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Retino-Collicular Projection in the Rabbit

by

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The topographic representation of the rabbit's retina on the cortical and sub-cortical visual centres has been demonstrated by histological methods. Brouwer and Zeeman (1926) made localised retinal lesions and succeeded in demonstrating a consistent topographical projection of the retinal quadrants on the lateral geniculate nucleus and superior colliculus, while Putnam and Putnam (1926) studying the effect of localised cortical lesions produced evidence of a fixed and definite anatomic projection on to the lateral geniculate nucleus. More recently electrophysiological methods have been used to confirm and extend these findings. Thompson, Woolsey and Talbot (1950) using a small photic stimulus determined the retinal representation on the exposed surface of the rabbit's cortex; Hamdi and Whitteridge (1953) established the projection of the meridians of the visual field on the collicular surface, while Choudhury and Whitteridge (1965) have described the visual field projection on the rabbit's geniculate nucleus. The experiments described below were designed to map the visual field of the rabbit on the collicular surface in sufficient detail to enable a quantitative description of the visual field projection to be made.

METHODS

Rabbits were anaesthetized with chloralose 100 mgm./kg., and urethane 1 mgm./kgm given intravenously and fitted in a stereo-taxic head-holder specially designed to achieve rigid head fixation and yet allow a clear field of vision to the laterally placed eye. The head-holder was so arranged as to keep the eye at the centre of a perimeter with the sagittal suture of the skull at right angles to a horizontal axis passing between the eye and the reference point of the perimeter. The stereo-taxic co-ordinates of Sawyer, Everett and Green (1954) were used to reach the colliculus and the responses evoked by a small spot of light in the visual field were recorded through stainless steel needle microelectrodes of tip diameter 2-10μ connected through a cathode-follower to a conventional RC amplifier. These responses were displayed on a cathode-ray tube and monitored through an audio-amplifier and speaker. The visual field was searched using a neon flash of short duration and more accurate localization made with a circular spot of light 1 mm. in diameter on the perimeter arm subtending an angle of 10' at the eye. The position of the stimulus spot in the visual field was defined using a system of spherical polar co-ordinates with a horizontal axis of reference and in each experiment several of these field localizations were obtained corresponding to the different electrode placements on the colliculus. At the end of each experiment the projection of the myelinated nerve fibre band of the retina on the perimeter was determined using an indirect binocular ophthalmoscope. The animal was then killed and perfused through the aorta with 10% buffered formol-saline and serial sections of the brain made to check on the accuracy of the electrode placements.

RESULTS

The collicular surface is devoted to the representation of a relatively narrow band shaped area of visual field. Along the horizontal axis of the field the band extends for nearly 180°, but projects further peripherally into the nasal field than into the temporal. This horizontal axis is represented along the antero-posterior diameter of the collicular surface, the nasal field being projected to the anterior end of the colliculus. In the vertical axis of the field the band is of near uniform width, the greater portion of it lying below the horizontal field axis. This narrow extent of field is represented across the transverse diameter of the colliculus, the limited upper field projecting medially, the larger lower field laterally.

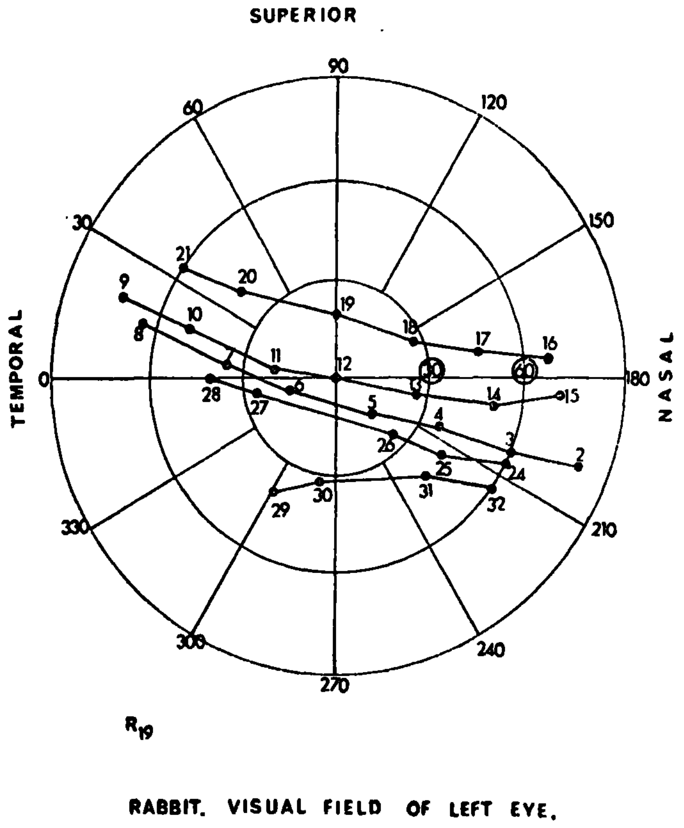

FIG. 1a. Visual field localization of the surface responses as recorded on a spherical polar co-ordinate perimeter. The successive responses, from an antero-posterior row of numbered electrode placements on the dorsal surface of the colliculus, are joined by lines. The axis of the perimeter is horizontal, passes through the rabbit's eye and is at right angles to the axis of the rabbit's head. Due to the rotation of the eye, the field band axis is parallel to the 15°-0-195° meridian.

In the experimental animal whose head is fitted in the head holder, the long axis of the visual field does not coincide with the true horizontal meridian, but is tilted down in the nasal field through 20°—30°. The projection maps (Fig. 1) however, show the long axis of this tilted band lying parallel to the perimetric projection of the myelinated nerve fibre band. In the intact and unanaesthetized animal, however, direct ophthalmoscopic examination shows that the eye is so held that the myelinated and is truly horizontal; it is thus inferred that the visual field band of the intact rabbit is also a horizontal one.

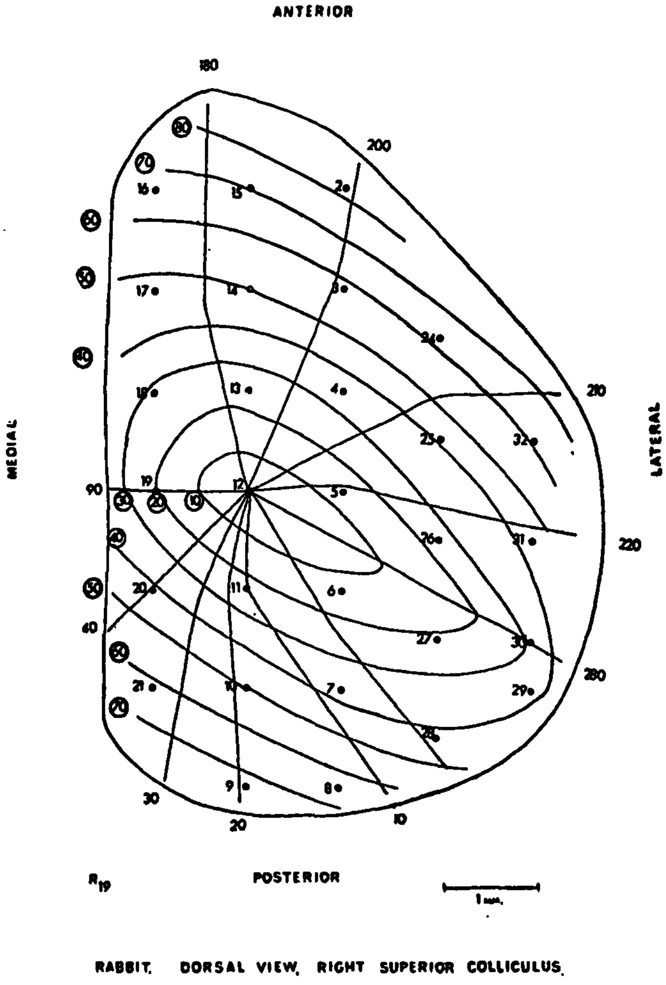

FIG. 1b. Visual field localization of the surface responses as recorded on a spherical polar co-ordinate perimeter. The successive respons, from an antero-posterior row of numbered electrode placements on the dorsal surface of the colliculus, are joined by lines. The axis of the perimeter is horizontal passes through the rabbit's eye and is at right angles to the axis of the rabbit's head. Due to the rotation of the eye, the field band axis is parallel to the 15°-0-195° meridian.

No localized responses could be obtained from the collicular surface for stimulus positions lying outside this limited extent of field. If such areas do have a collicular representation, they must then be on a very narrow rim of collicular substance situated at its extreme periphery. The retinal convergence to such an area would then be so great as to preclude the likelihood of localised field responses.

The representation of a band shaped area of field on the colliculus distorts the projection of the circles of equi-angular deviation of the field into ellipses on the collicular surface. Magnification factors, i.e. the linear extent of surface devoted to the representation of 1° of visual field (Daniel and Whitteridge, 1961), have been used to describe quantitatively the extent of this distortion. Thus for points along the horizontal axis the magnification factor is almost uniform at 0.035 mm./degree, whereas along the vertical axis they are nearly 0.16 mm./degree at the centre, falling off to 0.022 mm./degree for field positions 30° above and below the field centre. (Fig. 2).

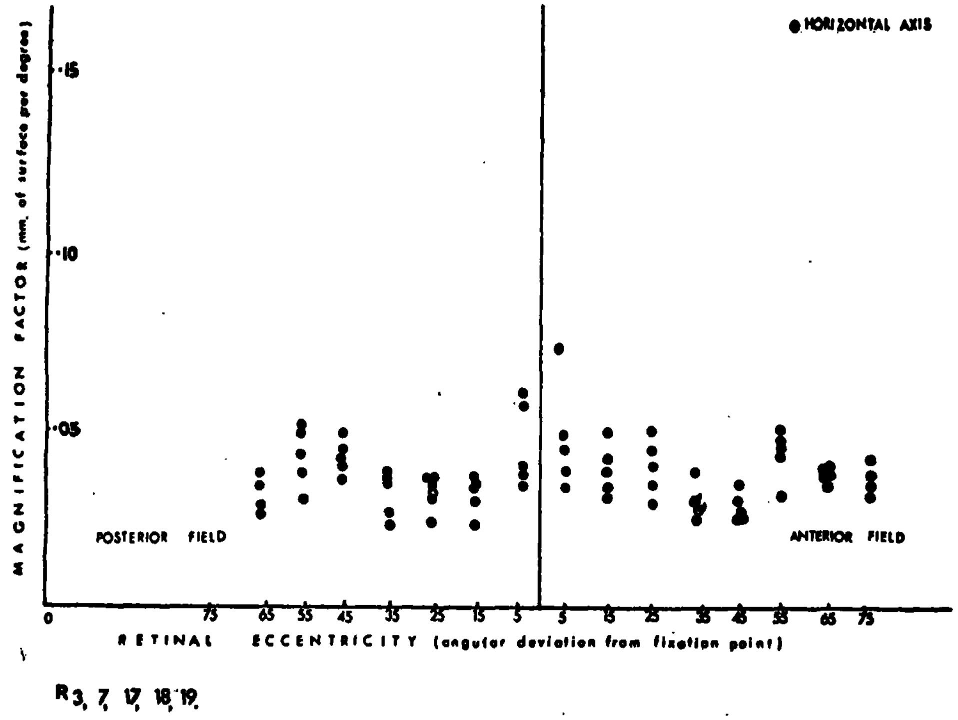

Fig. 2a. Magnification factors from five experiments along the horizontal and vertical axes of the visual field.

DISCUSSION

In inframammalian vertebrates the optic tectum receives the bulk of the optic tract, whereas in the mammalian forms the tract is distributed partly to the tectum and colliculus, and partly to the lateral geniculate nucleus and cortex. In the lower mammals, the insectivores and rodents, the fibres terminating in the cortex do not exceed the collicular ones,

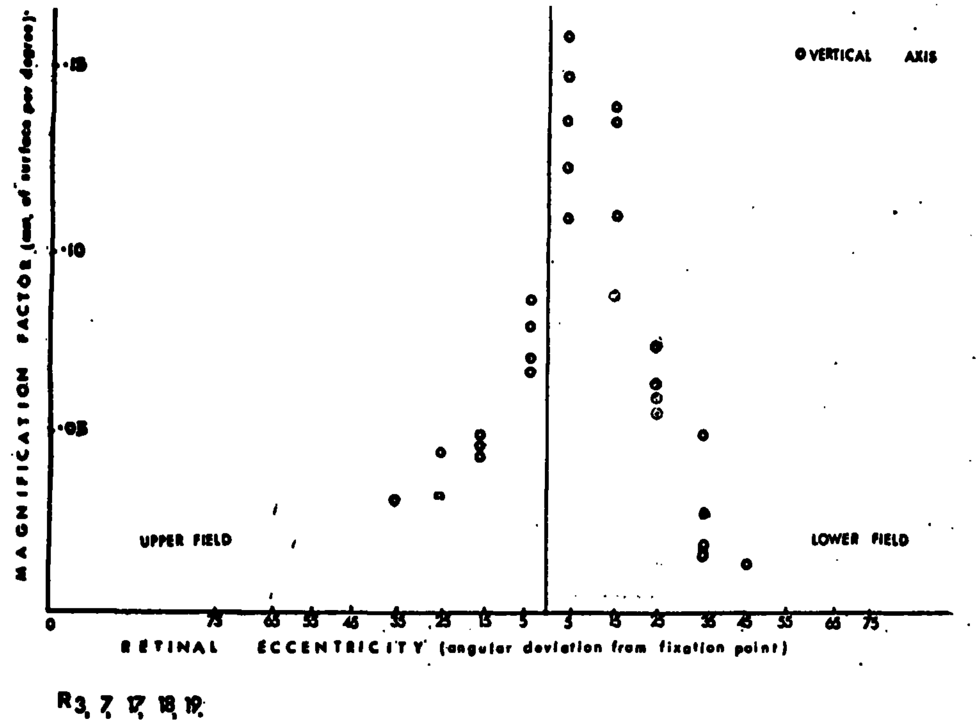

FIG. 2b. Magnification factors from five experiments along the horizontal and vertical axes of the visual field.

whereas in the higher mammals and primates the colliculus receives only a small fraction of the tract (Altman and Malis, 1962). These features indicate that as evolution proceeds sensory functions assume greater and greater preponderance and although the reflex aspects of vision are retained in the colliculus, eventually in the higher vertebrates the epicritic visual functions are transmitted through the thalamus in an ever increasing degree to the cortex. This translation from a reflex to a highly integrative level allows the development of the central nervous system to advance from mass reflex reactions to more restricted but complicated patterns of behaviour (Duke-Elder, 1958).

There is, however, little experimental evidence at present regarding the functional differentiation of the phylogenetically older collicular and the more recent geniculo-cortical visual systems. The study of conduction velocities in the optic nerve and tract of the cat in relation to fibre size have led to very divergent views with respect to the segregation of fibre groups. Bishop, Jeremy and Lance (1953) described two well segregated groups of fibres, Chang and Kaada (1950), and Lennox (1958) claim segregation into three groups, while Bishop and Clare (1955) claim four groups. The largest fibres 8-12 microns in diameter conducting at 40-50 m./sec. were destined for the geniculate nucleus, while the two groups of thinner fibres were less than 4 microns in diameter conducted at less than 12 m./sec. and terminated in the tecto-collicular regions. Hayhow (1958), however, could find no evidence for such a segregation and Le Gros Clark (1962) denies that such a segregation according to fibre size or function or locus of destination exists. The origin of the collicular afferents remains as much in doubt. Barris, Ingram and Ranson (1935), and O'Leary (1940) were of opinion that the collicular afferents were thin collateral branches of thicker tract fibres passing to the geniculate nucleus, whereas Cajal (1911) and Bishop and Clare (1955) believed that the colliculus was innervated by a special variety of retinal afferents that constituted a structural and functional entity.

Evidence for a functional differentiation between the collicular and geniculo-cortical pathways has been suggested by Altman and Malis (1962). Evoked potentials from the colliculus in response to a flash of light or electrical stimulation of the optic nerve require a higher stimulus threshold and exhibit significantly longer latencies than cortical responses obtained under the same conditions.

In view of these differences, the patterns of retino-topic projections on the colliculus in contrast to that on the geniculo-cortical system assumes a special significance. In the cat the projections on the lateral geniculate nucleus, (Seneviratne, 1963), and the primary visual cortex (Bilge, Seneviratne and Whitteridge, 1963) show an identical pattern of distortion, the lower quadrant of the hemi-field being represented on an area much larger than that devoted to the upper quadrant. Apter's (1945) data for the collicular projection, however, is not sufficiently precise to allow for a direct quantitative comparison between the cat's collicular and geniculo-cortical projections.

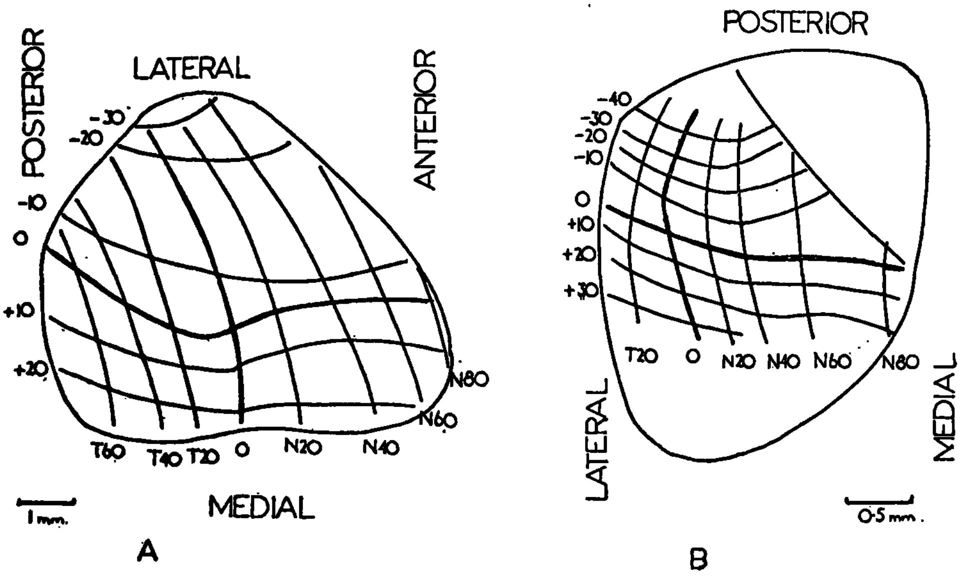

FIG. 3. A. Visual projection map on the surface of the colliculus in parallel co-ordinates as obtained by converting the experimental data of Fig. 1. In the construction of this map the 15°-0-195° meridian which passes through the long axis of the visual field band is chosen as the horizontal meridian, and the 105°-0-285° as the vertical. '+' indicates meridians of the upper field, '–' meridians of the lower field. N and T indicate nasal and temporal fields respectively.

B. Visual projection map on the surface of the lateral geniculate nucleus of the rabbit (after Choudhury and Whitteridge, 1965).

Choudhury and Whitteridge's (1965) study of the retinal projection on the geniculate of the rabbit enables a direct comparison to be made between the collicular and geniculate projections, (Fig. 3). The geniculate projection shows a magnification only in the part representing the anterior nasal field, i.e. the area of the rabbit's limited field of frontal binocular vision, whereas the collicular projection shows a marked increase in the areas representing the vertical plane extending from the nasal to the temporal fields. These morphological differences could correspond to the functional needs of the rabbit; geniculo-cortical areas of high resolution subserving the binocular anterior nasal field, and the collicular band of high resolution along the whole narrow extent of the vertical plane compensating for its limited extent. These results would accord well with de Kleijn's (1921) demonstration that the rabbit can accurately stabilize the horizontal meridian of its eye while the head is moved through 100° in a fore and aft plane, i.e. rotated about a bi-temporal axis. It is hence likely that the colliculus is concerned mainly with the integration of the vestibulo-ocular reflex, enabling the rabbit to keep within its narrow visual field objects of interest to it, while the phylogenetically newer geniculo-cortical pathway analyses in detail, the object of its concern.

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