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CORTICOCORTICAL PROJECTIONS OF A VISUALLY RESPONSIVE AREA IN THE CAT BRAIN

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ABSTRACT

The Clare-Bishop (CB) area bears the name of the investigators who first (1954) demonstrated a cortical area in the cat brain located along the lateral aspect of the middle suprasylvian gyrus which responded electrophysiologically to both optic nerve and striate cortex (area 17) stimulation. More recent studies of CB or the lateral suprasylvian (LS) area have supported its role in visual and/or oculomotor functions. Silver degeneration methods were undertaken to clarify some of the corticocortical connections of this cortical region. The data accumulated provides a morphological basis in support of the CB area's role in visual and/or oculomotor activities.

INTRODUCTION

Neurophysiological studies by Clare and Bishop (1954) revealed an area of the cat cerebral cortex which apparently is interrelated with the visual cortex (areas 17, 18, and 19). These investigators located a region, commonly referred to as the Clare-Bishop area (CB), along the lower one-half of the medial bank of the middle suprasylvian sulcus that was shown to respond to both striate cortex and optic nerve stimulation. The region of cortex, the CB area, is believed to be synonymous with the lateral suprasylvian area (LS) described by Heath and Jones in 1971. Recently, it has become apparent, based on electrophysiological recording studies (Palmer et al., 1978), that the LS area is much more extensive than its original description. Their investigation indicated that the LS area is made up of six mirror-symmetrical, topographically-organized representations of the visual fields having as the axes of symmetry fundi of the middle and posterior suprasylvian sulci.

Some experimental data based on silver impregnation, autoradiographic and HRP techniques have been accumulated regarding the efferent fiber connections of the CB area; however, disagreement still exists.

The cortical output of this area is both ipsilateral and contralateral. Cortical projections from the CB area primarily include efferent fibers to ipsilateral area 17, 18, and 19 and to the contralateral CB area (Heath and Jones, 1971; Jones, 1974; Maciewicz, 1974; Gilbert and Kelly, 1975; Ravizza et al., 1978).

It is thus apparent from a review of the available literature that this extra visual cortical region has not been extensively studied with respect to its neural connections. The purpose of this study was to provide more completely an anatomical basis for CB's proposed role in visual and oculomotor functions by elucidating more precisely the efferent cortical projections of this area of the cat brain.

List of Abbreviations

CB	Clare-Bishop area
LAT	lateral sulcus
RPS	posterior rhinal sulcus
SC	superior colliculus
SF	suprasylvian fringe area
SPL	splenial sulcus
SSPL	suprasplenial sulcus
III	oculomotor complex

MATERIALS AND METHODS

Seven adult cats of either sex and within a weight range of 2.0-3.5 kilograms were used in this study. Under diethyl ether anesthesia (35 mg/kg

body weight) an aseptic craniotomy was performed to expose the Clare-Bishop area along the lateral wall of the left middle suprasylvian gyrus for the placement of an unilateral cortical ablation into CB. The efferent connections of this area could then be identified by orthograde (silver impregnation) methods. Survival times used in the degeneration studies ranged from 3-7 days. It was apparent in this study that the optimum time for the simultaneous recognition of degenerating axons (Nauta and Gyax, 1954) and preterminal degeneration (Fink and Heimer, 1967) was seven days. After seven days, each animal was sacrificed by deep Nembutal (heparinized) anesthesia, given intravenously. Subsequently, the heart was exposed and the cat was perfused transcardially with room temperature physiological saline wash followed by 10% formalin. Following careful removal, the brains were immediately placed in cold 10% formalin for 24 hours and then maintained in the same fixative at room temperature for at least six weeks. Each brain was then photographed, blocked, and placed in 30% sucrose/formalin until it sank. Coronal serial sections of 50 μ m and 25 μ m were cut, using a freezing microtome, and collected in a compartmentalized plastic tray containing 10% formalin. Serial sections were then stained with the cresyl violet (50 μ m sections) and silver (25 μ m sections). Trajectories and the distribution of degenerated axons and preterminal degeneration were charted in projection drawings of appropriate sections by using light and/or darkfield microscopy. Cortical designations were based on Heath and Jones (1971) and Reinoso-Suarez (1961), while subcortical landmarks were localized according to Rioch (1929), Snider and Niemer (1961) and Berman (1968).

RESULTS

The selective silver impregnation techniques of Nauta and Gyax (1954) and Fink and Heimer (1967) were employed to study the efferent cortical connections. The Nauta method was especially useful in defining the origin, course and trajectories of fiber degeneration resulting from unilateral cortical ablations, while the Fink and Heimer method was essential for visualization of preterminal and terminal degeneration.

In each of the seven cases, fiber degeneration entered the sub-cortical white matter and was followed from the lesion site in one of three primary trajectories: 1) to the ipsilateral cortex as association fibers, 2) commissural fibers to the contralateral hemisphere by way of the body of the corpus callosum, 3) descending projections primarily through the capsules (internal, external, extreme) toward ipsilateral sub-cortical structures (Fig. 1).

Ipsilateral preterminal degeneration was observed in cortical areas 5, 6, 7, 17, 18, 19, 20, 21, the suprasylvian fringe region and the posterior suprasylvian gyrus (a part of area 21). Contralaterally, the homologue of the lesion site exhibited degeneration.

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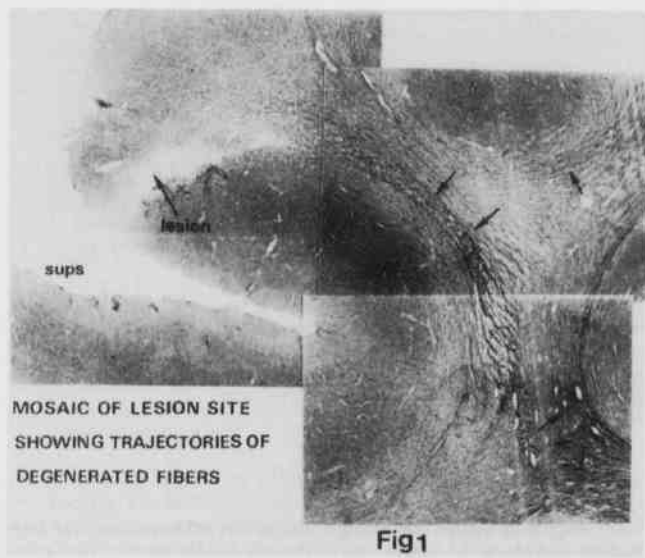


Figure 1. Photograph of Nauta section of cat brain showing fiber trajectories from the lesion site. Notice (at arrows) degenerated fiber in route to cortex, corpus callosum and subcortical areas.

The most rostral cortical connections from the CB area appear to be with areas 5 and 6. The degeneration appeared somewhat heavier in the lateral portion of area 5 in its caudal extent. Caudal progression through the ipsilateral cortex revealed preterminal degeneration in area 7. Finally, in the suprasylvian gyrus heavier degeneration, as would be expected, was encountered in the vicinity of the lesion site.

A caudal progression through the ipsilateral hemisphere revealed a connection between the CB area and areas 17, 18, 19, 20, 21, the suprasylvian fringe area and the posterior suprasylvian gyrus. The amount and rostrocaudal distribution of the degeneration in those areas varied with the size and rostrocaudal extent of the lesion. Generally, a larger and more rostral ablation produced, as would be anticipated, heavier degeneration in the more rostral portions of these cortical areas and vice versa. In particular, preterminal degeneration was most pronounced in the caudal portions of areas 17 and 19. The heaviest degeneration in area 19 was seen as the fibers left the white matter in a lateral direction (Fig. 2) to terminate throughout laminae III-IV. Degeneration also was seen in lamina I, although lamina II was almost free of degenerating debris. Light to moderate degeneration was found in area 17 involving mainly lamina III-IV but also lamina I. The projections to areas 19 and 17, were also visualized with autoradiographic methods and orthograde HRP transport (Fig. 3), evidence from which supported the observation of termination of CB efferents in laminae III-IV and I in areas 19 and 17. Similarly, area 18 was observed to receive efferents from CB area. These fibers primarily terminated in lamina III-VI of area 18, although there was, again, some degeneration in lamina I (Fig. 2). Finally, within the ipsilateral cortex, moderate degeneration was apparent in the suprasylvian fringe region, areas 20 and 21, and the posterior suprasylvian gyrus.

Preterminal degeneration was observed in the contralateral CB area homologous to the lesion, with termination located primarily in laminae III-VI (Fig. 2). The main focus of degeneration was along the medial wall of the middle suprasylvian sulcus with some extension into the depth of the sulcus. The fiber degeneration reached this destination by traversing the body of the corpus callosum.

DISCUSSION

The results of the present study provide an anatomical basis which suggests that the Clare-Bishop or lateral suprasylvian area is a cortical

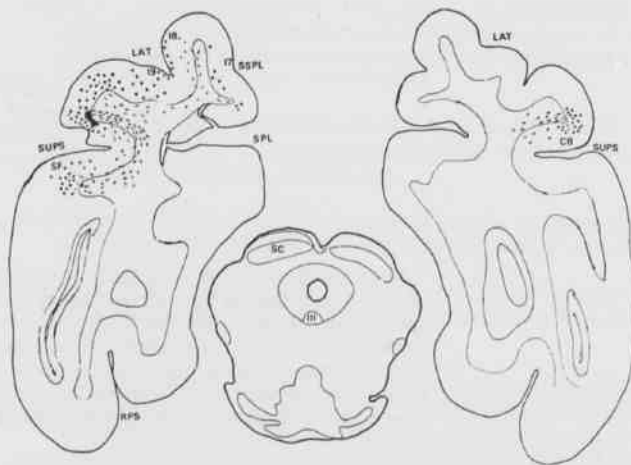


Figure 2. Charting of a Nauta section showing degeneration in ipsilateral visual cortices (areas 17, 18, and 19) and contralateral CB area.

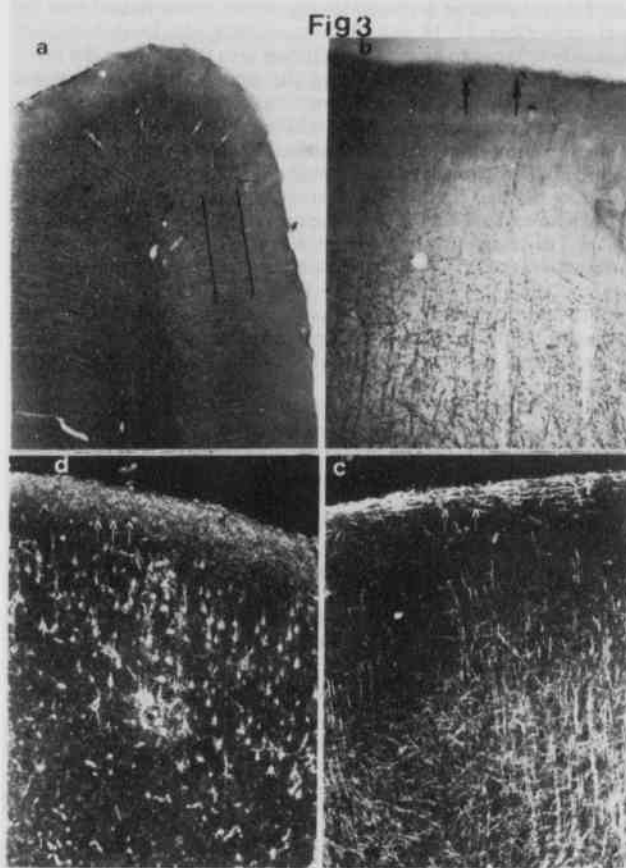


Figure 3. a. Low power photograph of Nauta section showing degeneration in area 17. Notice band of degeneration in laminae III-IV (between lines). b. High power view of above section. Notice degeneration in lamina I (at arrows). c. Darkfield Nauta section showing degeneration in lamina I (at arrows). d. High power photograph of HRP section showing labelled cells as well as orthogradely transported enzyme to area 17. Notice orthograde transport to lamina I (arrows).

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region in the cat brain primarily associated with visual mechanisms. This concept can be adduced from the information provided in this investigation which showed that the CB entertains connections with cortical regions classically known to be involved in visual functions. These connections include efferent projections from CB to other visual cortical areas (17, 18, and 19) and the frontal eye field (FEF).

The cat visual cortex (areas 17, 18, and 19) share the heaviest cortical input from the Clare-Bishop area. Data accumulated from the silver cases showed that the CB projects to laminae III-IV of these areas, with the heaviest degeneration being observed in laminae III-IV and some involvement of lamina I. Orthogradely transported HRP confirmed the lamina I termination in the other cortical visual areas after a HRP-gel placement in CB (Fig. 2d). Recently, Bullier et al. (1984), using retrograde fluorescent techniques, indicated that the CB cells projecting to areas 18 and 19 are found in laminae I, III, V, and VI.

The projection from CB to lamina I of area 17 is further supported by autoradiographic information presented by Lund et al. (1979) indicating that laminae I and VI of area 17 contain terminal fields after an injection of tritiated proline into the CB area.

Additional morphological support for a possible role of the CB area in visual activities comes from information showing its connectivity with the frontal eye field (FEF) of the cat. In agreement with Heath and Jones (1971) this study showed, with silver impregnation data, that the CB area projects to most of area 6 including that portion considered to be part of FEF.

In summary, the results from the present investigation provide an anatomical substratum for a possible role of the Clare-Bishop area in visual and/or oculomotor functions based on the fact that this cortical region entertains connections with areas distinctly concerned were visual activities, including areas 17, 18, and 19 and the frontal eye field (FEF). Further investigations are needed in order to clarify CB's efferent projections to subcortical visual structures.

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