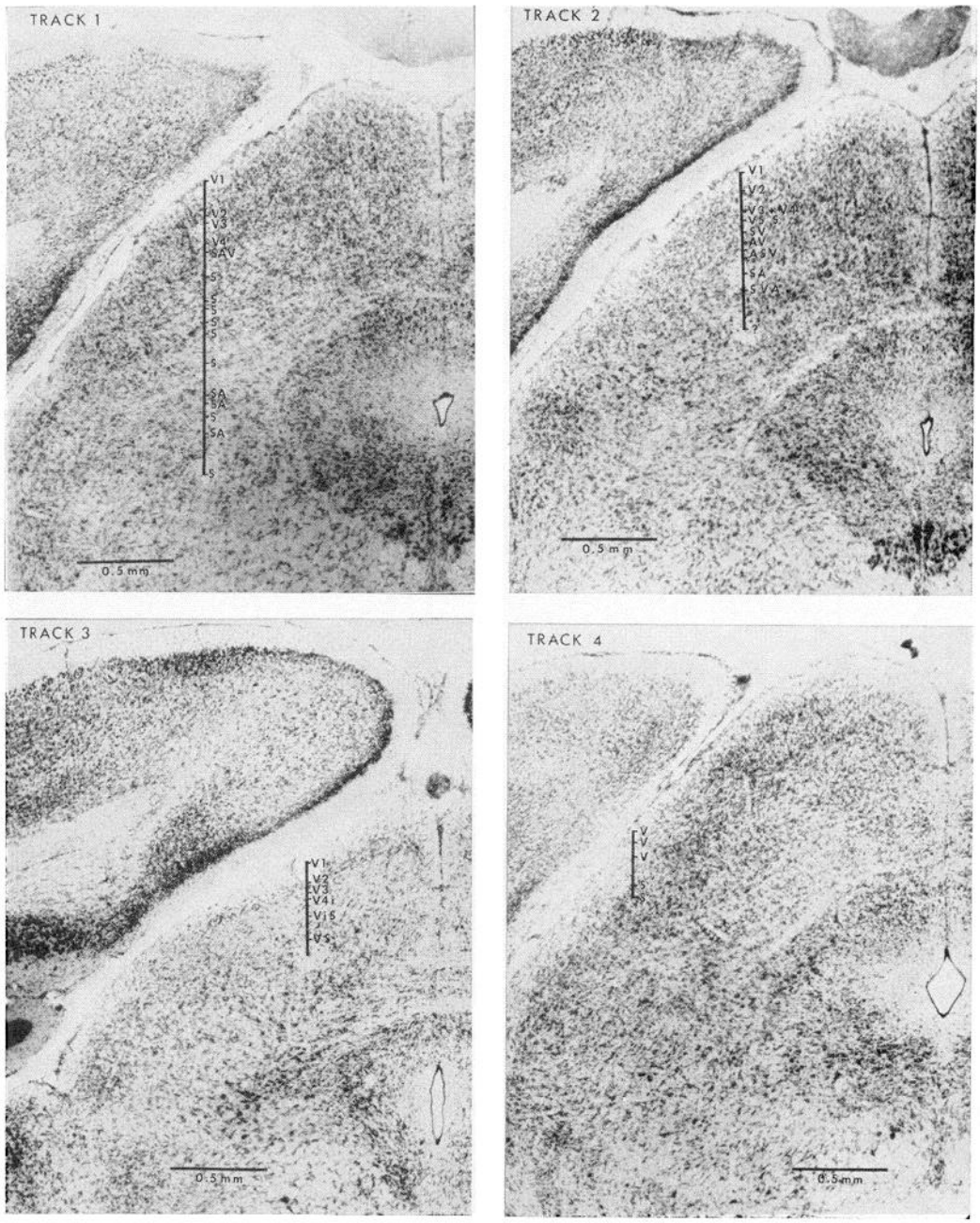

FIG. 15. Reconstructions of the four electrode tracks, receptive fields of which are shown in Fig. 14, coronal sections, Nissl stain. These four penetrations, in contrast to all others in the series, were in the true vertical and, consequently, passed through the tectal layers obliquely. Several lesions can be seen along each electrode track. V1, V2, etc., refer to visual receptive fields outlined in Fig. 14. S, somatosensory units or unit clusters; A, auditory. Vi, in track 3 indicates a binocular cell whose ipsilateral field is not shown in Fig. 14. Note that in each track, somatosensory or auditory responses were first recorded at a depth of 250–350 μm, roughly in the intermediate gray. Track 1 was exceptional in penetrating deep into the mesencephalic reticular formation: somatosensory receptive fields, from the intermediate and deep tectal layers to these deepest reticular cells, progressed steadily from the position shown in track 1, Fig. 14, to a final more anterior position (C3, C4, D3, D4), as expected from the oblique angle of the penetration, and suggesting that the topography of the deep reticular cells may be correlated with that of the tectal cells above.

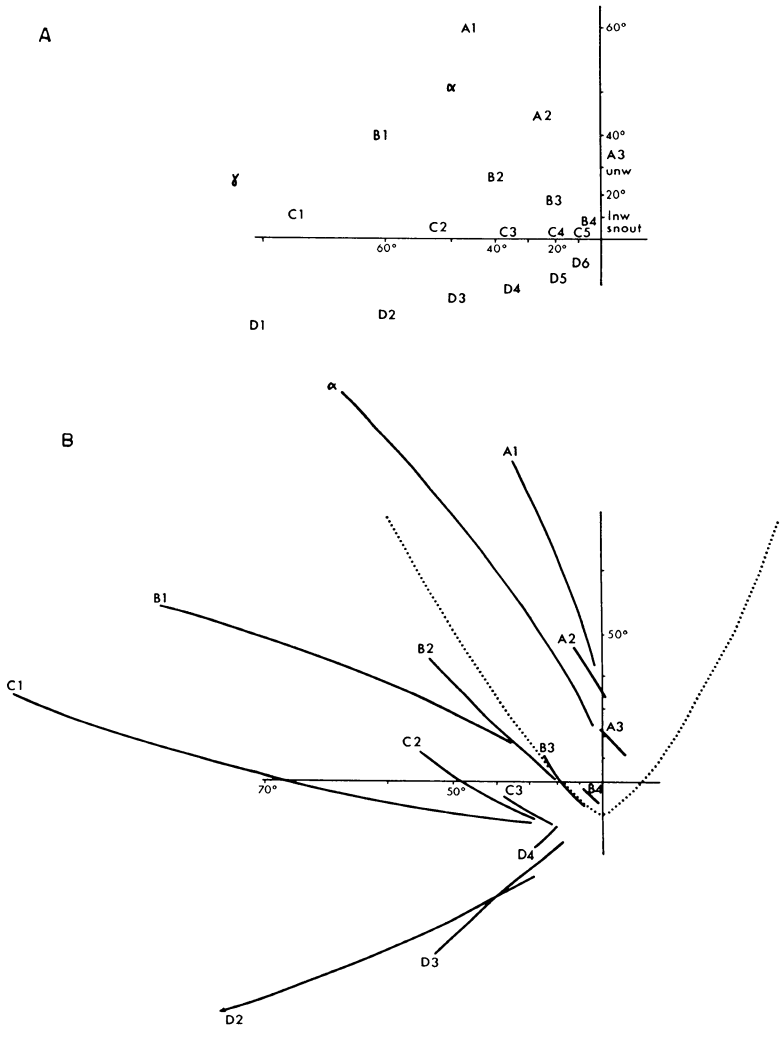

FIG. 16. *A:* diagram of visual fields showing correlation of visual and whisker receptive fields mapped in the same perpendicular penetration through the tectum. Each symbol refers to a position on the tectal surface; the letter and number indicate the whisker evoking maximal response from the intermediate and deep layers in that part of the tectum; the visual-field position indicates the average location of visual receptive fields of superficial cells in the same region. For whisker-numbering system, see Fig. 11. unw, lnw refer to pairs of tiny hairs on the tip of the nose (upper nose whiskers, lower nose whiskers); the upper pair are conspicuous in the upper photograph of Fig. 1. *B:* map of visual fields showing projections of whiskers. To construct this diagram a mouse was placed in a head holder and each whisker was lined up with the right eye and traced on the tangent screen. Dotted line partially encloses the binocular field of vision.

the colliculus, although there was a suggestion that somatosensory responses occurred slightly more superficially (Fig. 5). In most penetrations that were roughly perpendicular to the tectal surface the electrode recorded over long distances exclusively somatosensory or exclusively auditory responses. This is demonstrated in the six electrode-track reconstructions from one experiment in Fig. 18. Cells responding to one or other modality thus seemed to occur in clusters. There was no separate distribution by layers of auditory as opposed to somatosensory cells. Bimodal or trimodal cells were most often found at the transitions between visual and deeper layers or between clusters of cells giving somatosensory and auditory responses. More subtle forms of interactions between modalities might be detected if one stimulated with two or three

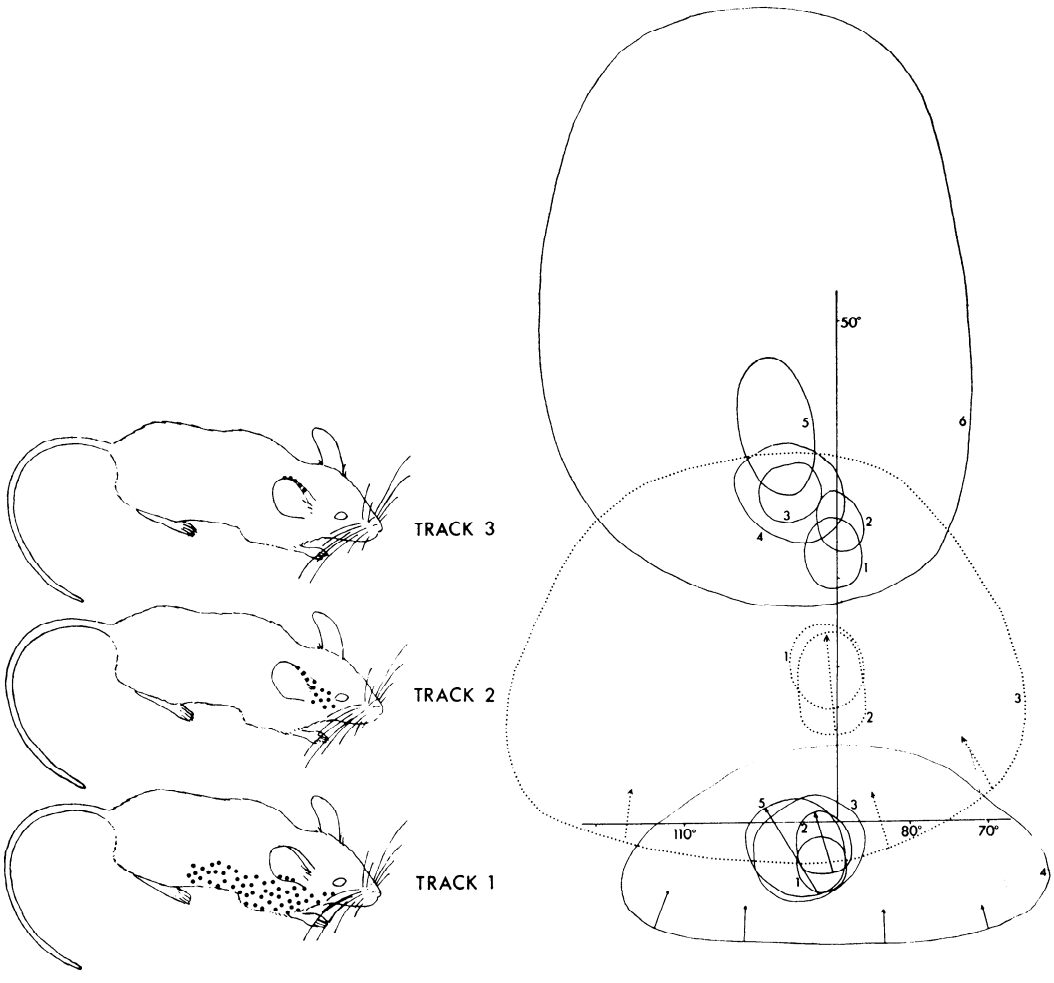

FIG. 17. Three penetrations going roughly from lateral to medial in the tectum. Screen is positioned parallel to the long axis of the mouse; axes intersect at the 90° point on the horizontal, on a line joining the two eyes. Visual receptive fields move up, from track 1 (solid lines), to track 2 (dotted lines), and finally track 3 (solid lines). Numbers refer to successively recorded visual receptive fields in each track. Associated somatosensory fields are indicated by dotted areas on figurines.

modalities simultaneously. This was not attempted in the present experiment.

Auditory responses

Auditory responses were commonest in tectal regions underlying the temporal representation of the visual fields. We never recorded auditory responses in the region of representation of the vertical midline. Pure tones, mainly in the human audible range, were tried in a number of cells but were not effective. Electronically produced clicks evoked some response, but the best stimuli were more complex sounds rich in high frequencies, such as clicks made by two fingernails or the crackling of cellophane. As the distance between the two ears is only in the order of 1 cm, it may not be surprising that only relatively high frequencies are useful for sound localization, regardless of whether time or intensity differences are used (30). The extent of auditory receptive fields was tested only in the horizontal plane and, given the relative lack of control over intensity, were determined only rather roughly. If a vertical component is also encoded in the superior colliculus, it could not be tested with the present preparation in which the scalp was cut longitudinally and the ears displaced downward.

In the majority of recordings in which the extent of the response in the horizontal

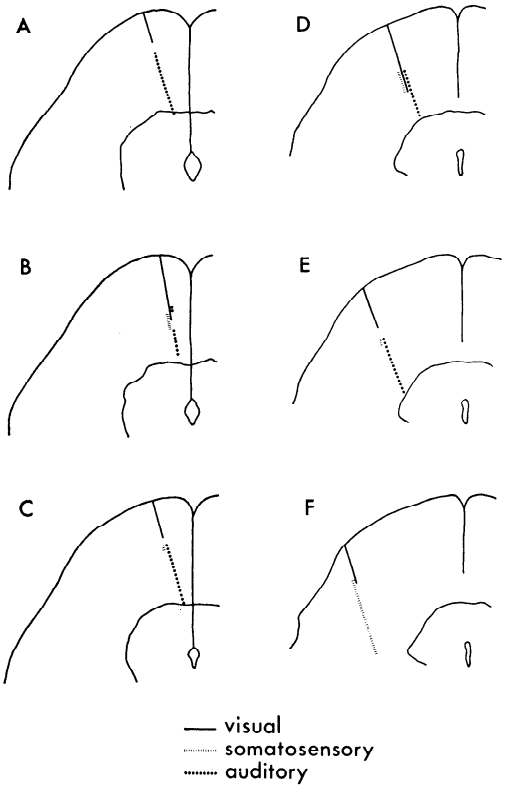

FIG. 18. Reconstructions of six consecutive electrode tracks from one experiment to indicate the tendency for segregation of visual, somatosensory, and auditory responses. Sections *A–F* are from posterior to anterior. Though there were short periods of overlap of sense modalities, responses over much longer distances were evoked exclusively from one modality. In this experiment auditory responses dominated, on the whole, but in most other experiments tactile responses were more common. We could never elicit responses in cells of the periaqueductal gray with the stimuli we used, i.e., complex sounds, light touch, or visual stimuli.

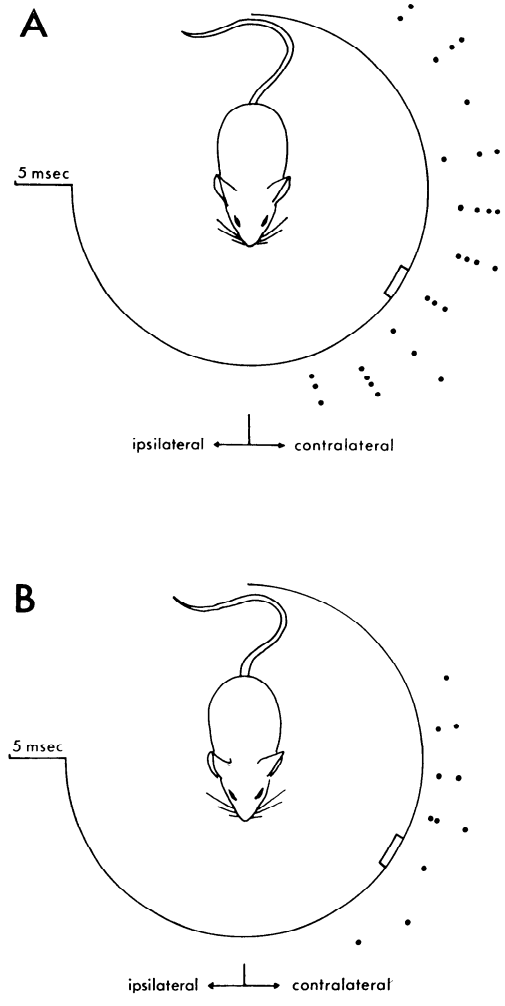

FIG. 19. Dot diagrams of two auditory cells recorded in the right superior colliculus in the same penetration, 630 μm (*A*) and 816 μm (*B*) below the tectal surface. The visual receptive field recorded at the tectal surface projected 58° temporal to the midline, as indicated by the segments just inside the circles, and 30° above the horizontal. Circles indicate the range over which auditory responses were tested, using complex clicks rich in high frequencies.

plane was determined (18 cells, 27 multiunit recordings), all but one cell gave responses that were greater on the contralateral side. The degree of selectivity was variable, from cells in which some response could be evoked all around the mouse, but with contralateral sounds more effective, to the most selective cells, which responded only over a certain rather broad angle, ranging from 70 to 150°. The most selective auditory cells were thus far less selective than the visual or somatosensory cells, especially in the extent of the receptive field in the temporal direction.

Figure 19 shows in dot-diagram form the recordings from two auditory cells, which responded over an angle of less than 180°. These cells were observed in the same penetration; the visual receptive fields recorded at the beginning of this track were situated 58° out from the midline and 30° above the horizontal. As for all such cells, the auditory receptive fields included the visual and somatosensory receptive fields, but the response maxima were somewhat further temporal, though usually $<90°$ from the vertical midline. On the contralateral side these

two cells were exceedingly sensitive, responding to clicks generated several meters away, which at that distance were inaudible to us. On the ipsilateral side, even a very loud click a few centimeters from the animal's ear evoked no response. This suggested that there was an inhibitory influence from the ipsilateral ear.

To examine this we made the test illustrated in Fig. 20, the cell was trimodal, with best responses to auditory stimuli. As shown in Fig. 20*A*, it responded about equally well to sounds coming from all angles on the contralateral side, but not at all to sounds on the ipsilateral side; in Fig. 20 only the anterior 180° are plotted. The right ear was closed over by pressing the folded pinna firmly with a plastic rod, with the result shown in Fig. 20*B:* responses could now be evoked from all angles, those from the ipsilateral side being only slightly weaker than those from contralateral. Similar results were obtained for all eight cells tested in this way, strongly suggesting an inhibitory influence from the ipsilateral ear.

DISCUSSION

In previous work on the superior colliculus three important interrelated functions have been described, one involving the processing of visual information, a second the bringing together and integration of several sense modalities, and a third having to do chiefly with the control of head and eye movements. All three of these are well recognized and have already been studied (3, 6, 11, 12, 14, 16, 17, 20, 22, 25, 29, 32–36, 38, 40, 41, 43, 44, 50, 54). In this paper we are concerned with the first two functions, in an animal whose tectal physiology has not previously been examined.

The visual receptive fields of cells in the upper tectal layers were small, compared with fields in the lower layers and also compared with fields of cortical cells. The increase of visual-field size with depth in the tectum is in agreement with results obtained in other mammals (e.g., ref 6, 16, 41). That the smallest fields occur in the upper layers is consistent with the anatomical finding, in rat and mouse, that the retinal afferents end mainly in the upper layers rather than in the stratum opticum, along which they enter (21, 47). Upper-layer cells reacted very briskly without habituation to repeated stimulation, and most of them preferred moving stimuli of any shape but of limited size; they closely resembled the prevailing cell type described in upper tectal layers of

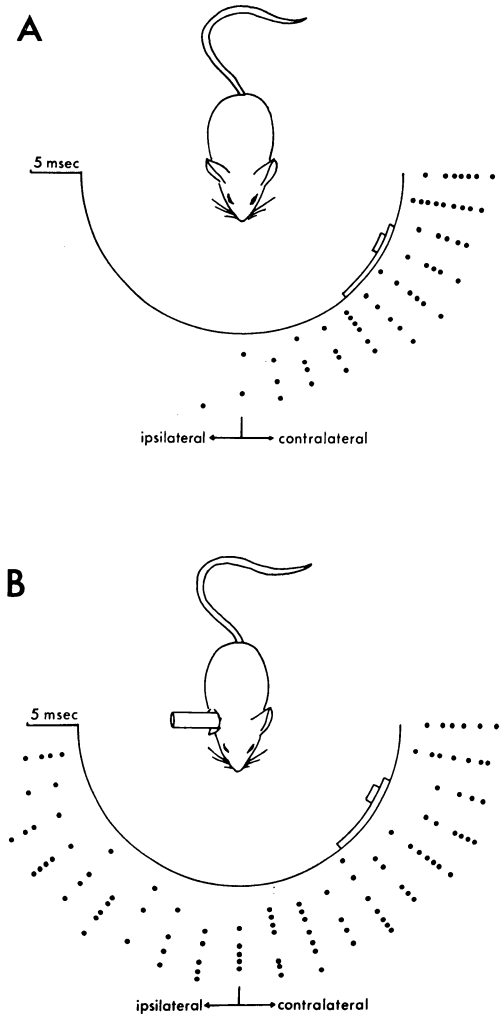

FIG. 20. Two dot diagrams of auditory responses of a trimodal cell, recorded 512 μm below the surface of the right superior colliculus, to illustrate binaural interaction. Visual receptive fields at the tectal surface projected 65° temporal to the midline, as indicated by the smaller segment, and 20° above the horizontal. The larger segment indicates the position of the visual receptive field of the cell under study. Somatosensory responses in this cell were evoked mainly from whisker β, but also from B1 and B2. *A:* with both ears open, the cell responded over the entire contralateral side, but not at all on the ipsilateral side. (Only the anterior 180° are plotted.) *B:* blocking the ipsilateral ear mechanically made the cell responsive to clicks from all around the mouse.

other mammals (e.g., ref 6, 32, 35). In the mouse, directional cells were present only in relatively small numbers, more than are seen in the monkey (6, 11, 35), but far fewer than occur in the cat (43), rabbit (22), or ground squirrel (25). For the deeper visual cells our results likewise agree with those found in most other species; the cells had large visual-receptive fields, but nevertheless responded best to small stimuli and showed marked habituation.

These properties of tectal cells may arise as a result of internal tectal circuits, but they may also be present in the retinal afferents, or be dependent on input from visual cortex. The optic nerve in several mammals is known to contain directionally selective axons (e.g., ref 2, 9, 25); in the cat and ground squirrel most or all of them are reported to project to the tectum. In the monkey it is not known whether any retinal ganglion cells are directional; the scarcity of such cells in the tectum suggests that there may be few if any in the nerve. Of animals in which retinal ganglion cells have been recorded, the rat is most closely related to the mouse. Brown (4), studying rat retinal ganglion cells, found no directional selectivity, nor did Humphrey (16) find directional cells in the rat tectum. Thus to answer the question of where the directional selectivity seen in the mouse tectum originates, comparisons with other species are not too helpful; what is most needed is a study of the mouse optic nerve.

A similar marked species variation seems to exist with respect to the cortical contribution to the tectum. The effects of cortical ablation or cooling are most dramatic in the cat, with a loss of sensitivity to moving stimuli, a decline in the influence of the ipsilateral eye, and a virtually complete loss of directional selectivity (31, 51). In the rat and rabbit (16, 22) no effects were observed, while in the monkey cooling the cortex produced only slight effects on upper layer cells, but rendered the cells in the deeper layers unresponsive (37). In the mouse, anatomically, there is an apparently faint projection from visual cortex to the stratum griseum superficiale and stratum opticum (47); physiologically, the experiments of extirpation or cooling have not yet been done. In mouse visual cortex, cells preferring horizontal or near-horizontal orientations occur more frequently than would be expected if the distribution were random; there is thus a preference for up- and downward movement (7). The presence of direction-specific cells in the tectum mostly favoring upward movement may therefore suggest a possible cortical influence, but this must be weighed against several marked differences, including a tendency for cortical cells to favor white stimuli and tectal cells to favor black spots and, especially, the observation that about two-thirds of cortical cells with fields in the region of binocular overlap are binocular, contrasted with the rarity of binocular cells in the tectum.

There are marked differences among mammalian species, not only in the frequency with which directionally selective cells occur in the tectum, but also in the directions of preferred movement—these are random in the ground squirrel (25), mainly centrifugal in the cat (43, 44) and, according to our results, mainly nasal and upward in the mouse. In the rabbit, Schaefer (32) found that movement preferences of most cells had a strong horizontal component with a centripetal direction. At present we have no idea why there should be such differences. It is not easy to see why the mouse should be more interested in up and nasally moving objects and the rabbit in horizontally moving ones, or why the monkey should be so deficient in these cells.

The presence of cells that respond to auditory and somatosensory stimuli in the deeper tectal layers is in agreement with previous evidence, anatomical and physiological. One source of the somatosensory input is probably fibers diverging from the spinothalamic pathway and from its fifth-nerve homologue (23). In addition, by making lesions in either primary or secondary somatosensory cortex of the cat, Garey, Jones, and Powell (10) observed degenerating fibers in the deeper tectum. This projection was confirmed by Tamai (45) using the evoked-potential method. For the auditory input both the inferior colliculus (27) and the auditory cortex (10) seem to be possible sources.

Physiologically the work of Gordon (12) in the cat is most closely related to our study; in both species there is not only a

strong input from somatosensory and auditory systems as well as the visual, but in both there is a similar correlation between optimal positions of stimuli in the three modalities. In the cat the auditory input was more prominent than the somatosensory, whereas in the mouse both were conspicuous, although the somatosensory was, on the whole, stronger. The direction-specific responses to moving auditory stimuli that Gordon noted in the cat were not found in the mouse, but for technical reasons we cannot rule out their existence. Cells responding to whisker stimulation are apparently rare in the cat, whereas in the mouse by far the commonest somatosensory responses were to whisker stimulation. Bilateral tactile fields, which were comon in the cat, were seen only once in the mouse in a cell whose receptive field extended over the dorsal surface of the nose up the ipsilateral whiskers A2 and A3 (which are visible to the contralateral eye, see Fig. 16*B*). These differences in detail should not obscure the more fundamental similarities, such as the presence of multimodal convergence to this structure and the close correlation, within one tectum, of the topographies.

A striking and somewhat puzzling feature of the multimodal convergence was its distribution: the laminar separation of visual input from the other two, and separation of the somatosensory and auditory inputs in the intermediate and deep layers in what seem to be clusters arranged perpendicular to the tectal surface. Gordon (12) makes no mention of such a grouping in the deeper layers but her track reconstructions suggest that the arrangement in the cat may be similar. A bringing together of functionally different units according to a topographic plan but with an apparent arm's length reluctance to intermix has many precedents in the nervous system. Groupings of diverse inputs by layers (lateral geniculate body), columns (somatosensory and visual cortex), or by clusters (ventrobasal nuclei, ref 28) have all been observed. It is as if it were advantageous to have multimodal convergence in a limited number of cells or to a limited degree, while avoiding a complete blending. That is exactly what we found in the mouse tectum, where the majority of cells were unimodal. Bimodal cells were found mainly at the borders between clusters, or the transition area between superficial (visual) layers and the deeper (nonvisual) ones. Of course there is probably also an advantage in grouping together cells whose axons have a common destination.

While the prominence of the mouse whiskers in the sensory input to the tectum was not predicted, it should, in retrospect, be no great surprise. The very size of the whisker organ as a whole (Fig. 1), together with the elaborate structure of the receptor organs (1, 24), suggests that the whiskers play an important part in the animal's perception. That a large portion of the somatosensory cortex is devoted to a special structure concerned with the whiskers, the "barrels" of Woolsey and Van der Loos (53), is a clear reflection of this. But especially, as pointed out earlier, it is the pervading and constant physical relationship between whiskers and visual fields that makes it reasonable to find a strong relationship in their representations.

It occurred to us that the whiskers, standing in the way of the visual field, might themselves produce responses in visual units. This seems unlikely, since a 25-μm-thick whisker at 1 cm distance subtends an angle of only 0°9′, which is far too small to be effective (the smallest fields were 3° in diameter, probably in retinal ganglion cell axons). The whiskers, moreover, move far too rapidly for tectal cells, to judge from the responses to moving objects. Actual attempts in several cells to stimulate by moving a hair at a distance of 1 cm from the eye were unsuccessful, except when the hair was lit by a very bright light from just the right angle (as was done in taking the photographs of Fig. 1), and it is doubtful that these conditions are met with very often in the life of a mouse.

The range of angles over which auditory responses could be evoked in tectal cells deserves some comment. Most auditory cells responded only to clicks generated over the contralateral half of the body and many responded over a horizontal range less than the entire 180°. The test shown in Fig. 20 makes clear that for most, and perhaps

all, of these cells this lateralization depended on inhibitory influence from the ipsilateral ear. At the high frequencies used, it would not be surprising if, in addition, the orientation of the pinna played a part in the directionality. This is indeed suggested by the optimal stimulus direction of these cells, which was generally somewhat less than 90° out from the vertical midline and roughly in the direction that the pinna faced in these anesthetized mice. Reflex movements of the pinna toward the source of an interesting sound (Pryer reflex) are well developed in the mouse, as is obvious by simple observation, and probably play an important part in determining the source of a sound.

Finally, while the part that the tectum plays in orientation of the head and eyes toward environmental stimuli has not been directly addressed in the present paper, the topographic representation that occurs in three modalities, ordered and roughly in register, must surely be related to this function. It seems likely that a given location in the mouse tectum represents some point in the space around the animal, that the information is mediated by any of these modalities, and that the result is a motor movement designed to orient the animal toward the stimulus.

SUMMARY

The superior colliculus was studied in anesthetized mice by recording from single cells and from unit clusters. The topographic representation of the visual field was similar to what has been found in other mammals, with the temporal part of the contralateral visual field projecting posteriorly and the inferior visual field laterally. At the anterior margin of the tectum receptive fields recorded through the contralateral eye invaded the ipsilateral visual hemifield for up to 35°, suggesting that the entire visual field through one eye is represented on the contralateral superior colliculus.

Cells located closest to the tectal surface had relatively small receptive fields, averaging 9° in center diameter; field sizes increased steadily with depth. The prevailing cell type in the stratum zonale and superficial gray responded best to a small dark or light object of any shape moved slowly through the receptive-field center or to turning a small stationary spot on or off. Large objects or diffuse light were usually much less effective. Less than one-quarter of superficial layer cells showed directional selectivity to a moving object, the majority of these favoring up and nasal movement.

The chief visual cell type in the stratum opticum and upper part of the intermediate gray resembled the newness neurons described for many other vertebrates: they had large receptive fields and responded best to up and nasal movement of a small dark or light object, whose optimal size was similar to the optimum for upper-layer cells. If the same part of the receptive field was repeatedly stimulated there was a marked tendency to habituate. Only very few cells responded to the ipsilateral eye.

Intermixed with visual cells in the upper part of the intermediate gray were cells that responded to somatosensory or auditory stimuli. Here bimodal and trimodal cells were also seen. In deeper layers somatosensory and auditory modalities tended to take over. These two modalities were not segregated into sublayers but rather seemed to be arranged in clusters. Responses to somatosensory and auditory stimuli were brisk, showing little habituation to repeated stimulation.

All but one tactile receptive field was found on the contralateral body side and the commonest input was from whiskers. The somatosensory topographic representation was arranged so that the region of visual field projecting to a particular area in the upper tectal layers was crossed by just the whiskers that projected to the tectum directly below. The whisker map was thus strongly correlated with the visual map and could be superimposed on it. Tectal areas representing extreme temporal and inferior fields of vision received input from the fur of the head, ear, flank, shoulder, and forepaw, also with a systematic relationship to the visual fields.

Auditory cells responded best to clicks rich in high frequencies. Maximal responses were obtained from a sound source in the contralateral half of the animal's surround, but within this semicircle there was often

a segment of heightened effectiveness whose position included the visual and somatosensory fields in the same penetration.

The mouse superior colliculus thus contains a representation of the environment of the animal, with superimposed maps of the surroundings from visual, auditory, and somatosensory sources.

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