J. Physiol. (1976), **256**, *pp.* 497–508
With 7 text-figures
Printed in Great Britain

THE CORTICAL VISUAL AREAS OF THE SHEEP

BY P. G. H. CLARKE AND D. WHITTERIDGE

From the University Laboratory of Physiology, Parks Road, Oxford OX1 3PT

(*Received 24 January 1975*)

SUMMARY

1. A stereotaxic method for the sheep brain is described.

2. At its widest part the primary visual area (Visual I) of each hemisphere extends approximately 20 mm anteroposteriorly and, when unfolded, approximately 35 mm from side to side. It occupies both walls of the lateral sulcus, and extends medially to the medial wall of the hemisphere and to the depth of the ectolateral sulcus laterally.

3. The most lateral part of the primary visual area includes 10–15° of the ipsilateral field; the contralateral field is represented to 135° from the mid line.

4. Visual II also includes a strip of ipsilateral representation on its medial edge and extends to the supra-sylvian sulcus on the lateral surface of the brain. The furthest lateral representation recorded was 130° lateral.

5. Most of both visual areas is concerned with the area centralis and the visual streak. The remainder of the retina has very little cortical representation.

6. Most cells in Visual I are simple with orientational and sometimes directional sensitivity. Some complex and hypercomplex cells have been seen in Visual I, and these predominate in Visual II. Receptive field sizes from 0·25 to 10° were found. Within 15° of the vertical meridian, binocular cells are common in both Visual I and II.

INTRODUCTION

The visual cortex of the sheep has been identified cytoarchitectonically by Rose (1942), and in rough outline by electrophysiological methods by Woolsey & Fairman (1946). We have set out to map it and to identify its subdivisions partly because the wide interocular distance of the sheep, 11–12 cm, makes it very suitable for the study of stereoscopic mechanisms. It has an area centralis as well as a streak in its retina (Hughes & Whitteridge, 1973) and has 20–30° of binocular overlap each side of the

vertical mid line. Although it is believed neither to accommodate nor to converge, its rich supply of muscle spindles in the extraocular muscles (Cooper, Daniel & Whitteridge, 1955; Harker, 1972) makes it very suitable for the future investigation of controlled eye movement.

We have tried to map the cortical visual areas and to relate them to the retinal ganglion cell distribution. The connexions of the lateral geniculate nucleus to the retina and the cortex have also been studied (P. G. H. Clarke, I. M. L. Donaldson, M. Glickstein & D. Whitteridge, in preparation).

We have investigated the properties of visual cortical neurones and compared them with those of cat and monkey.

METHODS

Welsh sheep of 20–50 kg were used. Black-face or Black-face crosses were avoided in case they had a genetic abnormality similar to that of Siamese cats (Guillery, 1970). The sheep were anaesthetized by I.V. pentobarbitone 30 mg/kg given slowly and varied according to the state of the corneal reflex. Subsequent doses of 100 mg were given during the morning and the rate of utilization was determined. Pentobarbitone was then given at this rate by infusion pump throughout the rest of the experiment (usually at 6–7 mg/kg per hour). If necessary, halothane ½% in O_2 was given during the initial operation only. Later, a mixture of 65% N_2O and 35% O_2 was added. After about 3–5 hr of preparation, tubocurarine chloride 0·5 mg/kg per hour and gallamine triethiodide 15 mg/kg per hour were given as paralysant in a 0·9% saline drip to give about 125 ml. fluid/hr.

Arterial pressure was recorded continuously and end-tidal CO_2 was determined by an infra-red CO_2 meter when the animal was being ventilated by a Starling Ideal pump. End-tidal CO_2 was kept between 5 and 6%. Body temperature was kept at about 39° C. An increase up to 41° C, liable to occur when unshorn sheep are brought into a warm building, could be controlled by passing cold air through the nose.

The methods of head fixation used for the sheep are in principle the same as those for stereotaxic techniques in the cat and monkey. We have used ear bars inserted into the external auditory meatus, usually without slitting it. The lower edge of the orbit was adjusted to the same horizontal plane as the ear bars by an insulated mouth bar which supported the hard palate. The head was then fixed by two screwed bars which pressed on the maxillae above the back teeth.

The co-ordinates used are relative to the interaural plane, the mid line and the basal plane in the usual way. We have made our own atlases for the cortex, but for the mid-brain we have referred to the atlas by Richard (1967) of a different breed of sheep, the 'Préalpes du Sud'.

If necessary, the horns were cut off close to the skull. The skull was opened for about 2 cm^2 over the visual cortex. The dura was removed and the hole closed with 2½% agar in normal saline. If the skull had been laid bare and dried for about 1 cm all round the hole and the agar was 10–20 mm thick this gave satisfactory immobilization. Electrodes were tungsten wires sharpened electrolytically to tips of about 1 μM, insulated with Bakelite varnish and with impedances of 1–5 MΩ at 1000 Hz. In some experiments, slightly lower impedances were used to make sure of getting some response every 200 μM.

The pupils were dilated with 1% atropine and contact lenses were applied.

Visual stimuli were usually hand-held targets moved against a screen about 100 cm from the eyes.

In some experiments, mechanically driven targets, light bars of adjustable orientation, were used.

Receptive fields were plotted on a tangent screen 90–114 cm in front of the sheep's eyes and the position of the vertical retinal artery and the blind spot were plotted on Perspex extensions using a Fison indirect ophthalmoscope without the +20D lens. The main blood vessels and the blind spot could be accurately located. The point of emergence of the artery from the blind spot could be plotted reproducibly to 0·5° or better. Subsequently, the vertical meridian for each eye was determined using the method of Joshua & Bishop (1970). The angular distance between the vertical meridian and the projection of the blind spot was measured. In adults this averaged 48°, but it was found to decrease linearly with body weight; the regression equation of angular distance (y) on body weight (x kg) was $y = 55{\cdot}4 - 0{\cdot}29x$, giving $r = -0{\cdot}69$, $P < 0{\cdot}1\%$.

At the end of the experiment, after 17–33 hr, the animal was killed by an overdose of pentobarbitone and perfused with saline and formalin while still in the stereotaxic machine. Marking needles were introduced and left in the brain during fixation. Some hours later the brain was removed, left in neutral buffered formalin 10% for some days and blocked either frozen or in celloidin. Frozen sections take less time to prepare and shrink less, but it is so difficult to get good sections of a structure as large as the posterior third of the brain, that embedding in celloidin was preferred in later experiments. Shrinkage was measured from the spacing of needle tracks. Sections were drawn or photographed at ×10 or ×15 and the data marked on the reconstructed electrode tracks. Depths were measured from electrolytic lesions made by passing 10 μA for 10 sec through the electrode as anode at known depths.

Co-ordinates

'Spherical polar co-ordinates with axis vertical' were used (Bishop, Kozak & Vakkur, 1962). The co-ordinate system was centred on the area centralis. The first co-ordinate denotes the number of degrees contralateral from the vertical meridian through the area centralis, and the second denotes the number of degrees below the horizontal. Hence, ipsilateral and high field positions have negative co-ordinates.

RESULTS

Anatomy

The best account of the sulci of the sheep's brain is that given by Krueg (1878) and Landacre (1930) and used by Rose (1942) in his study of the cytoarchitectonics of the sheep cortex. Our findings agree closely with those of Landacre, and we have used his terminology rather than that of Barkholder (1904, quoted by Landacre) (Fig. 1).

According to Kappers (1921), the lateral sulcus is the deepest and most conspicuous sulcus in the posterior part of the sheep's brain, and it is readily identifiable in transverse sections. In our experience it always contains visual cortex representing the contralateral field from 6 to 60° lateral with points 25–30° lateral occupying the depth of the sulcus. Medially, the visual field from 60 to 140° extends into the small and variable entolateral sulcus and for 2 to 3 mm on to the medial wall of the

hemisphere. Laterally, the representation extends on to the gyrus ectolateralis with 0° in the middle convexity of the gyrus. So far, receptive fields have been described by their lateral co-ordinate as one follows the representation of the horizontal meridian, as, owing to the large ganglion cell density in the retinal streak, most of the cortical representation is concerned with the horizontal meridian and the 10° above and below it. The lower part of the streak is represented anteriorly and the upper part posteriorly, and, apart from an anterior extension to deal with the anterior lower field (which has an increased ganglion cell density in the upper temporal retina), there is very little other cortical representation.

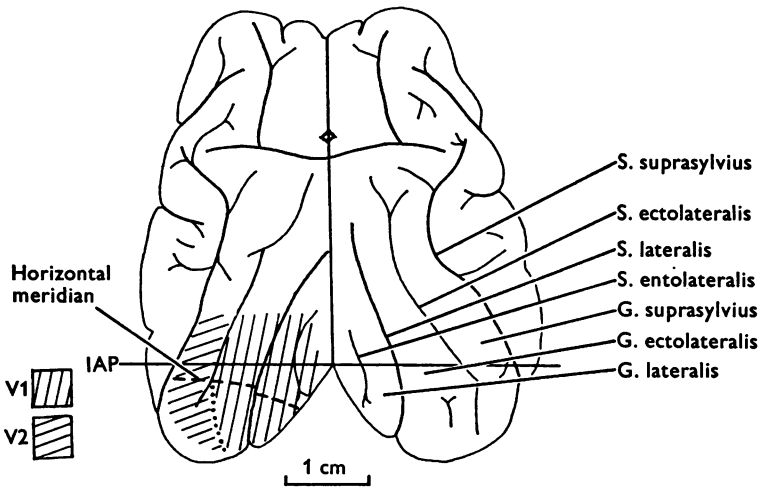

Fig. 1. Sheep's cortex from above. Sulci from Landacre (1930). The horizontal meridian runs medially and a little posteriorly. Only the posterior part of V1 extends about 12 mm on to the medial surface of the hemisphere. IAP, inter-aural plane.

The whole of the visual map extends about 20 mm anteroposteriorly on the surface and has a total mediolateral extent, including the buried cortex, of about 35 mm (Figs. 1 and 2).

One unexpected finding was that about 10–15° of the ipsilateral visual field was represented binocularly immediately lateral to the representation of the vertical meridian, and extending to the bottom of the ectolateral sulcus. The field positions then returned to the mid line and, in the ectolateral gyrus, there was a clear mirror-image representation of the field which extended down the lateral cortical surface as far as the suprasylvian sulcus. The fields furthest out which have been found so far are about 30° contralateral. This mirror-image representation is, by the usual

criteria, Visual II (Fig. 3). So far no Visual III has been identified, but few experiments have been devoted to this point. Some visual responses have been obtained from deep layers of cortex which open into the suprasylvian sulcus. These could be either Visual III or an area corresponding to the Clare–Bishop area of the cat.

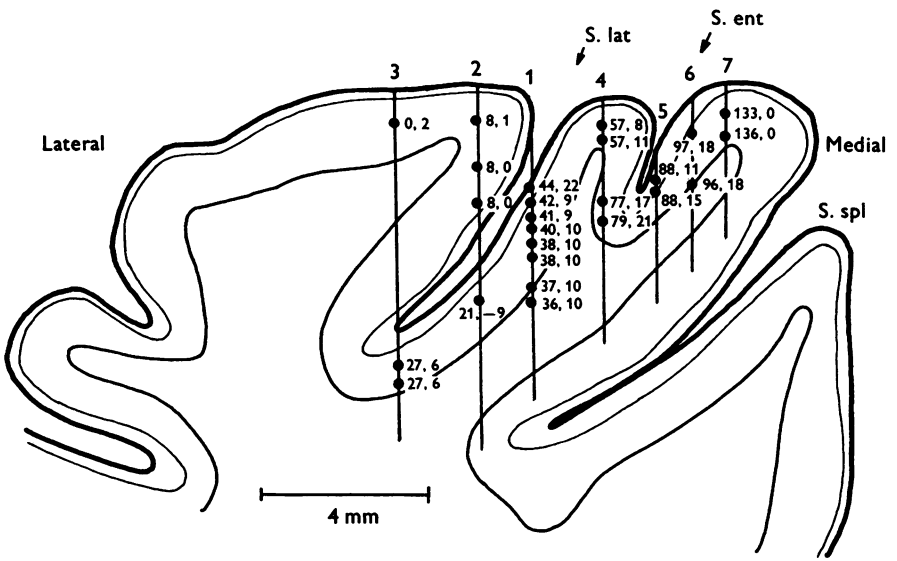

Fig. 2. Transverse section of the left hemisphere of the sheep 1 mm in front of the interaural plane. All needle tracks are in the primary visual area. S. spl., the splenial sulcus, and S. lat., the lateral sulcus, are constant features. S. ent, the entolateral sulcus, is variable in size.

Receptive fields

In both V1 and V2, most cells responded optimally to a moving bar or edge of a particular orientation. The cells in V2 were particularly sensitive to orientation. Because of the special role of vertical edges in stereoscopic vision we were interested to discover if units sensitive to vertical orientation occurred more commonly than others. As shown in Fig. 5, all orientation-preferences were observed; if all orientations were equally represented the expectation for each of the six classes of this Figure would be 1/6. In fact, among the 118 cells examined in V1 there were significantly more units which preferred vertical edges (12-6) than expected on the hypothesis of equal representation of orientations ($\chi^2 = 5{\cdot}31$ for 1 degree of freedom, $P < 0{\cdot}05$). This is also true of 216 cells in V2 ($\chi^2_{[1]} = 12{\cdot}03$, $P < 0{\cdot}001$). For all other orientations there was no significant deviation from expectation.

Cells with simple, complex and hypercomplex receptive fields were

found in V1, with a predominance of simple cells, but in V2 most cells were complex or hypercomplex as in the cat (Hubel & Wiesel, 1965). There were very clear differences between V1 and V2 in binocular interaction, which are described at length in the next paper (P. G. H. Clarke, I. M. L. Donaldson & D. Whitteridge, 1976). The functional boundary based on receptive field properties coincided with the point of reversal of the retinotopic map, where the fields were about 15° ipsilateral. Units with ipsilateral receptive fields did not have noticeably different properties from those of cells in the rest of V1 and V2.

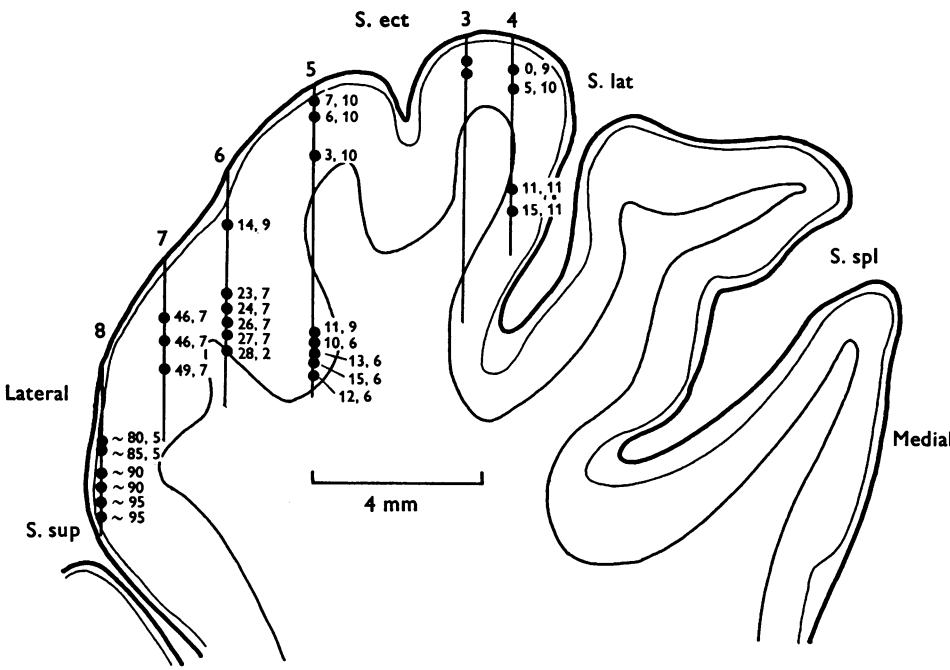

Fig. 3. Transverse section of the left hemisphere in the interaural plane. The V1/V2 boundary lies in S. ect., the ectolateral sulcus. From S. ect. to S. sup., the suprasylvian sulcus, is V2. The ipsilateral fields were not mapped in this experiment.

Magnification factors

In the representation of the area centralis, magnification factors were approximately equal when measured along horizontal and vertical meridians of the visual field. At the extreme periphery, the vertical magnification factor was about twice the horizontal magnification factor, as it is in the cat. If one follows the horizontal magnification factor along the horizontal meridian (Fig. 7), it is clear that it falls off more slowly

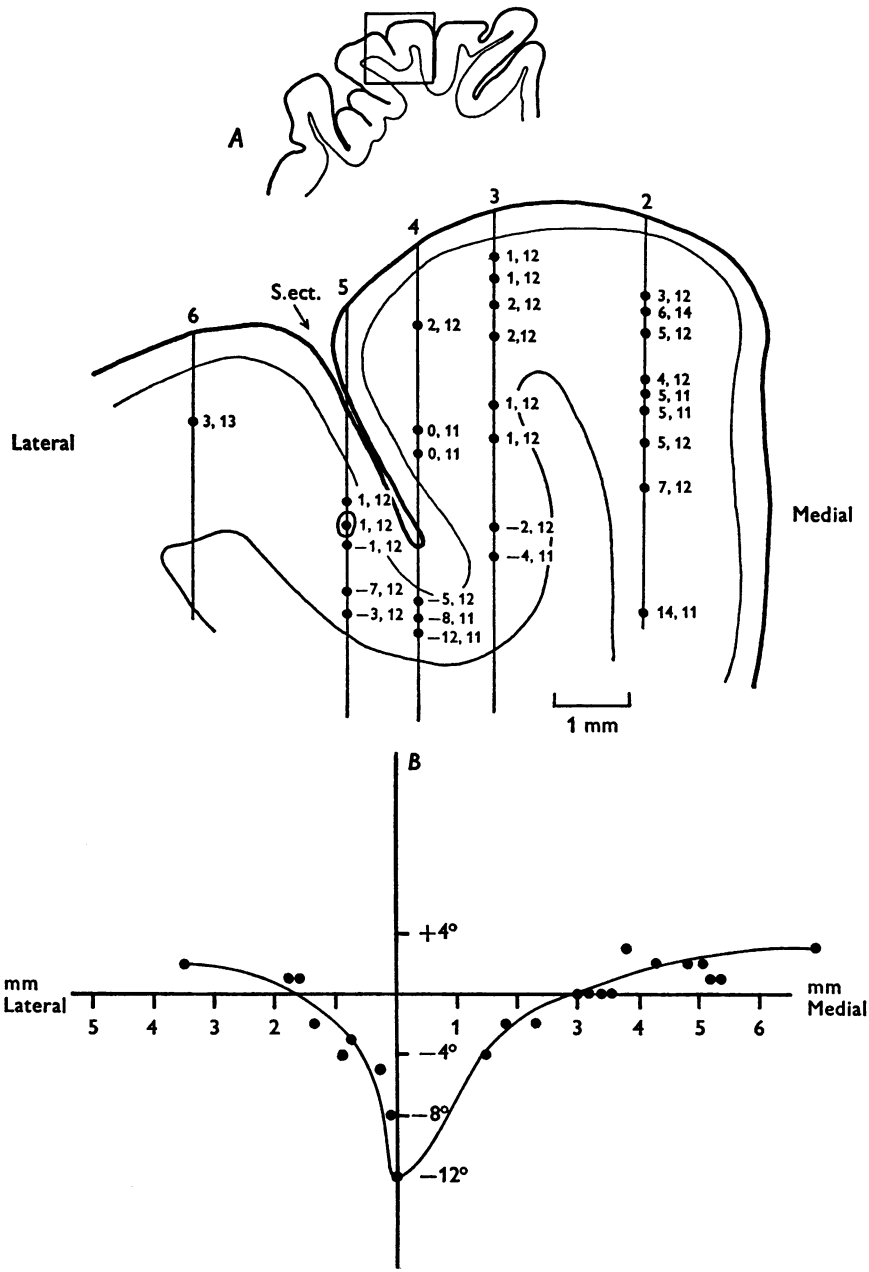

Fig. 4. *A*, transverse section of the ectolateral gyrus. The boundary between V1 and V2 is at the bottom of S. ect., the ectolateral sulcus. Its medial wall is formed by ipsilateral V1, its lateral wall by ipsilateral V2. *B*, ordinate: horizontal position of receptive fields of cells in the walls of the ectolateral gyrus. Contralateral field positions positive, ipsilateral fields negative. Abscissa: distance parallel to the surface of the cortex. The slope of the curve gives the reciprocal of the magnification factor.

than in the monkey (Daniel & Whitteridge, 1961), and the ratio between largest and smallest values is about 14:1, compared with 50:1 in the cat and 60:1 in the monkey. Magnification factors fall off sharply on each side of the representation of the retinal streak, so much so that it is difficult to find much cortical area dealing with retinal areas other than the streak.

The magnification factors in the ipsilateral region start high near to the representation of the area centralis, fall off as the fields move out to 10–12° ipsilateral and rise again as the fields approach 0° again in V2 (Fig. 4*B*).

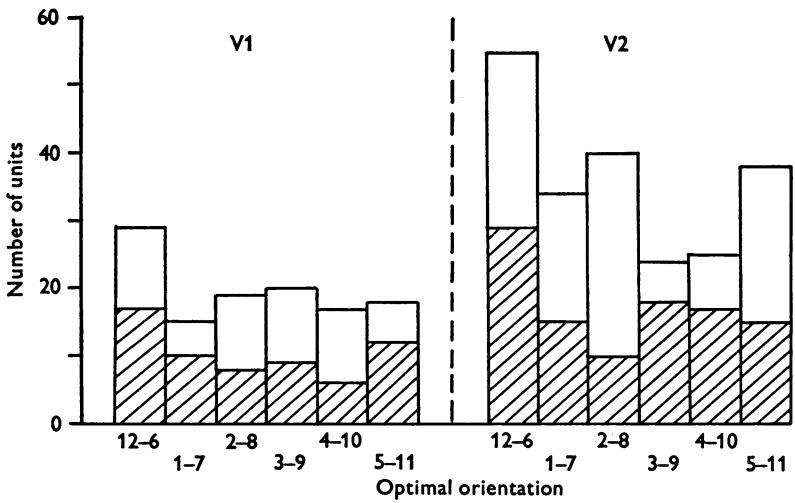

Fig. 5. Distribution of optimal orientations of cells in V1 and V2. Binocular units shaded, monocular units open. The excess of vertical orientations for all V2 and for binocular cells in V2 is significant at 1 % level (see text).

DISCUSSION

The cortical representation of the retina is dictated by the presence of a visual streak as is that in the rabbit (Hughes, 1971) with the addition that the sheep possesses an area centralis (Fig. 6) and the rabbit does not. Comparison of ganglion cell density of retina and magnification factor in V1 shows that both fall off more slowly along the streak than elsewhere (Figs. 6 and 7). A peculiarity of the sheep is the large ipsilateral representation extending up to 15°. It is possible that this is the visual equivalent of its large ipsilateral sensory area for lips and nostrils (Adrian, 1943; Woolsey & Fairman, 1946) which we confirmed in one experiment. This was attributed by Adrian to the dominance of smell for which

connexions are ipsilateral. We have seen binocular cells in V1 with both receptive fields 10° or more into the ipsilateral field. These cells cannot, therefore, be concerned with that wedge of visual field which would have no representation if the fields of two eyes 12 cm apart split exactly at 0° without overlap. Cells with ipsilateral fields of 10–12° have been found in the lateral geniculate nucleus (P. G. H. Clarke *et al.* in preparation).

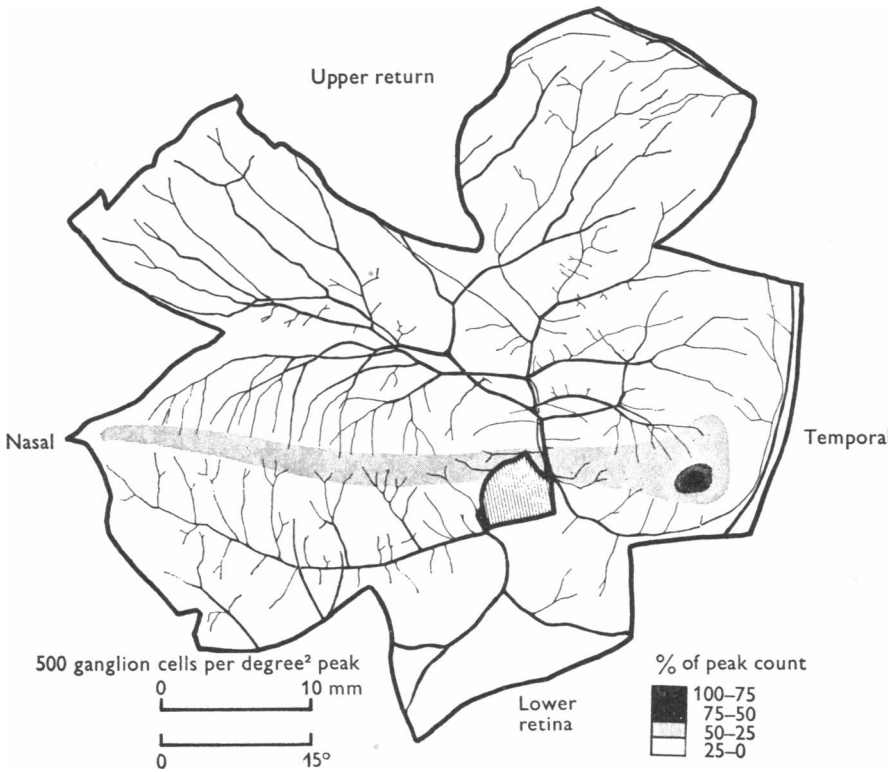

Fig. 6. Ganglion cell counts from a flat mount of the sheep's retina made by A. Hughes. Peak count 500 ganglion cells degree². Contours in ganglion cells/mm².

It is noteworthy that a high proportion of cells with ipsilateral fields have binocular corresponding fields. In this they differ from cells in the Siamese cat, in which nearly all cells with ipsilateral fields are monocular, but a few have binocular and non-corresponding fields (Hubel & Wiesel, 1971). We have found binocular cells whose fields are in the contralateral visual field up to 20° from the mid line. The blind spot seems to be close to the optic axis, laterally about 48° from the mid line. If the visual field extends out 90° laterally from the optic axis, one would expect a binocular

field of 42° on each side of the mid line. Any cells with binocular fields more than 20° from the mid line must be rare and difficult to find. The whole of the rest of the contralateral field is of course monocular.

It would be helpful to know the exact projection of callosal fibres to the area between contralateral V1 and contralateral V2. We have tried to obtain such evidence by fibre degeneration, so far without success. Pia and arachnoid are so adherent in the longitudinal fissure that it is difficult to cut the corpus callosum without producing some damage to the splenial gyrus and adjoining structures.

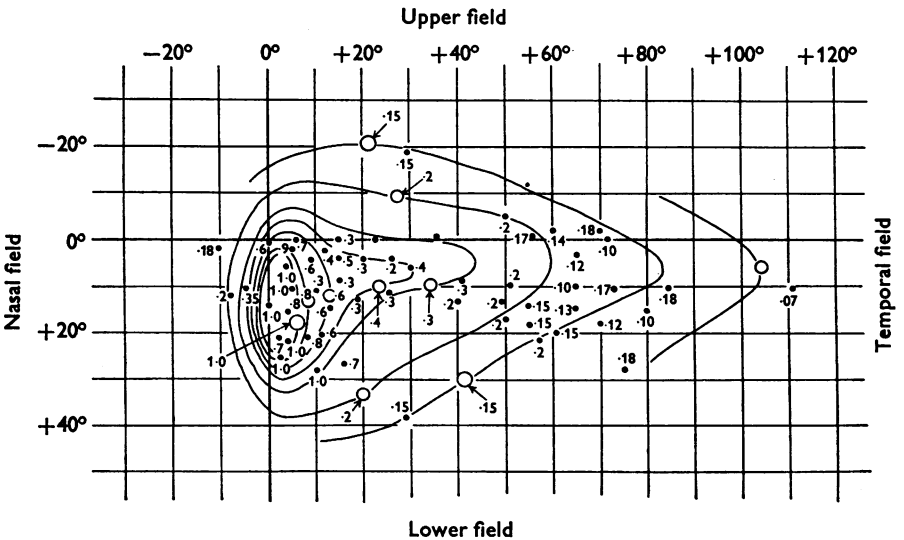

Fig. 7. Magnification factors (mm cortex/degree in visual field) plotted on a 'Mercator' projection of the visual field. At the equator this causes negligible error.

V1, V2 and cytoarchitectonics

It cannot be said that classical architectonics has been of much assistance in our physiological work. According to Rose (1942), the peristriate area is on the medial surface of the hemisphere. We have not identified a further visual area here though there may be one corresponding to the splenial visual area in the cat (Kalia & Whitteridge, 1973). Rose's peristriate area does not correspond with our V2 which lies entirely lateral to V1.

From physiological data, we think the boundary between V1 and V2 lies at the limit of the ipsilateral representation which extends 15–20° into the ipsilateral field. Cells with ipsilateral fields medial to this boundary behave like cells in contralateral V1. If binocular, they have closely

corresponding receptive fields with small or no retinal disparities. Cells lateral to this suggested V1/V2 boundary have larger fields, large disparities and behave like the cells of adjacent contralateral V2. Near the representation of the area centralis this boundary lies at the bottom of the ectolateral sulcus (Fig. 3*A*, *B*).

This means that area V1, which includes ipsilateral as well as contralateral components, coincides with the area striata (17) of Rose.

We do not find the transitional features that are obvious in the cat at the 17/18 border, thick myelinated radial fibres and an increase in large cells in layer III, to be as marked in the sheep and the correlation of cytoarchitectonics and physiological findings needs further work.

Magnification factor and acuity

The very clear organization of ocular dominance columns or stripes in the monkey (Hubel & Wiesel, 1972) has raised the question of a possible discontinuity in the magnification–eccentricity curve at the boundary between binocular and monocular fields. This would hardly be detectable in the monkey at 50–60° lateral, but at about 20° it should be detectable in the sheep if more precise data were available.

We know nothing so far of peripheral acuity in the sheep. For central acuity, the best figures for stationary stripes on a background matched for total illumination is 11 min (Backhaus, 1959). If one compares the available figures for the highest density of ganglion cells and the visual acuity in monkey, sheep and cat, there is a curious discrepancy (see Table 1).

TABLE 1

	Ganglion cells/deg²	Separation of ganglion cells*	Visual acuity
Rhesus monkey	3050†	1·1′	0·65′
Sheep	500‡	2·7′	11′§
Cat	300‖	3·5′	5′

* Assuming a regular rectangular array.
† Assuming cones to ganglion cells are 1:1 at the fovea.
‡ Hughes (personal communication).
§ Backhaus (1959).
‖ From Stone (1965).

Comparison of ganglion cell density and visual acuity in various animals.

One would expect an acuity of 3–4′ rather than 11′ if this is to be related to ganglion cell density. Possibly much lower figures would be given by moving targets. Hughes & Whitteridge (1973) remark that rapidly adapting units are common in the optic nerve of the goat and these are present even at the area centralis. Field experience strongly suggests that red deer are much better at the detection of moving objects, when a man may

cause a herd to move when he is downwind and over half a mile away. It is likely that sheep are similarly not good at the identification of stationary patterns but readily perceive movement.

We are indebted to Dr A. Hughes for Fig. 6, we thank Mrs J. P. Donaldson for preparing the histological material and Mrs Vivienne Harris for technical assistance, and we are grateful to the Medical Research Council for support.

REFERENCES

ADRIAN, E. D. (1943). Afferent areas in the brain of ungulates. *Brain* **66**, 89–103.

BACKHAUS, D. (1959). Visual acuity in ungulates. *Z. Tierpsychol.* **16**, 454.

BISHOP, P. O., KOZAK, W. & VAKKUR, G. J. (1962). Some quantitative aspects of the cat's eye: axis and plane of reference, visual field, co-ordinates and optics. *J. Physiol.* **163**, 466–502.

CLARKE, P. G. H., DONALDSON, I. M. L. & WHITTERIDGE, D. (1976). Binocular visual mechanisms in cortical areas I and II of the sheep. *J. Physiol.* **256**, 509–526.

COOPER, S., DANIEL, P. M. & WHITTERIDGE, D. (1955). Muscle spindles and other sensory endings in the extrinsic eye muscles. *Brain* **78**, 564–583.

DANIEL, P. M. & WHITTERIDGE, D. (1961). The representation of the visual field on the cerebral cortex in monkeys. *J. Physiol.* **159**, 203–221.

GUILLERY, R. W. (1970). The laminar distribution of retinal fibres in the dorsal lateral geniculate nucleus of the cat: a new interpretation. *J. comp. Neurol.* **138**, 339–368.

HARKER, D. W. (1972). The structure and innervation of sheep superior rectus and levater palpebrae extra ocular muscles. *Investve Ophth.* **11**, 970–979.

HUBEL, D. H. & WIESEL, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *J. Neurophysiol.* **28**, 229–289.

HUBEL, D. H. & WIESEL, T. N. (1971). Aberrant visual projections in the Siamese cat. *J. Physiol.* **218**, 33–62.

HUBEL, D. H. & WIESEL, T. N. (1972). Laminar and columnar distribution of geniculo-cortical fibres in the Macaque monkey. *J. comp. Neurol.* **146**, 421–450.

HUGHES, A. (1971). Topographical relationships between the anatomy and physiology of the rabbit visual system. *Documenta ophth.* **30**, 33–159.

HUGHES, A. & WHITTERIDGE, D. (1973). The receptive fields and topographical organization of goat retinal ganglion cells. *Vision Res.* **13**, 1101–1114.

JOSHUA, D. E. & BISHOP, P. O. (1970). Binocular single vision and depth discrimination. *Exp. Brain Res.* **10**, 389–416.

KALIA, M. & WHITTERIDGE, D. (1973). The visual areas in the splenial sulcus of the cat. *J. Physiol.* **232**, 275–283.

KAPPERS, A. C. U. (1920–1). *Vergleichende Anatomie des Nervensystems.* Haarlem: E. F. Bohn.

KRUEG, J. (1878). Uber die Furchung der Grosshirnrinde den Ungulaten. *Z. wiss. Zool.* **31**, 297–345.

LANDACRE, F. L. (1930). The major and minor sulci of the brain of the sheep. *Ohio J. Sci.* **30**, 36–51.

RICHARD, P. K. (1967). *Atlas Stéréotaxique de Cerveau de Brébus 'Préalpes du Sud'.* Paris: INRA.

ROSE, J. E. (1942). Sheep cytoarchitectonics. *J. comp. Neurol.* **76**, 1–37.

STONE, J. (1965). A quantitative analysis of the distribution of ganglion cells in the cat's retina. *J. comp. Neurol.* **124**, 337–352.

WOOLSEY, C. N. & FAIRMAN, D. (1946). Contralateral, ipsilateral and bilateral representation of cutaneous receptors in somatic area I and II of the cerebral cortex of pig, sheep and other animals. *Surgery, St Louis* **19**, 684–702.