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TOPOGRAPHY OF VISUAL AND SOMATOSENSORY PROJECTIONS TO THE SUPERIOR COLLICULUS OF THE GOLDEN HAMSTER

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SUMMARY

The topography of visual and somatosensory projections to the superior colliculus in the Syrian hamster was studied using electrophysiological techniques. The visual projection to the superficial layers of the colliculus is similar in general topography to that described for other rodents. The magnification of the visual field on the colliculus surface was greatest for nasal visual field. The magnification factor paralleled retinal ganglion cell density for corresponding visual field sectors.

In the deep layers of the colliculus, a somatosensory projection is found in register with the visual projection such that the anterior somatosensory field and nasalmost visual field are both represented in rostral colliculus; posterior somatosensory fields and temporal visual fields are found in caudal colliculus. Likewise, upper visual and somatosensory fields are found in medial colliculus, and lower visual and somatosensory fields are found in lateral colliculus. Large receptive fields make the somatosensory topography less precise than the visual topography, but this lack of precision could serve to keep the two maps generally in register during eye and body movements.

INTRODUCTION

Much convergent evidence indicates that the superior colliculus is a structure important in the analysis of visual space and in the control of orienting movements in mammals. Deficits in orienting ability of varying severity have been demonstrated in

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numerous species after collicular lesions[4,5,7,13,14,26,33]. After the superior colliculus has been undercut, a hamster loses the ability to turn toward objects in space in response to visual cues, but retains the ability to make pattern discriminations if visually elicited turning movements are not required[22].

The representation of the visual field on the surface of the colliculus in various species has been the subject of numerous electrophysiological studies[3,6,8-10,17-19,25,28,32]. Intraspecific differences in the relative areas of tectum devoted to different parts of the visual field are related both to the lateral placement of the eyes, and the degree of specialization of an area centralis or visual streak.

Recent evidence also suggests that not only visual space, but also somatosensory and auditory space are represented in the superior colliculus. The deep layers of the superior colliculus are known to receive multimodal inputs from the spinal cord[1,2,14], from the caudal midbrain[20] and from non-visual cortical areas[12,14,15]. A correspondence of the topography of the somatosensory and visual projections has been demonstrated in both cat[30] and mouse[8,9].

This study was undertaken to examine in detail, using electrophysiological methods, the visual and somatosensory topography in the superior colliculus of the hamster. Numerous examples of plasticity of the organization of the hamster retinotectal projection have been demonstrated anatomically[11,16,23]. This study is designed to provide normative data for further experiments on the physiology of altered projections in the hamster, in a representation suitable for direct comparisons with extant neuroanatomical data. In addition, a detailed study of the comparative organization of cat, mouse and hamster colliculus allows analysis of the adjustment of the relationship of visual and somatosensory topographies to suit respective body proportions.

METHODS

Subjects were Syrian hamsters of both sexes that were at least three months old at the time of electrophysiological recording. Animals were anesthetized intraperitoneally with urethane (0.7 g/ml, 0.3 ml/100 g body weight) mixed with prednisolone (Depo-Medrol, 4 mg/ml, 0.2 ml/100 g body weight), which served to reduce cerebral edema and counteract the local inflammation produced by the urethane. The cranium overlying the colliculi was removed, the sagittal sinus was ligated, cut and retracted, and overlying cortex (including area 17) was aspirated to give a full view of both superior colliculi. The exposed colliculi were covered with warmed saline agar for protection.

Prior to recording, two small marks were made on the corneal margins at the midpoints of the attachments of the lateral and medial rectus muscles. These marks were used to define the horizontal meridian, and served as a control for eye rotation. The optic disc was used as an intraocular landmark; it was located by reversible ophthalmoscope and plotted on a 22" translucent hemisphere centered about the hamster's eye. These landmarks are the same as those employed in prior neuroanatomical studies of the hamster colliculus[16,24]. The hamster's eye was protected by a contact lens of zero refractive power and the pupil was dilated with a dilute solution of

atropine. No attempt was made to correct for refractive error. A 3–8° white spot, back-projected onto the dome, was the principal visual stimulus used. Somatosensory stimulation was given by light touches or tugs with blunt forceps.

Electrode penetrations were made approximately perpendicular to the surface of the colliculus, with the skull inclined 30°, nose up, from normal stereotaxic horizontal[22], with a maxillary clamp. Single unit potentials were recorded with glass-coated platinum-iridium microelectrodes 1–2 μm at the tip, with capacitances ranging from 25–40 pF. Signals were amplified conventionally, and monitored by oscilloscope and audio monitor. The receptive field properties of single units, when encountered, were assessed informally. The depth and location of all electrode penetrations, identified by microlesions, were assessed histologically. Retinal ganglion cell counts were done on eyes prepared for a prior study[11]. Eyes were injected with formalin to preserve their normal shape during fixation. After hardening, the eyes were embedded in albumin-gelatin, and cut in 30 μm frozen sections parallel to the nasotemporal or superior-inferior axis of the eye, as determined by the attachments of the extraocular muscles. Sections were stained with cresylecht violet. The geometric center of the eye was determined, and the eye was divided into 10° sectors. All retinal ganglion cells in each sector were counted, including whole cells and parts of cells; endothelial cells were excluded. Two eyes were counted for relative cell density on the horizontal meridian, and one on the vertical meridian.

To determine if the topographic maps generated were derived from recordings from postsynaptic tectal units or presynaptic retinal ganglion cell arbors, we recorded in the colliculus of one hamster while stimulating the optic nerve electrically. Two stimulating electrodes, with tips 1 mm apart were positioned so they bracketed the optic nerve head. Single or paired pulses of 200 μsec duration and up to 15 V were applied across the stimulating electrodes. The variability of response latency to optic nerve stimulation, and the rate at which units would follow high frequencies of stimulation, were used to distinquish pre- and postsynaptic elements. Of the 60 identifiable single units and additional unresolved background activity, all had response properties characteristic of postsynaptic units. Units in the superficial gray had latencies of 6–15 msec to stimulation of the optic nerve head, with variabilities in latency from 0.5 to 1.5 msec (second trace, Fig. 1). The shortest interstimulus interval for twin pulses for which a response could be elicited for both pulses was 3 msec, well above the refractory period expected for axonal stimulation. An example of the evoked response of a group of collicular units to 10 successive pairs of pulses appears in the first trace of Fig. 1. While the response to the first pulse is identical to the response to the single pulse, there is no corresponding response to the second pulse occurring 4 msec after the first.

RESULTS

Superficial layers of the superior colliculus

The normal projection of the visual field onto the superior colliculus was studied in 8 hamsters with a total of 279 penetrations. The visual data from a further 10
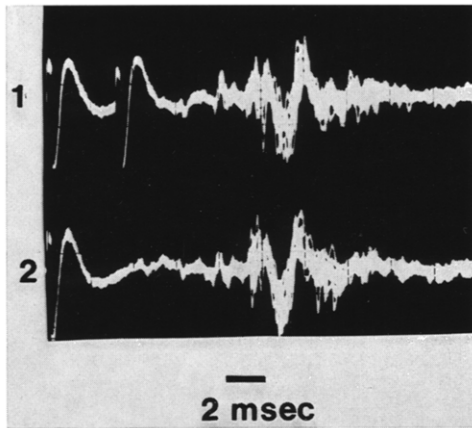
Fig. 1. Two oscilloscope traces of the evoked responses of units in the superior colliculus to 10 shocks of the optic nerve head. The upper trace shows the response to paired pulses of 12 V, 200 μsec duration. The lower trace shows the response of the same units to a single pulse. The initial pulse triggers the oscilloscope trace.
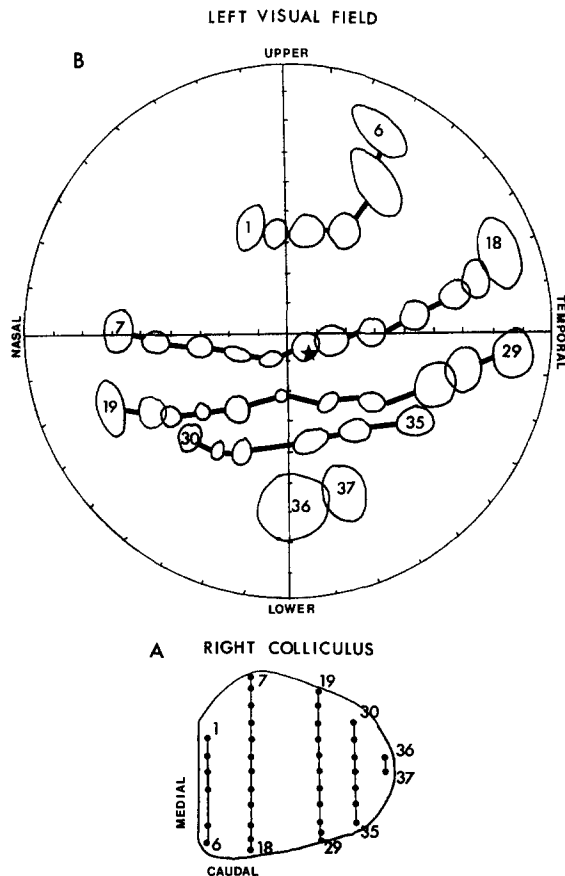

Fig. 2. Positions of electrode penetrations in the right superior colliculus and corresponding visual receptive fields. Each receptive field in the visual field map corresponds to a point on the superior colliculus represented by a dot. Rostral to caudal series of penetrations in the colliculus are connected by lines, as are corresponding nasal to temporal series of visual receptive fields. The visual field map is marked off every 10° and is centered on the optic disc. The horizontal and vertical meridians are defined by the centers of the attachments of the external eye muscles, and the geometrical center of the eye is marked with a star
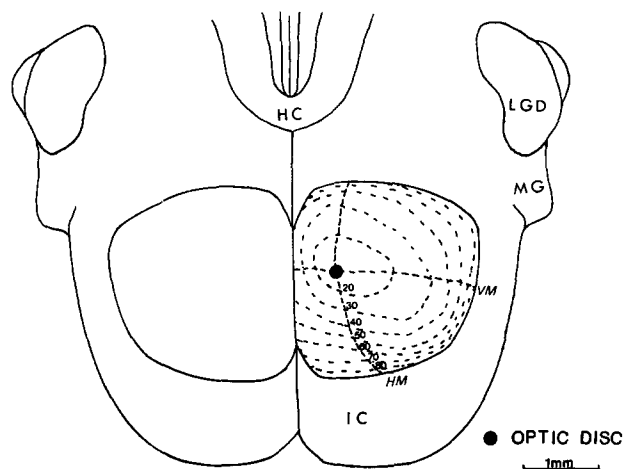
Fig. 3. Composite contour map of the visual field represented on the surface of the right superior colliculus. The midbrain is shown reconstructed in the plane used for electrophysiology. The representation of the optic disc, at the center of the map, is indicated with a large dot. Each 10° isocontour in the visual field relative to the optic disc is represented with a broken line (– · – · –). The horizontal meridian (HM) and vertical meridian (VM) are represented with dashed lines (– – – –). Other structures represented are inferior colliculus (IC), medial geniculate (MG), dorsal nucleus of the lateral geniculate body (LGD) and habenular commissure (HC).

hamsters in which both visual and somatosensory data were collected was used to amplify and confirm these data. The most complete source of data for the visual topographic map was one hamster in which 110 penetrations were made.

Results from one experiment, expressed as a reconstruction of the series of penetrations and a map of the corresponding receptive fields, appear in Fig. 2. The attachments of the eye muscles define the horizontal and vertical meridians of the visual field, the optic disc is at the center of the map, and the geometrical center of the eye is marked with a star. As expected from studies of other species reported in the literature, the entire contralateral field appears to be represented. The nasalmost fields are found for penetrations made most rostrally, temporalmost fields for caudalmost penetrations, upper fields for medial penetrations and lower fields for lateral penetrations in the colliculus. The extreme uppermost visual fields are represented in the midline declivity of the superior colliculus and were not investigated extensively in this study. Seventy degrees of visual field (± 5°) are found nasal to the optic disc, and 90° of visual field (± 5°) are temporal to the optic disc. Between animals there is little variability in the representation of the visual field on the surface of the superior colliculus. The maximal dispersion of the representation of the optic disc after histological reconstruction was 0.2 mm for 8 hamsters.

The 8 visual field reconstructions obtained were used to make a composite isocontour map of the projection of the visual field onto the surface of the superior colliculus (Fig. 3). The same coordinate system is used that is described for Fig. 2, and isocontour lines measured from the optic disc show the relative magnification of visual field areas onto the colliculus surface. The hamster shows an expansion of the area
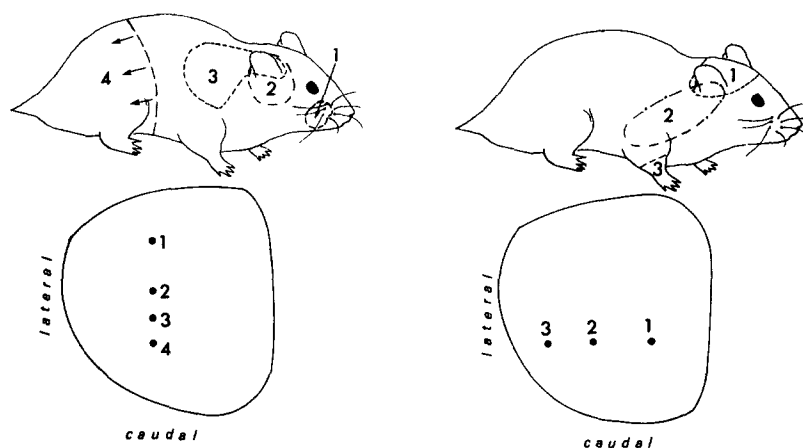
Fig. 4. Somatosensory receptive fields and corresponding penetrations in the colliculus. The somato-sensory fields delineated on the hamsters' body were recorded in a row of rostral to caudal pene-trations, and a row of medial to lateral penetrations in the left superior colliculus in one hamster The numbers within each receptive field correspond to the numbered penetrations. The paw field recorded on pass three included the dorsal and ventral surfaces of the foot and the under surface of the limb.

allotted to central visual field in its superior colliculus, an expansion that is more pronounced in nasal and lower nasal visual field. The greatest magnification appears in central nasal visual field. Measured along the horizontal meridian, the ratio of collicular surface length per visual field angle for the 30° of central nasal visual field is 0.025 mm/deg. In the nasal and temporal periphery, for similar angular extents, magnification is 0.020 mm/deg and 0.015 mm/deg respectively.

These changes in magnification factor are reflected in the receptive field sizes of single units in the upper layers of the superficial gray. Within 35° of the optic disc, receptive field diameters rarely exceed 10°, and occasionally are only 3–5°. In peripheral visual field, receptive field diameters may approach 20° (Fig. 2).

Retinal ganglion cell density and the representation of the visual field

Tiao and Blakemore[28] have reported that the magnification factor for visual field onto colliculus surface is 'uniform and low, with perhaps a very slight elevation in the immediate vicinity of the area centralis', in contrast to their report of marked regional specialization in the hamster retina[29]. In view of this contrast, we undertook to compare directly visual field magnification in the superior colliculus with retinal ganglion cell density, assessing retinal ganglion cell density by a different method.

Relative retinal ganglion cell density along both the horizontal and vertical meridians was determined by complete retinal ganglion cell counts of 30 μm sections along these meridians, and our relative estimations confirm Tiao and Blakemore's complete counts[28].

We then compared retinal ganglion cell density along the horizontal meridian to the representation of the visual field along the same meridian in the colliculus, for peripheral and central nasal retina and for peripheral and central temporal retina. For

this analysis, the percentage of cells counted in each sector relative to the total count was obtained, and compared to the percentage of total length for that sector along the representation of the horizontal meridian in the superior colliculus. The ratios are the following: peripheral temporal retina, 1.35; central temporal, 0.89; central nasal retina, 0.96; peripheral nasal, 0.88. All ratios fall close to 1, with the exception of the peripheral temporal retina, where a somewhat larger number of retinal ganglion cells is represented per unit length in the colliculus. The peripheral temporal retina is the source of the ipsilateral projections, which may account for the deviation in ratio of cell number to surface representation. In all other sectors, the relationship of retinal ganglion cell number to representation of visual field on the surface of the colliculus remains constant.

Intermediate and deep layers

In the deep part of the superficial gray layer and through stratum opticum and intermediate gray, the visual receptive fields of cells are larger, the receptive field boundaries less distinct, and the response to both moving and flashes stimuli is more erratic and often shows habituation with repetitive stimulation. The recovery period after habituation is not long, however; 5–10 sec suffice for a full recovery of initial response rate. The retinotectal topography, as defined by receptive field centers, remain identical. In intermediate gray, units appear that were sensitive to auditory or somatosensory stimulation as well as visual stimulation. Many cells are bimodal, and a few may trimodal; since we did not investigate auditory response exhaustively, we cannot be certain of the actual number of trimodal cells. Deeper into intermediate gray, visual response disappeared, while auditory and somatosensory responses remained. A representative rostral-to-caudal series of penetrations and medial to lateral series of penetrations and corresponding somatosensory fields shown in Fig. 4. The presence of somatosensory fields only visible to the hamster in particular grooming postures, such as the underside of the tail, feet and body, occurred regularly in caudal and lateral penetrations. All fields represented contralateral body parts.

Somatosensory fields were large, particularly those representing the posterior body, but were clearly defined. They responded well to light brushes or pinches; thermal and painful stimuli were not tested. All responded in an excitatory manner to stimulation, and none appeared to be specialized for the direction of stimulus movement or to have separate excitatory and inhibitory zones. Most habituated with repetitive stimulation. Many units showed ongoing spontaneous activity at a low rate of about 2–3 spikes/sec. Whisker fields did not appear to be as specialized in the hamster as those reported for cat[30] and mouse[9]. Occasionally, units were found that responded preferentially to stimulation of the upper versus the lower vibrissae, or the anterior versus the posterior vibrissae, but more commonly, fields were found in which all vibrissae on one side would produce a response. A unit with a receptive field limited to only one vibrissa was never encountered.

It was noted that when stimulation of a body part was accompanied by reflex movement of that part, the unit response was vastly more vigorous than the response
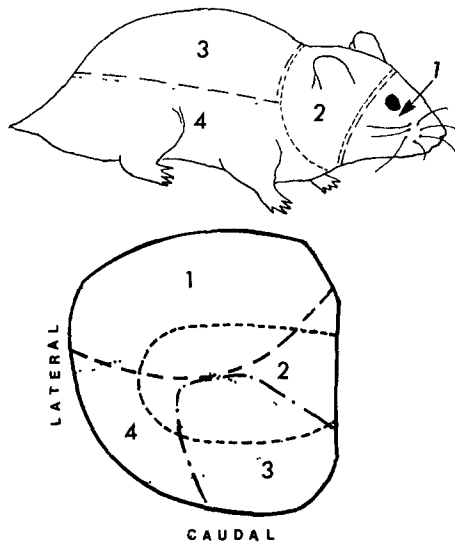
Fig. 5. Composite somatosensory topography within the colliculus, derived from the penetrations shown in Fig. 7. The hamster is divided into 4 regions: face (— — —); ear, neck and head (-----); upper body (— · — · —); and lower body (.   ..). If any portion of one of these areas was included in the somatosensory receptive field recorded on a penetration, then that penetration was included within the appropriate contour line on the superior colliculus.

to stimulation alone: for example, if a touch to the ear was accompanied by an ear twitch, the response of the unit was much greater in frequency and duration than if no movement occurred. The same was true for leg retractions. Since the hamsters did not produce independent movement in our experimental conditions, we could not test the relationship of response rate to self-produced movement. Nevertheless, the striking alteration in the response rate after movement suggest that units responsive to somatosensory stimulation might well show different properties in the alert, behaving hamster.

A composite topography for 64 passes in 6 hamsters is shown in Fig. 5. The hamster is divided into 4 areas, and a penetration which included any part of each delineated area in its somatic receptive field is included within the appropriate contour line on the superior colliculus. The colliculus represented is reconstructed in the electrophysiology plane. Since this method of representation reflects both the large size of somatosensory fields, and the large area of colliculus devoted to the representation of each body part, further delineation of body areas does not produce appreciably more specificity in the map. The low somatosensory specificity contrast markedly with the high specificity of the visual fields in the superficial gray (see Fig. 2).

For 44 penetrations, the location of units sensitive to somatosensory stimulation was determined directly from electrolytic lesions made while recording.

An electrolytically located somatosensory area, and 4 other locations determined by depth estimation where units sensitive to somatosensory stimulation were found, are shown in the drawing in Fig. 6. All 5 penetrations were found in one section, and the lesion location was used to calibrate the depth estimations. All of the
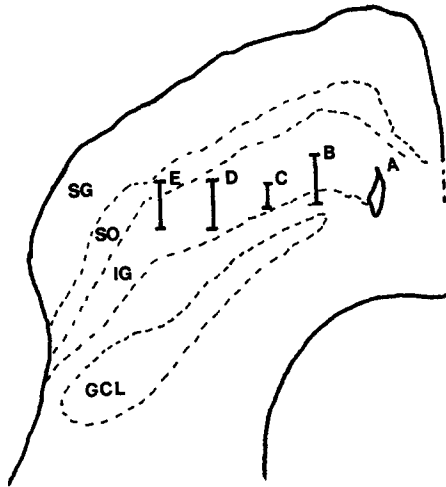
Fig. 6. A drawing of a section through the superior colliculus in the plane used for electrophysiology showing 5 penetrations in which units sensitive to somatosensory stimulation were found. A marks an electrolytic lesion made at the center of the area sensitive to somatosensory stimulation. Bars B–E represent the extent of the area sensitive to somatosensory stimulation in each penetration based on depth estimates from the surface of the superior colliculus, as calibrated by lesion A. Abbreviations: SG, superficial gray; SO, stratum opticum; IG, intermediate gray; GCL, the giant cell area of the deep gray layer of the colliculus.

units in these penetrations responded to stimulation of the vibrissae and cheek. The right penetration was marked by electrolytic lesion in the center of the area sensitive to somatosensory stimulation (A): the 4 passes to the left (B–E) have the extent of the penetration in which somatosensory units were located marked with a bar. The giant cell layer (GCL) shown on this drawing often marked the end of the layer in which somatosensory units were found. Units in this giant cell area showed a high level of spontaneous activity, and were unresponsive to visual, somatosensory or auditory stimulation under the conditions of these experiments.

In approximately 65% of the 44 penetrations, units sensitive to somatosensory stimulation were confined to the intermediate gray. In 20% of the passes, somatosensory neurons or cell processes were recorded in stratum opticum. In the remaining penetrations, somatosensory units extended to the deep gray layers.

The ipsilateral projection

We attempted to record visual evoked reponses from the ipsilateral eye in 60 penetrations in the anterior half of the colliculus in three different hamsters. We failed to find any binocularly responsive units or monocular units sensitive to the stimulation of the ipsilateral eye alone.

DISCUSSION

Retinotectal topography

As we were preparing this report, we received a report of similar experiments by Tiao and Blakemore[28]. Many of our results are in general agreement, particularly for

the visual response properties of single neurons. Some of the differences will be described below.

The superior colliculus is remarkable in the regularity of its retinotectal topography. Like the rat[25], rabbit[19], squirrel[17,32], mouse[8,9] and tree shrew[17], the entire visual field of the contralateral eye appears to be represented in each superior colliculus. The visual topography we report is similar in general form to that described by Tiao and Blakemore[28], however, they have reported all field positions in a coordinate system based on head position, whereas our coordinate system is based entirely on the eye. An advantage of our system is that it allows us to compare results directly with experimental neuroanatomical findings on topography of the retinal projections[11,16]. In addition, we have found the relation of the eye muscle derived horizontal meridian and true horizontal to be quite variable in the anesthetized hamster, so a control for eye rotation is of critical importance. The hamster 'area centralis' is very poorly defined compared with the cat or monkey, and thus has limited usefulness for precise visual field localization.

The hamster superior colliculus does show magnification of the central visual field relative to the periphery, particularly in the central nasal and lower field. We have shown that the ratio of retinal ganglion cell density to surface representation on the colliculus remains relatively constant throughout the visual field. This contrasts with Tiao and Blakemore's finding of uniform magnification in the superior colliculus[28], our method of precise visual field orientation by eye coordinates, plus histological reconstruction of the superior colliculus, would seem more advantageous for direct retina-to-colliculus comparisons. Relative magnification of visual field areas in the colliculus may be a direct result of a constancy of the total number of retinal ganglion cell axons converging upon individual tectal cells. Since the tectum, unlike the retina, has approximately uniform cell density throughout, differences in retinal cell density will be reflected in differences in total tectal area devoted to particular field sectors, provided that the same proportion of ganglion cells project to the tectum from various parts of the retina. This proviso may be violated slightly in the temporalmost retina (nasalmost field) where there may be an additional population of cells which project ipsilaterally — a projection which goes predominantly to the lateral geniculate body[24].

The superior colliculus and visual orienting behavior

The superior colliculus has been considered part of the visual pathway concerned with the analysis of visual space and the directing of orienting movements. The presence of a somatosensory map in register with the visual map indicates that the superior colliculus may also be involved in the control of tactually elicited orienting movements. In addition, the input from stimulation of body surface and hairs may modulate the flow of visually elicited effects before the latter reach the efferent neurons necessary for elicitation of turning movements.

In order for the colliculus to serve as an integrator of visual and somatosensory information for orienting behavior, the projections must remain congruent in the presence of both eye and body movements. In the hamster, there appear to be two solutions to this problem. It appears likely that the hamster, as well as the mouse[8],

does not make large eye movements to attend to interesting stimuli, although no detailed behavioral studies of eye movements in these small mammals have been done. Rather, since the whole head and body are moved, the relative topography of the visual and somatosensory projections would be maintained. Secondly, while the visual topography is very precise, the somatosensory topography is much less precise, as in the mouse[8]. Visual receptive fields are small (less than 10° in diameter for central visual field), while corresponding somatosensory fields subtend at least 30–40° of visual field, and may subtend up to 120°. In addition, large, overlapping collicular areas are devoted to the representation of each body part. Only if the hamster assumed a highly acrobatic posture or a highly deviant eye position could the two topographies become significantly divergent; the colliculus appears to be mapped according to the set of most probable eye and body positions.

An interesting inter-species difference appeared in the nature of receptive fields including the vibrissae for the hamster versus the mouse. In the mouse[8,9], whose vibrissae cover a much more extensive part of the visual field than do the hamster's, and whose cortex shows a marked degree of specialization for vibrissae innervation[31], collicular cells whose receptive field was confined to a single vibrissa and others that responded to the stimulation of only two or three could be found. Such a specialization was never found in the hamster colliculus; often all the vibrissae on one side of the head formed part of a single somatosensory field.

The presence of single cells sensitive to both visual and somatosensory stimulation suggests that, in some cases, the somatosensory and visual inputs are both excitatory and synergistic. This suggests that the animal would be more likely to make a turning movement if visual stimulation were accompanied by somatosensory stimulation from a corresponding spatial locus.

It is also possible that orienting responses are modulated by inhibition in the colliculus from somatosensory or proprioceptive pathways[1]. The effect of visual stimulation caused by self-produced movement is a candidate for such modulation. Two types of self-produced movement may be considered: movement of the visual world caused by movement of the hamster's eyes or body; and isolated movement in the visual field created by movement of some body part, such as the ears or paws. Schaefer has presented evidence that cells in the colliculus are selectively influenced during the first type of visual movement: in the alert rabbit, deep tectal units are apparently inhibited during self-initiated head movements[21]. Vestibular or cortical input may also play an important role in the observed inhibition.

We have observed that cells sensitive to somatosensory stimulation in deep parts of the colliculus show a much more vigorous response when reflex movement follows tactile stimulation than to tactile stimulation alone. Such a differential response might be used in the control of orientation to a self-produced movement of a body part. Separation, as well as integration, of information concerning self-produced movement and other movement in the visual field might be achieved by such a system of overlaid topographies.

ACKNOWLEDGEMENTS

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