COMPARISON OF RECEPTIVE-FIELD ORGANIZATION OF THE SUPERIOR COLLICULUS IN SIAMESE AND NORMAL CATS

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SUMMARY

1. The superior colliculus has been studied in Siamese and normal cats by recording the responses of single tectal units to visual stimuli.

2. The retinotopic organization of the superior colliculus has been compared in the two breeds. In the normal cat, the contralateral half-field is represented in the central and caudal part of the colliculus, and a vertical strip of the ipsilateral half-field, 15–20° wide, is represented at the anterior tip. The Siamese cat superior colliculus receives an abnormally large projection from the ipsilateral half-field so that units with visual receptive fields which extend as far as 40° into the ipsilateral half-field can be found. The area of the tectal surface devoted to the representation of the ipsilateral half-field is about twice as large in Siamese cats as in normal cats. The enhanced representation of the ipsilateral half-field in Siamese cats is reflected in a displacement of the vertical meridian and the area centralis on the tectal surface.

3. The area centralis in the Siamese cat is located at about the same point on the tectal surface as would be occupied by a point in the visual field about 6–7° contralateral to the area centralis in the normal cat. The smallest receptive fields in both breeds are located near the area centralis. The size of the receptive field for a tectal unit seems to be determined by the retinal location of the receptive field and not by the absolute position of the unit on the tectal surface.

4. The receptive-field characteristics of tectal units show many similarities in the two breeds. The receptive fields of individual units consist of activating regions flanked by suppressive surrounds. Units respond well to stimuli of different shapes and orientation provided they are moving. The optimum stimulus for a given unit can be much smaller than the size of the activating region. About two thirds of the units studied in both breeds show directional selectivity. Most of the units studied in normal cats can be activated by stimulation of either eye, while in Siamese cats,

80 % of the units studied can be driven only by the contralateral eye. A few monocularly driven units with two separated receptive fields have been observed in Siamese cats.

5. In the left tectum of both breeds, units respond well to left-to-right stimulus movement. The reverse situation obtains in the right tectum. In Siamese cats, units located at the anterior tip of the tectum with their receptive fields located in the visual half-field ipsilateral to the tectum under study respond better to stimulus movement toward the area centralis than away from it. The preferred direction for a tectal unit seems to be determined by its tectal location rather than by the location of its receptive field in the retina.

6. Visual cortex lesions in both breeds increase the responsiveness of tectal units to flashing spots and almost entirely remove the directional selectivity exhibited by tectal units, although units with asymmetric surrounds are still found. In normal cats, the lesions change the ocular dominance distribution, skewing it more strongly toward the contralateral eye. In Siamese cats, the ocular dominance distribution remains unchanged after a visual cortex lesion.

7. The squint commonly exhibited by Siamese cats is regarded as a compensation for the anomalous retinotectal topography. It is suggested that, in the absence of an adaptive modification, the anomalous retinotectal projection would lead to mislocalization in Siamese cats just as it does in frogs and hamsters whose retinotectal projection has been experimentally altered. The convergent strabismus which Siamese cats commonly exhibit may be a cure for the abnormal retinal projections rather than a disease.

INTRODUCTION

Several recent studies have demonstrated that the retinal projections of Siamese cats show marked abnormalities, and it has been suggested that these abnormal projections are related to the convergent strabismus commonly exhibited by Siamese cats (Guillery & Kaas, 1971; Kalil, Jhaveri & Richards, 1971). Siamese kittens usually become cross-eyed at 6–8 weeks of age, and preliminary evidence suggests that this abnormality may be dependent on visual experience (Hubel & Wiesel, 1971). In the normal cat, the lateral geniculate nucleus receives input from the contralateral half of the visual field from both eyes. The pretectal area and superior colliculus receive fibres from both retinae although the projection from the contralateral retina is more dense (Garey & Powell, 1968; Laties & Sprague, 1966). In the Siamese cat, an abnormal projection from the ipsilateral half-field to the lateral geniculate nucleus has been demonstrated, and the retinal projections to the pretectal area and the superior

colliculus are derived almost totally from the contralateral eye (Guillery & Kaas, 1971; Kalil *et al.* 1971).

The retinotopic organization of the lateral geniculate nucleus and of the visual cortex in Siamese cats has also been studied by electrophysiologic techniques. It has been shown that the abnormal projection to the lateral geniculate nucleus comes from a vertical strip of the contralateral temporal hemiretina about 20° in width that lies just temporal to the area centralis (Guillery & Kaas, 1971). Units in the left lateral geniculate nucleus of the Siamese cat, therefore, have receptive fields which extend 20° into the left half-field as well as covering the entire right half-field. Similar abnormalities have been observed in the retinotopic organization of the visual cortex in Siamese cats (Hubel & Wiesel, 1971) in which receptive fields also extend 20° into the ipsilateral half-field. In the normal cat, units in the cortex and the lateral geniculate nucleus usually have receptive fields confined to the contralateral half-field, though some overlap into the ipsilateral half-field has been noted (Leicester, 1968; Sanderson & Sherman, 1971).

The retinotopic organization of the superior colliculus of the normal cat has been studied by electrophysiologic and anatomic methods (Feldon, Feldon & Kruger, 1970; Straschill & Hoffman, 1969; Garey & Powell, 1968). The periphery of the contralateral half-field is represented in the posterior parts of the structure while the central field is represented in the anterior portions. In the cat, the anterior tip of the tectum receives an input from the contralateral temporal hemiretina (Laties & Sprague, 1966). This results in a representation of a vertical strip, up to 15–20° in width in some cases, of the ipsilateral half-field in the cat colliculus (Feldon *et al.* 1970).

The anatomic and physiologic findings in normal and Siamese cats suggest an investigation of the retinotopic organization of the Siamese cat's colliculus. It is possible, for example, that fibres from the contralateral temporal hemiretina might be misrouted and project to the lateral geniculate nucleus rather than the tectum. This would result in no representation of the ipsilateral half-field in the Siamese cat tectum. Alternatively, the representation of the ipsilateral half-field in the Siamese cat colliculus might be even more pronounced than has been been found in the visual cortex with receptive fields extending perhaps 40° into the ipsilateral half-field, i.e. 20° more than has been found in the visual cortex and lateral geniculate nucleus of the Siamese cat.

In the normal cat superior colliculus, many of the units encountered exhibit a directional preference in their responses to visual stimuli (McIlwain & Buser, 1968; Sterling & Wickelgren, 1969; Straschill & Hoffman, 1969). The horizontal component of the preferred direction of

units in the left tectum is usually from left to right and in the right tectum from right to left (Sterling & Wickelgren, 1969; Straschill & Hoffman, 1969). Since, except for units located at the rostral tip of the colliculus, the receptive fields are located in the contralateral half of the visual field, this statement is functionally equivalent to the statement of Sterling & Wickelgren that 'most of the cells have preferred directions away from the centre of gaze' (1969). This statement implies that the preferred direction of a tectal unit is determined by the retinal location of its receptive field. It is equally possible, however, that units in the left tectum might prefer left to right stimulus movement regardless of the location of their receptive fields. If an enhanced representation of the ipsilateral half-field exists in the tectum of the Siamese cat, then it would be possible to decide between these alternatives. Some evidence exists favouring a retinal determination of the preferred direction. Sterling & Wickelgren report that three of four directionally selective units encountered at the rostral tip of the tectum with receptive fields within the ipsilateral half-field had preferred directions toward the periphery of the ipsilateral half-field, i.e. away from the area centralis (1969). Feldon *et al.* report directional selectivity in the rostral zone of the tectum, where cells with their receptive fields located in the ipsilateral half-field are found, but they do not comment on the distribution of the preferred directions (1970). This evidence is clearly far from conclusive. As we were interested in the role of the retinal afferents versus that of factors intrinsic to the tectum in determining the preferred direction in tectal units, it seemed worth while to study this problem again in the Siamese cat where the dissociation between unit location in tectum and receptive-field position in the visual field might be exceptionally clear.

There have been conflicting reports on the effects of visual cortex lesions on receptive-field properties of units in the cat tectum. Some workers have found that lesions of the visual cortex remove the directional selectivity for moving stimuli commonly exhibited by tectal units in the intact animal (Rosenquist & Palmer, 1971; Wickelgren & Sterling, 1969) while others have found less pronounced changes or no changes at all in the receptive-field properties of tectal units after visual cortex lesions (Hoffman & Straschill, 1971; Marchiafava & Pepeu, 1966; Rizolatti, Tradardi & Camarda, 1970). In view of these conflicting results, we decided to study the problem again in both the normal and Siamese cat.

METHODS

Seven Siamese cats, identified by their blue eyes, characteristic fur colouring and facial features, and eight normal cats were studied. By normal cats we mean the domestic, mixed-breed cats commonly used in experimental investigations. In four of the Siamese cats and four of the normal cats the visual cortex was removed unilaterally 4–15 days before examination of the receptive-field properties of units in both colliculi. To do this, animals were anaesthetized with I.V. sodium pentobarbitone (Nembutal, Abbott). Under sterile conditions, 4 g mannitol (Osmitrol, Travenol Laboratories) in 20 ml. water was administered by I.V. injection to reduce brain oedema. Then, the visual cortex of one hemisphere was removed by subpial suction.

Two of the four Siamese cats which sustained visual cortex lesions were used for both anatomic and electrophysiologic procedures. The lesions were made unilaterally, and after 6 days the animals were prepared for electrophysiologic experiments. After 30 h of recording, the animals were perfused with saline and 10 % formalin. The brains were stained using the Fink–Heimer technique for selective staining of degenerating axons (Fink & Heimer, 1967).

The procedures for preparing the animals and for visual stimulation, recording, histology and reconstructing the shape of the colliculus were similar to those used in our previous investigation (Cynader & Berman, 1972). Cats were anaesthetized initially with I.V. sodium thiopentone (Pentothal, Abbott) and during recording were maintained on a mixture of 60 % nitrous oxide and 40 % oxygen. We recorded extracellularly from single tectal units using glass-coated platinum-iridium microelectrodes. A 19-gauge needle containing the micro-electrode was lowered at an angle 20° lateral to the Horsley–Clarke vertical to a point 4 mm above the colliculus surface. The lateral approach minimized damage to the overlying visual cortex. Residual eye movements were reduced by paralysis induced by continuous infusion of a mixture of tubocurarine chloride (2·8 mg/hr), gallamine triethiodide (14 mg/hr) and 5 % lactated dextrose in Ringer (Hartmann's solution) (3·4 ml./hr).

RESULTS

Of the seven Siamese cats studied, two showed no muscle imbalance and the other five all exhibited a convergent strabismus. The size of this strabismus was between 10 and 14° in four of the cats, and the other exhibited a 20° convergent strabismus. Units were identified by constancy of shape and size of their electrical wave form. We concentrated mainly on receptive-field properties of units in the superficial layers in this investigation, since it has been reported that units in the deeper layers of the tectum are sensitive to even small doses of anaesthesia (Hoffman & Straschill, 1971). The results will be presented in three parts: first, retinotopic organization, then receptive-field properties of the units and finally the effects of lesions in the visual cortex.

A. Retinotopic organization of Siamese cat superior colliculus

In two Siamese cats, both cross-eyed (11° and 13°), and three normal cats, a total of seventy penetrations were made through the superior

colliculus and the relationship between receptive-field location in the visual field and unit position on the collicular surface was established. This map was derived from stimulation of the contralateral eye only. This relationship was verified by histological reconstruction. The areae centrales and optic disks were mapped on to the tangent screen several times during the course of this experiment to control for residual eye movements.
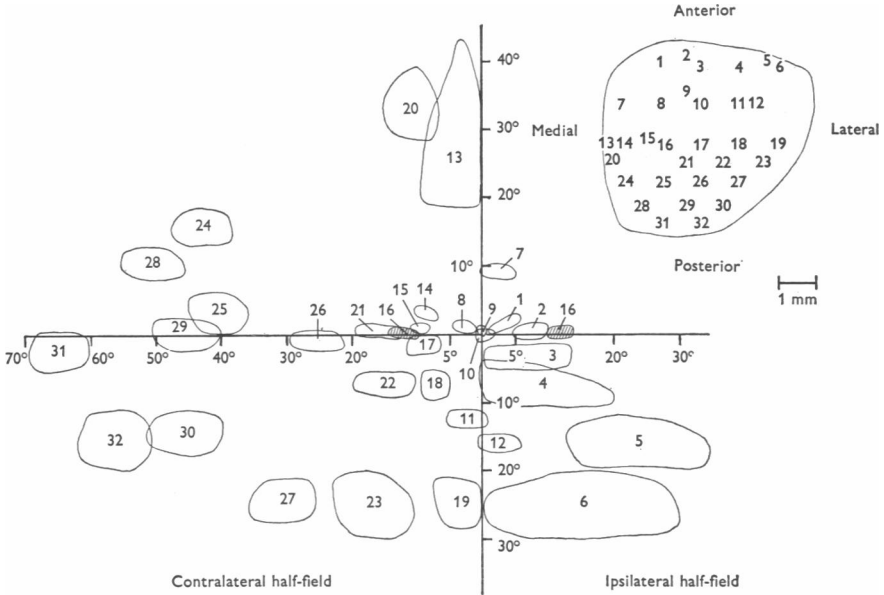

Fig. 1. The relationship between receptive-field location, receptive-field size and unit location on the colliculus surface in the Siamese cat.

The upper right of the Figure shows a reconstruction of the right superior colliculus as viewed from above in the Horsley–Clarke plane. The numbers on the collicular surface show the locations of our penetrations. The rest of the Figure shows the visual field. The horizontal and vertical axes represent the horizontal and vertical meridians of the visual field respectively. The intersection of the axes represents the area centralis. The scale is in degrees along the axes. The encircled numbers show the location and size of the visual field over which the neural background could be influenced on the penetration corresponding to this number. The shaded areas numbered 16 on the left-hand side of the Figure are discussed in the text.

Fig. 1 shows all thirty-two penetrations made in the two Siamese cats. As can be seen, there is a strong projection from the ipsilateral half-field on to the superior colliculus, and it is possible to record responses to visual stimulation as far as 40° into the ipsilateral half-field. Units with receptive fields extending 40° into the ipsilateral half-field are not seen at the collicular surface, but they can be observed as the electrode is advanced into

the colliculus. The shaded areas marked 16 in Fig. 1 require some explana-
tion. On this penetration, the neural background responded to visual
stimulation in two distinct areas. The areas were mirror symmetric about
the vertical meridian, and no response could be evoked from the neural
background in the area of the visual field between the two shaded areas.
The receptive-field properties of units encountered on this penetration
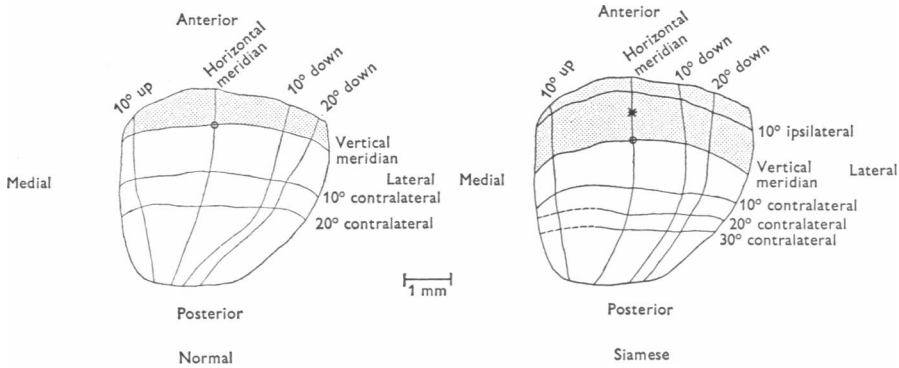will be considered in the subsection on unusual units.

Fig. 2. The representation of the visual field on the surface of the right
superior colliculus in the Siamese and normal cat.
   The left-hand side of the Figure shows the normal cat superior colliculus
and the right-hand side shows the Siamese cat superior colliculus. The
stippled area shows the representation of the ipsilateral half-field on the
colliculus surface in the two breeds. The location of the representation of
the area centralis on the tectal surface is encircled in both parts of the
Figure. The asterisk within the stippled area on the right-hand side of the
figure shows the expected location of the area centralis on the tectal sur-
face of the Siamese cat. This expected location is equivalent to the position
of the area centralis in the normal cat.

   A comparison of the maps of the visual field on to the superior colliculus
in normal and Siamese cats is shown in Fig. 2. The map for the normal cat
is similar to that obtained by Feldon *et al.* (1970) and shows the marked
magnification of the visual field near the horizontal and vertical meridians
and the existence of a zone of representation from the ipsilateral half of the
visual field at the anterior tip of the tectum. The upper fields are repre-
sented in the medial part of the tectum and the lower fields more laterally.
The periphery of the contralateral half-field is represented at the posterior
pole of the tectum while the central visual field is represented more
anteriorly. The map of the Siamese cat colliculus is similar, but the area of
the tectum devoted to representation of the ipsilateral half-field is about
twice as large in Siamese cats as normal cats. The representation of the

area centralis shown encircled in Fig. 2 is on a different point on the colliculus surface in the two breeds. The expected location of the area centralis on the tectal surface in Siamese cats is shown by an asterisk.

The relationship between the size of the activating region of the receptive field and the distance from the area centralis in Siamese and normal cats is shown in Fig. 3. In the Siamese cat, cells with receptive fields in the ipsilateral half-field are represented by triangles in this Figure while cells in the contralateral half-field are represented by circles. As can be seen,
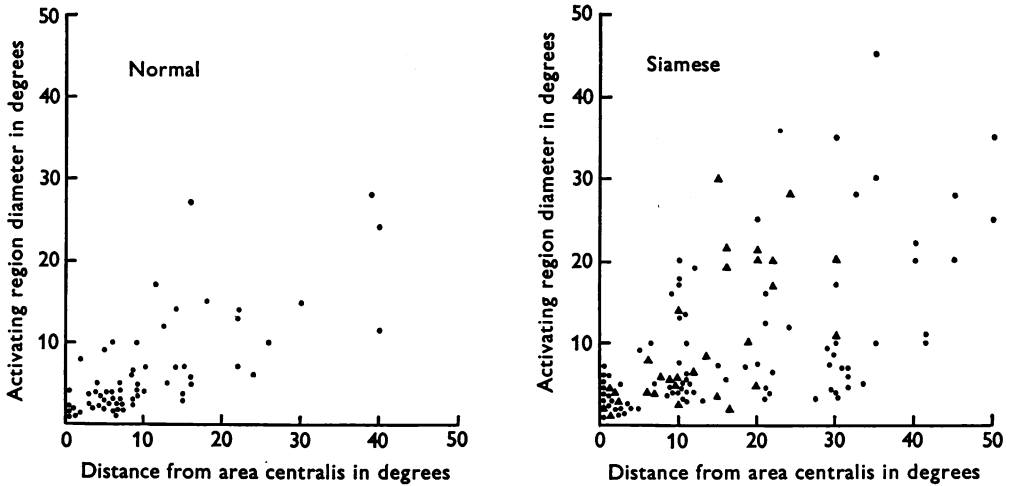

Fig. 3. The relationship between the diameters of the activating regions and distance from the area centralis for normal and Siamese cats for cells in the superficial layers. For cells with elliptical receptive fields, we took half the sum of the wide and narrow axes as our measure of the diameter. In the right-hand part of the Figure dealing with Siamese cats, triangles represent cells with receptive fields located in the ipsilateral half-field (stippled area in Fig. 2).

there is a tendency for larger receptive fields to occur in the periphery of the visual field, and this trend is evident in both the ipsilateral and contralateral half-fields. The units with the smallest receptive fields are located around the area centralis in both breeds, and units whose receptive fields are more than 10° from the area centralis have on the average larger fields. This is true in both breeds although the area centralis is represented in a different place on the tectal surface in the two breeds. These data suggest that the size of the receptive field of a tectal unit is determined by the retinal location of the receptive field and not by the absolute position of the unit on the tectal surface.

B. Comparison of receptive-field properties of units in the Siamese and normal cat colliculus

1. *Receptive-field characteristics common to both breeds.* One hundred and seventy-seven units were studied in thirty-eight electrode penetrations in Siamese cats and ninety-three units in fifteen penetrations in normal cats. The receptive fields of single colliculus units in both breeds of cat
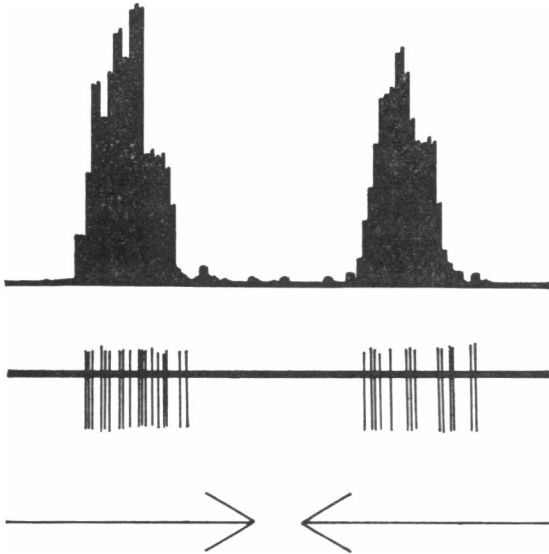

Fig. 4. A histogram representing the sum of twenty-five sweeps and a record showing the unit firing during a typical sweep of a 1° spot over the receptive field of a cell in the superficial layers of the superior colliculus of a Siamese cat.

The arrows represent the direction of stimulus movement. The two nearly equal peaks represent responses to movement in opposite directions. Receptive-field size: 6°, stimulus velocity: 8°/sec, stimulus cycle: 4 sec.

consisted of activating regions flanked on one or more sides by suppressive zones, the stimulation of which could inhibit the response to stimulation of the activating region, but from which no response could be evoked. These units responded well to a wide variety of stimuli showing little specificity for different stimulus shapes. Most units responded well to black stimuli on a white background and also to light stimuli on a dark background. The response of a unit showing no directional preference to a spot sweeping back and forth across the receptive field is shown in Fig. 4. The two roughly equal peaks represent the responses in opposite directions. The strength of the suppressive zone could be asymmetric in some cases.
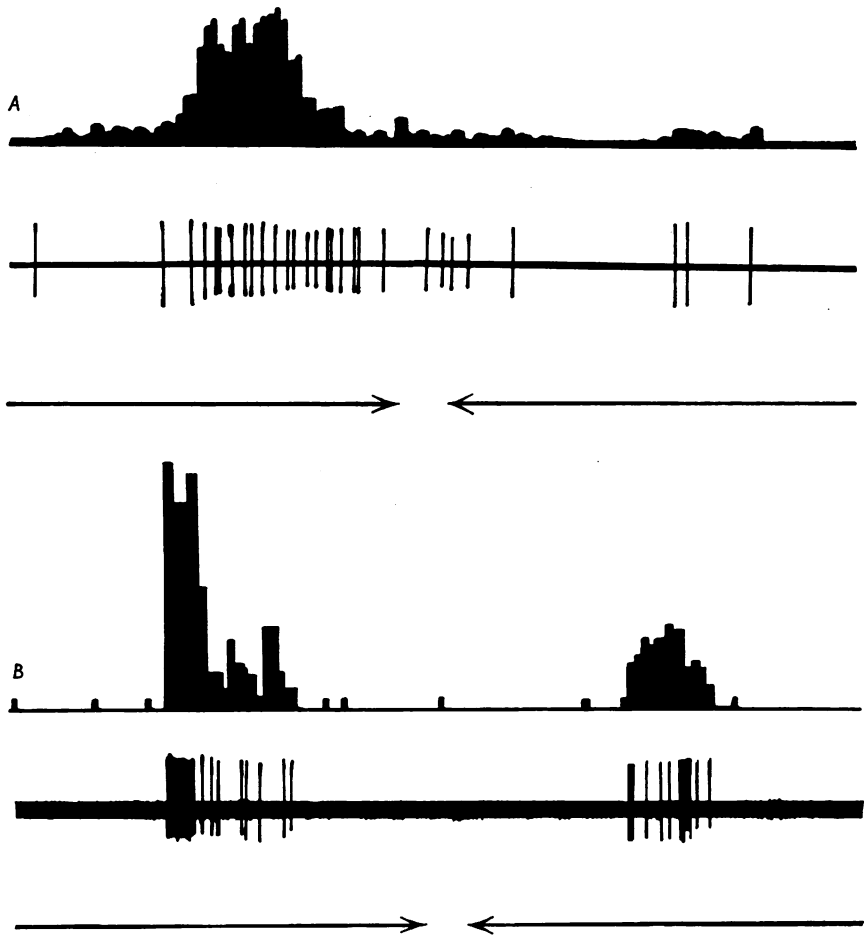
Fig. 5. Part *A* shows a histogram representing the sum of twenty-five sweeps and a record showing the unit firing during a typical sweep of a 1° spot over the receptive field of a directionally selective cell in the superficial layers of the superior colliculus of a normal cat. The arrows represent the direction of stimulus movement. Note the large response to movement in one direction and the slight inhibition of the rest discharge rate by movement in the opposite direction.

Part *B* shows a histogram representing the sum of twenty sweeps and a record showing a unit firing during a typical sweep of a 1° spot over the receptive field of a cell exhibiting an asymmetric surround. The arrows represent the direction of stimulus movement. Note the strong burst when the spot enters from the left. Receptive-field size: 3°, stimulus velocity: 6°/sec, total time: 4 sec.

Fig. 5*B* shows the response of a unit with an asymmetric surround. This response is easily confused with the response of a directionally selective unit (Fig. 5*A*), but it is clear that in Fig. 5*B* the difference between the responses in the two directions of movement lies in the burst evoked by the spot entering the activating region from the strong surround. These units show no directional selectivity when the movement of the stimulus is confined to the activating region. Spatial summation, up to the size of the activating region, a common property in the retina and lateral geniculate nucleus of cat and monkey, was rarely seen in collicular units in either breed. Most units responded as well to stimuli much smaller than the
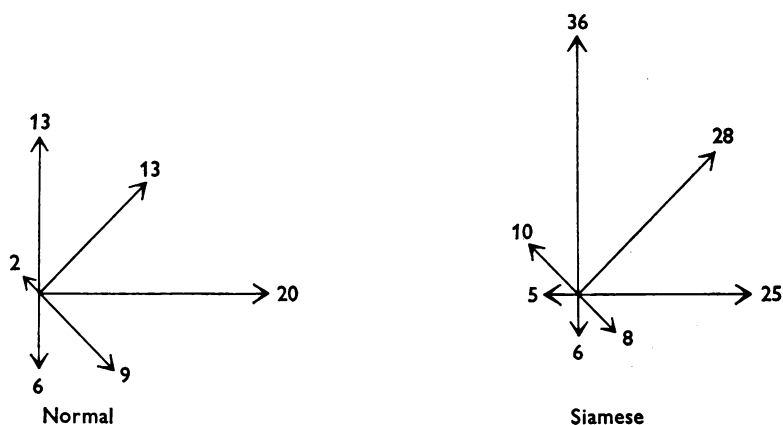

Fig. 6. The distributions of preferred directions of directionally selective cells in the left superior colliculus of the normal and Siamese cat.

The number at the end of each arrow shows the number of units having their preferred direction in the direction in which the line radiates from the intersection point. The relative length of each line is proportional to the number of units whose preferred directions are in the direction indicated by the arrow.

activating region as to stimuli filling it, and for many units the optimum stimulus size was much smaller than the activating region. Collicular units showed a strong preference for moving stimuli over flashing stimuli, and for many units it was impossible to evoke any response at all by flashing stimuli on and off. Fewer than 10 % of all units studied gave some response to a 1 log unit change in the level of background illumination.

2. *Directional selectivity.* Sixty-five percent (118/147) of all units tested for directional selectivity in Siamese cats and 66 % (61/93) in normal cats responded well to movement in one direction and poorly or not at all to movement in the opposite direction. In a few cases, inhibition of resting discharge could be noted with stimulus movement in the direction 180°

from the preferred direction. The unit in Fig. 5*A* responded well to move-
ment in one direction and was inhibited during movement in the opposite
direction. As has been previously noted, in the normal cat (Sterling &
Wickelgren, 1969; Straschill & Hoffman, 1969) the range of preferred
directions over which a given unit responded was often rather wide, and
some units responded well to movements 90° from the preferred direction.
In other units, the range of directions over which strong responses could
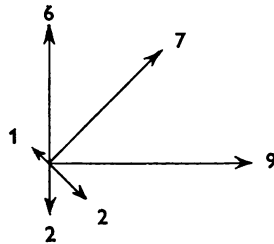be evoked was as narrow as 30°. For classification purposes, we compared

Fig. 7. The distribution of preferred directions for cells in the left superior
colliculus of the Siamese cat with receptive fields located in the left half of
the visual field.
    As in Fig. 6, the length of each arrow is proportional to the number of
units whose preferred directions lie along it and the number is shown at the
point of each arrow. It can be seen that units in the left colliculus with
receptive fields in the left half-field respond preferentially to stimulus move-
ment from left to right although the preferred direction is now toward the
area centralis rather than away from it.

the units' responses to upward *vs.* downward movement and leftward
vs. rightward movement. For example, a unit which responded pre-
ferentially to upward stimulus movement and to stimuli moving to the
right was categorized as having its preferred direction at 45°. The distri-
bution of preferred directions for units in the left tectum of Siamese and
normal cats is shown in Fig. 6. Sixty-five per cent (76/118) of the direc-
tionally selective units studied in Siamese cats and 72 % (44/61) in normal
cats showed a horizontal component in their directional selectivity. Of
the units in the left tectum which had horizontal components in their
directional selectivity, 80 % (61/76) in Siamese cats and 95 % (42/44) in
normal cats preferred movement from left to right. Seventy-five per cent
(88/118) of the units studied in the Siamese cats and 70 % (43/61) in
normal cats showed a vertical component in their directional selectivity.
In normal cats, about 65 % of the units with vertical components in their
directional selectivity (23/43) preferred upward movement. This trend was
even more pronounced in Siamese cats with 85 % (74/88) of the units with
vertical components responding better to upward movement.

The preferred directions of directionally selective units in the ipsilateral half-field in the Siamese cat are shown in Fig. 7. Units in the left tectum with their receptive fields located in the left half of the visual field show a strong preference for left-to-right movement over the opposite direction. The preferred stimulus direction for these units is, therefore, toward the area centralis rather than away from it. It seems clear that the tectal location of the unit rather than the location of the receptive field in the retina determines the preferred direction of a tectal unit. Units in the left tectum respond better to left-to-right stimulus movement regardless of whether the movement is toward or away from the area centralis. If the
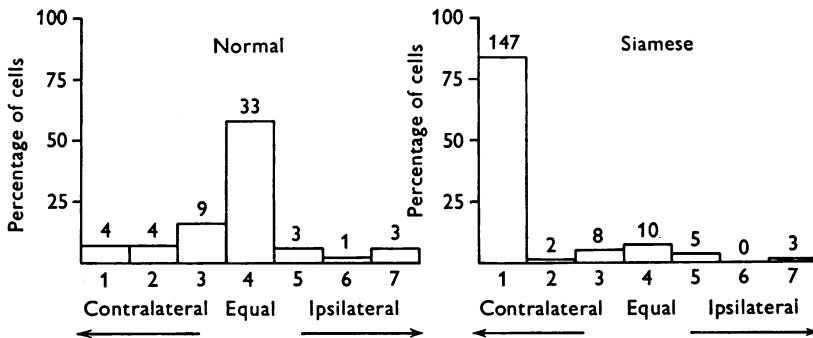

Fig. 8. The left-hand side of the Figure indicates the ocular dominance distribution for fifty-seven cells in the superior colliculus of the normal cat, and the right-hand side indicates the ocular dominance distribution for 175 cells in the superior colliculus of the Siamese cat. The categories correspond to those defined by Hubel & Wiesel (1962). Groups 1–7 represent a contralateral to ipsilateral trend with cells in group 1 totally dominated by the contralateral eye, cells in group 4 driven equally by either eye, and cells in group 7 driven exclusively by the ipsilateral eye.

preferred direction of a tectal unit were determined by the retinal locus of its receptive field, one would expect that units located in the anterior part of the left tectum with their visual receptive fields in the left half-field would prefer right-to-left movement (away from the area centralis).

3. *Ocular dominance.* Fig. 8 shows the ocular dominance distribution for units in the superior colliculus of Siamese cats as compared with normal cats. It is evident from inspection of these data that the contralateral eye is overwhelmingly dominant in driving the tectal units in the Siamese cat, whereas 87 % of all tectal units can be influenced by both eyes in normal cats. Except for the far contralateral periphery, which is not represented in the ipsilateral eye, it was always possible to hear a clear response in the neural background to stimulation of either eye in the normal cat. By

contrast, in the Siamese cat it was often impossible to elicit any background responses at all from stimulation of the ipsilateral eye, and when there was a response it tended to be distributed over a large diffuse area and showed a marked tendency to fatigue with repeated stimulation. On a few penetrations, however, over small patches of the visual field clear responses
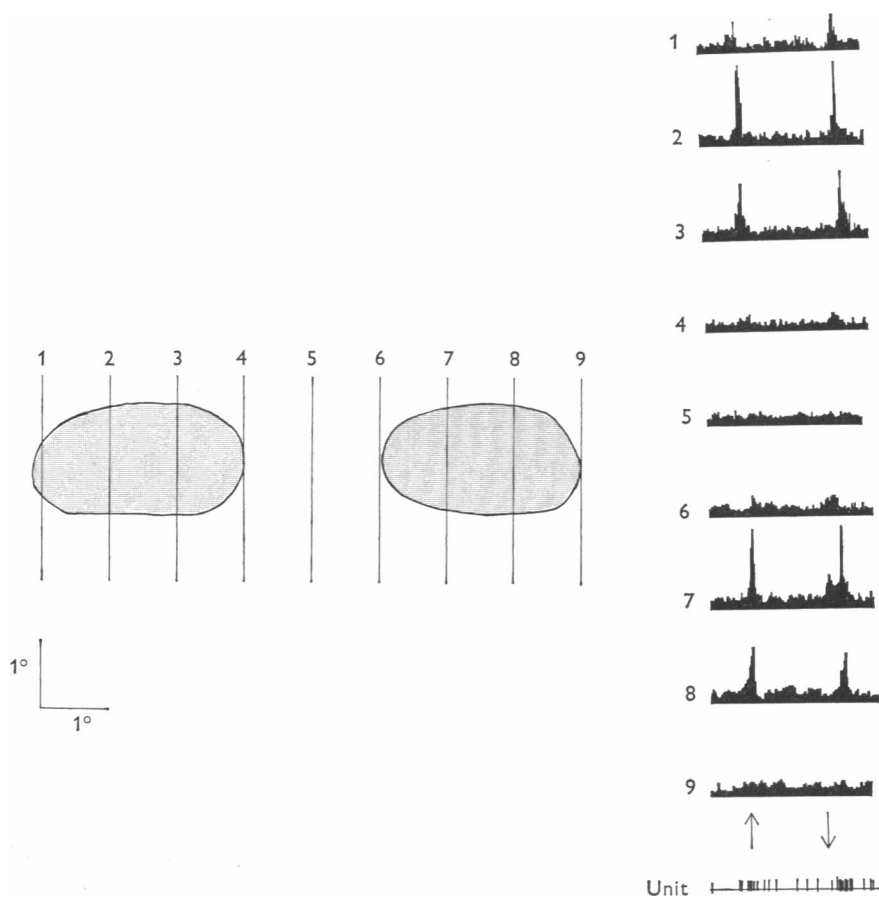

Fig. 9. The stippled area of the left-hand side of the Figure shows the locations of the two activating regions of a monocularly driven unit in the superior colliculus of a Siamese cat as plotted using a hand projector. The right-hand side of this Figure shows 9 histograms, each representing the sum of 20 sweeps of a 1/2° spot over the positions in the receptive field indicated in the left-hand side of the Figure. The arrows under histogram 9 show the direction of stimulus movement. The record of the unit firing is taken from a typical sweep through the position labelled 3. Receptive-field size: 1–1/2° × 3°, stimulus excursion: 6° in each direction, stimulus velocity: 6°/sec, stimulus cycle: 2 sec.

could be elicited by stimulating the ipsilateral eye. Most of the units influenced by the ipsilateral eye in Fig. 8 were encountered during these few penetrations.

An interesting correlation was observed between ocular dominance and directional selectivity in the Siamese cat. It was found that 96 % (27/28) of all units which had inputs from the ipsilateral eye (groups 2–7) exhibited directional selectivity, whereas only 60 % of the units driven exclusively by the contralateral eye (group 1) showed a clear directional preference in their response. No similar correlation was observed in normal cats, but only four units dominated exclusively by the contralateral eye were studied.

4. *Unusual units.* A number of cells were observed in Siamese cats which possessed unusual properties. In two penetrations, five units were observed which were driven exclusively by the contralateral eye and which had two separated receptive fields mirror symmetric about the vertical meridian. On one penetration, the neural background was centred around the area centralis. An illustration of the receptive fields of a unit encountered on this penetration is shown in Fig. 9. An examination of the histograms in Fig. 9 reveals the existence of an unresponsive area of the visual field interposed between the two receptive fields. The locations of the neural background on the other penetration are shown by the shaded areas marked 16 in Fig. 1. In this case, the size of the unresponsive zone separating the two responsive areas is about 20° Three of the units encountered in this penetration exhibited directional selectivity and the horizontal component of their preferred direction was the same in both receptive fields. They were recorded in the left superior colliculus, and in all cases they preferred left-to-right stimulus movement in both receptive fields. This resulted in a preference for movement away from the area centralis in the receptive field in the contralateral half-field and a preference for movement toward the area centralis in the receptive field in the ipsilateral half-field.

One binocularly activated unit was found in a Siamese cat in which the sizes of the receptive fields in the two eyes were grossly unequal. This unit was encountered in one of the penetrations in which a small patch of ipsilateral retina was responsive. The activating region was 1° in diameter for the ipsilateral eye and 5° by 7° for the contralateral eye. This unit was directionally selective, and in the large field it responded well to stimuli from 1 to 5° in diameter while in the small field it responded well to stimuli from $\frac{1}{4}$ to 1° in diameter. Less marked size differences were observed in several other units in Siamese cats.

Two units were found, one in a Siamese cat and one in a normal cat, which responded to stimuli moving within their receptive fields by having their firing suppressed. These units could be inhibited by movement of either a

dark or light stimulus in any direction. Flashing stimuli were less effective in reducing the discharge rate of these units.

C. Effects of visual cortex lesions

The effects of visual cortex lesions were studied for three reasons:

1. We wished to re-examine the retinotectal topography in the absence of the visual cortex.

2. In view of conflicting reports (Wickelgren & Sterling, 1969; Hoffman & Straschill, 1971 and Rosenquist & Palmer, 1971), we wished to examine the role of the visual cortex in the determination of directional selectivity in tectal units.
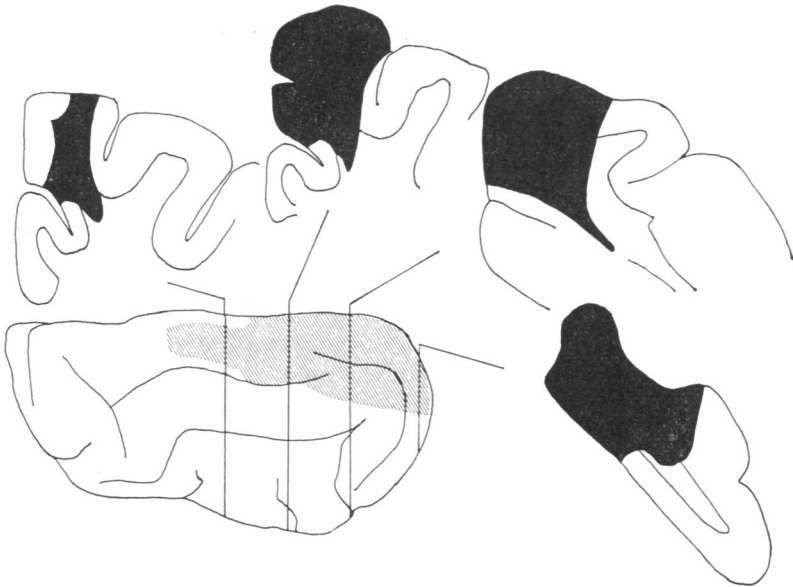

Fig. 10. The lower left of the Figure shows a schematic surface view of one hemisphere of a Siamese cat. The cross-hatched area shows the extent of a typical visual cortex lesion as seen by surface reconstruction. The rest of the Figure shows representative tracings of frontal sections taken at A 12·0 A 6·0 A–P 0, and P 6·0 in the Horsley–Clarke plane. The blackened area shows the extent of the lesion.

3. Since the retino-tectal and retino-geniculate pathways in Siamese cats show anomalous crossings, we wished to determine whether the cortico-collicular projection is strictly homolateral in the Siamese cat as it is in the normal cat (Wickelgren & Sterling, 1969; Garey, Jones & Powell, 1968).

1. *Anatomical results.* The lesions included most of areas 17, 18 and 19 but spared the Clare–Bishop area (1954). A reconstruction of a typical

lesion is shown in Fig. 10. In such cases of visual cortex lesion in Siamese cats, the Fink–Heimer method (1967) demonstrated a dense aggregation of degenerating fibres and terminals in the ipsilateral superior colliculus. As in the normal cat, this degeneration was distributed mainly in the stratum griseum superficiale and in the stratum opticum, and none appeared in the contralateral superior colliculus. Fig. 11 shows an electrode penetration through the superior colliculus ipsilateral to the visual cortex lesion and also shows the dense terminal degeneration observed in this structure after a visual cortex lesion.

2. *Electrophysiologic results*. The topographic organization was not studied systematically after cortical lesions, but units with receptive fields extending 35–40° into the ipsilateral half-field could still be found in the colliculus on the side of the visual cortex lesion. There was no indication that the representation of the visual field on the superior colliculus was changed by cortical ablations, nor was there any effect on the size of receptive fields.

Ninety units were studied in the superior colliculus ipsilateral to the visual cortex lesion in five normal cats, and seventy-two units were studied in four Siamese cats. The receptive fields of single units still consisted of a central activating region with a suppressive surround. The strength of the surround was still asymmetric in some cases. These asymmetries were found in about 10 % of all units studied after visual cortex lesions, and while the responses of these units are similar to those of directionally selective units, it is clear that no directional selectivity exists if stimulus movements are confined to the activating region of the receptive field. Units still exhibited no shape specificity and responded equally well to lines of all orientations. In contrast to the results of Wickelgren & Sterling (1969), we did not find changes in spatial summation of collicular units after visual cortex lesions. Units still responded well to stimuli smaller than the activating region, and for many units the optimum stimulus size was much smaller than the size of the activating region.

In agreement with the results of others (Rizolatti *et al.* 1970; Wickelgren & Sterling, 1969; Rosenquist & Palmer, 1971), we found that visual cortex lesions resulted in an increased responsivity to flashing spots in tectal units and in substantial changes in the ocular dominance distribution of colliculus units in normal cats. The ocular dominance distribution for cells in the colliculus ipsilateral to the visual cortex lesion in normal cats and Siamese cats is shown in Fig. 12. In the normal cat, the data shown in this Figure compared with that of Fig. 8 show a trend toward greater dominance by the contralateral eye, although almost 50 % of all units were still driven rather well by the ipsilateral eye. In Siamese cats, there appears to be no effect of the visual cortex lesion on the ocular dominance distribution. The

overwhelming superiority of the contralateral eye in driving tectal units is similar in intact and decorticate Siamese cats. Most of the units in ocular dominance groups 3–7 in Fig. 12 for Siamese cats were derived from one Siamese cat which showed several patches of the visual field from which
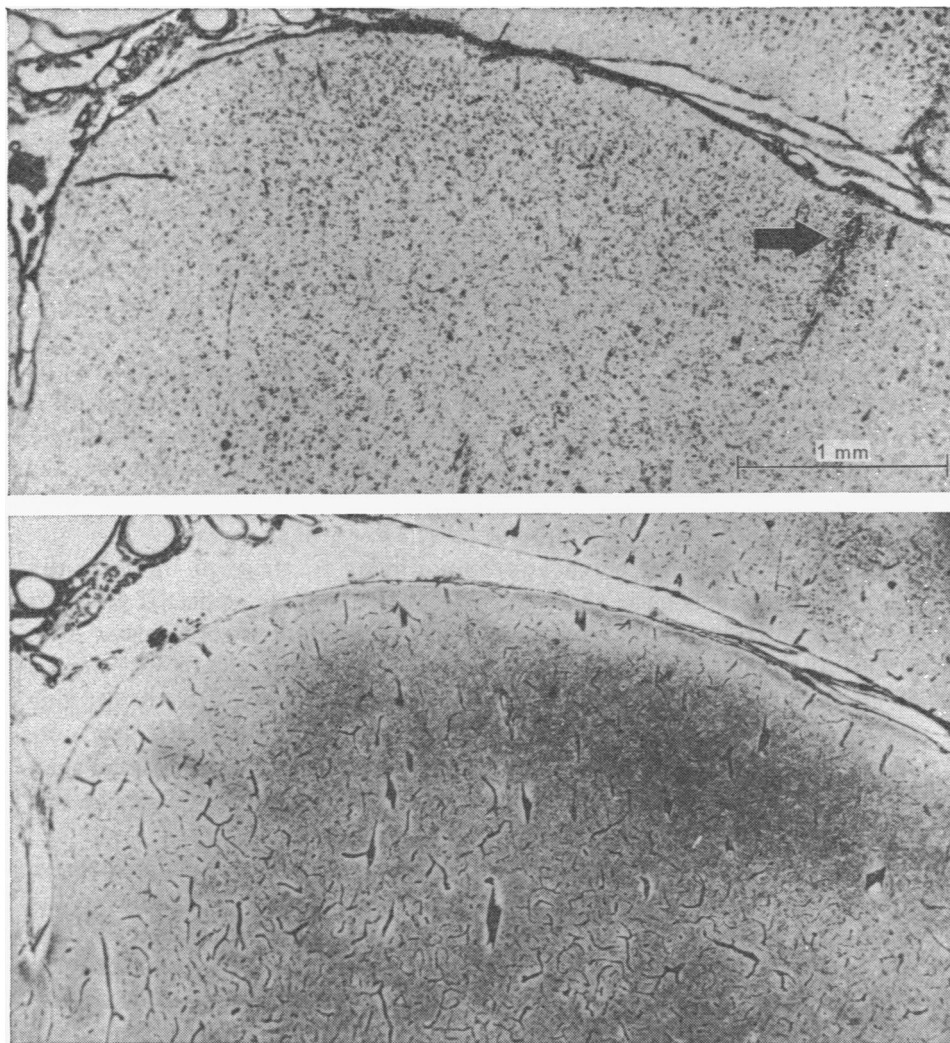

Fig. 11. Two nearby frontal sections through the right superior colliculus of a Siamese cat. The top section, stained with cresyl violet, shows an electrode track through the structure. The lower section, stained with the Fink–Heimer method, shows dense degeneration resulting from an ipsilateral visual cortex lesion 7 days earlier.

responses to stimulation of the ipsilateral eye could be elicited. In the other Siamese cats, there was only a negligible contribution from the ipsilateral eye. In most of the penetrations we were unable to elicit any response at all from the neural background by stimulating the ipsilateral eye.

Only five of the ninety units studied in the superior colliculus ipsilateral to the visual cortex lesion in normal cats exhibited directional selectivity. This finding confirms the report of Wickelgren & Sterling (1969) that visual cortex lesions abolish the directional selectivity exhibited by tectal units in the intact cat. Two units were found which gave good responses to movements in all directions when stimulated through the ipsilateral eye.
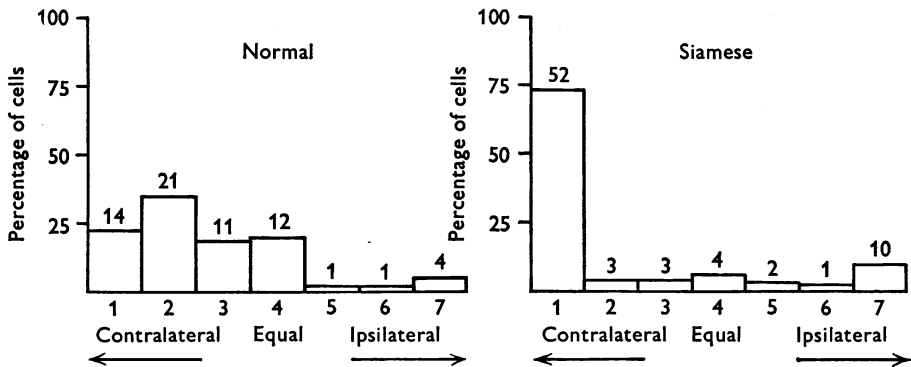

Fig. 12. The left-hand side of the Figure shows the ocular dominance distribution of sixty-four cells in the superior colliculus of normal cats following lesions of the ipsilateral visual cortex. The right hand side shows the comparable distribution for Siamese cats. As in Fig. 6, groups 1–7 represent a contralateral to ipsilateral trend in ocular dominance.

These units could not be driven when the contralateral eye was stimulated. When both eyes were stimulated simultaneously, the response to downward movement was strongly attenuated, but the response to upward movement was relatively unchanged. These two units, therefore, showed clear directional selectivity with binocular stimulation, but this was not the case when the dominant (ipsilateral) eye was stimulated alone. These units had virtually no spontaneous activity, making it impossible to observe any inhibition when only the contralateral eye was stimulated.

Three units, located at the rostral tip of the tectum (stippled area in Fig. 2) had their receptive fields located 10° into the ipsilateral half-field, were binocularly activated and showed a directional preference whose horizontal component was in the wrong direction, in the sense that the units responded best to right-to-left movement despite their being located in the left tectum. We would suggest the possibility that these units receive

a significant input from the other tectum via the intertectal commissure and that this input may be the necessary condition for producing the directional selectivity.

In Siamese cats only three of the seventy-two units studied in the tectum ipsilateral to the visual cortex lesion exhibited directional selectivity. These units, which were all encountered on the same penetration, exhibited several other interesting properties. All three units were driven by the ipsilateral eye exclusively, and in the two units which had horizontal components in their directional selectivity, their preferred direction was from left to right even though they were recorded in the right colliculus.
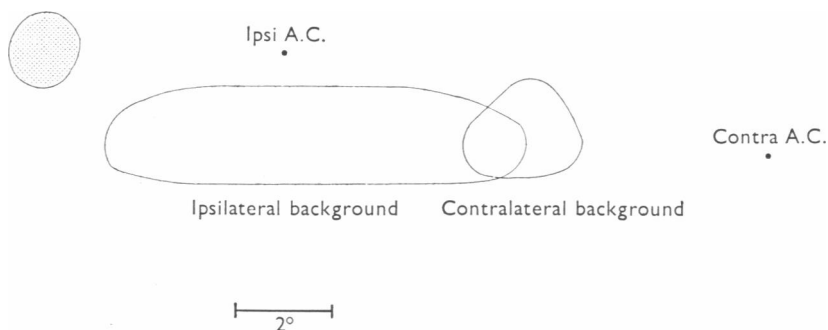

Fig. 13. The relative positions of the neural background from the two eyes on a penetration through the superior colliculus of a Siamese cat. The locations of the area centrales for the two eyes as plotted ophthalmoscopically are indicated by points labelled A.C., and the locations of the neural backgrounds from the two eyes are represented by the encircled areas. The expected location of the ipsilateral neural background is shown by the stippled area.

Also, as the electrode entered the colliculus on this penetration, the background from the ipsilateral eye was out of topographic registration with the background from the contralateral eye. The relative positions of the neural backgrounds from the two eyes are shown in Fig. 13. The distance between the area centrales on the screen corresponds to a crossed strabismus of 12 or 13°. The dotted area shows the expected area of the visual field over which the neural background from the ipsilateral eye should have responded were it in register with the background from the contralateral eye. The elongated area shows the actual location. Ophthalmoscopic examination at this time showed that the eyes had not moved. Taken together, the directional selectivity in the reverse direction, the dominance of the ipsilateral eye, and the lack of topographic registration with the contralateral background suggest that the origin of the responses of the units encountered is not directly from the retina but via the remaining

intact visual cortex or the contralateral tectum via the intertectal commissure. As our anatomic findings do not indicate a direct projection from the visual cortex to the contralateral superior colliculus, it seems likely that the contralateral tectum is contributing to the responses of these units. It should be noted that the locations of the neural backgrounds from the two eyes on this penetration are such that information about the same part of the visual world could be delivered to a single tectal locus in spite of the convergent strabismus which this cat exhibited.

<div align="center">DISCUSSION</div>

Retinotopic organization

The results reported here show that there is an abnormally large representation of the ipsilateral half-field in the superior colliculus of the Siamese cat. The abnormal projection from the ipsilateral half-field on to the anterior part of the tectum results in a displacement of the representation of the vertical meridian of the visual field on the colliculus surface. The area centralis is represented in the Siamese cat colliculus at the point on the tectal surface that, in the normal cat, would correspond to a point in the visual field about 6 to 7° contralateral to the area centralis.

It has been postulated that there is a fixed place-specificity between the retinal fibres and the tectum such that fibres from particular parts of the retina connect with cells at an appropriate point in the tectum (Sperry, 1944). This hypothesis, originally formulated for amphibians, agrees well with some data on the regeneration of retinotectal connexions (Sperry, 1963), but its validity has been called into question by more recent findings in an amphibian species (Gaze, Keating & Straznicky, 1970). It seems clear from a comparison of Siamese and normal cats that a given tectal locus may receive input from different points in the retinae in the two breeds. The results of these experiments suggest that either no 'place' to 'place' specificity of the type postulated for amphibians exists in cat retinotectal connexions or alternatively that the specification is different in the two breeds. The retinotectal map in Siamese cats is none the less a lawful one, since it appears clear that fibres from the most lateral part of the retina terminate in the most anterior part of the contralateral tectum with fibres from more medial parts of the retina terminating increasingly more posteriorly in the tectum.

The only exception to the lawfulness in the retino-tectal map was found in the units previously discussed which had two separated receptive fields in one retina. In the visual cortex of the Siamese cat, a few units have been described which also are monocularly responsive but have two separated receptive fields (Hubel & Wiesel, 1971). It is possible that cortical units like

those described by Hubel and Wiesel are necessary for the unusual properties exhibited by these collicular units. Alternatively, fibres from two separated parts of the retina may converge on a single tectal locus and confer the unusual properties of these units.

Receptive-field organization

The receptive-field properties of collicular units exhibit many similarities in Siamese and normal cats. In both breeds, collicular units are poorly responsive to stationary or flashing stimuli but respond well to a moving stimulus. Units do not respond preferentially to any particular stimulus shape. In both Siamese and normal cats, units respond well to stimuli much smaller than the activating region, and often the optimum stimulus size for eliciting responses is much smaller than the activating region of the receptive field. The receptive-field properties described above for the Siamese and normal cat are also properties of collicular units in the monkey (Cynader & Berman, 1972).

The major differences between unit properties in the two breeds appear in the distribution of preferred directions and in the degree of dominance by the contralateral eye. In the normal cat, 80 % of the units encountered can be activated equally or nearly equally by the two eyes (ocular dominance groups 3–5 in Fig. 6) and only 14 % of the units are strongly dominated by the contralateral eye. In Siamese cats, only 13 % of the units are activated equally by the two eyes and 85 % are driven entirely (or almost so) by the contralateral eye.

In penetrations through the superior colliculus of the normal cat it is almost always possible to hear responses in the neural background from stimulation of either eye, but in Siamese cats it was often impossible to hear any response at all to stimulation of the ipsilateral eye. These data are consistent with the recent anatomical work (Kalil *et al.* 1971) showing that the ipsilateral retinal projections to the colliculus are extremely sparse.

Sixty-five per cent of the units encountered in normal cats and 66 % in Siamese cats respond well to stimulus movement through the receptive field in one direction and poorly or not at all to movement in the opposite direction. In both breeds directionally selective units in the left colliculus show a strong preference for left-to-right stimulus movement and the reverse situation obtains in the right colliculus.

A consideration of the receptive-field properties in the part of the Siamese cat superior colliculus which receives input from the contralateral temporal hemiretina (the stippled area in Fig. 2) shows that the smallest receptive fields are found near the area centralis and that the size of receptive fields increases with increasing distance from the area centralis.

This is true even though the area centralis is represented at different points on the tectal surface in the two breeds. This trend is also evident in the visual cortex of the Siamese cat (Hubel & Wiesel, 1971). It seems clear that receptive-field position in the retina rather than unit position on the tectal surface determines the size of the receptive field for a given unit. By contrast, the preferred direction of tectal units appears to be determined by unit position in the tectum and not by the receptive-field location in the retina. In the anterior part of the Siamese cat colliculus (stippled area in Fig. 2), units exhibiting directional selectivity have the horizontal component of their directional selectivity toward the area centralis rather than away from it. In the units found which had two receptive fields whose location was mirror symmetric about the vertical meridian, the preferred directions in both receptive fields were the same. This resulted in directional selectivity for movement toward the area centralis for the receptive field in the ipsilateral half-field and for movement away from the area centralis for the receptive field in the contralateral half-field.

Effects of visual cortex lesions

The major effects of visual cortex lesions in normal cats are: (1) the almost complete removal of the directional selectivity normally exhibited by tectal cells; (2) an increase in units' responsivity to flashing spots and (3) a change in the ocular dominance distribution of tectal units skewing it more strongly toward the contralateral eye than in intact normal cats. In Siamese cats, the effects of visual cortex lesions on response properties of tectal units are similar to the effects in normal cats with the exception that the lesion causes no substantial change in the ocular dominance distribution in Siamese cats. The present findings in normal cats are in general agreement with those obtained by some workers (Rosenquist & Palmer, 1971; Wickelgren & Sterling, 1969), but differ from the results of others who find either no change or less pronounced changes in the directional selectivity after cortical lesions (Hoffman & Straschill, 1971; Marchiafava & Pepeu, 1966; Rizolatti *et al.* 1970). It is possible that differences in the criteria employed in classifying cells as directionally selective or unselective may account for some of the differences among the various workers. Wickelgren & Sterling defined the directional selectivity in terms of the null direction, that is the direction over which no response or inhibition could be obtained (1969). Others have defined the directional selectivity by simply comparing the strength of the responses to stimuli sweeping in opposite directions across the receptive field. We have found that units with clear null directions are virtually absent after visual cortex lesions. A consideration of the histogram in Fig. 5*B* shows that there is indeed a stronger response when the stimulus sweeps across the receptive field

in one direction than in the reverse direction, but that this difference is due to asymmetries in the strength of the suppressive surround. It seems reasonable to suggest that the units described as 'preferential' by Rizolatti *et al.* (1970) fall into this category. It should be noted, however, that the units with asymmetric surrounds are not directionally selective for stimulus movements confined entirely to the activating region of the receptive field.

Relationship to strabismus

Siamese cats often exhibit a convergent strabismus, and preliminary evidence suggests that it may be related to visual experience (Hubel & Wiesel, 1971). It is clear from both the previous anatomic and physiologic work (Guillery & Kaas, 1971; Hubel & Wiesel, 1971; Kalil *et al.* 1971) and from the results of the present study that the topographic organizations of the visual cortex and the colliculus of the Siamese cat are anomalous. There is preliminary evidence that the muscle imbalance which develops is related to the visual system abnormality since the strabismus is not present at birth and has been prevented by depriving a Siamese kitten of visual experience for the first 6 months of life (Hubel & Wiesel, 1971). It has been noted that the abnormal retinal projections would result in a reduced opportunity for binocular interaction in the Siamese cat's visual system (Kalil *et al.* 1971). This seems to be the case in both the visual cortex (Hubel & Wiesel, 1971) and the superior colliculus of the Siamese cat. In the normal cat, however, it is clear that an absence of binocular input during development is not a sufficient condition to produce a strabismus, even though it drastically reduces the number of units in the visual cortex which can be binocularly influenced (Hubel & Wiesel, 1965).

Abnormalities in the retinal projections have been produced experimentally in several ways in both amphibia and in mammals (Gaze *et al.* 1970; Jacobson, 1968; Schneider, 1970; Sperry, 1944). It has been shown that inversion of an eye in amphibia can result in inverted visuomotor reflexes. In *Xenopus*, the dorsal retina projects to the lateral part of the tectum while the ventral retina projects to the medial part. If the optic nerve is cut and the eye is inverted (after larval stage 30), the optic nerve regenerates, and the ventral retina now projects to the lateral part of the tectum while fibres from the dorsal retina terminate in the medial parts of the tectum. This results in a mismatch between the visual map and the tectal motor output. This mismatch results in inverted visuomotor reflexes for which no compensation is possible (Jacobson, 1968). Even much milder mismatches between the sensory and motor maps do not result in functional adaptation. Eye rotations as small as 15° in frogs result in permanent abnormalities in the retinotectal topography (M. Jacobson & H. V. B. Hirsch, submitted for publication). In hamsters, an abormal tectal

topography has been produced by removing one tectum at birth before the retinal fibres arrive at the tectum. This pattern of abnormal retinotectal connexions also results in mislocalization (Schneider, 1970), though this is partially compensated for by unknown mechanisms (G. Schneider, personal communication).

In the Siamese cat likewise, the pattern of retinotectal connexions is abnormal, and it is reasonable to expect that Siamese cats should mislocalize objects in space much like the hamsters and frogs in whom retinotectal connexions have been geometrically altered. Yet there is no evidence that this is the case. Siamese cats appear to be able to find visual targets in space, to avoid obstacles in their path and in general show none of the mislocalizing which would be expected. We suggest that the convergent strabismus exhibited by Siamese cats is an adaptive response to the abnormal retinal projections. In the monkey and the cat, the superior colliculus seems to play an important role in the oculomotor system. Unilateral colliculectomy results in strabismus in monkeys and bilateral colliculus lesions lead to a variety of oculomotor deficits in cats and monkeys (Denny-Brown, 1962; Sprague & Meikle, 1965). Stimulation of the colliculus in the alert monkey (Robinson, 1971) and cat (Apter, 1945) reveals the existence of an eye-movement map which is in register with the visual map on the tectal surface. In the deeper layers of the monkey colliculus, units have visual receptive fields but also fire before eye movements appropriate to bring a stimulus from the receptive field of the given unit to the fovea (Schiller & Koerner, 1971).

If one considers the Siamese cat topography in the light of these findings, it might be expected that a stimulus falling on the area centralis of the right eye of the Siamese cat should elicit a 7° eye movement to the right, assuming a normal tectal motor map. Our preliminary evidence based on tectal stimulation in the alert restrained Siamese cat supports this assumption. If one makes this assumption, it seems clear that some compensation must occur to allow a stimulus falling on the area centralis to result in no eye movement, rather than a 7° lateral eye movement. We suggest that the Siamese cat compensates by developing a convergent strabismus. For the purposes of this discussion, the lateral rectus muscle, the one which pulls the eye laterally, may be treated as a rope. We suggest that the Siamese cat compensates by introducing a 'slack' into the lateral rectus in the form of an additional length so that a 7° command from the superior colliculus motor map results in merely picking up the hypothetical 'muscle slack' rather than in an eye movement. On paralysis the increased length of the lateral rectus manifests itself as a muscle imbalance allowing each eye to rotate medialward by about 6–7° resulting in the 12–14° convergent strabismus which can be measured using ophthalmological techniques.

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