Topography of Visual and Somatosensory Projections to Mouse Superior Colliculus

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IN PREVIOUS WORK on mouse superior colliculus (7, 8), we showed that cells in the three upper layers—stratum zonale, stratum griseum superficiale, and stratum opticum—responded only to visual stimulation, whereas cells in the layers below were predominantly driven by somatosensory and auditory stimuli. The visual field projected onto the tectal surface in an orderly fashion, and the other sensory modalities, represented deeper in the tectum, were topographically arranged so as to be in spatial registration with the visual input. Thus, in a given perpendicular electrode penetration, somatosensory receptive fields recorded in the deeper tectum were always concerned with that group of whiskers or with those parts of the body that were in alignment with the position of the visual receptive fields recorded in the upper layers. The spatial registration between visual and auditory receptive fields was much looser, since auditory fields were always much larger than visual or somatosensory receptive fields.

Given this correlation between somatosensory receptive fields and visual-field coordinates, the next step was to establish the topographic coordinates of the somatosensory projection in terms of absolute distance on the tectum. We wished especially to compare the somatosensory projection onto the tectum with the projection to SI of the cortex (17, 32, 33), since our study had suggested that the two were very different. To do this it was first necessary to determine accurately the visual-field projection onto the tectum with the projection to SI of the cortex (17, 32, 33), since our study had suggested that the two were very different. To do this it was first necessary to determine accurately the visual-field projection onto the tectum with the projection to SI of the cortex (17, 32, 33), since our study had suggested that the two were very different. To do this it was first necessary to determine accurately the visual-field projection onto the tectum with the projection to SI of the cortex (17, 32, 33), since our study had suggested that the two were very different. To do this it was first necessary to determine accurately the visual-field projection onto the tectum with the projection to SI of the cortex (17, 32, 33), since our study had suggested that the two were very different.

METHODS

The seven animals used for this study were adult mice of the C57BL/6J strain; the breeding stock was obtained from the Jackson Laboratory. The mice were placed in a head holder, using ear bars and an incisor bar. The head inclination was the same as that used by Mon-temurro and Dukelow (20) for their stereotaxic atlas. Procedures for anesthesia and preparation were similar to those previously published (6), except that on one side the cortex overlying the tectum was removed by aspiration and the tectum covered with saline, thus permitting placement of the electrode under direct vision.

Recordings were made with fine tungsten microelectrodes. Near the tectal surface these electrodes usually recorded dense multiunit activity, which responded to visual stimulation over a small compact area. Deeper in the tectum, as in the cortex, the same electrodes recorded single units. Whenever it was possible to isolate single units from the surface activity, the receptive fields were almost identical in size and position to the multiunit field (8). Removal of the visual cortex did not, to any noticeable extent, influence the receptive-field properties of the multiunit activity at the tectal surface.

Visual stimuli were projected onto a translucent tangent screen placed either 10.5 cm in front of the mouse's eyes or parallel to the mouse's long axis 12 cm away from the contralateral eye. The readings from the tangent screen were converted into spherical polar coordinates (for details see RESULTS).

In the mapping procedure the electrode was moved horizontally in 200-μm steps in either the coronal or sagittal plane. In order to calculate distances between successive points, for determination of magnification, it was necessary to take into account the tilt of the tectum in the horizontal plane and the curvature of its surface. This was done by noting the depth reading at the earliest recording of tectal activity at each recording point. In three mice we
first mapped the visual projection on the tectal surface and then recorded somatosensory cells deeper in the tectum.

The mice were not paralyzed and artificially respirated nor was the eye mechanically fixed in any way, since eye movements in anesthetized mice seemed to be negligible for our purposes. Nevertheless, if the same tectal coordinates were remapped 3–5 h later there was frequently a general shift in the projection of up to 15° in one direction. There are several possible sources for such inconsistencies in the mapping: eye movements, swelling and hence distortion of the tectum, imprecision of the micrometer movements, and blood vessels or debris on the tectal surface which might deviate the electrode. Of all these sources of error swelling seemed to be the most severe and, we believe, the main reason for the observed slow shifts, since whenever we saw a shift on remapping a point the surface coordinates had moved up. The swelling could be considerable, amounting to a change in point of contact of 600 μm or more. This deformation had no obvious effect on the responses of the superficial tectal cells. There was marked swelling particularly in the three mice in which we also mapped the deep tectum, probably due to mechanical damage from the electrode. The distortion caused by the general edema led us to terminate these experiments. In the other experiments swelling did not become obvious until the mapping procedure was, in any case, almost finished.

RESULTS

Visual projection to tectal surface

In the present mapping experiments the ipsilateral eye was occluded; previous experiments have shown that this eye has a sparse and anatomically clustered representation in the anterior part of the tectum (8). A typical set of visual receptive fields on the anterior screen from one animal is shown in Fig. 1A. The dotted lines connect receptive fields recorded at the tectal surface at successive points separated

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**FIG. 1.** A: visual receptive fields of tectal surface activity recorded in one mouse, in a square array of successive penetrations 200 μm apart, solid lines connect fields recorded in the same sagittal plane; dotted lines, fields recorded in the same coronal plane. Fields were mapped on the anterior screen, 10.5 cm from the mouse, through the contralateral eye only. Star represents intersection of tangent screen with the mouse’s long axis. B: grid used to convert tangent-screen coordinates to spherical polar coordinates. Vertical lines represent azimuths; curves, lines of constant elevation. Same scale as A. This grid was used to determine azimuth and elevation coordinates for fields such as those shown in A. Curves of constant angular elevation were calculated after the formula: distance from horizon = (tan α/cos θ) • d, where d = screen distance from the eyes, α = elevation, θ = azimuth; α and θ in spherical polar coordinates.
The receptive-field borders extended for up to 45° into the ipsilateral field of vision, making it likely that in the mouse, as in several other mammals (14), the superior colliculus receives input from the entire contralateral retina.

In anesthetized mice both eyes are always diverted outward compared to the presumed position in the alert state, and consequently binocular receptive fields, mapped separately through each eye, usually lie 15°-20° horizontally apart on the screen (6). The projection of Fig. 2 was not corrected for this divergence: the designations of the vertical meridians (continuous lines in Fig. 2) apply only to the projection in an anesthetized mouse—in an awake mouse the numbers should probably all be 7°-10° less (and for i lines, more). In addition, the coordinate system of such a map is, in general, dependent on the choice of the tilt of the head in the head holder. Here the incisor bar was 2 mm below the interaural line. In a normal standing mouse the head is probably less extended. If corrections were made for this in our map the coordinates would change, and the line representing the projection of the horizon would come to lie more medially, in the anterior part of the tectum.

The anterior and lateral margins of the tectum, as drawn in Fig. 2, were determined during the mapping procedure. The location of the medial and posterior margins were measured postmortem after removing the occipital and the opposite parietal bones. Medially the tectal surface slopes down into a midline sulcus; this region receives projections from the uppermost part of the visual field (i.e., the ceiling). This medial slope was not mapped, since it is covered by the sagittal sinus and is, in any case, too steeply inclined to be shown in Fig. 2, which represents an orthogonal projection of the tectum onto the horizontal plane.

The projection of Fig. 2 appears rather uniform except for the representation of the anterior (nasal) upper visual field, which seems disproportionately large. (Compare, for example, the separation of elevation lines 30° and 40° with the separation between 0° and -10°.) It is difficult, however, to get more than an approximate idea of magnification in the different parts of the visual field from such a map, given the distortions inherent in any map of a spherical surface plus those arising from the curvature of the tectal surface itself.

To calculate magnification in the region of any two adjacent mapped points on the tectal surface, we first determined the angular separation Φ from the formula

$$\cos \theta = \sin \alpha_1 \sin \alpha_2 + \cos \alpha_1 \cos \alpha_2 \cos (\theta_1 - \theta_2)$$
FIG. 2. Map of visual field onto surface of right superior colliculus, prepared from two experiments such as shown in Fig. 1A. This figure represents a projection of the tectum onto a horizontal plane. Interrupted curves represent lines of constant elevation; solid curves, lines of constant azimuth. Star indicates the approximate position of the disc of the contralateral eye. Inset shows general plan of this visual-field representation.

where $\alpha$ and $\theta$ are the elevations and azimuths of the corresponding visual field positions. To determine the distance between two tectal points we required not only the separations in the coronal and sagittal planes, given by the manipulator, but also the vertical separations given by the difference in depth readings at which the electrode first recorded unit activity.

The tectal contour lines as determined by the surface micromanipulator readings for both the coronal and sagittal planes are shown in Fig. 3. The tectal surface is convex and slopes downward from medial to lateral and from posterior to anterior. The distance between two points $(x_1, y_1, z_1)$ and $(x_2, y_2, z_2)$ on the tectal surface is then given approximately by
FIG. 3. Contour maps of tectal surface, used to calculate distances separating points of recordings in successive electrode tracks. Diagram on the left shows projection of tectum on a horizontal plane. Grid lines indicate intersections of sets of parallel coronal planes (numbers) and sagittal planes (letters) with the tectum; members of each set are 200 μm apart. Middle and right-hand diagrams show profiles of tectal surface, intersected by sets of coronal and sagittal planes.

\[ r = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2 + (z_1 - z_2)^2} \]

and the reciprocal magnification by

\[ m^{-1} = \frac{\Phi}{r} \]

The results of determining magnifications in sagittal and coronal planes are shown graphically in Fig. 4: the coordinates mark the visual field. The lines represent, by their length, the movement in degrees in the visual field that corresponds to moving the electrode a constant distance on the tectal surface: direction of lines gives direction of movement in the visual field for a tectal movement in the coronal or sagittal plane, in the various parts of the tectum. The figure contains no data for the extreme upper, lower, and temporal field periphery, which either could not be mapped with our experimental setup or could not be determined with enough precision to justify calculation of magnification. In the sagittal plane the magnification was rather

FIG. 4. Lines indicating direction and magnitude of reciprocal magnification for various points in the visual field. Ordinates indicate elevation; abscissae, azimuths. To the left, values are shown for pairs of recordings 200 μm apart in the same sagittal plane; to the right, measurement pairs were in same coronal planes. The sagittal determinations have roughly the same magnitudes throughout the visual field. The coronal values, on the contrary, are smaller—about half the size—in the elongated region marked by dotted lines. Thus, within this streaklike area magnification is anisotropic.
uniform throughout, the reciprocal magnification \((m^{-1})\) averaging 66/mm of tectum. For the coronal plane the \(m^{-1}\) lines were shorter, with an average of 51/mm over the entire tectum. The discrepancy between magnification \(^-1\) values for the sagittal and coronal planes was particularly marked throughout a rather large, elongated central area, roughly indicated by dotted lines in Fig. 4. For this central area, 1 mm of tectum corresponded to 64° of visual field in the sagittal plane and 34.5° in the coronal plane.

The mouse thus seems to have an area of central vision with a relatively higher magnification, although the differences in magnification are rather subtle compared to those found in most other vertebrates (4, 5, 9, 11, 12, 15, 16). It is surprising that the magnification in this central area is anisotropic. For the two planes in which we measured magnification, an increase shows only in the coronal plane, that is, for a roughly vertical direction in the visual field.

**Projection to deeper tectum**

Cells in the upper tectal layers respond only to visual stimulation, and responses to tactile and auditory stimuli are first found in the stratum griseum intermedium. Here some cells can be driven by two modalities, a few by three. Responses to visual stimulation are rare below the intermediate gray, where most cells respond either to somatosensory or to auditory stimuli (8). In deep electrode tracks we found somatosensory cells over the entire tectum except very medially, where the electrode went down the medial slope of the superficial layers and never entered the deeper tectum. Auditory responses, on the contrary, were mainly found in the part of the tectum subserving the more temporal field of vision. They were never found in the part representing the anterior 30°.

These distributions are shown in Fig. 5, which gives the results from 75 deep electrode tracks in 16 mice; 3 of these mice were from the present series of direct-mapping experiments, whereas results from the 13 others have already been published (8). In Fig. 5 it was possible to include the information from these 13 experiments, since for each penetration the visual-field position of the overlying tectal cells was known, and consequently the tectal position could be determined by referring to the map of Fig. 2. Auditory responses, marked by stars, were recorded only in the posterior tectum; somatosensory cells (open circles) were common everywhere. In some tracks both modalities were found, and for these the two symbols are combined.

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**Fig. 5.** Distribution of sensory modalities represented in tectum, from 75 deep electrode penetrations in 16 mice; 3 of these mice were from the present series of experiments, whereas results from the 13 others, including the 4 penetrations with binocular visual input, have already been published (8).

The most striking feature of the somatosensory projection was its topographic organization relative to the visual field (8). A major part of the mouse's field of vision is crossed by whiskers. Whenever the visual receptive field recorded at the tectal surface fell within this part of the visual field, the somatosensory responses below were evoked from those whiskers that projected in the same direction in relation to the eye. Below the projections from the temporal and inferior field of vision other parts of the body were represented, such as the ear, the flank, and the forepaw. One could thus correlate certain areas in the field of vision with certain whiskers or other parts of the body.

A map of the somatosensory projection, constructed from 61 electrode penetrations (Fig. 5), is illustrated in the figurine of Fig. 6A. Over the major part of the tectum somatosensory receptive fields were located on whiskers. The nomenclature used for the vibrissae organ is indicated in Fig. 6B (29). First we made outline maps for the areas under which responses from single whiskers were recorded. Since these areas overlapped extensively, this map was rather confusing and in Fig. 6A we have, therefore, drawn only the outlines for complete rows plus the proximal whisker. The individual whisker designations are placed roughly in the centers of their areas. Whisker A1, for example, occupied about two-thirds of the area indicated by triangles for the entire a.A-row.
FIG. 6. Map of somatosensory projection onto tectum (A), based on penetrations shown in Fig. 5. Letters refer to whiskers, using terminology shown in B (29); these indicate centers of tectal areas in which responses from the whiskers were recorded. Ovals outline five overlapping regions within which the five rows of whiskers were represented. C shows general plan of visual-field projection, from Fig. 2.

In this map the projections of parts of the body and of the vibrissae organ follow spatial rules given by the visual projection. The ear is visible to the mouse only in the temporal field of vision, and the paw usually in the lowest part of the visual field. Of the whiskers, the A-row was associated with the highest visual-field coordinates, the E-row with the lowest. There were marked differences in the relative areas under which certain whiskers were found. For instance, whiskers A1 and B1 each projected to a much larger area than E1 or the short anterior whiskers. These differences have nothing to do with the innervation density of the whisker shafts, but can be directly accounted for by the difference in the projection from the eye. A1 stands close to the eye and crosses over a much larger sector of the visual field than E1; for the same reason, whisker movements in A1 subtend at the eye a much larger angle. In addition, A1 crosses over that part of the visual field whose projection is magnified in the tectum. The plan of the somatosensory projection in the tectum is thus determined by the way in which particular tactile body parts are seen from the eye, and is logically dependent on the visual projection to the tectal layers above rather than on the innervation density of the tactile periphery.

DISCUSSION

The superficial layers of the optic tectum receive a very precise projection from the retina in all vertebrates that have been studied. At deeper levels other systems are represented, all arranged so as to be in registration with the visual world coded above—a motor map (2, 21) devoted primarily to eye movements subserving foveation (24); an auditory representation of the space around the head, binaurally mediated (10); and a somatosensory projection, mapping mainly the parts of the body that the animal can see (7, 8, 10, 27). There are differences among species in the modalities emphasized in the deeper tectum. In the pit viper, for example,
the external world is mapped by the infrared-sensitive pit (28). In the mouse the somatosensory system seems to be prominent, with considerable detail of representation, particularly for the whiskers. This is in contrast to the cat, in which the auditory input is probably more important than the somatosensory (10). In the cat tectal somatosensory projection the whiskers seem not to be particularly conspicuous (10), but there is a topographic order in which the face is mapped anteriorly, below the general region of the visual area centralis representation, and the trunk and forelimbs more caudally, where the peripheral visual fields are represented (10, 27); the somatosensory projection is distorted in accordance with the disproportionately large representation of the central field of vision (27).

The present study, an extension of a previous one, has involved the preparation of a detailed tectal map of the mouse visual field and the charting of the deeper somatosensory map in terms of tectal coordinates. In precision the two representations are about an order of magnitude apart: roughly speaking, in the superficial visual map a displacement of the electrode of 30-40 µm would probably be just detectable; for the somatosensory map a 300- to 400-µm displacement was usually necessary to give discernable shifts in tactile receptive fields.

The general plan of the visual topographic representation on the tectum is similar for all vertebrate species so far studied (4, 9, 11-13, 15, 16, 25), with anterior or anterolateral on the tectum corresponding to nasal visual field, posterolateral corresponding to down in the visual field. In most species there is a considerable tectal representation of the ipsilateral field of vision via the contralateral eye (14), monkeys forming a conspicuous exception in lacking a significant ipsilateral field representation (4, 16). There are also differences among species in the degree to which a central region of retina has an enlarged representation on the tectum. In monkey and cat (4, 9, 16) the differences between the representation of the central area and the rest of the retina are pronounced; they are less obvious in the rabbit (12), tree shrew, squirrel (15), and frog (13), and the rat is said to have no disproportion in magnification of its central visual field (25). The present results show that the mouse has a rather large, elongated, and roughly horizontally oriented area of higher magnification subserving a region some 30° above the horizontal meridian used here. In the tectum of the frog (13) and rabbit (12) the central, horizontally oriented region of higher magnification has been shown to correspond to the retinal region of higher ganglion cell density. The mouse is reported to lack such a specialized central area of the retina (3), but contour mapping of retinal ganglion cell density may be necessary to reveal one.

The higher magnification in mouse superior colliculus was evident only in calculations from pairs of tectal surface points in the same coronal plane, subserving visual field points roughly along the same vertical meridian. For measurement pairs in the sagittal plane the magnification was fairly constant throughout the tectum. We measured magnification only in these two tectal planes and have no direct information about its magnitude in other directions and, in particular, the maximum and minimum values at each point.

Although the anisotropy in magnification was at first surprising to us, since it is not known to occur in cat or monkey, it seems in fact to be a rather common phenomenon. In the rat tectum Slinnoff et al. (25) conclude that magnification is anisotropic throughout the visual field, being constant for measurement pairs in a given plane in the tectum and having about twice the value for the vertical direction in the visual field as for the horizontal. In the rabbit (12) the area of representation of the visual streak has a vertical magnification factor that is 8-10 times the horizontal. The squirrel and tree shrew seem to resemble the mouse, to judge from the tectal maps of Lane et al. (15), with a horizontal magnification that is fairly constant throughout and a vertical magnification that is larger for a central visual field area. Jacobson (13) has shown that a similar organization exists in the frog: plots of magnification show a sharp central peak for points along a vertical meridian, with a ratio of magnification centrally as opposed to peripherally of 3:1 and relatively little variation for points on the horizontal meridian. Centrally the ratio of magnification, vertical to horizontal, is about 2:1. Thus the mouse is not at all exceptional, and in fact shows an anisotropy that is mild compared with that of the rabbit, tree shrew, or squirrel.

The biological meaning of this anisotropic magnification is not clear. It is tempting to think that the tectal anisotropy is in some way related to the shape of the area of increased ganglion cell density in the retina. In cats and monkeys, where no obvious anisotropy has been described, the area of increased ganglion cell density is fairly round (26). The frog (13), squirrel (26), and rabbit (12) have a horizontally elongated central area, and the magnification in the tectum is anisotropic, with the highest values in a direction perpendicular to the retinal streak or
streaklike structure. For the animal with the most pronounced streak, the rabbit, the anisotropy in magnification is by far the largest. There is thus a rather striking parallel between anisotropy and the degree of development of a streak. It is easy to think of biological advantages in an animal's having a specialized retinal region of high acuity along the horizontal (i.e., a visual streak), and an increased central representation of the area would seem to follow naturally, but what is unexpected is to find this increase expressed along the vertical dimension of the visual field, but not to any extent along the horizontal. An anisotropy throughout the tectum could be the result of an asymmetric stretching to adapt the surface to the space available—this is suggested by Siminoff et al. (25), but such an explanation cannot easily be used to account for an anisotropy confined to a limited area within the visual field. In the mouse one striking correlate of the anisotropic magnification is the marked tendency for directionally specific cells in the tectum to favor upward movement. This specialization might well be the reason for an increased precision of representation in this direction. If so, one would predict an absence of any preference for upward movement outside of the central area. Such a comparison has not been made, but would be of some interest. Admittedly, if a preference for upward movement has any bearing on the anisotropy in the mouse, such an association can hardly hold for the rabbit, in whose tectum cells were observed by Schaefer (23) to prefer the horizontal component of centrifugal movement.

As a general rule the central representation of sensory surfaces is related linearly or monotonically to peripheral innervation density—to ganglion cell density in the retina (5, 12, 13, 22), to the richness of afferent sensory fibers from skin or vibrissae (1, 17, 30, 31), and in auditory centers to distance along the cochlea (e.g., and for references, see 18, 19). Although in the mouse a monotonic relationship has not been established between retinal ganglion cell density and magnification, there is no reason to expect the mouse to be different in this respect from the frog (13), rabbit (12), or monkey (5, 22). For the somatosensory system in mice, Lee and Woolsey (17) demonstrated a linear relationship by comparing the number of cells in the barrel formations of SI, the primary somatosensory cortex, with the number of afferent fibers from single whiskers. The number of fibers supplying a single whisker shaft was similar for whiskers of similar size and larger for larger whiskers. There were 17 times as many cells in a barrel as fibers from the corresponding vibrissal capsule, and this ratio held true for measurement pairs from an entire row of whiskers, measured in several animals.

The somatosensory projection to the superior colliculus provides an exception to the rule that peripheral innervation density determines the richness of the central representation. Here the parts of the body are represented so as to be in registration with the visual coordinates in the upper tectal layers, and the somatosensory projection follows the rules dictated by the visual projection. Thus two large whiskers, such as AI and EI, may have a similar length and be associated with a similar number of afferent nerve fibers, but AI, being closer to the eye and subtending a much larger visual angle, commands a much larger space in the tectum. Likewise, the anterior part of the pinna, which stands close to the eye, is more prominently represented than the hindpaws or the tail. The figurine of Fig. 6 is, therefore, far more distorted than Woolsey's (32) figurine for mouse SI, and distorted in a different manner. This is not surprising if one remembers that the optic tectum probably serves the special function of orienting the animal's eyes, head, and body toward an interesting object in the environment. In the superior colliculus, which is primarily a center of the contralateral eye, the environment is coded in terms of visual coordinates of that eye, and other sensory modalities merely endorse the visual plan.

**Summary**

In adult mice of the C57Bl/6J strain the projection of the visual field was systematically mapped under direct vision. As in other vertebrate species the nasal (anterior) field projected anterolaterally, and the inferior field posterolaterally. Values of magnification $m^{-1}$ were calculated over most of the tectum, for measurements in the coronal and sagittal planes. Whereas $m^{-1}$ was fairly constant for measurement pairs in sagittal planes, for coronal planes there was a rather large, elongated, horizontally oriented area in the upper field of vision within which $m^{-1}$ was smaller than elsewhere. In this area $m^{-1}$ was anisotropic, with a ratio of almost 2:1 between sagittal and coronal planes.

In a previous study we had observed that many cells recorded in deeper tectal layers responded to somatosensory stimulation, with whiskers especially conspicuous. In a given penetration perpendicular to the tectal surface, somatosensory receptive fields recorded in the
deeper tectum were always concerned with that group of whiskers or with those parts of the body that crossed the regions of visual field represented in the superficial layers directly above. Given this information on the visual coordinates associated with certain somatosensory fields, the detailed mapping of the visual field onto the tectum made it possible to prepare a map of the somatosensory projection on the tectum. The resulting representation differed markedly from maps described for the classic somatosensory pathway. In the tectum the somatosensory map was dictated by the visual-field projection rather than by the peripheral tactile innervation density. Whiskers were thus featured much more prominently in the tectum, and structures close to the eye, such as the pinna and cheek, receive more representation than the tail or hindpaws.

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