

## THE VISUOTOPIC ORGANIZATION OF THE SUPERIOR COLLICULUS OF THE OWL MONKEY (*AOTUS TRIVIRGATUS*) AND THE BUSH BABY (*GALAGO SENEGALENSIS*)

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### SUMMARY

Microelectrodes were used to map the representation of the visual field in the superior colliculus of the owl monkey and bush baby. The results lead to the conclusion that the representation in these primates is restricted to the contralateral half of the visual field in each tectum, while the representation reported for several other species of mammals is more extensive including part of the ipsilateral half field and all or most of the retina of the contralateral eye. Thus, we conclude that at least two different basic types of visuotopic organization are found in the mammalian superior colliculus.

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### INTRODUCTION

Until recently, it has been commonly stated that each superior colliculus of mammals, like the dorsal lateral geniculate nucleus (LGN<sub>D</sub>), represents only the contralateral half of the total visual field<sup>2,26,29</sup>. There appear to be two main reasons for this conclusion. First, early anatomical studies were able to demonstrate that only the sectors of the two retinæ corresponding to the contralateral hemifield are represented in each LGN<sub>D</sub><sup>3,4,23,28</sup> and it was reasonable to conclude that a similar organization occurs in other structures receiving direct retinal projections. Second, some of the early anatomical and electrophysiological reports on the organization of the superior colliculus concluded that the representation was basically similar to that in the LGN<sub>D</sub>. Thus, Bodian's paper<sup>3</sup> on the projection of the retina to the superior colliculus and LGN<sub>D</sub> in the opossum included a summary diagram showing that only the portion of the retina of each eye that corresponds to the left hemifield projects to the right supe-

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rior colliculus and to the right LGN<sub>D</sub>. Moreover, Bodian stated that fibers from the temporal extreme of the retina (corresponding to the ipsilateral hemifield) 'do not pass to the opposite colliculus but appear to pass exclusively to the uncrossed superior colliculus'. Later, Apter<sup>2</sup>, using small spots of light to evoke electrical potentials at known sites on the surface of the superior colliculus of the cat, reported that only the contralateral hemifield was represented in each superior colliculus. Reviewing previous anatomical studies, Apter<sup>2</sup> suggested that the representation of the visual field was similar in this respect in the rat, rabbit and opossum. This view of superior colliculus organization was extended to other mammals, including primates, even though the experimental evidence did not warrant this extension. The early work of Brouwer and Zeeman<sup>4</sup>, for example, resulted in only 3 cases of partial lesions of the retina which produced detectable degeneration in the superior colliculus. Since the location of the lesions and the terminal degeneration differed in each case, Brouwer and Zeeman suggested that the retina is topologically represented in the superior colliculus of monkeys but concluded that the material was 'too limited to give a detailed scheme'. From such evidence, Polyak<sup>29</sup> concluded that 'the relation of the two retinae to the optic tectum in the monkey . . . duplicates that of the lateral geniculate nucleus'. Later, Daniel and Whitteridge were able to record from the superior colliculus of monkeys (unpublished study referred to by Whitteridge<sup>38</sup>), and obtained some responses which were to visual stimuli in the contralateral hemifield. However, the recordings were termed 'difficult' to obtain and details of the representation were not stated.

Early evidence that the superior colliculus represents more of the total visual field than just the contralateral half, and in this way differs from the LGN<sub>D</sub>, was included in Lashley's<sup>23</sup> paper of 1934. In describing the projections of the retina in the rat, Lashley<sup>23</sup> noted that after making a lesion in the extreme temporal retina completely within the sector corresponding to the ipsilateral hemifield, part of the fibers projected to the ipsilateral LGN<sub>D</sub> as one would expect, but another part projected *contralaterally* to the superior colliculus. More recently, as a result of a number of electrophysiological investigations<sup>8,13,24,32,35</sup>, it has become clear that the superior colliculus of the cat not only represents the contralateral visual hemifield but also represents at least 20–30° of the ipsilateral hemifield via the contralateral eye. Our own studies<sup>20</sup> on the grey squirrel and tree shrew revealed that the superior colliculus of these mammals represents the complete contralateral hemifield plus the portion of the ipsilateral hemifield that is seen by the contralateral eye. Thus, the complete retina of the contralateral eye is represented in the superior colliculus of the grey squirrel and tree shrew, while the most temporal 30° of the retina are represented ipsilaterally in the geniculostriate system<sup>12,17,18,20</sup>. Other electrophysiological studies on the rat<sup>30</sup> and ground squirrel<sup>41</sup> also indicate representation of the complete retina of the contralateral eye in the superior colliculus.

We are left with clear evidence that the early opinions on the amount of visual field represented in the superior colliculus were in error for at least some mammals and it is not clear what plan (or plans) of tectal organization applies to primates. To answer this question, we used electrophysiological mapping methods to determine the

representation of the visual field in the superior colliculus of a New World monkey, *Aotus trivirgatus*, and a prosimian, *Galago senegalensis*. In both primates, we found evidence of the representation of only the contralateral half of the visual field in each superior colliculus, and we conclude that in this way primates differ from a number of other mammals. A preliminary report of some of our results was presented elsewhere<sup>21</sup>. The evidence is described below and is supported by the results of recent studies on the squirrel monkey<sup>19</sup> and macaque monkey<sup>7,10</sup>.

#### METHODS

The method of electrophysiological mapping employed in this investigation has been described previously<sup>1,20</sup>. In brief, the 8 owl monkeys and 5 galagos used in this study were anesthetized with urethane. Both the ipsilateral and contralateral eyes were either sutured or glued to a rigid eye ring to prevent eye movements. The nerve head of each retina was ophthalmoscopically projected onto a translucent hemisphere centered in front of the contralateral eye. The dorsal dura was removed to expose the dorsal surface of the cortex. The superior colliculus was approached by penetrating tungsten microelectrodes through the exposed surface of the overlying cortex. The depth of the microelectrode's tip from the surface was monitored and recorded for each receptive field mapped. The determination of receptive fields was made by projecting small bars of light or shadows on the translucent hemisphere. Microlesions were made in each penetration to facilitate the reconstruction of the recording tracks. The recording sites were later identified in paraffin-embedded or frozen sections stained with cresyl violet for cells. The position and orientation of the zero vertical meridian of the visual field for both eyes was estimated prior to recording from the superior colliculus. This was accomplished by recording receptive fields from the portions of the striate cortex representing the vertical meridian<sup>1</sup>. Responses were obtained from both cortices. The horizontal meridian was estimated as passing through the projected blind spot on the basis of previous studies on the owl monkey<sup>1</sup> and ophthalmoscopic and whole mount examination of the retina of the galago.

#### RESULTS

##### *Histology*

As shown in Fig. 1, the superior colliculus in both the owl monkey and galago is a distinct structure with well defined boundaries and clear laminations. The stratum griseum superficiale and stratum opticum are readily identifiable. In the experiments described, the recordings were from neurons in these two layers. The sagittal sections show the ventral flexion or rotation of the caudal portion of the superior colliculus of the owl monkey as compared to the galago. Because of this rotation, in the illustrations that follow, the superior colliculus of the owl monkey is shown in a dorsocaudal view and the superior colliculus of the galago shown in a dorsal view.

##### *Visuotopic organization in the owl monkey*

Recording with microelectrodes in the superior colliculus of the owl monkey

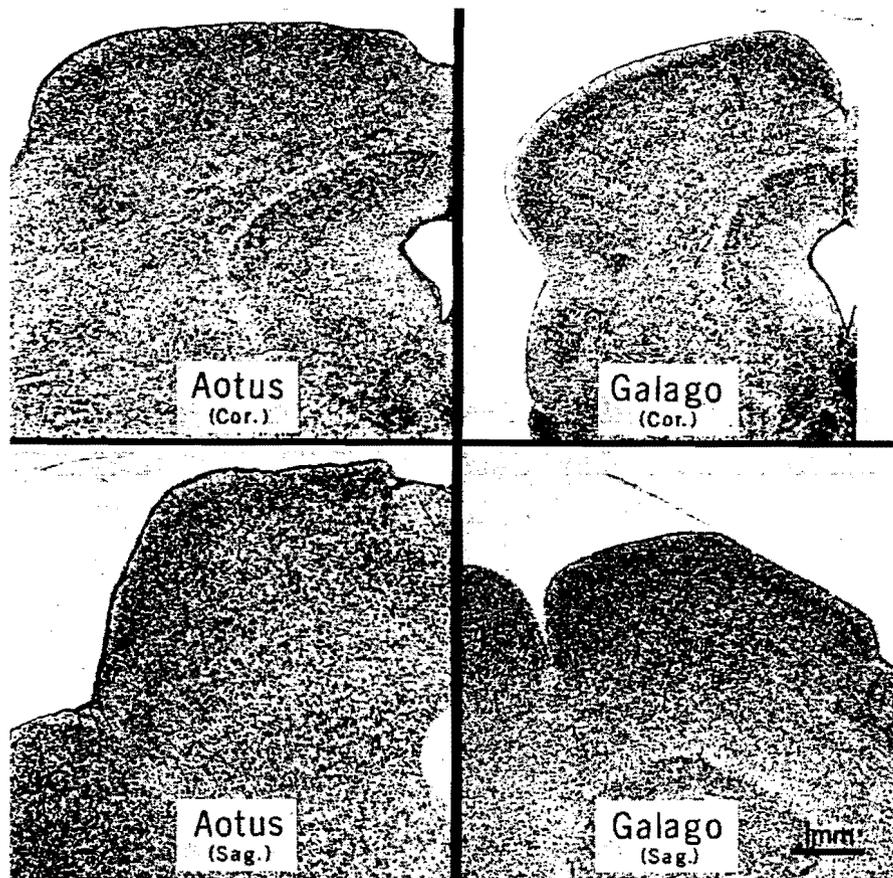


Fig. 1. The superior colliculus of owl monkey (left) and galago (right). The 30  $\mu$ m brain sections stained with thionine are in coronal (top) and sagittal (bottom) planes.

revealed a systematic representation of the contralateral hemifield (Figs. 2, 3 and 8). The centers of the receptive fields were all within the contralateral hemifield (Figs. 2–4) even when the receptive fields were for recording sites at the rostral margin of the superior colliculus (Figs. 2 and 3). Receptive fields for comparable recording sites in the rostral part of the superior colliculus of the grey squirrel and tree shrew were in the ipsilateral hemifield<sup>20</sup>.

The overall pattern of the representation of the visual field in the superior colliculus of the owl monkey can be reconstructed from the data illustrated from one experiment in Fig. 2. If the receptive fields for the row of electrode penetrations numbered 8–16 are considered, it is clear that the upper visual field is represented in the medial portion of the colliculus and the lower visual field in the lateral portion. Receptive fields for a second row of recording sites 5–17 indicate that vertical meridian and the center of gaze are represented near the rostral border, and the temporal periphery of the contralateral hemifield is represented caudally in the colliculus. More details are apparent when receptive fields for the other electrode penetrations are considered. In most electrode penetrations, the course of the electrode was somewhat oblique to the lamination of the colliculus and receptive fields for successively deeper recording sites

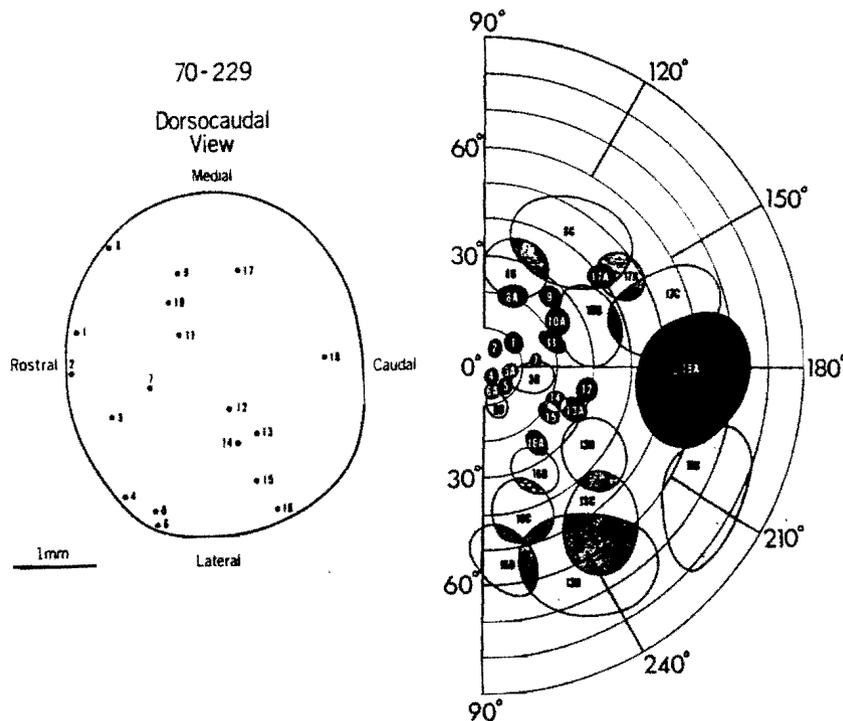


Fig. 2. Receptive fields for recording sites in the left superior colliculus of owl monkey 70-229. A reconstructed dorsocaudal view of the superior colliculus is shown to the left. Numbered dots mark electrode penetrations. To the right, receptive fields for the right eye corresponding to the numbered electrode penetrations are shown. The dark fields represent the first or only receptive fields recorded in each penetration while the gray fields depict receptive fields for successively deeper recording sites.

changed a little in position and became larger. When the shifts in position were minor, only the smallest receptive field for the most superficial recording site is shown. Other electrode penetrations near the curving sides of the colliculus passed along the layers for greater distances and successively deeper recording sites revealed greater displacement of receptive field centers. Thus, electrode penetration 8, for example, passed down the lateral bank of the colliculus and the deepest recording site (8C) was near the ventrolateral margin. Because of the rostrocaudal slope of the colliculus (see Figs. 1 and 3), the more caudal electrode penetrations (16, 18 and 17 in Fig. 2) extended along the caudal bank and receptive field positions changed accordingly with successively deeper recording sites. These results indicate that the zero vertical meridian of the visual field corresponds to much of the outer margin of the superior colliculus extending from at least recording site 16D near the rostromedial margin to 8B on the caudolateral margin. Receptive fields for recording sites 1-5 show that the center of gaze is represented near the rostralateral margin of the tectum.

The representation of central vision is also shown in Fig. 3. Recording site 1 was from neurons at the rostralateral margin of the colliculus and the corresponding receptive field was centered near the intersection of the horizontal and vertical meridians. Fig. 3 also shows the usual angle of the electrode penetrations in these experiments.

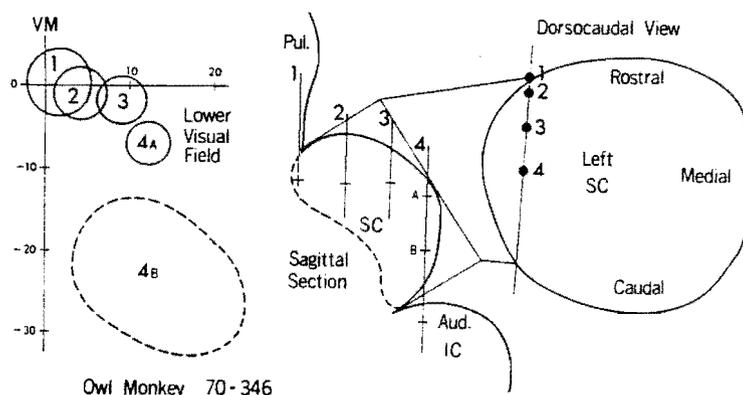


Fig. 3. Receptive fields for a rostrocaudal row of penetrations in the left superior colliculus of owl monkey 70-346. The reconstructed colliculus is shown with numbered penetration sites in a dorso-caudal view. A sagittal section of the colliculus through the electrode tracts is illustrated depicting the recording sites. Corresponding receptive fields for each penetration are shown to the left. The vertical line (VM) represents the vertical meridian of the visual field for the right eye. The solid line fields depict the first or only receptive fields of the penetrations while the dashed line illustrates that for the deep recording site of penetration no. 4.

Receptive fields for two additional experiments are shown in Fig. 4. While some receptive fields overlap the estimated zero vertical meridian by a few degrees, all are centered in the contralateral hemifield. In no experiment was there any evidence of a representation of the ipsilateral hemifield other than these few degrees of overlap along the vertical meridian.

It is also apparent that receptive fields near the center of gaze are smaller than those in the periphery of the visual field. Most recording sites were activated by stimuli presented to either eye, although the response from the contralateral eye was usually stronger. Responses for neurons representing central vision were usually much weaker than for more peripheral parts of the visual field. This observation might be explained by the report of Wilson and Toyne<sup>39</sup>, in which it was noted that the caudal portions of the superior colliculus of the macaque representing the periphery of the visual field received a stronger retinal fiber projection than the more rostral regions representing central vision.

The results of our experiments on the visuotopic organization of the superior colliculus of the owl monkey are summarized in Fig. 8. The superior colliculus represents the contralateral hemifield with the vertical meridian corresponding to most of the outer margin of the structure. Central vision is represented in the rostrolateral zone of the tectum, and proportionally more tissue corresponds to the central 10° of horizontal visual angle than the next 10°, to the central 20° than the next 20°, and to the central 40° than the next 40°. The temporal periphery of the visual field is represented along the caudomedial margin of the colliculus.

#### *Visuotopic organization in the galago*

The same procedure was employed in investigating the galago superior colliculus as with the owl monkey. The basic organization of the visual field representation

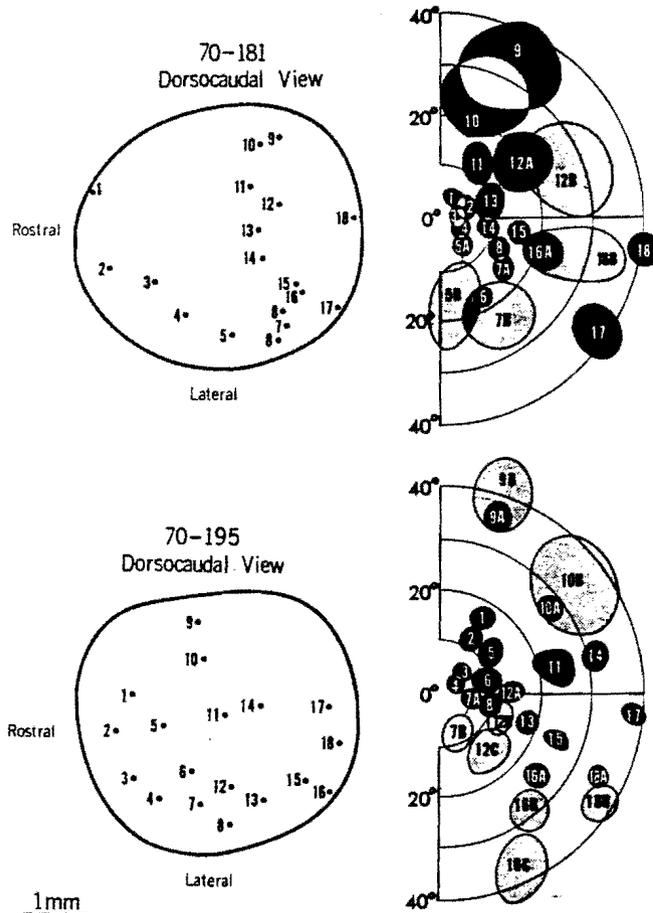


Fig. 4. Receptive fields for recording sites in the left superior colliculus of owl monkeys 70-181 and 70-195. The reconstructed superior colliculi are shown to the left in dorsocaudal views. Receptive fields within the central 40° of the visual field for the right eye are shown. The receptive fields correspond to the numbered electrode penetrations. The dark fields represent the first or only receptive field recorded in each penetration while the gray fields depict receptive fields for successively deeper recording sites. The receptive fields do not cross the vertical meridian by more than a few degrees.

was found to be similar to that shown for the owl monkey (Fig. 8). The centers of the receptive fields were all within the contralateral hemifield (Figs. 5-7). Recording sites approaching the rostral margin of the superior colliculus reveal corresponding receptive fields that approach but do not cross the vertical meridian by more than a few degrees (Figs. 5-7). As in the owl monkey, the upper and lower visual fields are represented medially and laterally, respectively (Fig. 8). The horizontal meridian courses in a rostralateral to caudomedial manner, although the lateral to medial rotation is less in the bush baby than in the owl monkey (Fig. 8). Receptive fields were readily obtainable with stimuli presented to either eye (the monocular crescent in the temporal periphery being an exception).

The results from one galago experiment are illustrated in Fig. 5. A reconstructed dorsal view of the superior colliculus is shown. The dorsal view provides the maximal view of the surface of the structure in the galago (vs. the dorsocaudal view in the owl

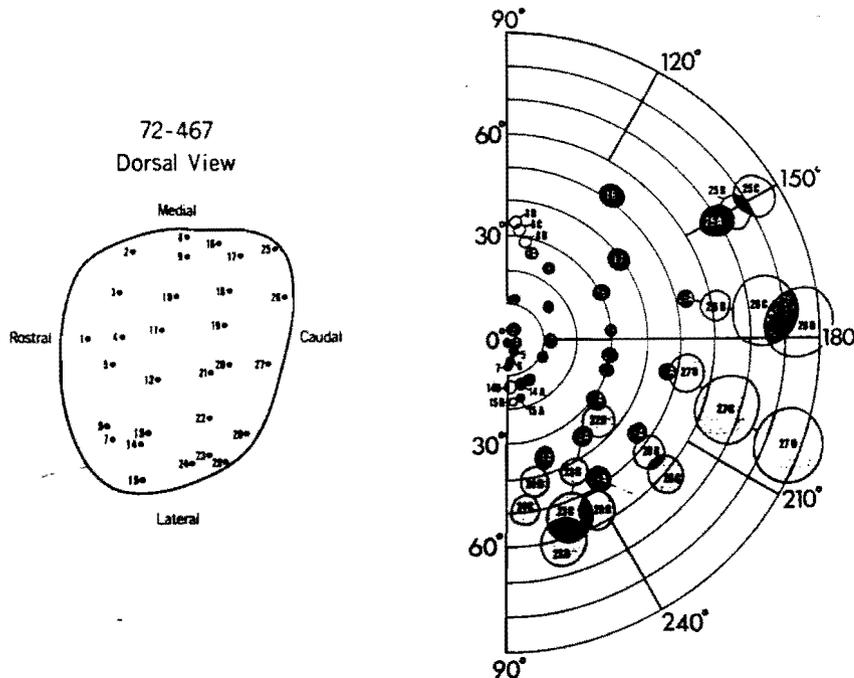


Fig. 5. Receptive fields for recording sites in the left superior colliculus of galago 72-467. A reconstructed dorsal view of the superior colliculus with numbered electrode penetrations is shown to the left. The numbered receptive fields for the right eye correspond to the electrode penetrations.

monkey, see Fig. 1). Receptive field positions are shown for 29 electrode penetrations. The dark receptive fields depict the initial or only field recorded in a given penetration with the numbered shaded fields representing responses for successively deeper recording sites. The receptive fields for penetrations 1-7 indicate that the center of gaze is represented in the rostral segment of the colliculus. Equally, a consideration of the receptive fields for penetrations 25-29 reveals that the periphery is represented caudally. By comparing the receptive fields for the rostral penetrations (1-7) with those for the caudal penetrations (25-29) the tendency for the peripheral fields to be larger than those in central vision can be appreciated. Unlike the findings in the owl monkey, the responses near the center of gaze were usually as strong as those in the periphery. The receptive fields for the deeper recording sites are usually larger than those more superficial as can be seen in Fig. 5. There was also a noted tendency for the response from the contralateral eye to begin at a level superficial to the response from the ipsilateral eye in the binocular portions of the tectum.

Figs. 6 and 7 illustrate 3 additional galago experiments in which it can be seen that receptive fields recorded for one superior colliculus are limited to the contralateral hemifield. Although many electrode penetrations were made near or at the rostral margin of the superior colliculus, none of the receptive field centers were beyond the vertical meridian.

A composite of the visuotopic results from the galago experiments is shown in Fig. 8. As in the owl monkey, the representation is binocular and limited to the contra-

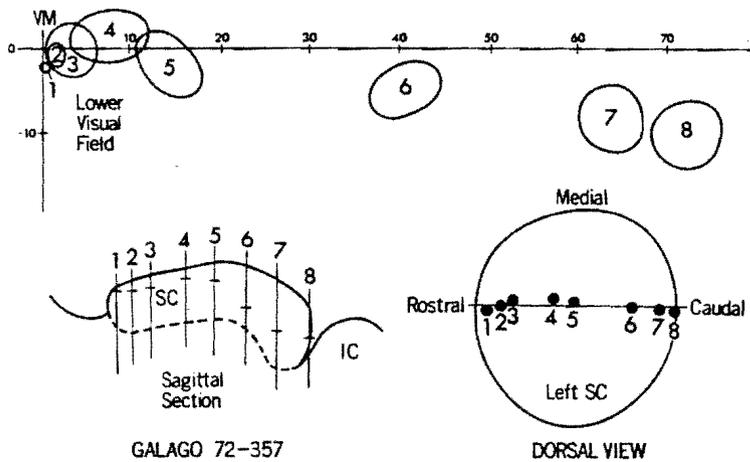


Fig. 6. Receptive fields for a rostrocaudal row of penetrations in the left superior colliculus of galago 72-357. The reconstructed colliculus is shown with numbered penetration sites in a dorsal view. A sagittal section of the colliculus through the electrode tracts is illustrated depicting the recording sites. Corresponding receptive fields for each penetration are shown at the top. The vertical and horizontal lines represent the vertical and horizontal meridians, respectively, of the visual field for the right eye.

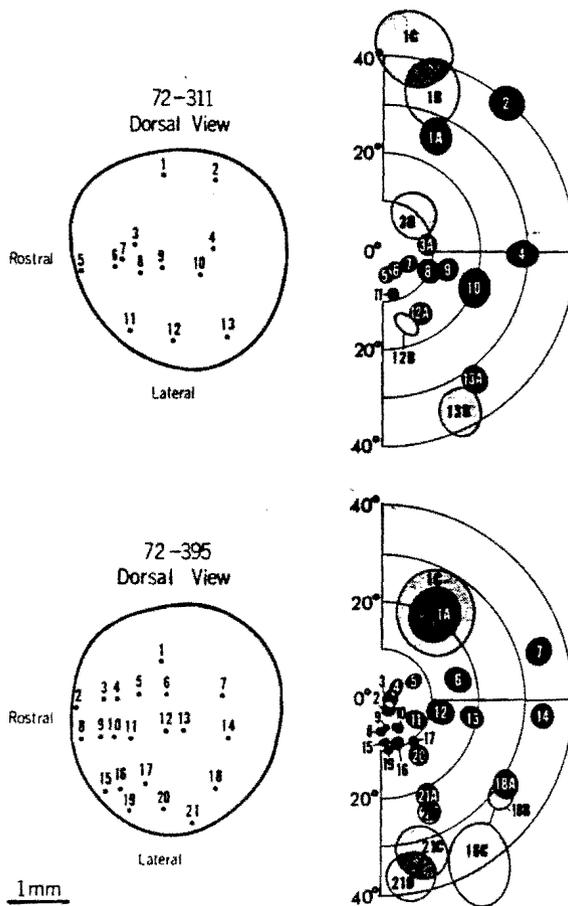


Fig. 7. Receptive fields for recording sites in the left superior colliculus of galagos 72-311 and 72-395. The reconstructed superior colliculi are shown to the left in dorsal views. Receptive fields within the central 40° of the visual field for the right eye are shown. The receptive fields correspond to the numbered electrode penetrations. The dark fields represent the first or only receptive fields recorded in each penetration while the gray fields depict receptive fields for successively deeper recording sites. The receptive fields do not cross the vertical meridian by more than a few degrees.

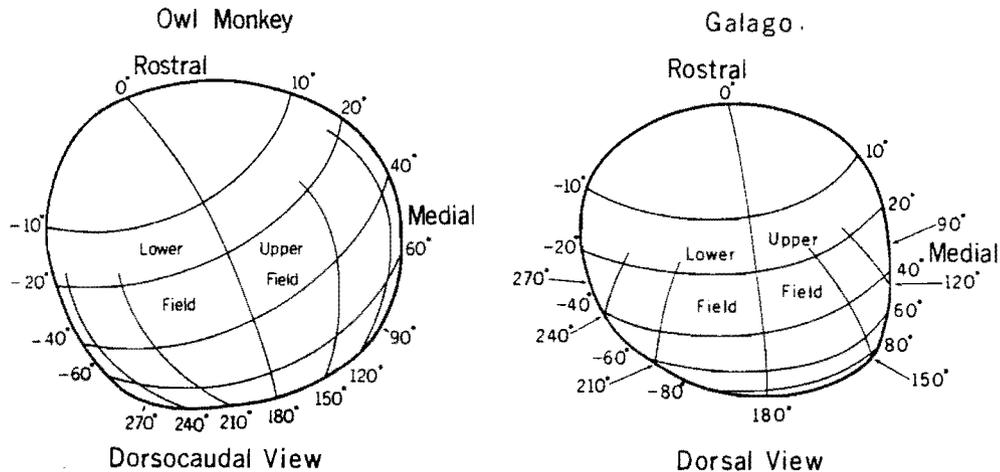


Fig. 8. Maximal surface view of the right superior colliculus of owl monkey (dorsocaudal) and galago (dorsal) with polar coordinates of the visual field representation superimposed.

lateral hemifield. The vertical meridian is represented at the rostral margin of the structure. There is a disproportionate amount of tissue devoted to central vision, with the central  $10^\circ$  portion of horizontal visual angle being greater than the next  $10^\circ$ , the central  $20^\circ$  portion greater than the next  $20^\circ$ , and so on. While the horizontal meridian courses in a rostralateral to caudomedial manner, the lateral to medial rotation is not as pronounced as in the owl monkey.

#### DISCUSSION

##### *Representation of the visual field in primates*

(A) *Extent of the representation.* The results of this investigation indicate that in two primates, a New World monkey and a prosimian, the amount of visual field represented in the superior colliculus is limited to the same portion that is represented in the geniculostriate system. Thus, both the superior colliculus and dorsal lateral geniculate body<sup>17</sup> (and unpublished observations) of these primates contain an isomorph of the contralateral half of the visual field. This finding is consistent with the results of recent microelectrode studies on other primates. In squirrel monkey, Kadoya *et al.*<sup>19</sup> found that the receptive fields of neurons in the superior colliculus were all within the contralateral half of the visual field or within  $2^\circ$  of the vertical meridian. In the macaque monkey, Cynader and Berman<sup>7</sup> and Goldberg and Wurtz<sup>10</sup> reported similar findings (see also Humphrey<sup>15</sup>). In addition, after small lesions of the retina in the macaque monkey, Wilson and Toyne<sup>39</sup> found that the nasal and temporal 'halves' of the retina project to the contralateral and ipsilateral colliculi, respectively. In contrast to the cat<sup>33</sup>, section of the optic tract in the macaque monkey results in total degeneration of the ganglion cells of the temporal hemiretina of the ipsilateral eye<sup>34</sup> indicating that it is unlikely that any of these ganglion cells project to the contralateral superior colliculus. Although these results are limited to only a few primates, the fact that the results are similar for a prosimian, two New World monkeys and one Old

World monkey, suggest that the limited representation of the visual field in the superior colliculus is a general feature of the primate brain.

A possible exception to the above generalization is found in the tree shrew. The tree shrew, often classified as a primate, has a complete representation of the retina of the contralateral eye in the superior colliculus. This difference from the representation known for other primates is part of an array of differences in neural organization in tree shrews<sup>5</sup> and emphasizes the now prevailing view that tree shrews either diverged from primates very early in the evolution of primates or both tupaiids and primates arose from the same ancestral group of insectivores<sup>6,11,25,31,37</sup>.

(B) *Topology of the representation.* In the superior colliculus of the owl monkey and galago, the upper field is represented medially and the lower field laterally as in other mammals. The presumed center of gaze is represented rostrally and rostrolaterally in the galago and owl monkey, respectively, with the vertical meridian forming most of the medial and lateral borders of the structure. Disproportionate amounts of tissue represent successively more central parts of the visual field. However, the expanded representation of the central few degrees of the field is less in these two nocturnal primates than in either the squirrel monkey<sup>19</sup> or the macaque monkey<sup>7,10</sup>.

A disproportionately large representation of central vision corresponding to a greater cell density of the central retina<sup>16,40</sup> is also found in striate cortex<sup>1</sup> and the dorsal lateral geniculate of the owl monkey<sup>17</sup> and galago (unpublished studies).

(C) *Input from the ipsilateral eye.* With the exception of the monocular crescent in the temporal periphery of the visual field, responses from the ipsilateral eye were routinely obtained in both the galago and the owl monkey. Typically, the response from the ipsilateral eye was weaker than the response from the contralateral eye for the same recording site. It has been reported for the prosimians, galago and potto, that the contralateral and ipsilateral retinal terminations are segregated within separate subdivisions of the stratum griseum superficiale<sup>9,36</sup>. The projections form partially overlapping sublaminar with the contralateral terminations lying immediately superficial to the ipsilateral terminals. This laminar segregation of input was reflected in our cluster recordings in the galago. As the electrode first penetrated the superior colliculus, the ipsilateral response was much weaker than the contralateral response, or absent. As the electrode was advanced 350–500  $\mu\text{m}$  deep to the surface the ipsilateral response became the stronger response.

#### *Comparison of primates with other mammals*

Data from a number of other mammals, in contrast to primates, suggest that part of the ipsilateral hemifield, as well as the contralateral hemifield is represented in the superior colliculus. Some of the evidence is reviewed below.

(A) *Rodents.* The first evidence for the representation of part of the ipsilateral hemifield in the superior colliculus was Lashley's<sup>23</sup> finding that retina temporal to the 'fixation point' projects to the contralateral superior colliculus. Lashley's contention that the superior colliculus of the rat represents the complete retina of the contralateral eye, while the dorsal lateral geniculate nucleus represents only the contralateral hemifield, appears to be supported by the results of microelectrode mapping studies.

Using the positions of the most nasal receptive fields obtained from neurons in the LGN<sub>D</sub> of the rat<sup>27</sup> as a guide, we estimate the 'line of decussation' or 'line of fixation' of the rat to be about 53° nasal to the blind spot or the position of the optic disc in the visual field. This figure is close to Lashley's earlier estimate of 52°<sup>22,23</sup>. However, if the blind spot is used as a reference for the most nasal receptive fields obtained for neurons in the superior colliculus of the rat<sup>30</sup>, it appears that at least 20 additional degrees of visual field beyond the 'line of decussation' are represented in the superior colliculus in comparison to the LGN<sub>D</sub>.

In another rodent, the grey squirrel, the evidence is more compelling. Receptive fields for neurons in the superior colliculus extended some 30° past the line of decussation and into the ipsilateral hemifield when the line of decussation and ipsilateral hemifield were defined by recording from striate cortex in the same animals<sup>20</sup>. It was concluded that the complete retina of the contralateral eye is represented in the superior colliculus<sup>20</sup> while about 30° of the temporal retina projects ipsilaterally to the geniculostriate system<sup>12,17</sup>. A similar representation of the complete retina of the contralateral eye appears to exist in the superior colliculus for the ground squirrel<sup>41</sup>.

(B) *Lagomorphs*. Microelectrode mapping studies of the superior colliculus and visual cortex of the domestic rabbit have revealed that the part of the ipsilateral hemifield seen by the contralateral eye, in addition to the complete contralateral hemifield, is represented in the superior colliculus (C. Sitthi-Amorn, personal communication). These findings are supported by the observations of Hughes<sup>14</sup> who reported occasional responses to stimuli presented beyond the vertical meridian of the contralateral eye in rabbit.

(C) *Carnivores*. The superior colliculus of the cat was initially mapped by Apter in 1945<sup>2</sup>. Recording evoked potentials, Apter gave a detailed account of the representation of the visual field in the superior colliculus. She was apparently unable to record responses to light stimuli presented beyond the vertical meridian, however, because she stated that her recordings corroborated 'the fact that only retina nasal to the vertical meridian projects to the contralateral colliculus and only the temporal retina to the ipsilateral colliculus'. Accordingly, the vertical meridian in her map of the colliculus was placed at the structure's rostral margin. This view of the superior colliculus representing only the contralateral visual hemifield in cat remained unchallenged for over 20 years. In 1968 McIlwain and Buser<sup>24</sup> and Sprague *et al.*<sup>32</sup> reportedly were able to record receptive fields beyond the vertical meridian. The recordings were few in number, but the evidence did suggest that the colliculus representation extended into the ipsilateral visual hemifield by at least 20°. This extended representation was subsequently confirmed in the detailed maps published by Strachill and Hoffmann<sup>35</sup>, Feldon *et al.*<sup>8</sup> and Hoffmann<sup>13</sup>. In a recent series of experiments in cats (in preparation) we obtained evidence which suggests that the representation in the superior colliculus of the contralateral retina is complete. In addition the representation beyond the vertical meridian (in the ipsilateral hemifield) is binocular.

(D) *Marsupials*. Quadrant projections of the retina in the opossum were first reported by Bodian<sup>3</sup>. Employing the Marchi method, Bodian observed that the pattern of degeneration in the superior colliculus subsequent to retinal lesions was much the

same for opossum as reported for other mammals. Unlike Lashley<sup>23</sup>, however, Bodian<sup>3</sup> found no evidence for a complete representation of the retina in the contralateral superior colliculus as noted above. Our own unpublished recordings from striate cortex and the superior colliculus in the opossum lead to another conclusion. From recordings in striate cortex, we estimate the projection of the line of decussation into the visual field is about 25–30° nasal to the optic disc. Receptive fields for recordings in the superior colliculus extended as much as 40° further nasalward in the visual field of the contralateral eye. These results suggest that the representation in the opossum superior colliculus is of the complete visual field of the contralateral eye and indicate, at least, that the question of extent of representation should be reopened.

#### *Functional implications*

It is clear that there are at least two basic types of visual field representations in the superior colliculus, the representation of the hemifield seen in some primates, and the more extensive representation found in a number of other mammals. In addition, the superior colliculus of different mammals varies considerably in size, architectonic differentiation and amount of input from the ipsilateral retina. These observations appear to be inconsistent with any view that the functions of the tectum are identical from species to species or vary along a single dimension and suggest a complex and varied role of the tectum in vision.

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