A function of the corpus callosum in the Siamese cat

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Recordings were made from 180 single cells, or cell clusters, in the Clare–Bishop area of two Siamese cats. In one cat, the corpus callosum had been sectioned prior to recording and all cells were driven by the contralateral eye exclusively. In the other recordings were made before and after callosal section. Before callosal section, most cells were binocularly driven but dominated by the contralateral eye. There were striking examples of binocular interaction and some cells could only be activated by simultaneous binocular stimulation. After callosal section, cells were driven by the contralateral eye only. The same experiment performed in a normal cat revealed no change in binocularity following section of the corpus callosum. We conclude that one of the functions of the corpus callosum in the Siamese cat is to generate binocular neurons.

Introduction

This paper addresses itself to the question of whether the corpus callosum is critical in mediating interocular interactions in the visual cortex. A direct and relatively simple way of studying this problem was to use the Siamese cat. In a remarkable series of studies, Guillery and his collaborators have shown that the retinogeniculate fibres in such cats are misrouted at the optic chiasm, giving rise to a strikingly abnormal lateral geniculate nucleus (Guillery 1969). One consequence of this is that the projections from the latter to the cortex do not allow any significant amount of binocular interaction there. In particular, cells in the part of the striate cortex representing the central 20° of the field of view on either side of the midline receive an input from the contralateral eye only (Hubel & Wiesel 1971). Elsewhere in the striate cortex, cells receive their input from either the ipsilateral or the contralateral eye, but not both (Hubel & Wiesel 1971; Kaas & Guillery 1973). In addition, in Siamese cats, most visual callosal fibres are monocular (Shatz 1977a). Although such findings might suggest a total absence of binocular neurons in the part of the visual cortex representing the central 20° of the field of view, we suspected intuitively that a significant amount of binocular interaction must occur in a visual area other than the striate cortex, especially in view of the apparently normal visual behaviour of our animals and
the absence of an obvious squint in them. We therefore undertook to explore the Clare–Bishop area (Hubel & Wiesel 1968; Spear & Bauman 1975; Palmer et al. 1978). Any binocular interaction that might occur there within the representation of the central 20° of the field of view would, necessarily, depend upon callosal connections.

**Material and methods**

Two Siamese and one normal cat were used in the present study. In addition, recordings were made from the motion area of the superior temporal sulcus (Zeki 1969, 1974) in two rhesus monkeys and from area MT (Allman & Kaas 1971) in two owl monkeys. Recordings from cats were done at the Ludwig Maximilians Universität, Munich, and those from monkeys, at University College London.

All operative and recording procedures were done under barbiturate anaesthesia. During the electrophysiological recording sessions the animals were, in addition, given a muscle relaxant (Flaxedil), and further doses of sodium pentobarbitone were given to maintain adequate anaesthetic levels.

Electrophysiological recording procedures were identical to those already described (Zeki 1974). In the cats, we took the precaution of using the same electrode (tungsten-in-glass) for all our recordings so that any sampling bias would be the same in all penetrations. No attempt was made, for the purpose of this study, to distinguish between the various subdivisions of the Clare–Bishop area (Palmer et al. 1978), but the positions of the needle tracks were histologically verified to have been in the cortex of the suprasylvian sulcus (see figure 2).

In one Siamese cat, the corpus callosum was sectioned six days before the recording experiment; in the other, it was sectioned during the experiment, both operations being carried out according to procedures already described (Zeki 1970). The corpus callosum was also sectioned in one owl monkey and in one rhesus monkey six days before the recording experiment. At the termination of the recording sessions, the animals were given a lethal overdose of barbiturate and perfused transcardially with physiological saline followed by a solution of 4% (by volume) paraformaldehyde. The brains were subsequently sectioned and stained with cresyl violet for Nissl substance, and by the Wiitanen (1969) method for degenerating fibres.

In the Siamese cats, except in two penetrations, all cells had receptive fields within 20° of the area centralis, estimated by plotting the optic disks as retinal landmarks on the screen (Fernald & Chase 1972) and reconstructing the position of the fovea (Bishop et al. 1969). Cells were classified in the conventional ocular dominance histogram for cats (Hubel & Wiesel 1962) and an ocular interaction histogram (Zeki 1979) was used to classify cells that showed summation in their response when binocularly stimulated. Six somewhat arbitrary categories were used, from one (definite but weak binocular summation) to six (cells responding only to simultaneous binocular stimulation).
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RESULTS

We began by sampling from 25 cells in a penetration through the right Clare–Bishop area of a Siamese cat with a sectioned corpus callosum, starting at the upper bank of the suprasylvian sulcus and terminating at its depth. All cells encountered were driven by the contralateral (left) eye only. In the next penetration, parallel to the first and 0.5 mm posterior to it, not only the 18 cells, but also the unresolved background in the cortex and, more strikingly, in the white matter could only be activated by stimulation of the contralateral eye (figure 1). The result was so clear cut that it seemed worth while to record from the Clare–Bishop area of the other (left) hemisphere. With the same electrode, 31 cells were sampled in one long penetration. All were driven by the contralateral (right) eye only. The ocular dominance histogram for this animal was easy to plot. All cells belonged in group 1 (figure 1).

Figure 2 shows a reconstruction of the two penetrations through the Clare–Bishop area of the right hemisphere. It illustrates the positions of the electrode tracks, the receptive field positions of cells and the cortical degeneration produced by sectioning the splenium of the corpus callosum. In confirmation of the results of Shatz (1977b), the entire upper bank and depth of the suprasylvian sulcus was occupied by degenerating fibres. Within this broad band of degeneration were two patches of heavy degeneration, surrounding a region of considerably sparser degeneration. The first group of cells (A in figure 2) were recorded from the latter region. These had their receptive fields well away from the midline, even though they were situated in a region containing degenerating fibres. This combined anatomical–physiological evidence suggested to us that, in the Clare–Bishop area of the Siamese cat, callosal fibres distribute to regions of the cortex in which parts
of the retina outside the vertical meridian are represented. Their function here would be to generate binocular neurons.

The second part of the recording was from the depth of the suprasylvian sulcus, in a region containing heavy degeneration. Cells here had their receptive field at the midline. Here, the function of the callosum would seem to be to generate binocular neurons in addition to uniting the representation of the midline (Whitteridge 1965; Hubel & Wiesel 1969; Zeki 1976; Zeki & Sandeman 1976) (figure 2, B).

![Diagram](image)

**Figure 2.** Reconstruction of two penetrations through the cortex of the suprasylvian sulcus (S.S.) in a Siamese cat with a sectioned corpus callosum. The callosal fibre degeneration is shown as dots. The receptive fields for penetration 1 only are shown; those in penetration 2 were closely similar. Receptive fields are drawn as squares for convenience. In the first part of the penetration (A) cells had receptive fields well away from the midline (---). In the second part, fields were at the midline (---).

It was important to establish the role of the corpus callosum in generating binocularity in another kind of experiment, in which neurons in the same animal could be studied for their ocular preferences before and after callosal section. Accordingly, we recorded from a second Siamese cat, with an intact corpus callosum. Three penetrations were made, still by means of the same electrode. Two were in the left hemisphere and one in the right. As in the first animal, units were sampled at intervals of 50–100 μm. Of the sixty cells sampled in the three pene-
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trations, most were found to be binocularly driven, 16% being equally well driven by either eye, the others mostly being dominated by the contralateral eye. Only 8% belonged in group 1 (figure 3a). Of the binocular neurons, no less than 60% showed some degree of binocular interaction, 7% being driven only when both eyes were simultaneously stimulated (figure 3b).

![Graphs showing ocular dominance](image)

**Figure 3.** (a) Ocular dominance histogram of cells in the Clare–Bishop area of a Siamese cat before sectioning the corpus callosum. Seven cells sampled could only be activated by simultaneous binocular stimulation, and therefore do not appear in this histogram. (b) Ocular interaction histogram for cells summing their response to binocular stimulation: 1, weak but definite summation; 6, cells responding to simultaneous binocular stimulation only. (c) Ocular dominance histogram of cells in the Clare–Bishop area of the same Siamese cat after sectioning the corpus callosum.

After these cells had been studied, the splenium of the corpus callosum was sectioned by gently retracting the left hemisphere only. After an interval of 90 min, three penetrations were made in the right hemisphere and 66 units were sampled. They were all driven by the contralateral eye exclusively, with no hint of an input from the ipsilateral eye (figure 3c). We concluded that, in the Siamese cat, the corpus callosum generates the binocularity of neurons and mediates interocular interactions in the Clare–Bishop area.

*The consequences of callosal sectioning on the binocularity of neurons in the common cat, rhesus monkey and owl monkey*

Because sectioning the corpus callosum had such a powerful effect on the binocularity of neurons in the Siamese cat, we decided to record from the same area in the common cat. Accordingly, a penetration was made in the Clare–Bishop area of the left hemisphere, and 33 units were sampled at intervals of about 50–100 μm, using the same electrode that we used in Siamese cats. Most cells were binocularly driven, and belonged to group 4 in the ocular dominance histogram.
Figure 4. Ocular dominance histogram for cells in the Clare–Bishop area of a common cat before (a) and after (b) sectioning the corpus callosum.

Figure 5. (a), (b) Ocular preference histograms for cells in area MT of an owl monkey with an intact (a) and one with a sectioned (b) corpus callosum. (c), (d) Ocular preference histograms for cells in the motion area of a rhesus monkey with a sectioned and one with an intact corpus callosum. c., Contralateral only; c.d., contralateral dominated; b., binocular; i.d., ipsilateral eye dominated; i., ipsilateral only; b.o., binocular only; m, monocular only (one eye inhibits the other).
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Following these recordings, the corpus callosum was sectioned as in the Siamese cat and two penetrations were made in the right hemisphere. The 24 units sampled did not show any significant change in binocularity compared with those of the previous penetrations; most cells still belonged to group 4 (figure 4b). The results obtained in the common cat resemble closely those obtained in two species of monkey. In the histograms of figure 5, the power of the two eyes to drive cells in the motion area of rhesus monkey superior temporal sulcus and in area MT of owl monkey is given, for animals with an intact and those with a sectioned corpus callosum. It is evident that sectioning the corpus callosum has little effect, as studied by present techniques, on the binocularity of these neurons.

Incidental observations

One of our two Siamese cats had an evident nystagmus. We thought it worth while to record the preferred directions of motion of cells in this particular animal, since most cells in the Clare–Bishop area are directionally selective (Hubel & Wiesel 1969; Spear & Bauman 1975). For comparison, we also recorded the distri-

Figure 6. The preferred directions of the directionally selective cells in (a) the right Clare–Bishop area of a Siamese cat with a sectioned corpus callosum, (b) the left Clare–Bishop area of the same cat, and (c) the left Clare–Bishop area of a normal cat.
bution of preferred directions in the Clare–Bishop area of the normal cat. Whereas in the latter this distribution was equally spread in all directions (figure 5c), without an evident bias, in the Siamese cat there appeared to be a definite bias: cells in the Clare–Bishop area of the left hemisphere were overwhelmingly responsive to motion to the right hemifield; those in the right hemisphere preferred motion to the left (figure 6). This type of observation is worthy of further study.

Discussion

The results reported in this paper show that, in the Siamese cat, binocular interaction occurs in a visual area other than the striate cortex, the Clare–Bishop area, and that this interaction is mediated by the corpus callosum. In the common cat, binocularity in the Clare–Bishop area is provided by ipsilateral cortico-cortical connections from areas 17 and 18 (Spear & Baumann 1979); the contribution of the contralateral side is negligible. In the Siamese cat, the cortical input from parts of area 17 representing the central 20° could only be monocular, because the mis-routing of fibres at the chiasm leads that part of area 17 to receive inputs from the contralateral eye exclusively, in both the Boston and Midwestern varieties (Kass & Guillery 1973). Hence any binocular interaction that occurs in regions of Siamese cat Clare–Bishop area representing the central 20° must be mediated by another route. The corpus callosum appears to fulfil that function. But, as the results show, it is also instrumental in mediating interocular interactions in regions of the Clare–Bishop area where more peripheral parts of the retina are represented (see figure 2). In theory, the binocular cells here could be established by direct ipsilateral inputs from area 17, since cells in more peripheral parts of Siamese cat area 17 receive inputs from either the ipsilateral or the contralateral eye (but not both). Presumably, once the strategy of using the corpus callosum to generate binocularity is developed, it is generalized to involve the whole area rather than just a segment of it.

In addition to generating binocular neurons, the corpus callosum appears also to mediate more subtle interocular interactions in the cortex of the Clare–Bishop area, as the presence of cells that responded to binocular stimulation only or cells that were inhibited to varying degrees by binocular stimulation shows. In this respect, it was surprising to find that sectioning the corpus callosum had no obvious effect in the common cat and in the rhesus and owl monkeys. In the latter especially, powerful binocular interactions occur even when the corpus callosum is cut (see also Zeki 1979). The functions of the corpus callosum in interocular interactions in these species obviously require the use of other techniques for their demonstration.

Finally, while answering one question about the function of the corpus callosum in the Siamese cat, the results reported here raise the question of why callosal fibres do not generate binocular neurons in area 17. Callosal fibres are found to extend throughout large parts of area 17 in the Siamese cat (Shatz 1977a) and
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visually active callosal fibres have receptive fields extending about 20° on either side of the vertical meridian (Shatz 1977b). In spite of this, the callosum appears to make no contribution to interocular interaction in area 17, either in the very cross-eyed Boston animals (Hubel & Wiesel 1971) or in the apparently non-strabismic Midwestern variety (Kaas & Guillery 1973). Why the corpus callosum should contribute to binocular interaction in one visual area and not in another is a problem that deserves study.

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References


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