Electrophysiological and behavioural studies of vision in the pigeon

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ELECTROPHYSIOLOGICAL AND BEHAVIOURAL STUDIES OF VISION IN THE PIGEON

by D.M. Parker

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ABSTRACT

The literature concerning the eye and the visual pathways in the pigeon is reviewed (Chapter 1).

An electrophysiological investigation of the forebrain of the pigeon using the method of evoked potentials revealed four main areas within this structure in which large amplitude responses were found. These areas were the hyperstriatum, neostriatum caudale, paleostriatum augmentatum and an area of tissue surrounding the ectostriatum. Comparison of the latencies of these potentials with the latencies of potentials found within the mesencephalon and diencephalon excludes the nucleus rotundus as being involved in the relay of these potentials to the forebrain. Previous work by other authors has suggested that this nucleus is a major source of telencephalic visual afferents. Only one area within the forebrain produced potentials which are compatible as regards latency with being relayed by the nucleus rotundus. This area is the dorsolateral corticoid area. These results are discussed and compared to previous work (Chapter 2).

An investigation of the effects of destruction of the centrifugal pathway to the retina, by lesioning the isthmo-optic nucleus or sectioning the optic tract, on the pigeon's electroretinogram has revealed no evidence of this pathway being involved in the control of this potential. Evidence from two birds suggests that previous reports of centrifugal effects on the electroretinogram of the pigeon can be attributed to metabolic abnormalities occurring within the retina as a consequence of optic tract section (Chapter 3).

Destruction of the hyperstriatum of the pigeon revealed no evidence of profound effects on visual discrimination tasks. Birds lesioned in this area show increased choice times on a compound colour-brightness discrimination but no increase in trials to criterion. No effects were apparent on pattern discrimination contrary to previous reports of such effects in the literature (Chapter 4).

Destruction of the hyperstriatum or the neostriatum caudale revealed no profound disturbance of the animals' ability to analyse visual stimuli in terms of orientation, brightness or size, when the performance of these animals was compared to controls using the method of stimulus generalisation. The gradients of the generalisation slopes to size, but not those to orientation or brightness, were significantly flatter in the experimental groups than in the control group (Chapter 5).

The implication of the findings concerning the visual projections to the hyperstriatum and neostriatum caudale and the effects of lesions to these areas on our understanding of the function of the pigeon's forebrain are discussed (Chapter 6).

CONTENTS

INTRODUCTION

The experiments reported in this thesis have their basis in the author's interest in the visual process in vertebrates. Among vertebrates, birds are one of the most interesting phyla in which the visual process can be studied. As they are the terminal branch of a separate phylogenetic tree from mammals, the similarities and contrasts in the development of the eye and related brain structures between birds and mammals should prove helpful in our understanding of both. Yet of the four main sub-human species, (the rat, the cat, the rhesus macaque and the pigeon), that have been used in laboratory studies of the visual process, probably less is known about the visual process of the pigeon than the other three. Because the pigeon offers such a wide scope for research in which the experimenter can acquire a wide range of skills, and still make a contribution to the elucidation of our understanding of its eye and brain, this experimental animal seems in many ways ideal for someone with an interest in vision and who has yet to acquire the basic research skills.

The report which follows begins with a review of the pigeon's visual system. This is followed by an investigation of visual projections to the pigeon's forebrain using the method of evoked potentials to visual stimulation of the eye. The information gained from this study was utilised in Chapters 4 and 5 for a study on the effects of forebrain lesions on visual learning in the pigeon. Chapter 3 contains a report of an investigation into centrifugal effects on the electroretinogram of the pigeon. While Chapters 2, 4 and 5 form a whole, Chapter 3 has been placed with the other electrophysiological work, because from the point of view of methodology they belong together. It was hoped at the time the investigation of centrifugal effects on the E.R.G. began, that the study would provide some information which could be utilised in a behavioural investigation of the function of the centrifugal tract to the eye. Unfortunately no information was found that could predict the animals' behaviour on

visual learning tasks.

While the studies reported in this thesis do not form a whole in the sense that only a single problem was investigated, they are unified in the sense that they were designed to provide insight into the visual process of the pigeon.

CHAPTER I. The Visual System of the Pigeon

Part I. The Eye

In the pigeon, as in other birds, the eyes are extremely well developed in comparison with the size of the brain. Chard (1938) estimated that the weight of the two eyes was equal to the weight of the brain in the homing pigeon. Superficial inspection of the pigeon's brain with the eyes and optic nerves attached confirms the relatively enormous development of the eyes (figure 1). The fact

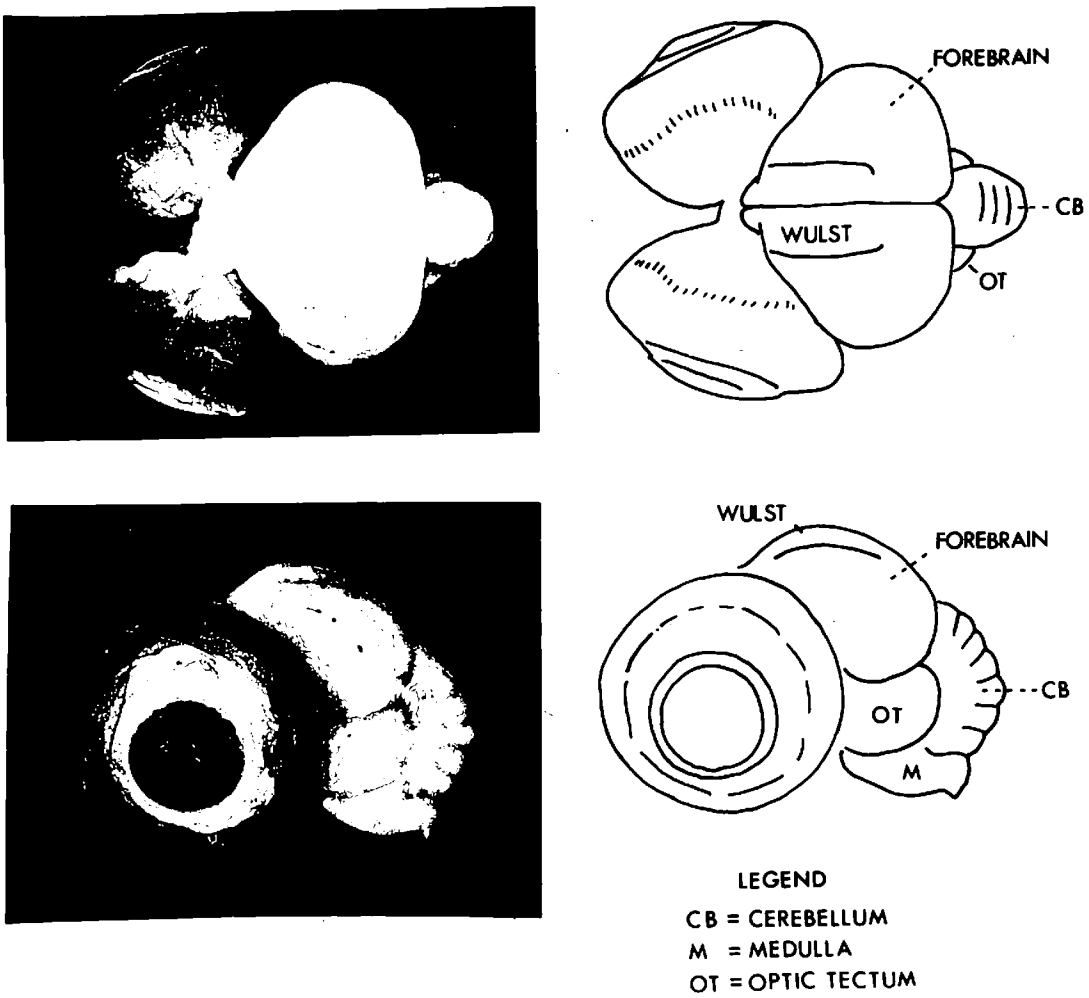

Figure 1. Superficial appearance of the brain and eyes of the pigeon from the lateral and dorsal inspection points.

that the eyes are so large means that there is only a thin septum of bone separating them in the midline; a fact which has been used to view the fundus of the eye using a transilluminating beam (Wolbarsht 1964). This passage of light across the midline may account for the sometimes reported consensual pupillary reflex in the pigeon (Levine 1955). In their normal resting position in the head, the axes of the eyes are approximately 150 degrees apart. Estimates of the visual field of the pigeon's eye range between 172 and 180 degrees, and this would mean that the binocular visual field is about 24 degrees in extent (Chard 1938). It would also mean that in the absence of head movements the pigeon would have a blind area behind of at least 24 degrees. The early investigators (Chard 1938, Gundlach, Chard and Shaken 1945) concluded that as the eyes fitted the sockets so tightly (the cornea collapses when eye is excised) that eye movements were practically absent. Recent work (Nye 1969) has shown that pigeons are capable of quite a wide range of eye movements; at least 5 degrees in the horizontal plane and about the same in the vertical plane. As the extent of the visual field may have been underestimated rather than overestimated, due to the difficulty of using opthalmoscopic instruments that were designed for human eyes on much smaller animal eyes, it seems likely that in the absence of head movements the pigeon's visual system encompasses the full 360 degrees. An incidental finding in Nye's (1969) study is the apparent absence of a fine tremor movement in the pigeon's eye movement spectrum. As tremor plays such an important part in the maintenance of human vision (Riggs et al 1953) this may point to a fundamental difference in the construction of the pigeon's visual apparatus.

The sphincter and dilator muscles of the pigeon's iris are usually described as striated and consequently do not receive autonomic innervation (Walls 1942). Certainly the speed of contraction of the iris in birds (between 60 and 100 milliseconds Gundlach 1934) lends support to this statement. However there is definite proof of the existence of adrenergic fibres in the avian iris (Ehinger 1967) that are similar to those found in the mammalian iris, although there is as yet no proof of the existence of unstriated

muscle in this region. The existence of a muscle system in the avian iris which received autonomic innervation would help to explain the phenomenon of pupillary constriction that occurs during the courtship bouts of pigeons (personal observations).

The eye is of the flat type, rather than the spherical type found among mammals. There is thus a considerable saving in space and weight without any loss of optical efficiency (Pumphrey 1961). The flatter shape of the eye, which brings the lens correspondingly closer to the retina should in fact give the eye relatively greater depth of focus than that found in a spherical eye. If the analogy of the eye being similar to a camera is used, then the pigeon's eye is more like the wide angle short focal length type than that of the humans, which is more like the medium angle, medium focal length type (the distance from the front of the lens to the retina in the pigeon is approximately 9mm as against 23mm in man). It is somewhat surprising then that estimates of the range of accommodation in pigeons and in other birds have usually referred to its extremely large extent (Walls (1942). In the pigeon according to the work of Gunlach et al (1945) the minimum range of accommodation is 17 dioptres and may be as much as 25 compared to a human range of 10 to 12. However these investigators (Gunlach et al 1945) confined themselves to investigating the dioptric power of the cornea, ignoring the possible contribution of the lens system. It is undoubtedly true that part of the advantage gained by having the lens closer to the retina is offset by the fact that the outer segments of the cones are not elongated (as they are in the specialised foveal cones of humans. Consequently, other things being equal, the bird must begin to focus sooner as an object approaches it and must maintain a closer control of accommodation once the object is within the focussing range. If one assumes that the advantages of the closer lens are exactly cancelled by the shorter outer segments of the retinal cones, then the dioptric power of the cornea alone would be enough to furnish the pigeon with as wide a range of accommodation as it could possibly need. However there is no evidence that the ciliary process, which controls the contraction of the lens, is in any way

degenerate, and in the absence of other evidence it seems wise to conclude that it is still functional. This presents a problem, because if we assume that both cornea and lens contribute to the accommodation mechanism of the pigeon then it would follow that the focussing mechanism is hopelessly redundant.

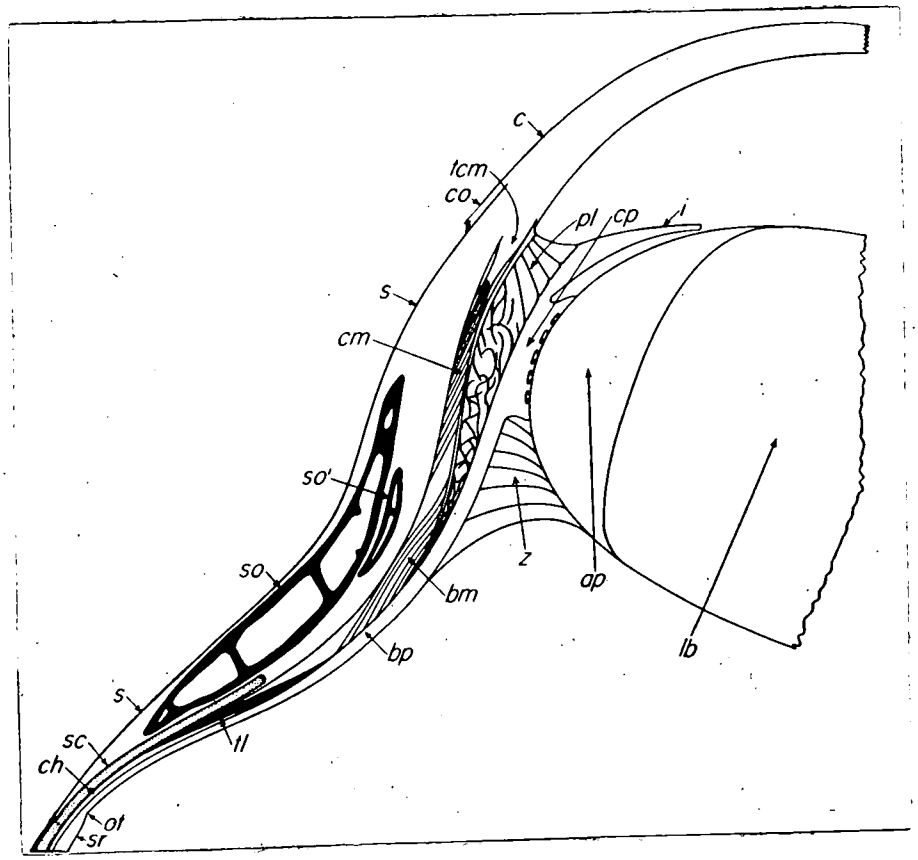

Figure 2. The ciliary region of the birds eye (schematic). ap - annular pad; bp - base plate of ciliary body; bm - Brucke's muscle; c - cornea; ch - choroid; cm - Crampton's muscle; co - conjunctiva; cp - ciliary process; i - iris; lb - lens body; ot - ora terminalis; pl - pectinate ligament; s - sclera; sc - scleral cartilage; so - scleral ossicle; sr - retina; tcm - tendon of Crampton's muscle; tl - tenacular ligament; z - zonule fibres. From Walls (1942).

Figure 2, shows a diagram of the cornea lens, and associated muscle system of the pigeon. Crampton's muscle, a muscle unique to birds but derived from the reptilian ciliary muscle, is the only

muscle which could alter the shape of the cornea. Brucke's muscle in birds is somewhat differently positioned to the muscle of the same name in the human ciliary process, and because of its different position would appear to serve a different function. In the human ciliary process contraction of Bruckes muscle results in a forward movement of the ciliary process, which relieves the tension on the zonule fibres thus enabling the lens to collapse under its own elacticity and so producing accommodation. In birds the position of the zonule fibres would not allow any change in the shape of the lens but would result merely in a forward movement of the whole ciliary process if Brucke's muscle is contracted. The ciliary process itself in birds appears to be similar to the corresponding structure in reptiles (Walls 1942), except that birds have in addition Crampton's muscle. Thus the pigeon would appear to posses three muscular systems which superficially at least, are all involved in the process of accommodation. If however, the data available from behavioural and opthalmic studies are taken into account the situation becomes even more confusing. As has been pointed out above, changes in the curvature of the cornea alone would be enough to provide the animal with all the range of focussing it would need; indeed if one assumed that the pigeon began accommodating at the same distance as humans do in metres, then with a focussing range of only 10 dioptres its near point would be 7 centimetres from the eye. Studies by Hamilton and Goldstein (1933), Chard (1938) and Gunlach (1933) however all suggest that the near point of vision in the pigeon is in the region of 40cm., and recently it has been suggested by Catania (1964) that while the pigeon is myopic in the frontal field it is hypermetropic in the lateral field. Hamilton and Goldstein (1933) mention that skiascopic examination of the pigeon's eye shows it to be hypermetropic. Taken together this data is obviously contradictory. A solution to what might in fact be happening is to consider what else would happen when the curvature of the cornea is changed. As well as increasing or decreasing the dioptric power of the eye it would also increase or decrease the acceptance angle of the eye thus changing the size of visual field; the binocular field would be affected in particular.

Concomitant with this increase in the size of the visual field however would be the tendency for the image to lose focus but this would be easily corrected if the lens were to move. These two effects could be easily accomplished by muscular systems known to exist in the pigeon's eye; tension on Cramptons muscle would change the curvature of the cornea, while simultaneous contraction of Brucke's muscle would move the lens to compensate for the change in focus. Focussing of the image could then be accomplished in the normal way by pressure by the ciliary process on the annular pad of the lense. The pigeon would thus be able to change the focal length of the eye while maintaining focus on an object at a given distance from it. It would thus have the equivalent of a zoom lens mechanism which could either shrink or expand the image of an object lying a given distance from it. A system like this seems necessary to account for the contradictions in the available data, although experimental verification of the above hypothesis presents several problems.

If the cornea, lens and ciliary process are removed and the eye is examined under a transilluminating beam (fig.3) the general structure of the retina of the pigeon can be clearly seen. The pecten, a structure unique to birds but derived from the reptilian conus, covers the optic nerve head. This structure is responsible for the nutrient supply to the inner retinal layers, particularly the supply of oxygen (Walls 1942, Wingstrand and Munk 1965). Such a structure is needed in birds because of the absence of any direct blood supply to the inner retina. It has been proposed that the pecten has a part to play in vision in addition to its role as a nutrient supply organ. Menner (1938) and Crozier (1943) have proposed that the pecten, by casting a shadow on the retina, could improve the detection of the images of small objects moving across the light dark boundary. It is pointed out that in diurnal birds of prey the pecten is particularly well developed, consisting of a number of fingerlike extensions from the optic nerve head into the vitreous, and that this refinement is there to detect the presence of small moving

images. However in those birds in which the pecten is most well developed it is also true that the cone density is highest (Walls 1942), and some improvement in the diffusion of substances from the pecten would appear to be required. The elaboration of the pecten in these avian species effectively increases the surface contact between the vitreous and the pectinate vanes and this would considerably speed up the diffusion process. The heavy pigmentation of the pecten should also help to cut down the amount of diffusely refracted and reflected stray light that a transparent structure in this position would normally introduce. Whether the pecten does have a dual role in avian vision or not seems a question that is not capable of easy resolution as its metabolic function precludes its removal in order to study the bird's psychophysical performance in its absence.

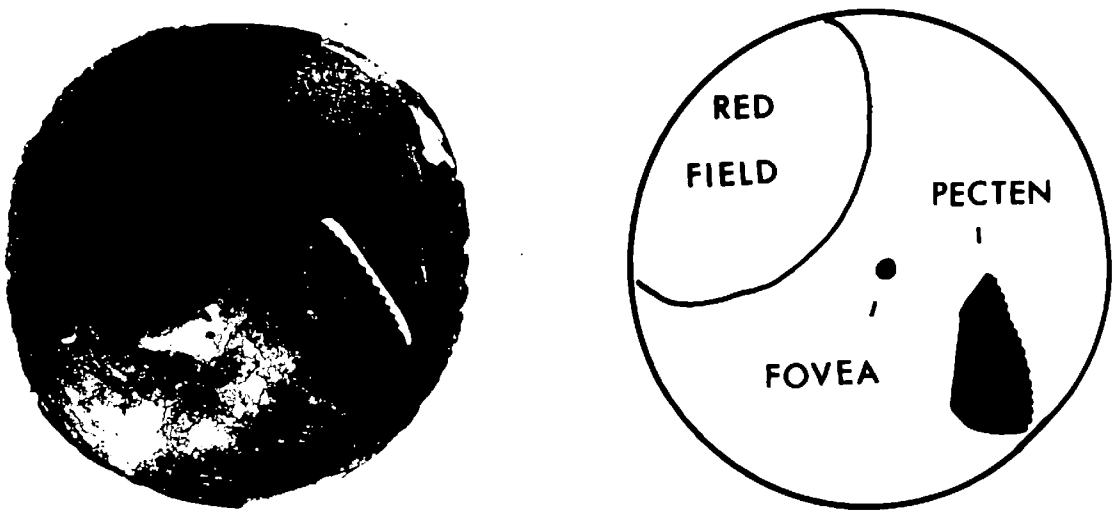

Figure 3 Fundus of the pigeon's eye, showing red field (area dorsalis), fovea and pecten.

The other immediately noticeable feature on superficial examination of the fundus of the eye is the dark elliptical area in the superior temporal quadrant of the retina (Fig.3). This area is the red field or area dorsalis, and is the region of the pigeon retina that

receives the image of the pecking field when the bird's head is in its normal orientation. Its darker appearance is due both to the very high density of large (3 μ diameter) red oil droplets in the outer cone segments and the small (.02 μ diameter) in the inner segments of the cones as well as the greater thickness of the choroid in this region. This background red colour, by filtering the short wave part of the spectrum, would remove the main source of stray intraocular light (the pigeon does not have a yellow pigment in its lens). It would also have the effect of raising the contrast of yellow and red objects lying against a background of green (Pedler and Boyle 1969), a featur e that may be of considerable importance to a ground foraging bird. It should be pointed out however that the red field also contains orange, yellow and green oil droplets as well as cones without oil droplets. Thus blue light can still be seen when it is reflected from an object in the environment and is partially or fully in focus on the retina. It is only the stray light within the eye that would be excluded by the red droplets. In contrast to the red field, the yellow field of the pigeon's eye, which comprises the area surrounding the fovea has a much higher proportion of yellow and greenish yellow oil droplets.

The retinae of all birds studied shows that in toto birds have the most well developed retinae of any group of living species. In diurnal birds the most striking features are the high density of receptors over the entire retina, the large numbers of coloured oil droplets found in the outer segments of the cones, and the extreme development of the inner nuclear layer. The retina can be conveniently divided into 10 layers, although of course sub-divisions exist within these layers. The layers are 1) pigment layer; 2) rod and cone layer; 3) external limiting membrane; 4) outer nuclear layer, containing within it three rows of nuclei; 5) outer plexiform layer; 6) inner nuclear layer, containing fifteen rows of cell bodies; 7) inner plexiform layer; 8) ganglion cell layer, containing 2 layers of cell bodies; 9) fibrous layer; 10) inner limiting membrane.

Receptor cell counts in the pigeon do not appear to have been carried out directly, although Galifret (1968) has counted the density

of cells in the outer nuclear layer. This count does indicate that the pigeon has a high density of receptors spread over the whole of the retinal surface; an average for the retina would appear to be in the region of 85,000 per square millimetre, but there are of course peaks and troughs. Close to the fovea the density rises to about 92,000 per square mm. and in the area dorsalis the receptor density is about the same. It is difficult however to extrapolate from the receptor nuclei density to the density of the actual pigment-containing outer segments. While overall the two counts must obviously coincide, in regions like the lateral fovea (fig.3) the receptor cell nuclei are pulled back producing a circular mound of receptor cell bodies surrounding the foveal depression. The areal density of receptor nuclei would give only a coarse estimate of the higher density found in this region, as there may be in fact a decreasing density of receptors from centre to periphery within the area. When calculating the resolving power of the fovea (assuming of course that the limitations on resolving power are imposed by the receptor cell density and not on factors occurring later in the visual pathway) another fact must be taken into account. Walls has pointed out that the refractive index of the retinal tissue is substantially higher than that of the vitreous (Walls 1937, Walls 1940). While this makes no difference when the light rays strike the retina at right angles, if the light strikes the retina at anything but a right angle it will be deflected. The fovea in birds, including the pigeon, is surrounded by a steep depression made up of the retinal tissue which has been pulled back from the centre of the fovea. Since any incoming light which strikes the side of this depression will be deflected outwards this will introduce a magnification factor which must be taken into account, since in effect it is the same as introducing a higher density of receptors. Walls (1942) states that the magnification factor may be as much as 30%, although the precise figure for the pigeon is not available.

Table I

Chimpanzee	0'28"	Spence	(1934)
Rat	26'00"	Lashley	(1930)
Cat	5'30"	Smith	(1936)
Rabbit	10'00'	Van.Hof.	(1968)
Pigeon	2'42"	Chard	(1939)

Grating measures of visual acuity from some vertebrate species (minimum separable).

Behavioural measures of the pigeon's visual acuity have always found the minimum separable angle to be greater for pigeons than for primates, but smaller than that found for the other infraprimate mammals measured (Table I). The one exception to this is the findings of Gundlach (1933) who found minimum separable angles of 22 and 26 seconds of arc for two birds. Gundlach, however, selected runs from his data that appeared to him to be free of position preferences and this makes the validity of his conclusions questionable. Later authors, Hamilton and Goldstein (1933) and Chard (1938) found the minimum separable angle for the pigeon to be between 2.7 and 3.8 minutes of arc. Recently Nye (1968) found, using a contrast sensitivity technique, that the peak of the modulation transfer function for the pigeon occurs at a lower spatial frequency than that for the human observer when the binocular acuity is measured. Of these studies mentioned here one feature separates Gundlach's (1933) experiment from the remainder. His is probably the only study where the birds would be biased towards using the lateral field of view (the area of the retina which contains the fovea). In the studies of Hamilton and Goldstein (1933) and Chard (1938) a jumping response was used, with the stimuli presented in a position ventral to the bird. Nyes (1969) study presented the stimuli in the frontal plane, so that again the stimuli would not fall on the lateral field of view. Catania (1964) has proposed that the pigeon is Hypermetropic in the lateral field of view and myopic in the frontal

field so that the pigeon is apparently unable to look at stimuli close to it and use its fovea. Obviously comparisons of the visual acuity of vertebrates demands that the area of the retina with the finest grain should be compared across species. Comparisons of the visual acuity of the pigeon with that of primates should then use a measure of the foveal acuity of the pigeon. It seems to be inherently difficult to obtain reliable discrimination from pigeons when the lateral field of view is used. An attempt by the present author to obtain an index of acuity for the lateral field of the pigeon met with no success despite the fact that the animals were trained daily for eleven months (see Appendix I).

The pigeon posseses a duplex retina and the proportion of rods appears to be higher than in a number of other diurnal species of birds (Waelchi 1883). Blough's work (1956) indicates a Purkinje shift, and comparison of the sensitivity of Blough's pigeons under scotopic conditions with the starlings used in Adler and Dalland's similar work (1959) shows the pigeons to be more sensitive under these low illumination conditions. It has been reported that pigeons can be trained to home at night (Hitchcock 1955, St. Paul 1962), a fact which is somewhat surprising as most diurnal birds are most reluctant to move about under conditions of dim illumination (Polyak 1957). The basis of the pigeon's scotopic vision would appear to be rhodopsin which was extracted from the pigeon retina by Hess (1923), Bridges (1962) and Sillman (1969). Comparison of the spectral absoption curve for rhodopsin with the scotopic spectral sensitivity curves derived both behaviourally (Blough 1957) and electrophysiologically (Donner 1953, Graham et al 1935, Ikeda 1965) shows a good agreement.

The cone mechanism is however the predominant one in the pigeon, as is to be expected in the structure of a diurnal animal. In common with a number of other vertebrates (chiefly reptiles and fish) the outer segments of the pigeons cones contain a single oil droplet through which the incoming light has to penetrate in order to reach the photosensitive pigment. These oil droplets are either red, orange, yellow or green. The droplets themselves act as lenses of extremely

short focal length and it has sometimes been argued that this would result in the light refracted by them penetrating a neighbouring outer segment (Pedler and Boyle 1969). This argument ignores the fact that under conditions of light adaptation the outer segments of the cones are surrounded by a dense pigment which originates in the pigment epithilial cells (Van Genderen Stort 1887) and also ignores the possibility that the cone membrane may be highly refractive. The oil droplets do not have a uniform spectral transmission curve within a given colour, the yellow oil droplets in particular may show quite large variations (King-Smith 1969), and it has even been claimed that between oil droplets in the yellow and red field there is a consistent difference, the droplets in the red field showing a significant bias towards sharper cut off of the shorter wavelengths. If the shift in the transmission of the oil droplets to the long wave end of the spectrum is due simply to the lower proportion of short wave light reaching the oil droplets because of the background filtering action of the red microdroplets in the inner cone segments, then the colour detection mechanism would be biased towards the long wavelength. Thus unless there was a correction factor at a later stage of the system, an object of a given hue when seen bu the red field. If the transmission shift is really a shift within the oil droplets themselves however, then this could be seen as a way of partially or perhaps even fully correcting for the red bias in the incoming light. However a shift in the transmission maxima of the oil droplets would only be effective if the shift was differential i.e. the green, yellow and orange droplets were shifted in preference to the red. As the shift seems to be uniform (King-Smith 1969) it appears that this is most probably due to the background filtering action of the microdroplets.

It has been assumed in the above discussion that the coloured oil droplets found in the pigeon's outer cone segments are involved in the mechanism of colour vision. The evidence, even though circumstantial, is reasonably strong that this is in fact the case, although a number of authors have held alternative theories (Walls 1942, Polyak 1957). In the first place, it is impossible for light to reach the cone outer segments

which contains the photosensitive pigment without passing through the relevant oil droplet in those cones that contain them. Thus the sensitivity of any cone depends not only on the absorption spectrum of the cone pigment but also on the spectral density of the oil droplet in the path of the light. Only one pigment has been extracted from the

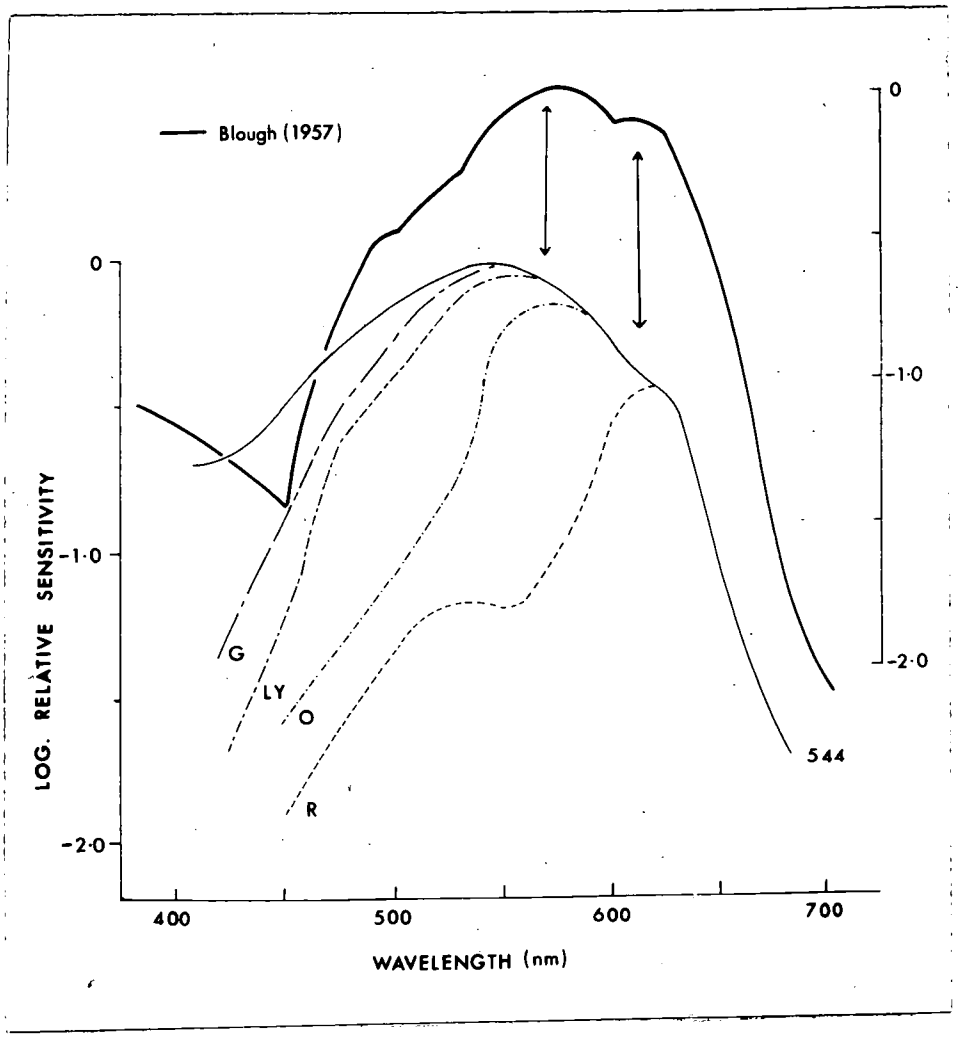

Figure 4. Spectral sensitivity curve from Blough (1957) compared with the relative absorption curve of pigment 544 (Bridges 1962). Curves for R (red), O (orange), LY (light yellow) and G (green) were obtained by subtracting the relative density curves for these oil droplets from the 544 pigment curve. Data on the oil droplets was obtained from King-Smith (1969) and Strother (1962).

retina of the pigeon that has its absorption maximum far enough towards

the long wavelength end of the spectrum to act as a photopic pigment exclusively. This is pigment 544 discovered by Bridges (1962). While the fact that other pigments have not been found in the pigeon retina does not preclude the possibility that they might be there, it appears that action of the oil droplets in conjunction with one pigment is enough to account for a very sensitive colour mechanism except in the blue region of the spectrum where a second assumption must be introduced. If the relative extinction curve of pigment 544 (Bridges 1962) is converted to a log. sensitivity curve and the optical density of the four oil droplets subtracted from it (taken from King-Smith 1969 and Strother 1963) then four primary light sensitive mechanisms are found which have their absorption maxima at different points on the spectrum. If the peaks of these hypothetical mechanisms are compared with the inflection points on the photopic spectral sensitivity curve of Blough (1957) then there appears to be good agreement, except in the blue region of the spectrum (Fig.4). Bridges (1962) also extracted rhodopsin from from the pigeon's retina, and this is usually accepted as being the basis of scotopic vision. There are however reasons for thinking that rhodopsin may be a cone pigment as well as a rod pigment. Bridges (1962) found that 85% of the pigment he extracted from the retina of the pigeon was rhodopsin despite the fact that the eye is cone dominated. Dartnell (1960) extracted rhodopsin from the all cone retina of the squirrel, an animal which is strongly suspected as having normal mammalian trichromatic vision. Since in Blough's (1957) study the increasing sensitivity in the blue region of the spectrum was found well above the cone-rod break (Fig.4) then it seems another photopic pigment might well be postulated. However it is still possible that the rising sensitivity with movement of the spectrum towards the shorter wavelengths is a function of mesopic vision only and in this case the discrimination of different hues in the blue range of the spectrum might be analagous to the case in the cat described by Daw and Pearlman (1966). They found that colour discrimination in the cat could be adequately described by a one-cone process operating in conjunction with the rods in the mesopic range of intensities. Whichever mechanism

operates in the pigeon (whether rhodopsin can be regarded as a cone pigment, or whether the blue sensitivity is due to the action of the rods and so is present only in the mesopic intensity ranges) could be decided by examining the ability of pigeons to discriminate hues in the blue region of the spectrum as a function of adaptation level. If the rod mechanism is responsible then hue discrimination of shorter wavelengths should fade with a high level of light adaptation.

The same arguement can be used in favour of the fact that iodopsin is the single cone pigment in the pigeon. A report by Wald (1958) quotes some unpublished work by Brown, who claimed to have extracted iodopsin from the pigeon retina although this claim has never been substantiated subsequently. It appears to make little difference to the argument whether one accepts iodopsin or pigment 544 as being the cone pigment of pigeons. The interaction of a single cone pigment with the coloured oil droplets known to exist in the cones of pigeons can explain how it is possible for the pigeon to discriminate different wavelengths in the spectrum above 500 nm. Donner (1958) has in fact argued that iodopsin can be considered as the cone pigment in the pigeon. Whichever assumption one makes about which pigment is in fact present in the pigeon the sensitivity in the blue region of the spectrum under photopic conditions is not explained and requires further assumptions.

The inner nuclear layer of the pigeon's retina is extremely well developed. In fact the increased thickness of the pigeon retina as compared to the primate retina is due to the expansion of the inner nuclear and inner plexiform layers (.31mm pigeon, .14mm man, Chard 1938), between the fovea and the ora serrata). This expansion of the inner nuclear layer may reflect the increased processing of visual information in the retina of this animal which is evident from the outputs of the ganglion cells (Maturana 1959, 1961). Dowling and Werblin (1969) have noted that in those animals whose retinal ganglion cells show high selectivity as regards their trigger features, such as the frog and the pigeon, there are very few direct bipolar - ganglion cell synapses, but the majority of contacts are bipolar - amacrine, amacrine - amacrine and amacrine - ganglion cell (Dowling 1968, Dowling and Boycott 1966).

Both the frog and the pigeon show highly specific types of ganglion cell response (Maturana 1961, Maturana et al 1960), while the cat and primate show a relatively uniform 'centre-surround' type of retinal receptive field, and correlated with this is the fact that the majority of synaptic contacts between the inner nuclear and ganglion cell layers are direct bipolar - ganglion cell synapses. In the rabbit and the ground squirrel which show ganglion cells like the primate - cat type as well as the more specialised type like the frog and pigeon, the types of inner nuclear layer - ganglion cell layer synapses show a distribution intermediate between the frog, pigeon and the cat - primate. (Dowling and Werblin 1969).

The ganglion cell layer of the pigeon retina shows a high density of cell bodies although there has been no really accurate estimate of the truly neural population of this layer. Perhaps the most accurate estimate can be taken by assuming that each true neuron sends an axon into the optic nerve and so take the number of optic nerve fibres as giving the neural density of the ganglion cell layer. The most accurate counts made so far of the number of fibres in the optic nerve of the pigeon are those of Bingelli and Paule (1969) using the electron microscope. They estimated the number of fibres to be 2,279,000 ± 6%, which is by far the largest number found in any vertebrate species. The animal that was previously thought to possess the largest number was man with an estimated 1,010,000 but this estimate was based on light microscopy (Bruesch and Arey 1942). Examination of the human optic nerve with the electron micropscope has failed to expand on this estimate (Cohen 1967). However it must be taken into account that approximately one percent of the fibres in the pigeons optic nerve are centrifugal fibres running to the retina (Cowan, Adamson and Powell 1961). These calculations are based on light microscopy and there remains a possibility that there may be centrifugal fibres which are not resolved by light microscopy. Even so it appears unlikely that these would make a substantial difference to the calculated number of centripetal fibres, considering the size of the isthmo-optic tract compared to the optic tract. It is highly unlikely that the pigeon will prove to have the largest number of optic nerve fibres, probably one of the hawks will prove to have far more, but it is interesting to speculate why such

a well developed eye brain channel has evolved in the pigeon. Presumably one of the most important contributory factors is that the diurnal bird's retina is in toto much more like the human macular area than it is like the human retina as a whole. Even 60 degrees outside the fovea the density of cells in the external granular layer (nuclei of rods and cones) is in excess of 70,000 per square millimetre (Galifret 1968). A considerable number of these receptors are cones even though the number of rods in this region of the retina is increasing rapidly (Waelchi 1883), and presumably the representation of these more peripheral areas in the optic nerve must be higher than if the eye in this region is rod dominated. A second factor that must be taken into account is the specialised nature of some of the receptive fields in the pigeon's retina. Maturana (1961) described six classes of ganglion cells in the pigeon retina; 1) verticality detectors,
2) horizontality detectors,
3) general edge detectors,
4) directional moving edge detectors,
5) Convex edge detectors,
6) luminosity detectors,

which included the brightness and colour sensitive cells. It is evident that a high degree of information processing goes on at the retinal level of the pigeon and furthermore it is evident from Maturana's description of these cells that they have in the majority of cases reasonably small fields ("a few minutes" up to about 2 degrees). This implies that from a given region of visual space highly specific features of the environment are extracted. This is in contrast to the case in mammals, and particularly cats and primates, where the retinal receptive field is of a reasonably uniform structure. Thus in the mammalian visual system very basic information can be transmitted and the important features analysed later, while in an animal like the pigeon a large amount of specialised information must be transmitted, thus calling for a larger channel capacity. Maturana has related the development of the more plastic mammalian system to the evolution of the visual cortex, but it seems unlikely that this is the only factor to

be taken into account. Holden (1969) has found cells in the pigeon retina that show responses similar to the mammalian 'centre-surround' and 'on-off' types which implies that the story in the pigeon is a lot more complex than Maturana implied, and that retinal cell types cannot so easily be used to predict the structure of central pathways in animals.

Part 2. Central Visual Pathways of the Pigeon

The optic nerve leaves the eye from the inferior temporal quadrant, beneath the pecten. The nerve enters the chiasma and crosses to the contralateral side of the brain and there is no obvious ipsilateral projection. Polyak (1957) did describe a direct ipsilateral projection which left the majority of the fibres after the chiasma when the projection has become the marginal optic tract, and recrossed the midline to synapse in the anterior thalamus. Cowan, Adamson and Powell (1961) did not confirm this projection but since a projection of this type is known to exist in the lizard, its existence in the pigeon cannot be easily dismissed (Armstrong 1950).

Posterior to the optic chiasma a group of large diameter fibres leave the optic tract and pass backwards to the ectomammillary nucleus. This tract has been called the basal optic root and appears to be homologous to the tract of the same name in mammals, where it is sometimes called the posterior accessory optic tract (Granit 1962), and the terminal nucleus the nucleus opticus tegmenti. In mammals it has been reported that this system may be concerned with the visual facilitation of motor cortex activity (Remond and Dobson 1961*). In birds no suggestion has been made to its function. Huber and Crosby (1939) report that it has connections with the oculomotor nuclei, and Jungherr (1945) states that its main efferent tract projects to the lateral geniculate nucleus pars dorsalis, another nucleus which receives a substantial direct input from the optic tract. Thus it seems that at least in birds this nucleus is more concerned with visual integrations than with interactions with other sensory or motor systems.

Lateral to the origin of the basal optic root, a group of fibres leave the marginal optic tract and penetrate an overlying cell structure, the nucleus lateralis anterior, where they terminate. This nucleus does not receive fibres of foveal origin according to Galifret (1966). It appears to be homologous to the nucleus of the same name in mammals where it projects to the parietal neocortex (Kappers 1936). In birds, according to Papez (1929), it contributes fibres to the thalamo-frontal tract and thus would seem to project to the forebrain. It should be

* The author has lost and is unable to trace the bibliographic reference to this paper.

noted however that Powell and Cowan (1961) did not find any retrograde degeneration in this nucleus after damage to the forebrain. While this does not invalidate Papez's finding it does suggest that this projection needs more definite evidence to confirm its existence.

Posterior and slightly medial to the nucleus lateralis anterior, fibres leave the optic tract and enter the overlying lateral geniculate nucleus pars ventralis. This nucleus is divided into a dorsal large-celled part and a ventral small-celled portion. Most of the degeneration following eye enucleation is confined to the dorsal large-celled portion (Powell and Cowan 1961). According to Galifret (1966) this nucleus receives fibres of foveal origin. This nucleus appears to be homologous to the praegeniculate gray of mammals (Polyak 1957) although in higher mammals it is not divided into large and small-celled sections. In mammals it shrinks considerably in relative size as we ascend the phylogenetic scale, so that in primates it is simply a strip of tissue overlying the anterodorsal surface of the laminated lateral geniculate nucleus. In the pigeon the only known projection of this nucleus is to the optic tectum (Papez 1929, Kappers et al 1936). There is no evidence of a projection to the forebrain (Powell and Cowan 1961).

Beyond the lateral geniculate nucleus pars ventralis, a band of fibres leave the optic tract to enter and terminate in a group of nuclei lying between the nucleus rotundus and the tectal layers (Fig.5). Different investigators have called these nuclei by different names (Table 2). The terminology used here is that of Karten and Hodos' stereotaxic atlas of the pigeon brain (1967) as this is the terminology that is most likely to become standard. According to Karten and Hodos (1967) these nuclei are the lateral geniculate nucleus pars dorsalis, nucleus lentiformis mesencephali pars magnocellularis and nucleus lentiformis mesencephali pars parvocellularis. This nomenclature represents a clear departure from previous authors and implies that they (Karten and Hodos) have concluded that the two divisions of the nucleus lentiformis mesencephali are homologous to the nuclei of the same name in the pretectal area of the rabbit (Kuhlenbeck 1942). Kuhlenbeck (1937) thought that all three of these nuclei were subdivisions of the lateral geniculate nucleus pars dorsalis, while Cowan Adamson and Powell (1961) thought that the

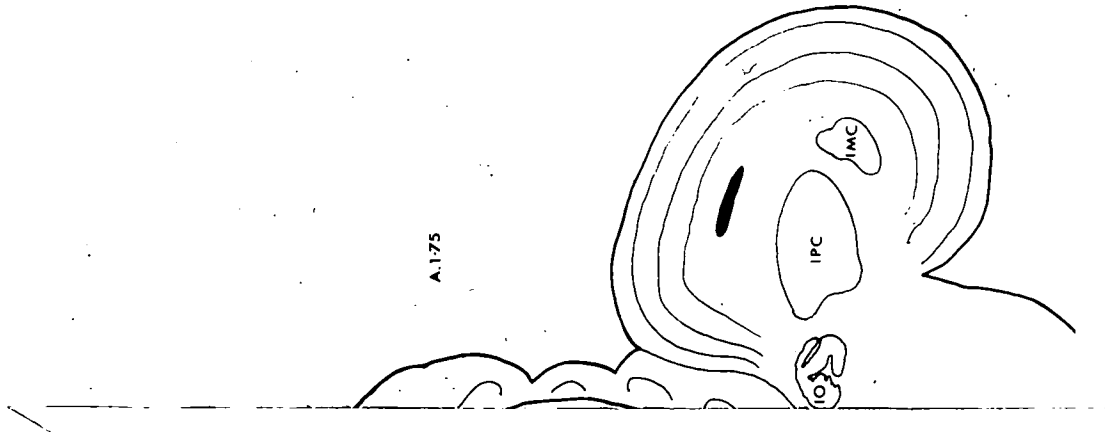

Table 2

Karten and Hodos (1969)	Others
Nucleus geniculatus lateralis pars dorsalis principalis	Nucleus externus of Rendahl (1924) Huber and Crosby (1929) Kappers et al (1936) Galifret (1966). Corpus geniculatum lateralis dorsale pars intercalatus of Kuhlenbeck (1937).
Nucleus lentiformis mesencephali pars parvocellularis.	Nucleus superficialis synencephali of Rendahl (1924) Huber and Crosby (1929) Kappers et al (1936) Galifret (1966). Tectal gray of Cowan et al (1961).
Nucleus lentiformis mesencephali pars magnocellularis	Nucleus superficialis magnocellularis of Rendahl (1924) Huber and Crosby (1929) Kappers et al (1936) Galifret (1966). Nucleus superficialis synencephali of Cowan et al (1961).
Nucleus lentiformis mesencephali pars magnocellularis and pars parvocellularis	Corpus geniculatum laterale dorsale pars principalis of Kuhlenbeck (1937).

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nucleus they call the n. superficialis synencephali (Nucleus lentiformis mesencephali pars magnocellularis of Karten and Hodos) was homologous to the dorsal section of the lateral geniculate nucleus. Although a decision as to the functional and anatomical homologies of these nuclei must await further work; at present there appears to a clear division of opinion as to which subdivision of the brain these nuclei belong in. Huber and Crosby (1929), Kappers et al (1936) and Kuhlenbeck (1937) group the mesencephali lateralis nuclei with the thalamus while Karten and Hodos (1967) group them with the mesencephalic pretectal nuclei.

Although in the last analysis the nuclei of the geniculate complex, like the pretectal nuclei, are derived from the optic tectum during ontogenesis (Stingelen and Senn 1969, Kuhlenbeck 1937, 1939) the classification of nuclei as thalamic or mesencephalic does reflect the extent to which investigators consider the visual thalamus of birds has evolved. In this context it should be mentioned that Galifret (1961) has recorded units in the n. lentiformis mesencephali pars parvocellularis that showed definite peaks in certain spectral regions; 449, 540 and 589 mu. It appears to be a general rule among vertebrates that colour coded cells are found in the thalamic visual nuclei known as the lateral geniculate nucleus pars dorsalis or those nuclei that are clearly related to it phylogenetically. This would tend to suggest that at least one division of the nucleus lentiformis mesencephali is more thalamic than pretectal. Galifret (1966) has reported that only the nucleus geniculatus lateralis pars dorsalis and the nucleus lentiformis mesencephalii pars parvocellularis receive fibres of foveal origin.

Despite previous reports of an absence of any direct visual thalamic projection to the telencephalon (Cowan, Adamson and Powell 1961) a recent report by Karten and Nauta (1968) has described such a system. Using a different anatomical technique from Cowan et al (1961) they described direct projections to a number of nuclei that had not previously been reported. The lateral portion of the area pretectalis receives a direct retinal projection and in addition two nuclei in the dorsal thalamus; nucleus dorsolateralis anterior pars lateralis and nucleus dorsolateralis anterior pars magnocellular is. In the burrowing owl this dorsal thalamic system was found to project onto the granule cell layer of the wulst (Hyperstriatum accessorium and hyperstriatum intercalatus superior). A similar projection in all probability exists in the pigeon (Fig.6). Although specific anatomical evidence is not available as proof there has been one brief report of visual evoked potentials in this region of the forebrain with a latency sufficiently brief (10-20m.sec) to imply that the projection was reasonably direct (Adamo and King 1967).+

+F.N. Recently Revzin (1969) has reported single cells in this area of the forebrain which are triggered by visual stimuli.

Having given off the previously described thalamic, and possibly some mesencephalic projections, the marginal optic tract sweeps around in latero-dorsal and ventral directions to cover the surface of the optic tectum, probably the most well developed and differentiated structure of the avian brain. The projection from the retina to the tectum is topographically organised, the antero-ventral quadrant of the retina projecting to the dorso-posterior quadrant of the optic tectum (Hamdi and Whiteridge 1954). The projection of the foveal region to the lateral surface of the tectum and its expansion relative to the more peripheral retinal areas has been confirmed electrophysiologically (Hamdi and Whiteridge (1954) and anatomically (McGill, Powell and Cowan 1966). This optic tectal projection undoubtedly comprises the greater part of the optic tract, despite the fact that there are so many independant and collateral projections elsewhere. While the evolutionary development of the tectum reaches its peak in birds, with the differentiation of the layers of the tectum in particular, no degenerating boutons are found deeper than the second layer following eye enucleation (Cowan Adamson and Powell 1961). The layers of the tectum usually distinguished are:-

A) Stratum opticum
B) Stratum griseum et fibrosum superficiale
C) Stratum griseum centrale.
D) Stratum album centrale.
E) Stratum griseum periventriculare.
F) Stratum fibrosum periventriculare.

While degenerating boutons are found only in layer A and B, layer B is extremely complex and can be further subdivided (Huber and Crosby 1933). As well as being the main afferent layer for the visual system, the stratum griseum et fibrosum superficiale is also the main receptive layer for sensory inputs from other modalities (Huber and Crosby 1933 Cobb 1963). A prime feature of the avian optic tectum as described by Huber and Crosby is the convergence of visual, auditory and somatic fibres on the stratum griseum et fibrosum superficiale, and this fact leads them to postulate that this structure should not be regarded as primarily a

visual one but as an intersensory correlation centre. This view of the function of the optic tectum has gained ground among investigators of mammalian brains recently (Schneider 1968, 1969), and there has been a move away from the view that the mammalian superior colliculus is that part of the brain whose function the striate cortex took over in evolution (Humphrey and Weiskrantz 1967). Perhaps it is worth emphasising that in birds the structure as well as the inputs to the optic tectum are fundamentally the same as in the mammalian colliculus where electrophysiological evidence about non-visual projections is available (Abrahams and Falchetto 1966, Jassik-Gerschanfeld 1966, Horn & Hill 1966). The expansion of the optic tectum in birds is probably demanded because of the necessity of creatures which move rapidly with respect to their environments possessing a highly efficient spatial orientation mechanism. The large visual input to the optic tectum probably reflects the importance of vision as a source of information about the relative positions of objects in the environment. The analysis of colour and pattern is probably carried out by the thalamic visual system. The proposition that the optic tectum is not the major centre for visual analysis is an important one because it influences the way in which one views the ascending projections of the optic tectum.

There are two major projections of the optic tectum in birds, one an ascending system that runs via the nucleus rotundus to the ectostriatal region of the avian forebrain, and the other a descending system that runs to the nuclei of the isthmi complex. Neither the nucleus rotundus or the ectostriatum on the one hand, nor the nuclei of the isthmi complex on the other have been identified as being homologous to any nuclear group found in mammals, although there is a possibility that the nucleus rotundus may have certain properties in common with the nucleus lateralis posterior of the mammalian thalamus. This nucleus has been described by Altman and Carpenter (1961) as receiving a substantial input from the superior colliculus in the cat and in the tree shrew (Tupaia glis) projects to the circumstiate cortex (Snyder and Diamond 1970). Just how far this similarity can be extended must await more information on the functional role of these nuclear groups in the behaviour of both species.

The descending projection from the optic tectum goes to the nuclei of the isthmi complex (Karten 1969). These nuclei are:-

A) Nucleus isthmi pars parvocellularis
B) Nucleus isthmi pars magnocellularis.
C) Nucleus isthmi pars semilunaris
D) Nucleus isthmo opticus.

The nucleus isthmo opticus is the source of the fibres that run in the centrifugal tractus isthmo opticus to the retina where they synapse in the inner nuclear layer. Thus this nucleus must be involved in a very direct way in influencing the afferent activity to the brain. The nucleus is topographically organised, a given region receiving its input via the tectum from a localised area of the retina and sending fibres back to the same retinal area. The other nuclei of the isthmi complex have not had their projections worked out in detail, but they are known to have connections with the oculomotor nuclei. According to Showers and Lyons (1968) the fibres of the isthmi complex project to the paleostriatum augmentatum and the neostriatum caudale.

The ascending projection from the optic tectum to the forebrain has been described by Karten and Revzin (1966) and Revzin and Karten (1967). Following lesions of the optic tectum dense degeneration is found in the ipsilateral nucleus rotundus. If the nucleus rotundus is stimulated electrically then short latency evoked potentials are found in the ectostriatal region of the forebrain. Kondo (1933) also described a projection from nucleus rotundus to the ectostriatum using the Marchi degeneration technique. Karten and Hodos have described this system as a major pathway subserving vision, but the evidence that it subserves vision in an exclusive or even in a major way appears to be lacking. The evidence that it is a visual pathway can be summarised thus: lesions in the optic tectum cause degeneration in the nucleus rotundus and electrical stimulation of the statum griseum and stratum album central cause large evoked potentials in the rotundus. However in the anatomical study all the lesions appeared to involve the central layers of the tectum (Karten and Revzin 1966) and in the electrophysiological study large potentials were produced in the rotundus only when the stimulating electrode was in the central layers of the tectum (Revzin and Karten 1967). It is noticeable in the latter study that

electrical stimulation of the marginal optic tract produced potentials equivalent in amplitude in the rotundus to those produced by stimulation of the nucleus mesencephalicus lateralis pars dorsalis, a nucleus that has been shown to be involved in the relay of auditory information to the thalamus. (Karten 1967, 1968). One of the main reasons why Karten and Revzin (1966) excluded the involvement of the nucleus rotundus in the relay of non visual information to the telencephalon was the fact that lesions of the spinal cord did not produce any anterograde degeneration in the rotundus. However it has been pointed out by Kappers et al (1936) and Baker-Cohen (1968) that a typical pattern in the non-mammalian brain is the tendency of ascending somatic and auditory fibres to synapse in the tectal layers before being relayed to the thalamus.

Two other facts need to be taken into account in considering the extent to which the nucleus rotundus may be involved in any major way in the avian visual system. Revzin (1966) found unit responses to light flashes in the rotundus, while in a study by Hodos and Karten (1966) lesions in the n. rotundus produced deficits in brightness and pattern discrimination. In considering the weight that should be asigned to the finding of visual units in a particular nucleus of the thalamus, consideration should be given to the work of Diamond and his associates (reviewed in Diamond 1967) that in mammals that have evolved from lines that were in existence before the evolution of carnivores the sensory projections to the thalamus are not highly specific. Thus visual auditory and somatic units were found in the medial geniculate body of the hedgehog (Diamond 1967) and studies of retrograde degeneration in the opossum the whole of thalamic projection onto the cortex had to be destroyed in order to produce degeneration in any given thalamic nucleus, and then of course they all degenerated. This argues strongly for a consideration of the relative size of the input to a particular area as being a criterion for deciding whether a given area is visual auditory or somatic.

Studies that show deficits in visual learning by animals need to be treated with care before they can be interpreted as offering evidence for the involvement of a particular structure in a particular

sensory system. The situation used by Hodos and Karten (1966) was a two-key situation in which the animals had to choose between one of two stimuli presented to it. Such studies in the past have produced results that have pointed to the importance of particular structures in visual discrimination. Blake (1959) claimed that lesions of the superior colliculus in cats produced deficits in brightness and pattern discriminations. Hers was a two choice situation, and the study was similar to that of Hodos and Karten in that it involved training the animals and after they had acquired the discrimination lesioning them. The work of Schneider (1969, 1968) with the golden hamster has shown that the apparent loss of ability to discriminate patterns after lesions of the colliculus is due to the difficulty that the animals have in orienting to either an auditory or a visual stimulus, and that the deficit is not properly described by calling it a visual pattern deficit. The work of Sprague (1963) on the cat suggests that the deficit resulting from collicular lesions in this species is a general one that involves difficulty in orienting to any stimulus whether it be auditory, visual or somatic. The relationship of the nucleus rotundus with the colliculus makes it a likely candidate for producing a similar sort of deficit if the organisation of the avian and mammalian brain is similar on very broad lines. At least the fact that in the cat spatial deficits can be construed as brightness and pattern deficits should make us wary of making the same mistake in the bird brain.

Karten and Revzin (1967) have stated that they have evidence of a projection from the ectostriatum to the overlying hyperstriatum and to the neostriatum caudale which lies posterior to the ectostriatum. The fact that visual evoked potentials have been found in the hyperstiatum (Adams and King 1967) does not directly support this finding, as they could, and probably are, mediated by the more direct pathway from the dorsal thalamus, as their latency appears to be too short to be mediated by the rotundo-ectostriatal system. Revzin (1966) found that the main response in the rotundus to a flash stimulus to the eye was a wave of inhibition with a latency of approximately 60 milliseconds whereas the latency of the evoked potential in the wulst occurs between 10 and 20 milliseconds (Adams and King). Karten and Revzin (1967) also reported

a pathway from the ectostriatum to neostriatum caudale. Concerning the existence of a visual pathway to the neostriatum caudale, Bremer Dow and Moruzzi (1939) found a response to illumination of the contralateral eye with an electrode on the dorsal cortex of the pigeon. They found that application of cocaine to the brain surface did not abolish the response and concluded that the response was probably subcortical in origin. They did not give any latency information, so that it is not possible to estimate whether this response was carried by the rotundo-ectostriatal system of Karten and Revzin, or whether the route was more direct. The only other report of a visual projection to the forebrain is that of Phillips (1966) who found a response to a flash of light in the archistriatum, a region of the avian forebrain probably homologous to the mammalian amygdaloid complex (Kallen 1953).

The organisation of the visual telencephalic projections in the pigeon brain appears to involve two major divisions; one system that ascends to the hyperstriatum via the dorsal thalamus and the other system that ascends to the ectostriatal region of the forebrain (Fig.6). These are described as the thalamofugal and tectofugal systems by Karten (1969). While the thalamic sectors of these ascending visual systems may be shown to be homologous to certain nuclear groups of the mammalian thalamus the possibility of finding functional and structural similarities between mammalian and avian brains in the terminal site of these projections does not seem so good. Karten (1969) has pointed out that the termination of the projection system from the dorsal thalamus on the hyperstriatum accessorium and hyperstriatum intercalatus superior is in many ways similar to the termination of geninculo-cortical system on a band of granule cells that comprise layer 4 of the cortex in mammals. However, since the currently accepted homologies of the dorsal geniculate of mammals are usually taken to be one or more of the group of nuclei that lie between the tectum and the nucleus rotundus of birds (Fig.5) then it is difficult to see this as more than a superficial resemblance. How meaningful it is to try to establish homologies, either morphological or functional, between the structures of animals that have evolved independently for so long is a question that can only be answered when more information is available on which to base the speculations. What

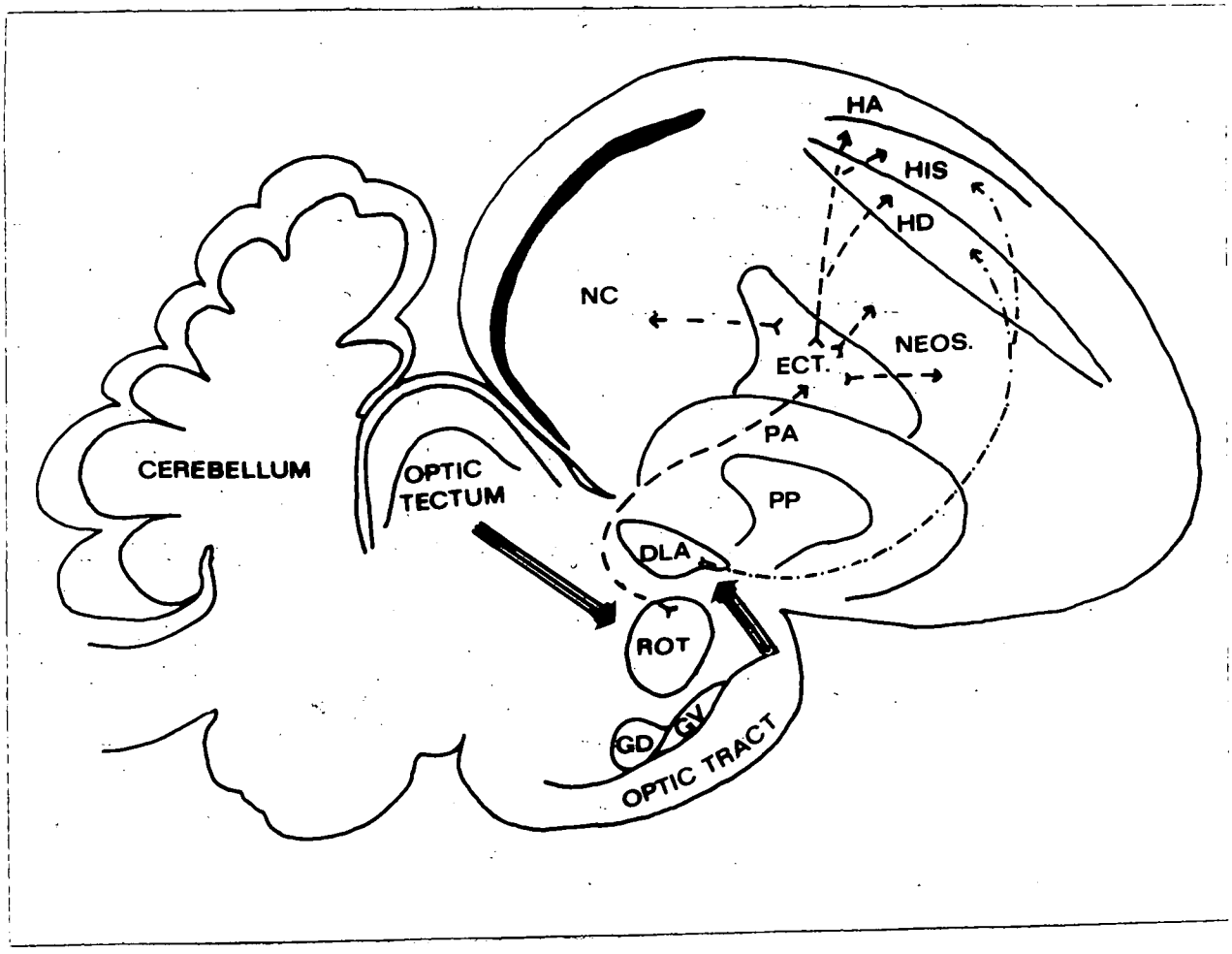


Figure 6. Visual projections to the forebrain of the pigeon, according to Revzin and Karten (1967) and Karten (1969a). The nucleus rotundus receives a large input from the optic tectum and sends its efferent fibres through tractus thalamo frontalis pars lateralis to the ectostriatum. The ectostriatum in turn sends fibres to the neostriatum and neostriatum caudale as well as to the hyperstriatum. This projection comprises the tecto-fugal system of Karten (1969a). The nucleus dosolateralis anterior thalami receives its input from the optic tract and sends its fibres through tractus thalamo frontalis to the hyperstriatum dorsale and ventral part of the hyperstriatum accessorium. This projection comprises the thalamo-fugal system of Karten (1969a). Abbreviations. DLA = N. dorsolateralis anterior. ECT = ectostriatum. GD & GV = lateral geniculate nucleus pars dorsalis and pars ventralis. HA = hyperstriatum accessorium. HD = hyperstriatum dorsale. HIS = hyperstriatum intercalatus superior. NC = neostriatum caudale. NEOS = neotriatum. PA = paleostriatum augmentatum. PP = paleostriatum primitivum. ROT = N. rotundus.

is striking is that the ability of pigeons to perform visual discriminations based on colour, pattern orientation or brightness should be so similar to the behaviour of the highest evolved mammals. Towe (1954) showed that pigeons trained to discriminate between a triangle and a square retained the discrimination, despite alterations in the figure ground brightness, alterations of size, and considerable distortion of the patterns themselves. Towe (1954) remarks "this extent of transfer to distorted figures is comparable to that which appears in rats and primates only after specific concept formation training". Hernstein and Loveland (1964) found that pigeons could be trained to discriminate coloured slides containing people from slides containing objects and the birds showed immediate transfer to black and white slides. This ability to make extremely subtle discriminations argues for a highly refined visual system and in mammals discrimination of this sort requires the integrity of the visual cortex. It seems likely that in birds too the forebrain must contain systems that play an important part in these types of complex discriminations.

Apart from the studies mentioned above, there has been little work carried out on visual inputs to the bird's forebrain. The studies described have all confined themselves to studying specific areas of the forebrain, and no systematic attempt has been made to examine the extent of its visual input. This question is an important one for it is possible that, as is the case with lower mammals, the sensory projections to the forebrain may be extremely diffuse (Diamond (1967). There is some slight indication that this may be the case from the work of Powell and Cowan (1961) who found that destruction of the ectostriatum, which according to Revzin and Karten (1967) is the target area for the rotundal projection did not produce retrograde degeneration in the rotundus. Only when the lesions invaded the underlying paleostriatum did the rotundus show degeneration. This type of finding is suggestive of a much wider distribution of rotundal efferents than the studies of Revzin and Karten would lead one to believe.

The projection of the pigeon's thalamic visual system on the forebrain appears to be divided into two major parts if the interpretation

of Karten and Revzin (1967) and Karten (1969) are to be accepted; a system that runs from the dorsal thalamus to the hyperstriatum, and a system that runs from the tectum through the nucleus rotundus to the ectostriatum. Other authors have reported finding evidence of visual projections to other parts of the pigeon's forebrain; Phillips (1966) reported visual evoked potentials in the archistriatum and Bremer Dow and Moruzzi (1939) found an evoked potential to light in the caudo medial area of the pigeon's forebrain. Whether areas outside those mentioned receive any visual input is not known as there has been no systematic exploration of the avian forebrain in search of visual projection areas. Evidence from the effects of lesions in the forebrain in birds is rare. Layman (1936) studied the effects of lesions in the forebrain of chickens on a triangle-circle discrimination task. She found that only lesions that involved the antero-medial sector of the forebrain produced severe impairment in learning, although some of the lesions involving the caudal sector of the forebrain also produced noticeable deficits. None of her lesions completely destroyed either the hyperstriatum of the ectostriatum bilaterally. Zeigler (1963) also studied the effects of forebrain lesions in pigeons on a triangle-circle discrimination. Like Layman (1936), his lesions did not completely destroy any known target area for visual afferents although he found that lesions to the hyperstriatal region resulted in impairment both on learning and memory tasks. The only other work of any relevance to the function of the avian forebrain in vision is that of Rolando (1823) who found that extirpation of tissue in the caudal forebrain area of chickens produced innaccuracy in seizing grain.

Experimental work on visual projections to, and the function of visual target areas within, the avian forebrain remain incomplete in several important respects. Firstly, there is the question of whether the projections to the forebrain as described by Karten (1969) in his summarising account of visual projections in birds are complete. Secondly, there is the question of what effect lesions to these visual target areas have on visual function in birds. Lastly, there is the problem that, except in the case of the hyperstriatum, each of the projections have been described only by one author using one technique:

the tecto-rotunduo-ectostriatal pathway by Karten and Revzin (1967), although previous authors (Kondo 1933, Kappers et al 1936) did provide inconclusive evidence of this projection system; the archistriatal projection by Phillips (1966); the projection to the dorsal cortical area by Bremer Dow and Moruzzi (1939). There is obviously a need to replicate these findings.

Chapter 2. VISUAL PROJECTIONS TO THE FOREBRAIN OF THE PIGEON

As stated in Chapter 1, the available information on visual projections to the forebrain of the pigeon is limited. The information we have is the result of studies of specific areas within the forebrain (Phillips 1966, Adamo and King 1967, Bremer Dow and Moruzzi 1939) or is the result of investigators following fibre tracts from the diencephalon using experimental, anatomical or electrophysiological techniques (Kondo 1933, Karten and Nauta 1968, Karten and Revzin 1966, Revzin 1969, Revzin and Karten 1967). There has been no systematic investigation of the forebrain in an attempt to delineate specific areas responsive to visual stimulation. Also there is a clear need to replicate the findings of Revzin and Karten (1967) concerning the projection from optic tectum to rotundus to ectostriatum using natural (photic) stimulation. The findings of Phillips (1966) on a projection to the archistriatum and of Bremer, Dow and Moruzzi (1939) on a projection to the caudo-medial surface of the forebrain also need replication as they have only been reported once. The experiments to be reported in this chapter were aimed at fulfilling these objectives, and also with the aim of using the results in studies of the effects of lesions to forebrain areas receiving visual input on visual discrimination tasks.

METHOD

30 pigeons were used in the experiments. The pigeons were anaesthetised with Equithesin (2.5 cc per kilogramme body weight) and placed in a modified rat stereotaxic apparatus. The skin overlying the skull was cut and held back with retractors and a few drops of 2% xylocaine placed on the wound. A small hole was made in the skull using a dental drill, the dura was cut with a sharp needle and the electrode introduced. The electrodes were either bipolar or monopolar, although bipolar electrodes were used in the majority of cases as these reduced interference considerably. The bipolar electrodes were made from .5mm diameter insulated stainless steel tubing and 36 s.w.g. insulated stainless steel wire which was pushed through the

tubing until the tip just appeared, and was then cemented in place with araldite. Monopolar electrodes were made from stainless steel insect pins which had received four to six coats of Schenvar varnish. Both types of electrodes were tested for the integrity of their insulation, after a small region of the tip had been ground bare using a small grindstone, by immersing them in a dish of saline and passing 2 volts D.C. between the electrode and the bath. Those electrodes that showed bubbling anywhere but the tip were discarded.

During recording sessions the stereotaxic instrument containing the bird was placed in a shielded enclosure open on one side to permit unimpeded photic stimulation. The potentials were amplified on a Tektronix 122 preamplifier using a low frequency cut-off of 5 cycles and a high frequency cut-off of 250 cycles. The output from the preamplifier was taken to a second amplification system and from there to a Biomac 500 signal averager. The output from the preamplifier was simultaneously displayed on an oscilloscope so that individual potentials could be monitored to see that the build-up on the averager was systematic. A triggering pulse, simultaneous with the start of the sweep of the signal averager, was used to trigger a Dawe model 1201E stroboscope positioned 18 inches from the birds eye. The output of the stroboscope was a 40 microsecond 90 joule flash. A Nuclear Chicago constant current stimulator was interposed between the Biomac 500 and the stroboscope in order to give sufficient current to trigger the stroboscope and to provide a slight delay so that the stimulus artefact, which was recorded by a photocell, could appear on the sweep of the averager. For some records the output from the preamplifier was displayed on a storage oscilloscope. Permanent records were made during the course of the experiment by photographing the display tube of the signal averager or the storage oscilloscope. At the conclusion of the experiment the bottom of the electrode track was marked by passing radio frequency current for 10 seconds. The pigeon was then decapitated and perfused through the carotid arteries with 10% saline followed by 10% formalin.

The heads were stored in formalin until ready for histological

processing, when they were blocked in the plane of the stereotaxic atlas of Karten and Hodos (1967). The brains were either embedded in paraffin wax and sectioned at 25μ, or else sectioned at 50μ, on a freezing microtome. The sections were stained either with haematoxylin or cresyl violet. The positions at which the potentials were recorded were located by noting the plate in the atlas of Karten and Hodos that corresponded to the plane of entry found on the sections and noting the position of the lesion that marked the termination of the electrode track. Notes made during the course of the experiment of the position of the microdrive when the tip of the electrode entered the brain (seen by the disappearance of 50 cycle hum) and the position when the lesion was made enabled the tip location for any given potential to be calculated fairly accurately. Subsequent penetrations through the same structure provided a check on the accuracy of this method and it was found to be highly reliable.

All potentials reported were recorded on the side of the brain contralateral to the stimulated eye. All these potentials are highly repeatable. They are, in the case of the averaged potentials, the result of 32 presentations of the stimulus with a minimum interstimulus interval of 600 milliseconds. In some cases this fairly fast presentation rate resulted in noticeable attenuation of the response as seen on the oscilloscope, and in these cases the presentation rate was slowed. A presentation rate slower than 1 stimulus every 1500 milliseconds was never needed to secure a maximum response. Where latency measurements are given in the results section the measurement is from the beginning of the stimulus mark to the first significant departure from baseline. Records were usually made at two sweep lengths, 62.5 milliseconds and 250 milliseconds. The shorter sweep speed was made in order to facilitate accurate latency measurements. Sometimes however, sweeps up to 2 seconds duration were used.

RESULTS

Figure 1 shows the positions of the penetrations superimposed on a drawing of the dorsal surface of the brain. While the penetrations do not cover the brain in a uniform fashion they do represent a good sample,

since all the major forebrain areas were penetrated and recordings taken. The uneven distribution of the penetrations is due to errors in positioning

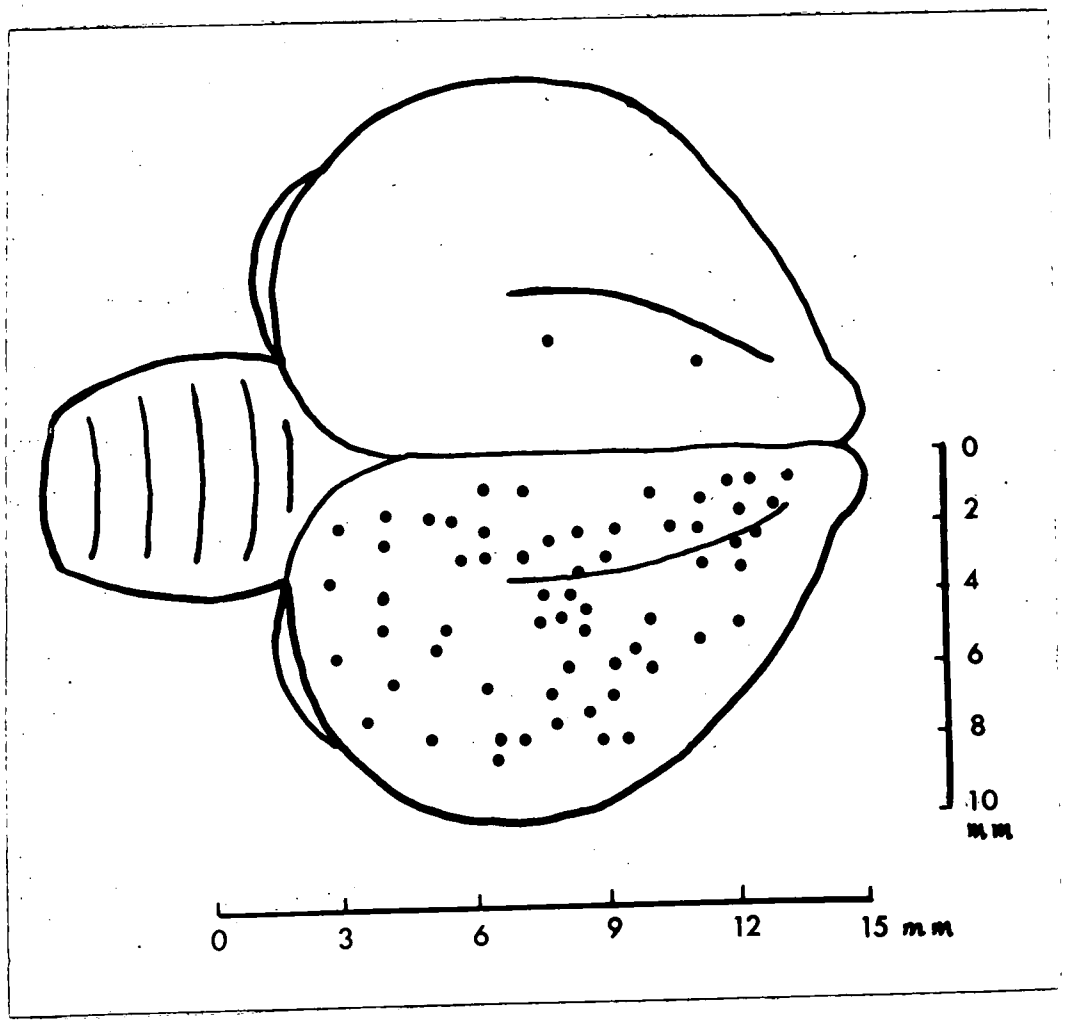


Figure 1: This drawing shows the distribution of penetrations through the forebrains of the pigeons used in this study.

the electrodes when using the co-ordinates of the atlas of Karten and Hodos (1967). These errors (in some cases as much as 2 millimetres) are undoubtedly due in part to the wide variation in skull size of the animals used in these experiments; also the ear bar sheaths of the stereotaxic instrument (Krieg modified) were rather large and rounded and this probably also contributed to the errors. The use of a different stereotaxic instrument in later experiments (Kopf with pigeon adaptor) greatly improved the accuracy of penetrations.

In order to determine the latencies of potentials in the principal diencephalic and mesencephalic centres, several penetrations into the diencephalon and mesencephalon were made. The latency of potentials in the optic chiasma is between 14 and 15 milliseconds. The potential is complex because potentials were produced in both optic nerves despite the fact that the eye contralateral to the stimulated eye was

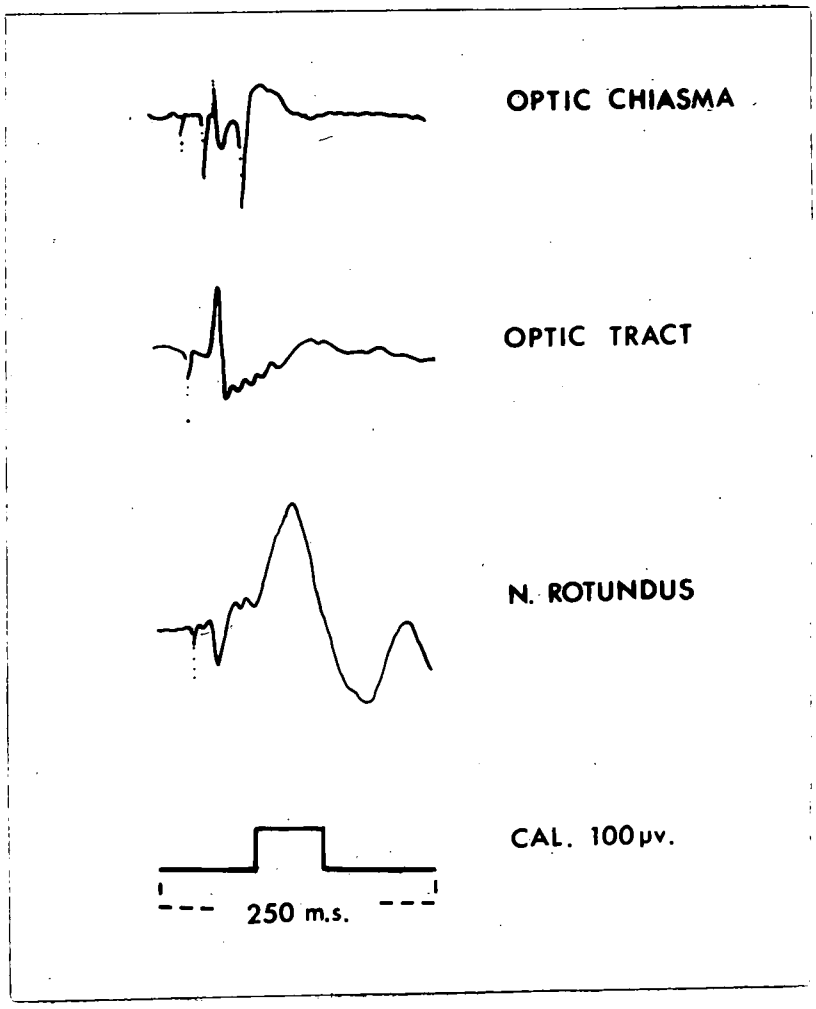


Figure 2: Tracings of the potentials recorded in the optic chiasma, optic tract and nucleus rotundus of the pigeon. Note that the first downward peak of the potential recorded from nucleus rotundus did not originate within the nucleus. The tip of the bipolar recording electrode was just ventral to the rotundus and recorded the volume spread from the optic tract.

covered. This precaution was taken because the lid is transparent and

light was reflected from the walls of the experimental room when the stimulus was delivered. The second peak in the potential is produced by light diffusing across the thin transparent lamina of bone that separates the eyes in the midline. This second peak can be seen to have disappeared when the potential from the optic tract is recorded

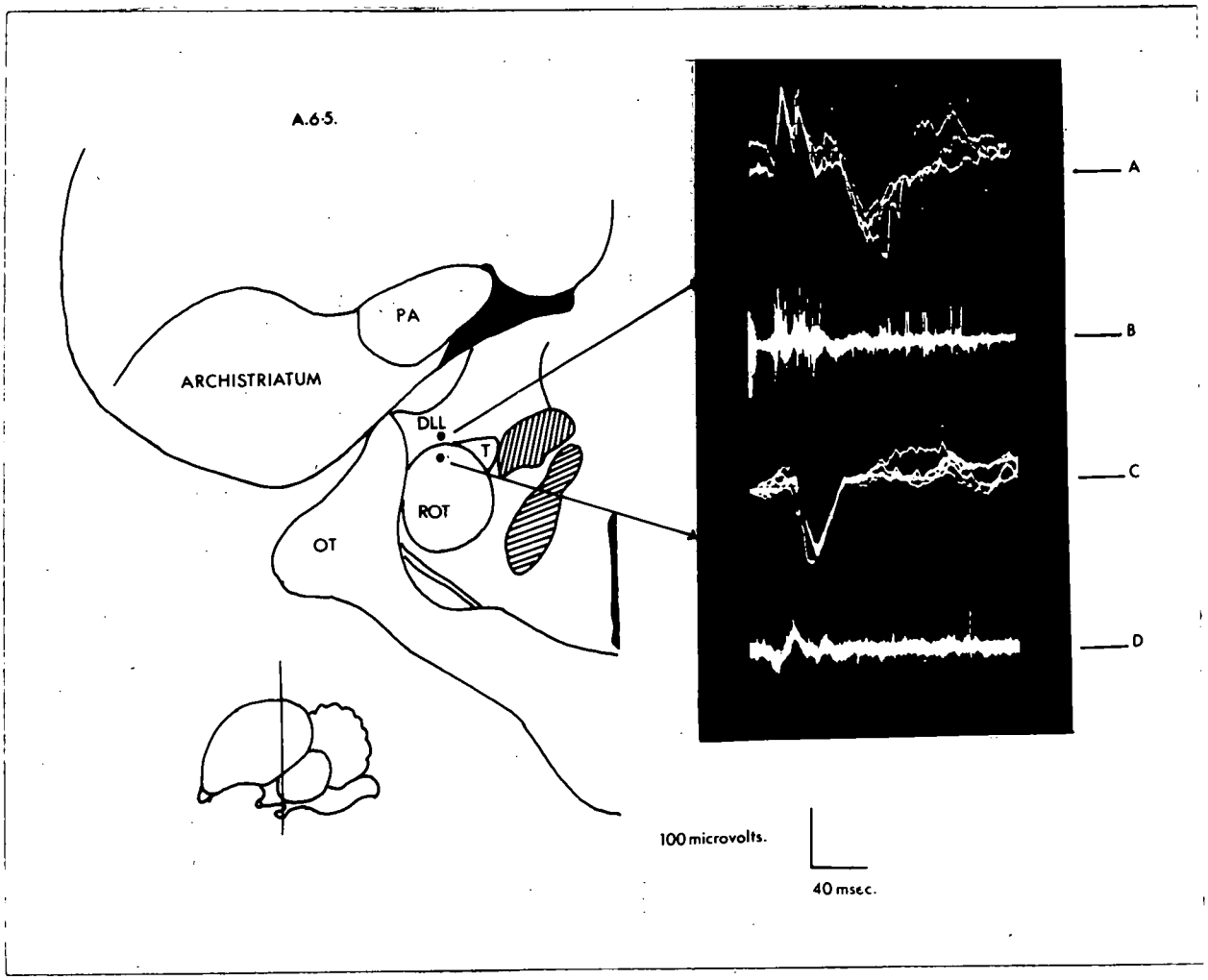


Figure 3: Recordings from the dorsal thalamus of the pigeon. A - shows the evoked potential recorded with the electrode tip in the nucleus dorsolateralis anterior pars lateralis. Time constant of amplifier 1 second. B - shows a recording from the same site with a low frequency cut off of 100 cycles. C - electrode tip in nucleus rotundus and the sheath in the dorsal thalamus. Time constant of amplifier 1 second. D - same as C but with low frequency cut off at 100 cycles. The reversal of the potential in C indicates that the recording was from the sheath of the bipolar (Concentric type) electrode.

(Fig.2). The optic tract potential is easily identifiable because of the series of high frequency oscillations (90 - 100 cycles per sec) that follow the primary potential. The latency of the potential at the medial surface of the optic tectum is between 15 and 16 milliseconds. By the time the afferent volley has reached the nucleus rotundus (Fig.2) the latency of the potential is 50 milliseconds or more. In those thalamic nuclei receiving direct input from the optic tract the onset of the postsynaptic activity is difficult to estimate as the potential is partly obscured by the incoming optic tract volley (Fig.3), but it can be seen that it does closely follow the optic tract input and is probably of the order of 17 milliseconds.

Evoked potentials found in the forebrain can be conveniently divided into four sections.

1) Potentials found in the hyperstriatum.
2) Potentials found in the neostriatum.
3) Potentials found in the paleostriatum.
4) Potentials found in the neostriatum caudale.

1. EVOKED POTENTIALS IN THE HYPERSTRIATUM

Small amplitude potentials with a latency of approximately 23 milliseconds were found throughout the hyperstriatum, from the surface through to the hyperstriatum ventrale. The potentials show reversal (in some cases more than once) indicating that the potentials arise within this area and are not due to spread from other sources (Fig.4). These potentials typically have an amplitude of between 20 - 30 microvolts except in a localised area of the anterior hyperstriatum. In the anterior hyperstriatum (planes A. 11 to A. 12.5 in the atlas of Karten and Hodos) potentials of much larger amplitude are found. These potentials of larger amplitude show 2 reversals during passage of the electrode from the surface of the brain through to the neostriatum. The first reversal takes place close to the border of the hyperstriatum dorsale and the second reversal takes place within the hyperstriatum ventrale (Fig.4). When the electrode enters the neostriatum the potential disappears. It should also be noticed that the potentials near the surface of the

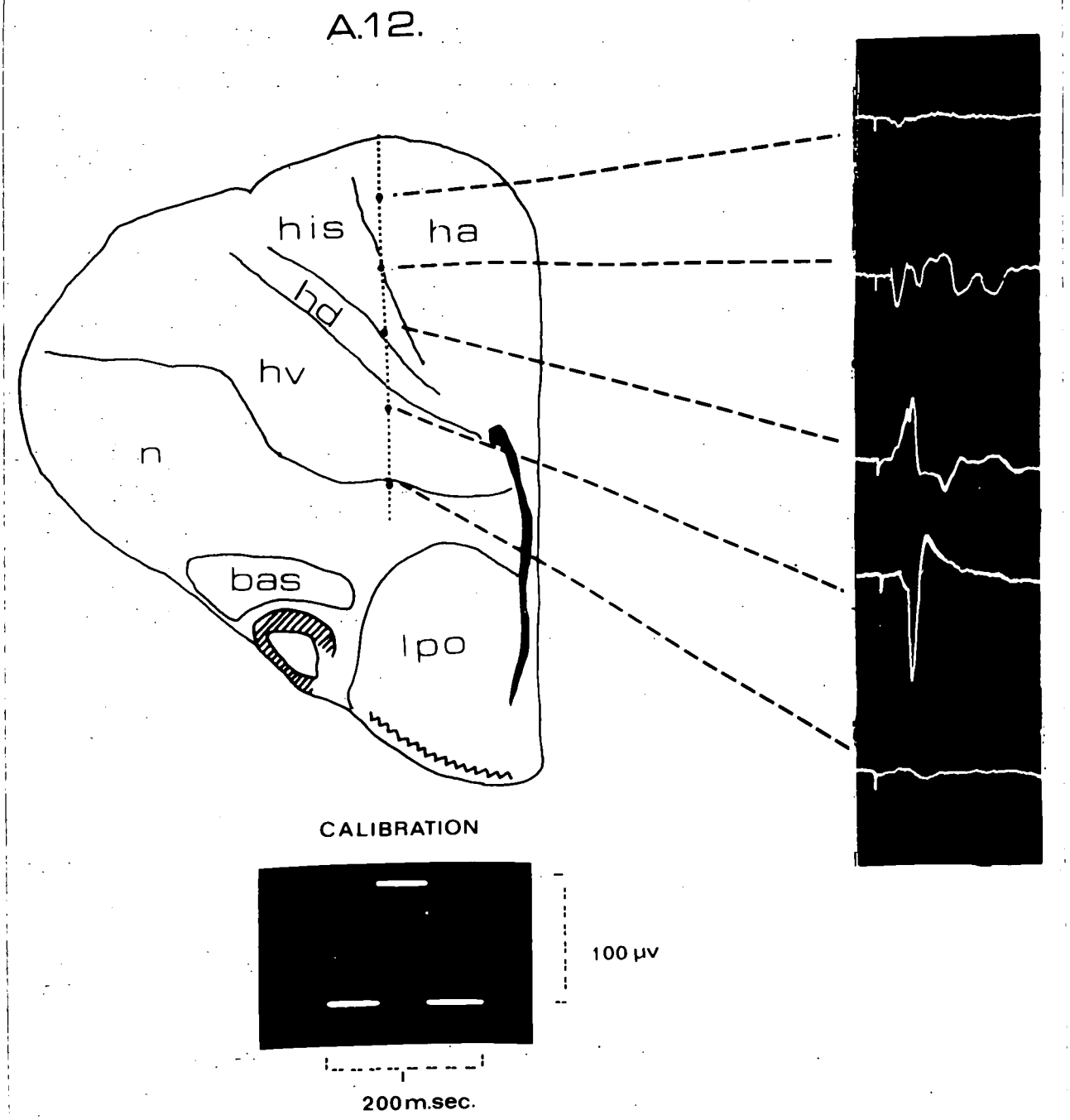


Figure 4: Recordings during a single penetration of the anterior hyperstriatum. The potential recorded from the upper border of the hyperstriatum intercalatus superior (his) is highly repeatable in this region despite its complexity. Note that the waveform of the potentials becomes simpler as the electrode advances through the layers. Abbreviations: bas - nucleus basalis, ha - hyperstriatum accessorium, hd - hyperstriatum dorsale, his - hyperstriatum intercalatus superior, hv - hyperstriatum ventrale, lpo - lobus para olfactorius, n - neostriatum. Recording was bipolar.

hyperstriatum is extremely complex and it becomes simpler in form as the electrode tip advances ventralward.

2. EVOKED POTENTIALS IN THE NEOSTRIATUM

In the anterior neostriatum evoked potentials are not found. Neither are they found in the posterior or medial neostriatum. Potentials are found consistently in a band of tissue surrounding the ectostriatum. When the electrode enters the brain overlying the anterior ectostriatum the tip of the bipolar electrode shows a potential positive with respect

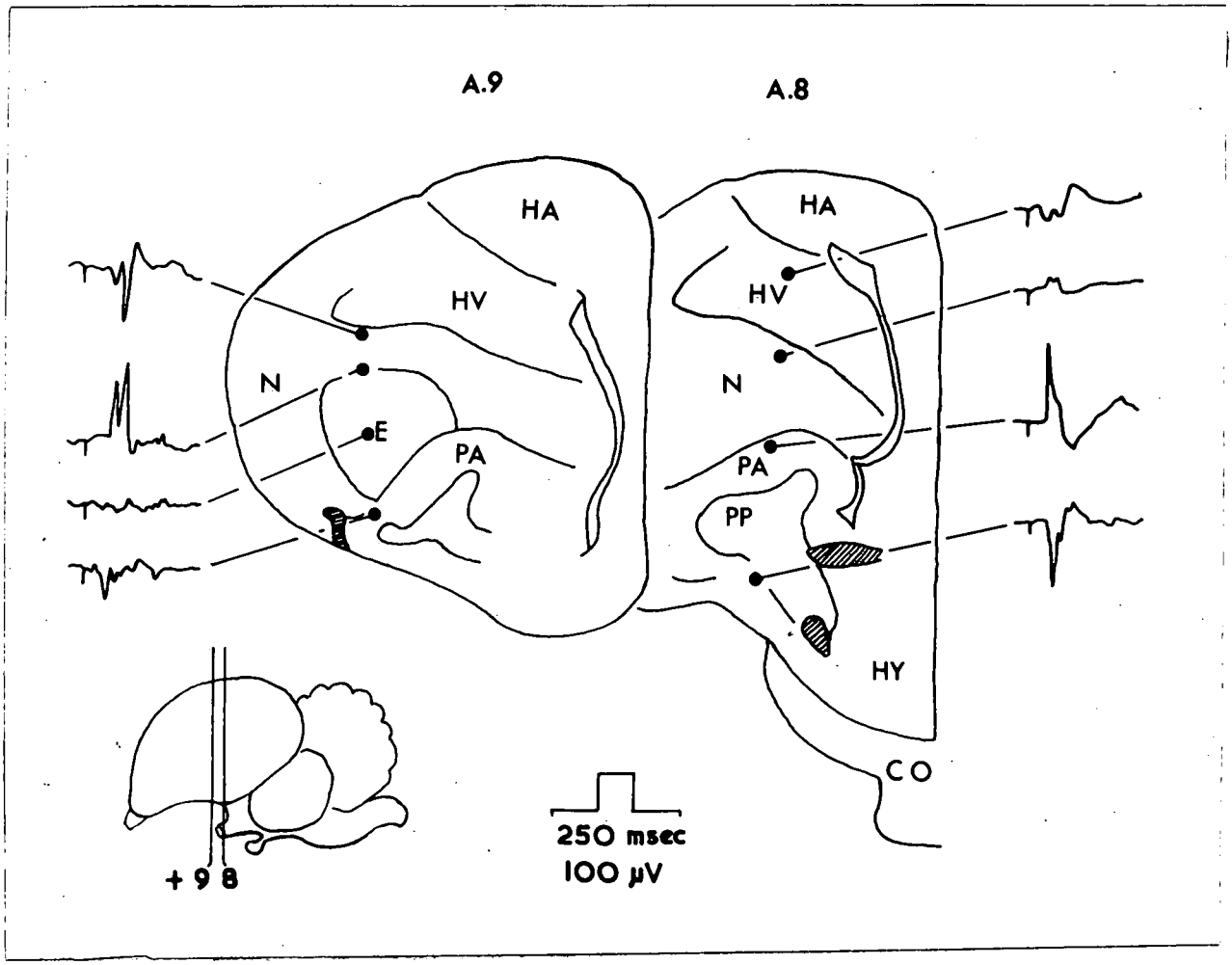


Figure 5: Recordings of two penetrations. Penetration shown on the left at anterior 9 (Atlas of Karten and Hodos) shows that potentials are not found within the ectostriatum proper. Penetration on the right shows potentials within the posterior sector of the hyperstriatum and potentials within the paleostriatum augmentatum (PA). Abbreviation: CO - Optic chiasma, HA - hyperstriatum accessorium, HV - hyperstriatum ventrale, HY - hypothalamus, E - ectostriatum, N - neostriatum, PA - paleostriatum augmentatum, PP - paleostriatum primitivum. Recordings were made with a concentric bipolar.

to the sheath. As the tip enters the ectostriatum the potential reverses (tip negative) and a potential does not reappear until the tip enters the lateral edge of the paleostriatum underlying the ectostriatum (Fig.5). In the more posterior regions of the neostriatum potentials are recorded close to the lateral edge of the ectostriatum and the potentials become more complex as the tip approaches the lateral border of the paleostriatum

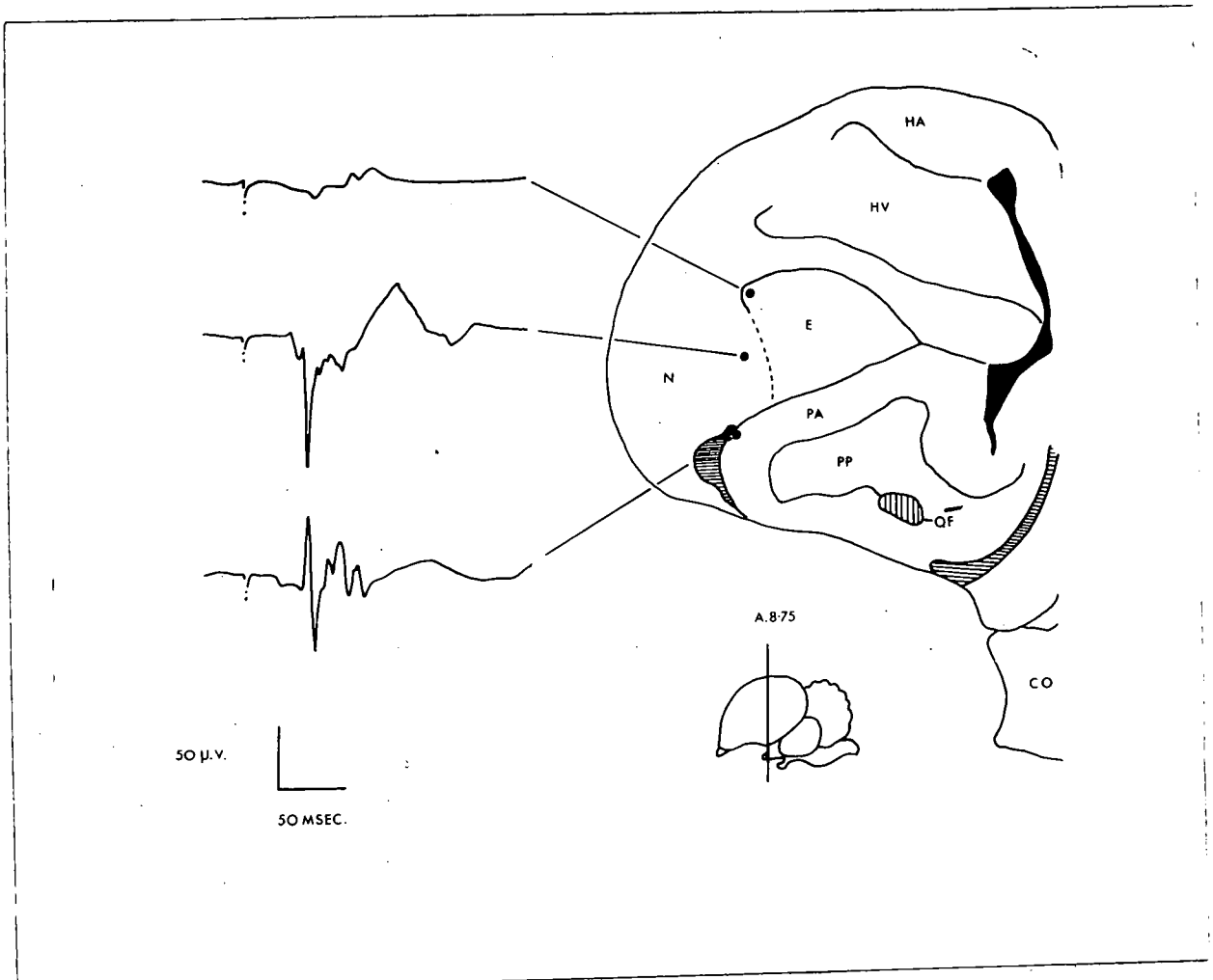


Figure 6: Recordings at the lateral edge of the ectostriatum. The major peak reverses when the electrode tip enters the lateral edge of the paleostriatum augmentatum but several other peaks of smaller amplitude appear. Abbreviations: CO - optic chiasma, E - ectostriatum, HA - hyperstriatum accessorium, HV - hyperstriatum ventrale, QF - tractus quinto frontalis, PA - paleostriatum augmentatum, PP - paleostriatum primitivum.

augmentatum (Fig.6). There is a reversal of this potential as the tip enters the paleostriatum augmentatum. In other parts of the neostriatum evoked potentials are not found. This area within which the potentials are found is definitly not the ectostriatum since the potentials are found outside the border, but it may correspond to what Karten (1969) has called the periectostriatal area. It is to the ectostriatum proper that the projection from nucleus rotundus goes, and the latency of these potentials (about 35 millsecs) is nearly 20 milliseconds faster than those recorded from the nucleus rotundus.

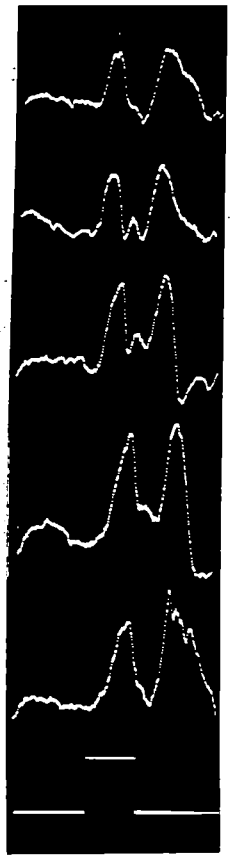
3. EVOKED POTENTIALS IN THE PALEOSTRIATUM

Potentials were found throughout the length and breadth of the paleostriatum, but not in the paleostriatum primitivum. The latency of these potentials (see Fig.5 above) is again faster than those found in the nucleus rotundus and is in the region of 33 - 35 milliseconds. The finding of potentials in this region of the avian forebrain is not surprising as all the fibre projections to the forebrain run through this structure. The potentials found here are too slow to give rise to hyperstriatal evoked potentials being almost 10 milliseconds too late, and on no penetration was any activity found that would be fast enough to represent a fibre tract projecting to that region. Whether the projection through this area is too diffuse to be picked up by the electrodes used in this study and that the potentials represent a true projection to the paleostriatum augmentatum itself cannot be decided on the present data.

4. EVOKED POTENTIALS IN THE NEOSTRIATUM CAUDALE

When an electrode is placed on the caudo-dorsal surface of the pigeon's forebrain a potential with a latency of approximately 23 milliseconds is recorded. Application of xylocaine to the surface of the brain does not abolish this potential. As the electrode is advanced through the ventricle into the neostriatum caudale the potential grows slightly in amplitude and can be recorded continuously through this area of the brain until it strikes the bone at the ventral surface of the forebrain. No reversal of the potential is apparent during the penetration

(Fig.7). The potential is too slow to represent current spread from the surface of the optic tectum and too fast to represent spread from those structures that border on the tectal ventricle. The potentials are almost impossible to record with large tip bipolar electrodes, but if bipolar electrodes of small tip size (50μ) are used, unit clusters firing at the appropriate latency (25 milliseconds) are found (Fig. 8).



CAL = 50. μv. 62·5m.sec. Total sweep.

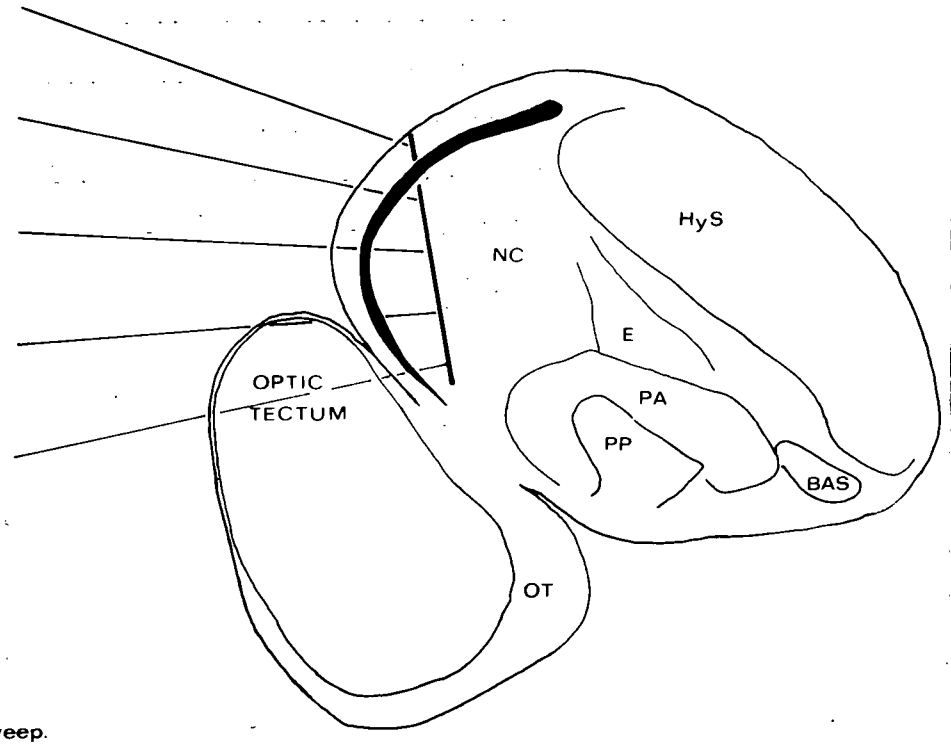


Figure 7: Recordings of a single penetration through the neostriatum caudale. Recordings are monopolar, tip size being approximately $\frac{1}{2}$ mm. Sagittal plane section.

Taken together this evidence suggest an extremely diffuse projection to this area of the brain.

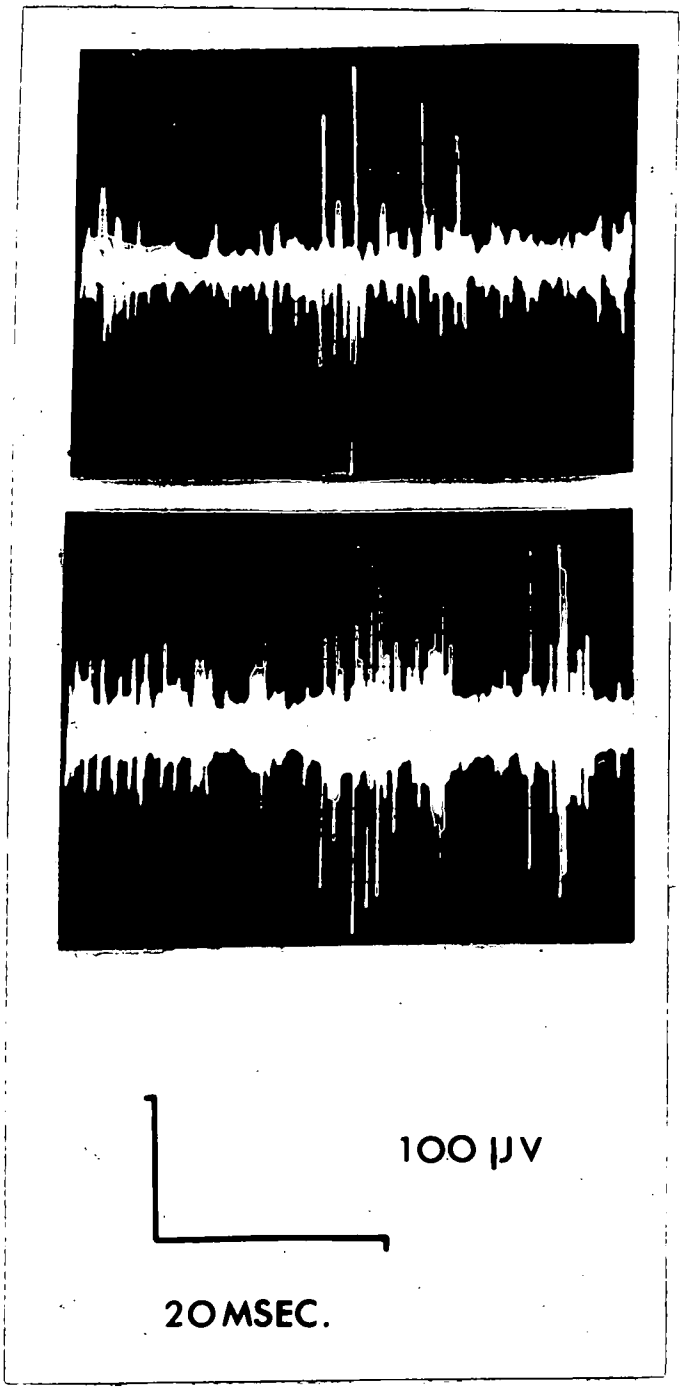


Figure 8: Unit clusters recorded in the medial part of the neostriatum caudale. Concentric bipolar with tip approx. 50 microns and sheath about 150 microns. Recordings made with a bandpass filter set to pass between 400 and 1400 cycles. Storage oscilloscope photographs. Stimulus coincidence with start of sweep.

The avian archistriatum has been reported as receiving short latency visual input from the diencephalon (Phillips 1966). Phillips (1966) recorded flash evoked potentials in the archistriatum of chickens and the latency he quoted when stroboscopic stimulation was used was between 10 and 20 milliseconds. In order to check on the existence of such a projection in the pigeon several penetrations of this area were made. On no occasion was a poential found within the nucleus with a comparable latency or

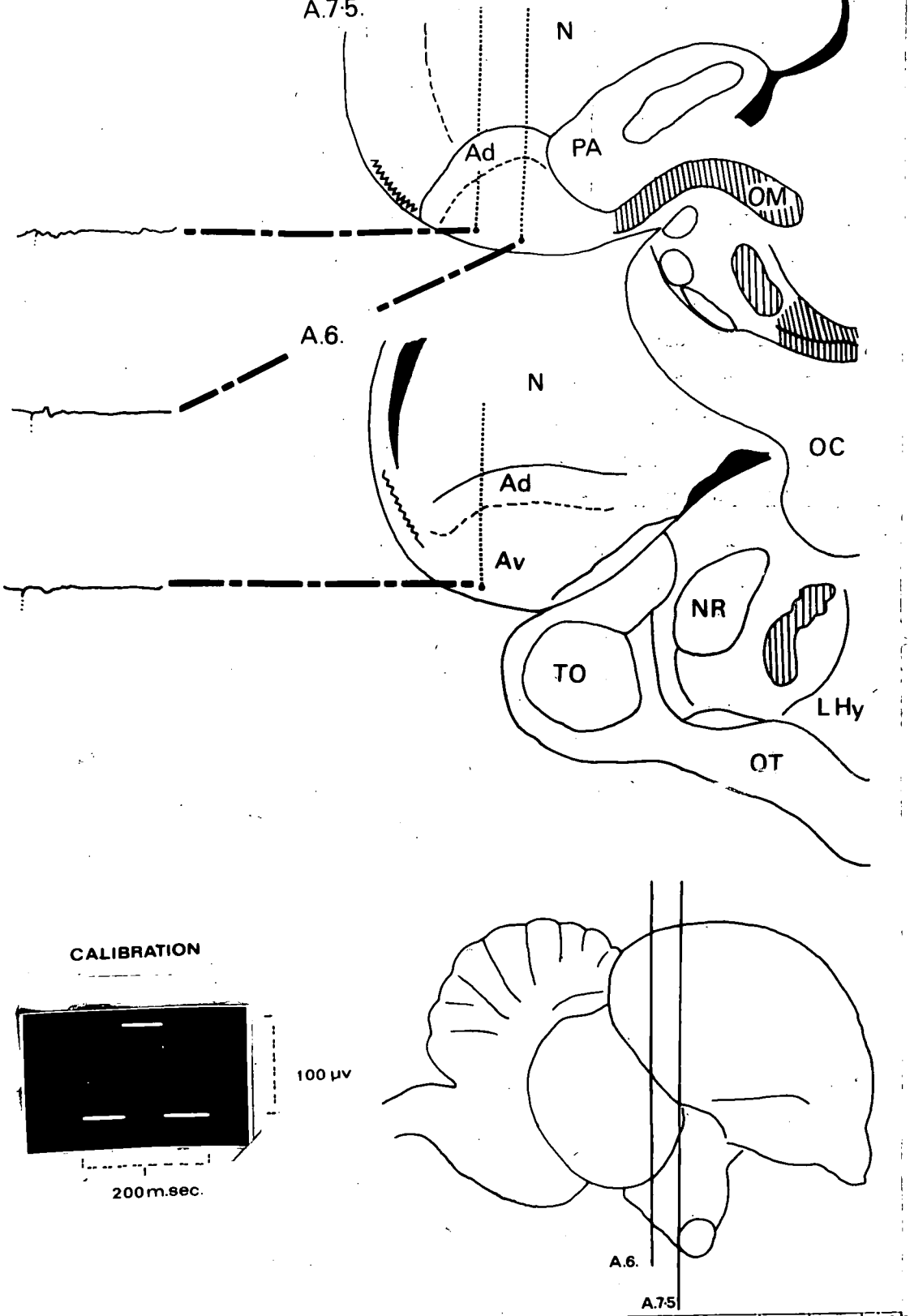


Figure 9: Recordings taken within the Archistriatum. Three tracks which terminated within the archistriatum and failed to show short latency evoked potentials.

amplitude (50 - 150 microvolts) to that reported by Phillips (1966), although very small long latency (80 - 200 milliseconds) potentials with extremely slow rise times were sometimes seen. These potentials resemble what are probably slow arousal responses recorded in every structure in the brain in the present study. On two penetrations made into the

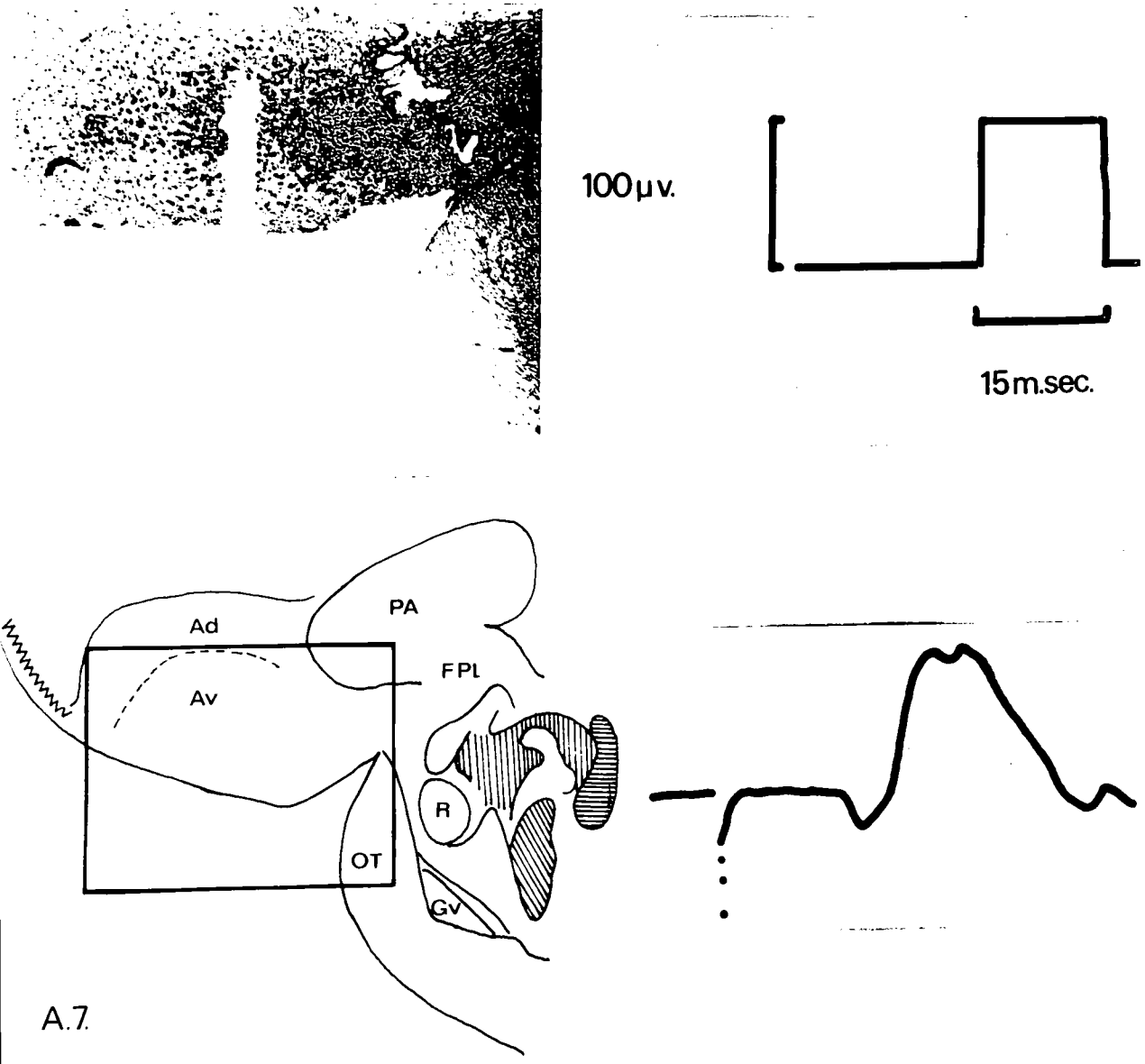


Figure 10: The photograph at the upper left shows the terminal portion of an electrode track which left the brain and touched the bone of the eye socket. Lower left drawing shows location of photograph. The potential on the right is a tracing of the potential recorded when the electrode tip was outside the brain. The peaks are, in order, a-wave (downward), b-wave (First bump on upward potential), 'off' response (second bump on upward potential) and secondary 'off' (final upward deflection).

archistriatum in the present study the electrode was pushed through the brain and into the bone surrounding the eye socket. On both these occasions large (100 microvolt) short latency (12 - 15 milliseconds) potentials were recorded. This response both in form and latency resembles the E.R.G. recorded to a stroboscopic flash, showing the 'a' wave, the 'b' wave and the 'off' response together with a small secondary 'off' response (Fig. 10). Bearing in mind the fact that potentials are produced in the eye contralateral to the stimulated eye in the pigeon it seems highly probable that these potentials, which are faster even than the optic nerve responses are in fact E.R.G's. It is of course a possibility that the conduction velocities in the chicken are much faster than those of the pigeon, but data from Crampton & Bogg (1959) which compare the latencies of E.R.G. and optic tectal evoked potential in the chicken show that even at extremely high intensity levels

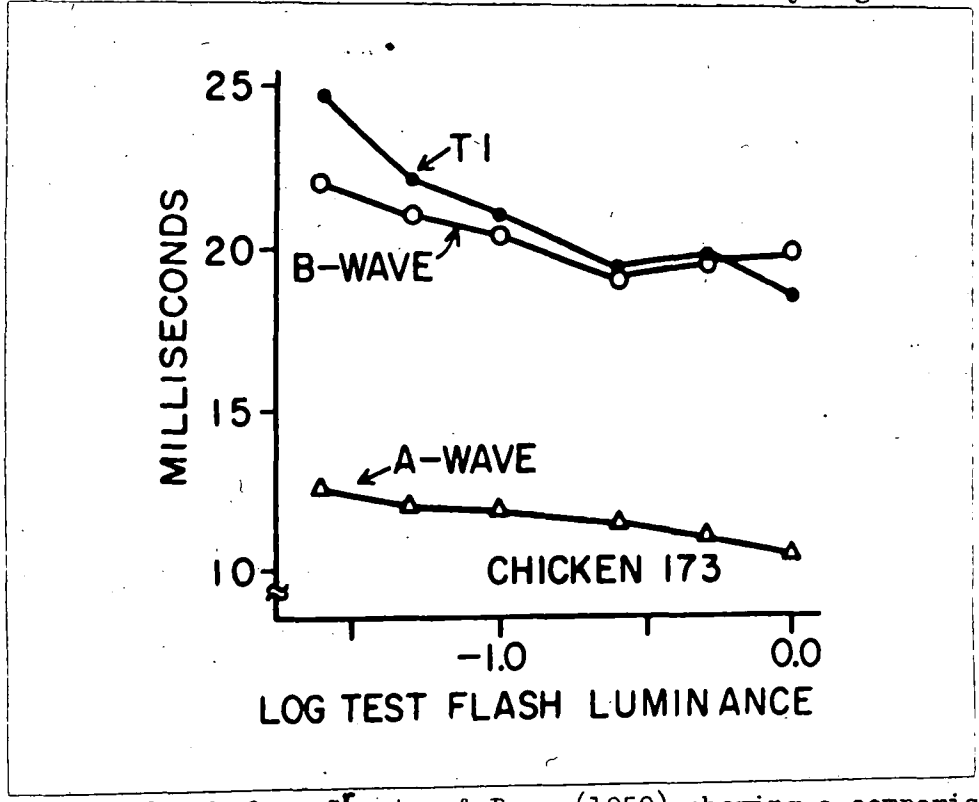


Figure 11. Graph from Crampton & Bogg (1959) showing a comparison of the latencies of the a - wave, b - wave and the first component of the potential recorded in the optic tectum.

the evoked potential is not fast enough to generate these responses in the chicken forebrain (see Fig.11). The conclusion that these potentials

reported by Phillips (1966) did not originate within the archistriatum seems justified.

Only one other area within the forebrain gave reliable evoked potentials. This was the dorsal cortical surface area, where small amplitude responses were recorded on the surface but disappeared one millimetre below the surface (Fig.12). This area has been reported as receiving an input from the nucleus rotundus (Belekova 1966) and the latency of the potential is appropriate for such an interpretation (50 + milliseconds).

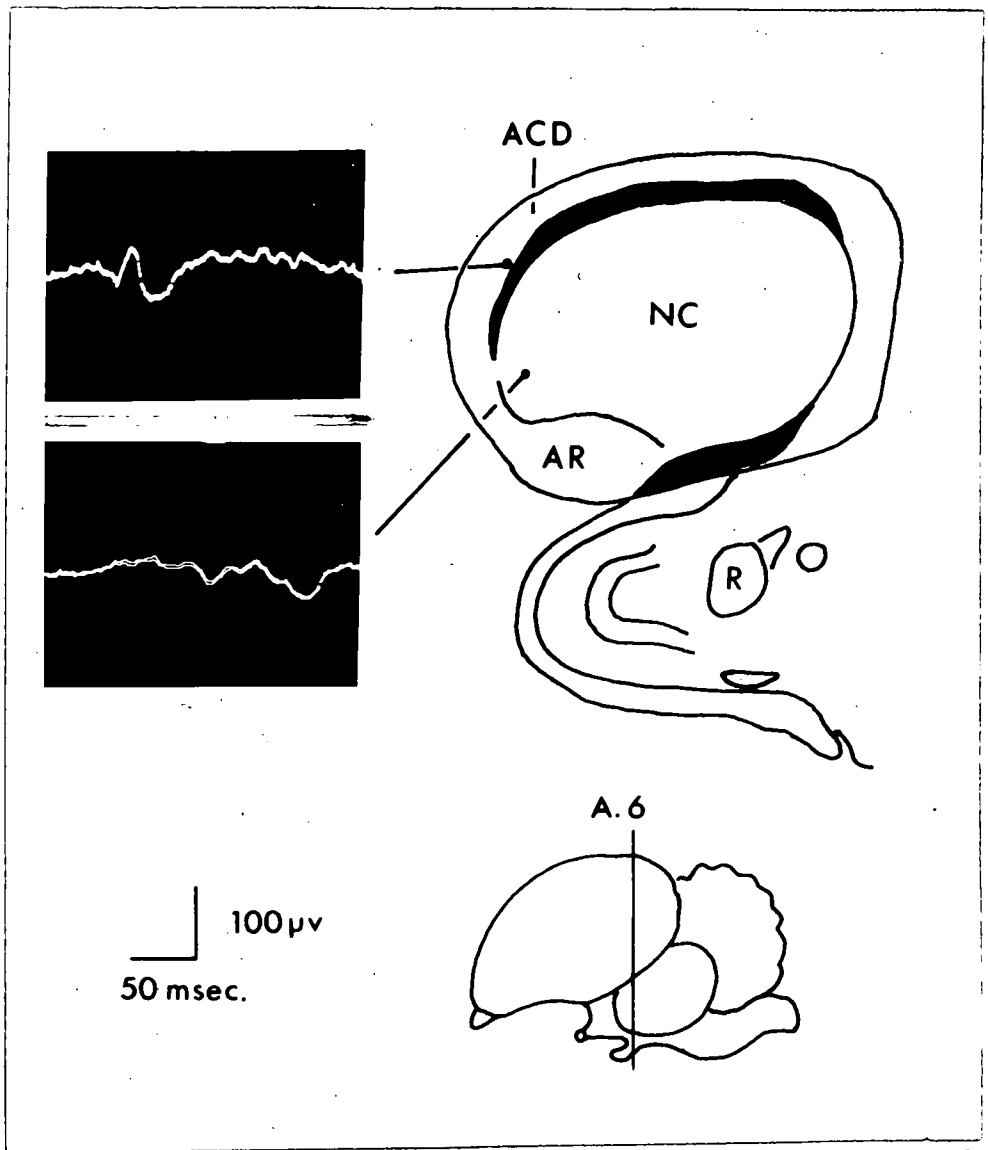


Figure 12: Potentials recorded in dorsal corticoid area. ACD - dorsal corticoid area. AR - archistriatum, NC - neostriatum caudale, R - nucleus rotundus. Bipolar recording.

A general feature of all responses found in the forebrain is the time-dependent attenuation of the responses that occurs at stimulus repetition rates below one second (see Fig.13). This feature was not noted at any diencephalic or mesencephalic sites. Revzin and Karten (1967) report a similar observation when stimulating the nucleus rotundus electrically and recording from the ectostriatum. This time-dependent attenuation may be a specific feature of forebrain sensory areas since it occurs in tactile and auditory systems as well. (Delius pers com).

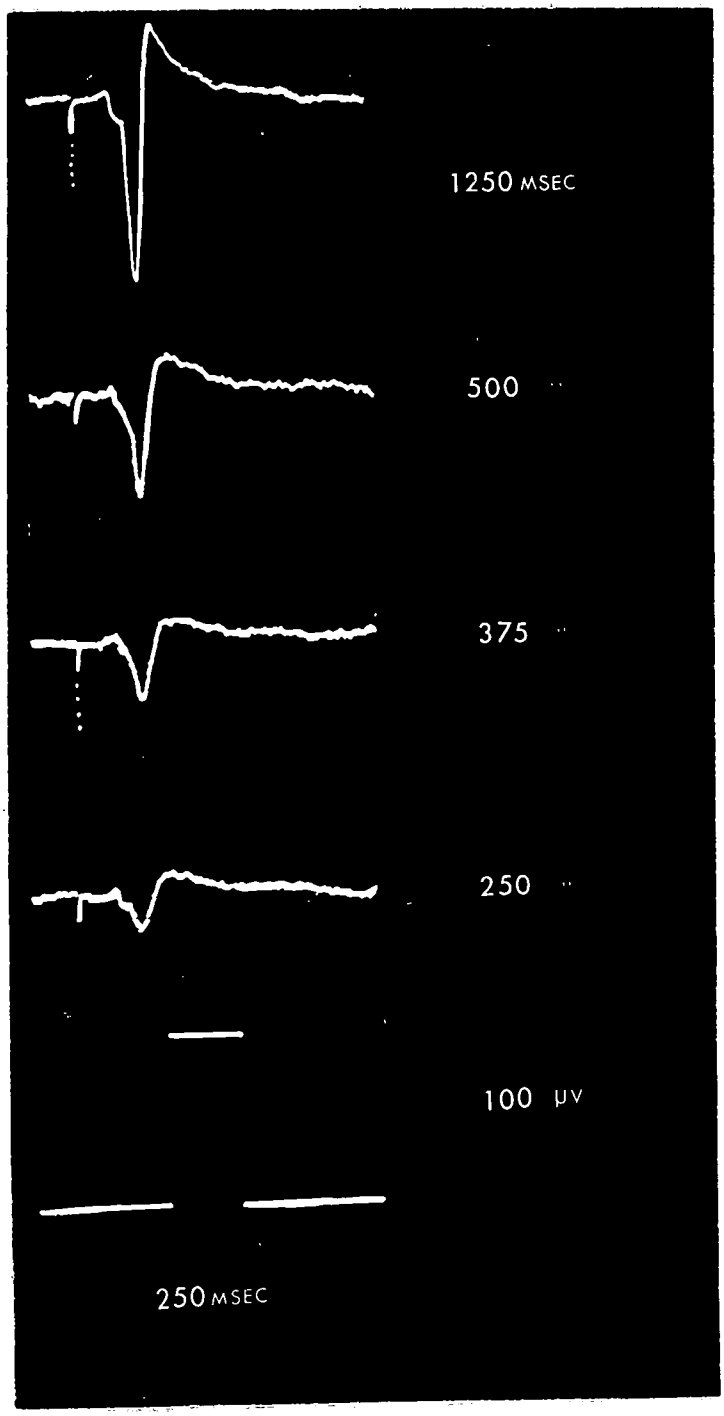


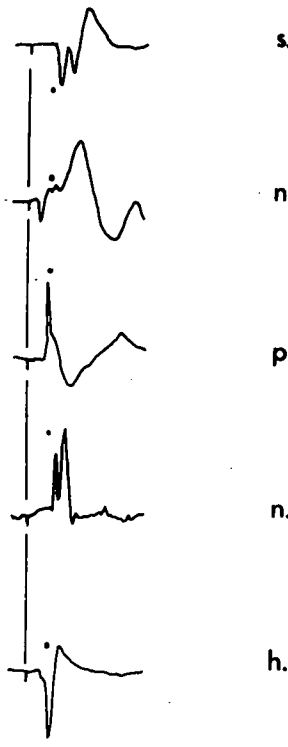
Figure 13: Potentials recorded in the hyperstriatum ventrale at various interstimulus intervals. Average of 32 presentations of the stimulus.

DISCUSSION

The finding that stimulation of one eye produces evoked potentials in the eye contralateral to the stimulated eye is of interest for two reasons. In the first place it confirms Levine's (1955) prediction that the consensual pupillary reflex that had been reported in birds by earlier workers was due to the transmission of light across the midline tissue separating the two eyes. Levine (1955) noted that when he shone light into one eye along the optic axis, small and variable pupillary responses were seen in the contralateral eye, whereas when the light beam was directed into the temporal sector of the eye no pupillary reflex is seen in the contralateral eye. Levine concluded that there was no true consensual pupillary reflex in birds. In the second place it points to the need for care when describing neurophysiological responses that occur later in the birds visual pathway, since these could be the result of interactions from the two eyes, especially when high contrast stimuli or direct light stimulation is used. In the present study when recording from structures in the ventral part of the forebrain overlying the eye socket small amplitude E.R.G's. could be recorded even when the electrode tip had not touched the bone surrounding the eye socket. That these potentials were in fact spread from the eye was concluded because of their short latency and waveform.

The evoked potentials found in the dorsal thalamus (nucleus dorsolateralis anterior pars lateralis) confirms the findings of Karten and Nauta (1968) of a direct projection from the optic tract to this nucleus. This projection was not described by Cowan Adamson and Powell (1961) using the Nauta technique so it is interesting that the results of Karten and Nauta are confirmed by another method. The responses found in the nucleus rotundus are of exceptionally long latency for a diencephalic nucleus, but it should be remembered that it receives its input from the central output layer of the optic tectum, the stratum griseum centrale, and the afferent volley from the optic nerve must pass through eleven tectal layers before it reaches this point (Fig.14) The latency of the rotundal evoked potential (50+ milliseconds) agrees with the descriptions of Revzin (1966) that units in the rotundus fire with a

latency of 60 to 80 milliseconds. The long latency response in this nucleus is important because it excludes the nucleus as a source of the early components of nearly all evoked potentials recorded in the forebrain in the present study.



LEGEND

S.G.C. = Stratum Griseum Centrale.
N.R. = Nucleus Rotundus.
P.A. = Paleostriatum Augmentatum.
N. = Neostriatum.
H.S. = Hyperstriatum.

Figure 14: Comparison of potentials recorded at different locations in the brain. The dot above or below the tracings of the potentials indicates the 40 millisecond point.

The potentials found in the hyperstriatal region of the forebrain are expected as the existence of a visual projection to this region has been reported by a number of authors (Adamo and King 1967, Karten and

Nauta 1968, Revzin 1969). The wide distribution of these potentials within the hyperstriatum is somewhat surprising since Revzin (1969) reported that this projection was confined to a fairly localised area within the anterior part of the hyperstriatum. It is possible that in the present experiments that the responses found outside this region are due to current spread from a generator within the anterior hyperstriatum, but this appears unlikely because there was no sharp decrease in amplitude when the electrode was in the posterior hyperstriatal area. The potentials found in the hyperstriatal area all showed reversal as the electrode tip passed out of the hyperstriatum which suggests that the generator lies in a band running coronally through the hyperstriatum.

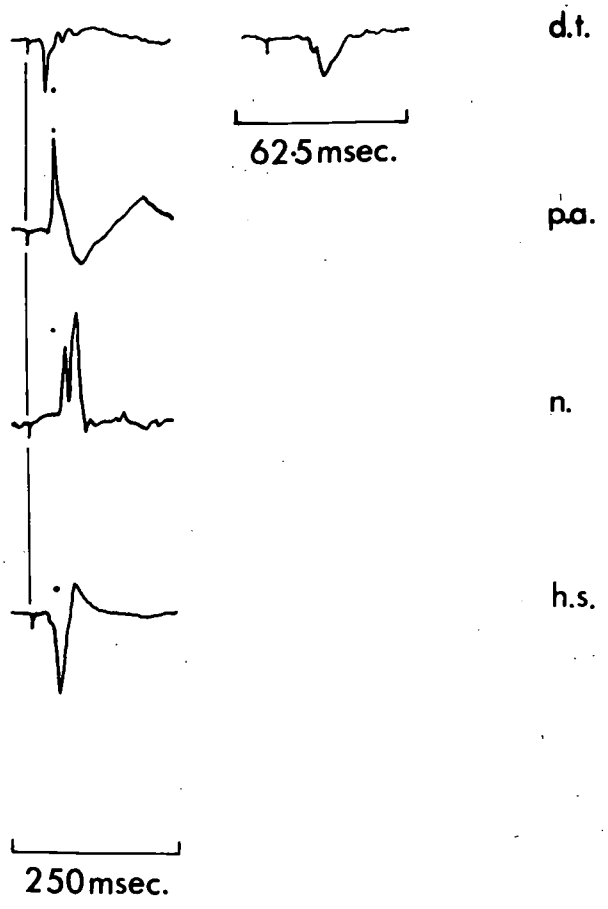
The failure to find evoked potentials in the ectostriatum is somewhat surprising as Revzin and Karten (1967) have pointed to the rotundo-ectostriatal system as a major pathway subserving vision. There are a number of possible explanations for this. Revzin (1969) reported that units in the ectostriatum fire to moving stimuli and it is possible that they do not respond to light flashes. It should be noted however that an evoked potential is found to light flashes in the rotundus where Revzin (1966) reported that moving targets were the optimal stimulus also. In the report by Revzin and Karten (1967) an illustration appears of a light evoked potential in the ectostriatum although no mention is made of it in the text, and the latency (30 + milliseconds) appears too fast to come directly via the nucleus rotundus. Another possibility is that the state of anaesthesia of the animal is all important to secure potentials in this region of the forebrain, and in the present studies the animals were too deeply anaesthetised for these potentials to be recorded. As the units recorded by Revzin (1969) in the ectostriatum responded to movement anywhere in the visual field of the animal, it is possible that a large area stimulus, as used in these studies, results in an inhibitory interaction and prevents the appearance of any postsynaptic activity. On the results of the present experiments it is not possible to choose between these alternatives.

The potentials found in the area surrounding the ectostriatum are too fast to be attributable to the efferent pathway from the nucleus rotundus. These potentials are found in the area referred to by Karten (1969) as the periectostriatal area. In the owl this area receives a

projection from the hyperstriatum and it is possible that this area is the source of the potentials found in the present study. Comparison of the latencies of the potentials found in the various diencephalic and forebrain structures (see Figs.14 & 15) shows that the paleostriatal potentials precede the neostriatal projection by a millisecond or so and are excellent candidates for relaying visual afferents to this region. Which area is the source of the potentials in this area must be decided by further experiments.

The finding of potentials in the neostriatum caudale was gratifying because it confirms both the results of Bremer Dow and Moruzzi (1939) and supports the assertion of Edinger (1895) that the caudal portion of the pigeon's forebrain has visual functions. It also helps to explain why the lesions produced in this area by Layman (1936) produced deficits in visual discrimination learning (although see Chapter 5 for fuller discussion). The projection does not seem to be organised in any lamelar pattern however, as penetration through this area does not show the typical reversal of potentials that is found when the electrode passes through the generator. However the finding of unit clusters that fire with the appropriate latency to visual stimuli does confirm that the potentials are generated within this area and are not due to spread from other sources. As with the hyperstriatum, the potentials found in this area are faster than found in any other structure except the dorsal thalamus. The dorsal thalamus seems to be in fact a good candidate for the production of these short latency forebrain responses (Fig.15).

The failure to find potentials in the avian archistriatum with a latency comparable to those reported by Phillips (1966) is not too suprising when one considers the latency of potentials found in the diencephalic nuclei receiving direct input from the optic tract (about 17 milliseconds). Phillips (1966) readily accepted the finding of visual evoked potentials in the archstriatum because Kalischer (1905) had stated that lesions to the archistriatum, or its main efferent fibre tract, the tractus occipito mesencephalicus produce blindness in birds. This may have been because when the archistriatum is damaged birds become remarkably nonreactive to visual stimuli (or any other form of



LEGEND

D.T. = Dorsal Thalamus.
P.A. = Paleostriatum Augmentatum.
N. = Neostriatum.
H.S. = Hyperstriatum.

Figure 15: Potentials recorded at different locations in the brain. The dot above or below the tracings of potentials indicates the 40 millisecond point. The expanded version of the potential recorded from the dorsal thalamus is shown in order that the incoming optic tract volley (small initial peak) can be distinguished from the potential generated within the nucleus.

sudden sensory stimulation for that matter). My own observations on two birds that sustained damage to the archistriate area shows that they do not avoid the experimenter and can be easily picked up by hand. This is in marked contrast to normal animals which make furious attempts to escape when the experimenter tries to sieze them. However observation of the animals shows that they are capable of feeding, drinking and flying as well as carrying out visual discrimination tasks. The birds also

show normal pupillary and nystagmic reactions, so the conclusions of Kalischer must have been based on a very superficial inspection.

In conclusion then it can be said that some of the findings concerning visual projections to the avian forebrain reported previously have been confirmed and extended, while others have not been confirmed (Fig.16). Of particular note is the fact that nearly all the potentials found in the forebrain precede the potential found in the nucleus rotundus (Fig.14), a nucleus that has been reported by Revzin and Karten (1967) and Karten (1969) as being one of the major sources of visual afferents to the avian

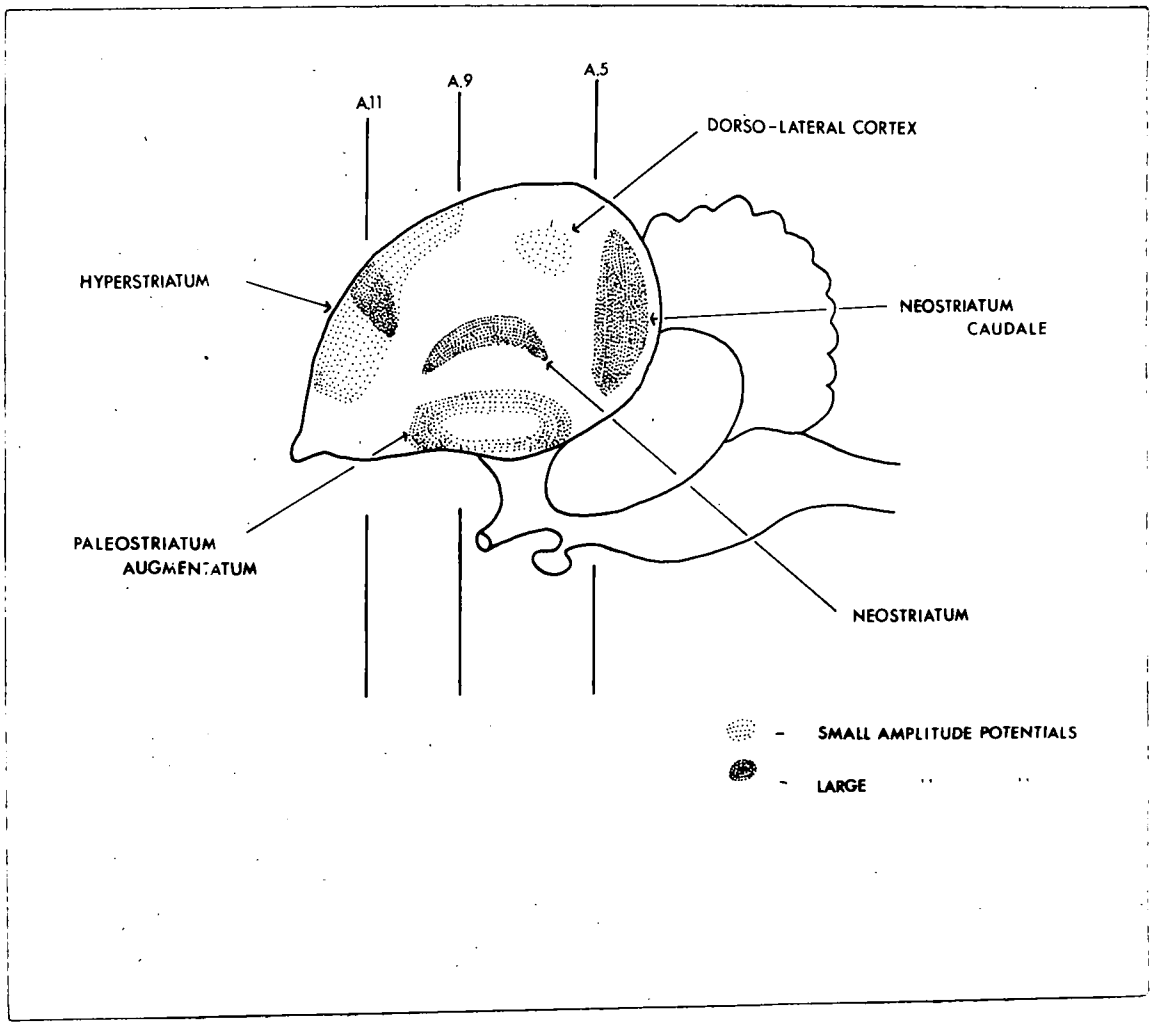


Figure 16: The areas within the forebrain from which potentials to a visual stimulus can be recorded.

telencephalon. The only diencephalic nucleus in which evoked potentials were found with a latency sufficiently short to account for the potentials

found in telencephalic structures was the nucleus dorsolateralis anterior thalami pars lateralis (Fig.15). This nucleus cannot however directly account for all the potentials found in the forebrain. The potentials in the hyperstriatum and the neostriatum caudale follow the postsynaptic wave found in this thalamic nucleus by about 4 to 5 milliseconds. However the potentials found in the neostriatum surrounding the ectostriatum are over 10 milliseconds longer than the potentials found in the other forebrain areas outside of the paleostriatum augmentatum. It is possible that these potentials are relayed by a pathway similar to that described by Karten in the burrowing owl (Spectyto cunicularia) which runs from the hyperstriatum to the periectostriatal region. However it should be noted that the potentials found in the paleostriatum augmentatum precede the potentials found in the neostriatum by a short period and it is possible that these potentials are generated by structures that relay the visual afferents to the neostriatum. However these potentials themselves (paleostriatum augmentatum) occur too late to be directly relayed by the dorsal thalamus. It should be noted however that in no case was any activity recorded in the paleostriatum with a latency sufficiently fast to account for the short latency potentials found in the hyperstriatum and the neostriatum caudale. Completely satisfactory reasons cannot be given for this, but it is possible that either the electrode did not penetrate the fibre tract that carries the afferents to these areas, or alternatively the fibre tract that runs from the dorsal thalamus through this region is too diffuse to be picked up by the electrodes used in this study. If either of these alternatives is true, then it is possible that the potentials found within the paleostriatum augmentatum are postsynaptic potentials which reflect a visual projection to this area since when the electrode penetrated the paleostriatum primitivum no potentials were found. The paleostriatum primitivum is also traversed by afferent fibres running to the overlying forebrain areas, and so this may suggest that there is a projection to the paleostriatum augmentatum proper and that the activity found there does not simply represent fibres of passage.

Chapter 3.

AN INVESTIGATION OF CENTRIFUGAL EFFECTS ON THE ELECTRORETINOGRAM

In contrast to mammals, the existence of centrifugal fibres in the retina of birds is a well confirmed fact (Ramon Y Cajal 1911, Cowan and Powell 1963, McGill Powell and Cowan 1966, Maturana and Frenk 1965). Cowan and Powell (1961) estimated that approximately 1% of the fibres in the optic nerve of the pigeon were central in origin. These fibres originate in the nucleus isthmo opticus which is situated just below the fissure separating the medial margin of the optic tectum from the cerebellum. The projection from retina to tectum is topographically organised as is the projection from the tectum to the nucleus isthmo opticus. The retina is thus represented on the nucleus isthmo opticus and it in turn sends fibres to the same retinal area from which it receives its input (McGill et al 1966 a,b). The anatomical picture gives the appearance of what may be seen as a feedback system designed in some way to modulate the visual input to the brain. Physiological work by Holden (1968 a,b) has confirmed that the direction of conduction of this system is from the nucleus isthmo opticus to the retina.

Within the pigeon retina four types of centrifugal terminals have been described (Cajal 1911, Maturana and Frenk 1965): 1) the convergent type, where the fibres form a nest on the body of the small amacrine cells near the border of the inner nuclear layer; 2) the divergent type which synapses on small amacrines lying at the inner border of the inner nuclear layer; 3) each displaced ganglion cell (Dogiel cell) at the border of the inner nuclear layer receives a fibre that synapses on its axon hillock; 4) a small number of endings penetrate deeply into the inner nuclear layer to an unspecified termination point. The density of the terminals is even over the entire retina, which seems to suggest that they are designed to perform one or more very basic functions in vision.

The existence of centrifugal fibres to the retina of mammals has never been shown conclusively. Most of the reports dealing with the existence of these fibres in the optic nerve were based on the conclusion that prograde degeneration is more rapid than retrograde degeneration. This claim has never been substantiated, and at least in the cat Brindley

and Hamasaki (1966) have shown that the time course of degeneration for optic nerve fibres isolated both peripherally and centrally is indistinguishable from that of optic nerve fibres cut only peripherally. The inconclusive and contradictory evidence concerning the anatomical existence of these fibres in mammals has not inhibited the flow of claims that definite centrifugal effects are detectable on the electroretinogram and optic nerve discharge. Except for the finding of Dodt (1956) in the rabbit and Spinelli and Wiengarten (1966) in the cat, the evidence all seems attributable to circulatory disruption or metabolic abnormalities resulting from optic nerve section (see Ogden 1968 for a review). Dodt (1956) found that spikes, delayed relative to the antidromic wave following stimulation of the optic nerve, could be recorded near the optic nerve head. Since these spikes could be blocked by high levels of light adaptation and could not follow electrical stimulation rates above 6 per second the responses do not seem attributable to the excitation of recurrent collaterals. Spinelli and Weingarten (1966) found single units in the cat's optic nerve that could be selectively fired by sound or shock. Because of the impedance of the recording electrodes (3-10 megohms) it seems unlikely that these responses could be recorded from sources outside the optic tract. Despite the lack of anatomical evidence for centrifugal fibres in the visual system of mammals there does seem to be some physiological evidence that can at least stand up to preliminary criticism.

Physiological work on the function of the centrifugal system in birds has been scarce. Holden (1968 a,b) has shown physiologically that the direction of conduction of the isthmo-optic tract is from the nucleus isthmo-opticus to the retina. Holden (1966) has also suggested two possible functions for the centrifugal system. He has proposed that it may be concerned with supressing the visual input during an eye movement, or that it may supress one eye while the bird is attending to some stimulus in the other eye. There appears to be no physiological evidence that would support either of these propositions. The only work that the present author is aware of that is directly concerned with function is that of Wylie and Ogden (1965) and Ogden (1968). Ogden (1968) found that when the intraretinal E.R.G. of the pigeon was recorded 3 hours

centrifugal system by radiofrequency current. The response to single flashes would enable a comparison of the relative amplitudes of the components of the E.R.G., while the response to flickering light would show whether there was any change in the temporal interaction of exitation and inhibition that occurs in the normal E.R.G. of the pigeon. The normal E.R.G. of the pigeon changes in a non-monotonic fashion as flicker frequency is increased, showing first a reduction in amplitude then a recovery before decreasing regularly in amplitude (Dodt and Wirth 1953). It was decided to plot the amplitude of the response to flicker as a function of frequency rather than plot the critical flicker fusion points (C.F.F's) at a range of intensities. This was decided because the decision of where flicker fusion frequency occurs is highly subjective.

The flicker amplitude curve was of particular interest because it has been suggested (Autrum 1958) that in insects the presence of centrifugal fibres is correlated with high flicker fusion frequencies. While Autrum's observations were not confirmed by Ruck (1958, 1961), the hypothesis that the very high fusion frequencies found in the pigeon may be in part attributable to the presence of centrifugal fibres appeared a reasonable one. These high fusion frequencies that have been reported for the pigeon by workers using both electrophysiological and behavioural techniques (Dodt and Wirth 1953, Powell 1967) have not been found even among mammals possessing all-cone retinas (Bornschein and Szegvari 1958).

APPARATUS

The optical system employed for stimulation and the associated recording apparatus is shown in Figure 1 (Page 66). The light source was a tungsten filament lamp run at six amps. d.c. from a ten volt supply. Lamp current was monitored during the experiment to check on fluctuations and to correct them where necessary. After passing through a heat filter, a small sector of the beam was focussed, where it was chopped by a sectored disc. The beam was then divided by a beam splitter. One beam was reflected by a mirror and focussed onto a photocell to provide a stimulus marker. The other beam was focussed at the birds eye to provide a 14 degrees evenly illuminated field seen in Maxwellian view by the pigeon. Neutral density filters could be inserted in the

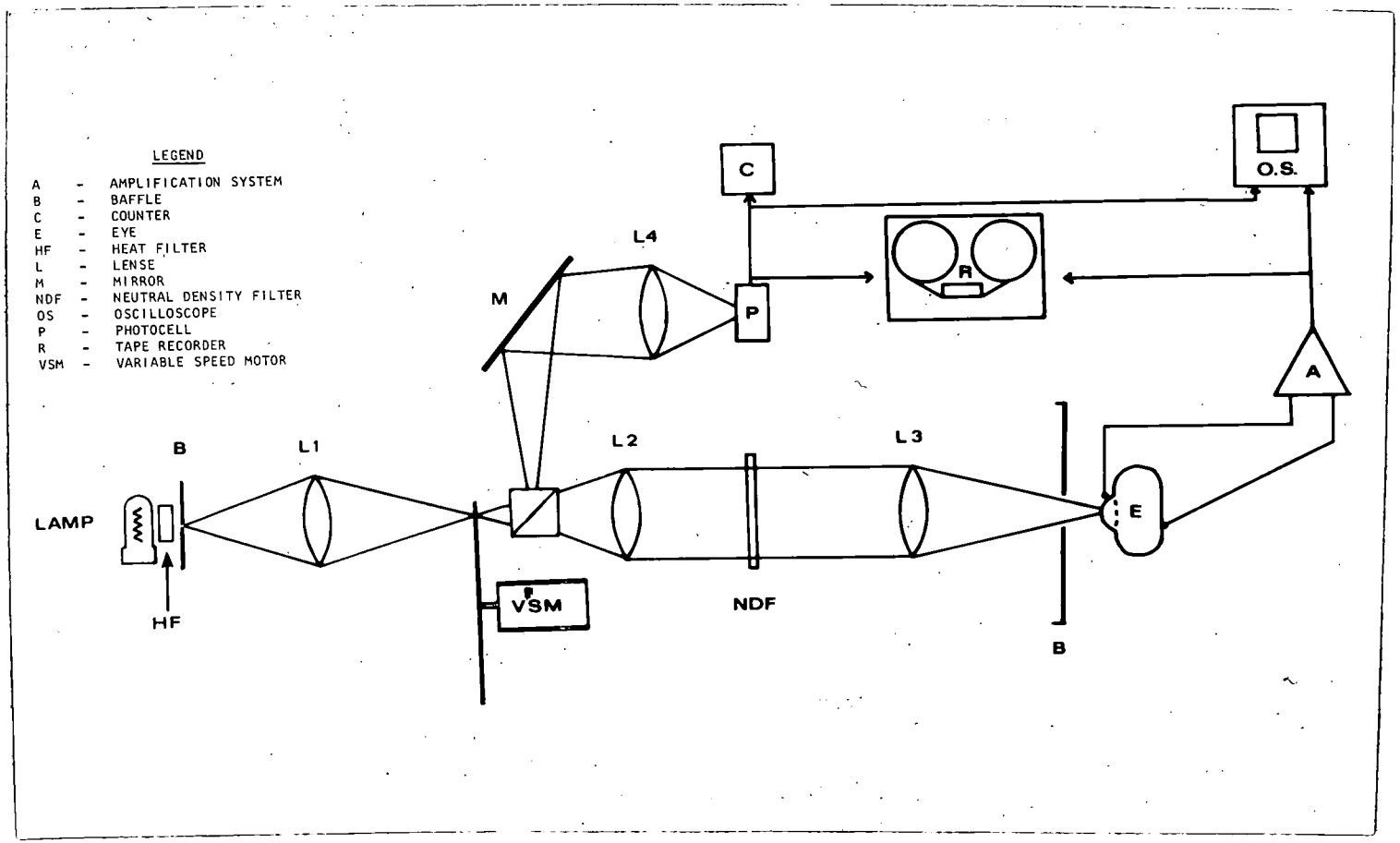


Figure 1. Shows the optical system employed for stimulating the eye and the apparatus used for recording the E.R.G. in experiments 1 and 2 .

parallel sector of this beam in order to provide attenuation of the maximum intensity which was 4.7 log. ft. Lamberts. Wratten neutral density filters of .5, 1.0, 1.5, and 2 log. units attenuation were used. The sectored disc was powered by a velodyne variable speed motor which was controlled by a servomex control unit. In order to ensure reproducible flicker frequencies the output from the photocell was taken to a Racal universal counter timer and the number of beam interuptions per second accurately counted. For the occasions when single flashes were used a Compur shutter was placed in the beam just in front of the sectored disc. The experimental animal was held by ear bars and a beak rest on a specially designed platform which could be moved in all three planes in order to enable rapid positioning of the birds eye.

The corneal contact electrode was made from a length of silver wire, which was coated with silver chloride according to the method given in Donaldson (1958). It was covered with black cotton thread and bent so that the end of the electrode consisted of a ring 6 millimetres in diameter. This ring fitted snugly around the birds cornea allowing passage of the light beam through the centre. The indifferent electrode consisted of a length of platinum wire inserted into the bone of the eye socket.

Signals were amplified using a Tektronix 122 preamplifier driven by batteries, which was placed inside the copper mesh enclosure that contained the bird. The amplifier was set with a time constant of 1 second and a high frequency cut off at 250 cycles. A second amplification system raised the signal to a level acceptable to an Ampex S.P. 300 tape recorder which was used for storage of data. During the experiment signals were monitored on an oscilloscope. At a later date, the data on the tape was analysed using a Biomac 500 signal averager, or by photographing either single sweeps on a storage oscilloscope, or by photographing long runs of the record using an oscilloscope camera.

EXPERIMENTAL PROCEDURE

The pigeon was anaesthetised with between 3.5 and 5 cc's of 20% urethane (ethyl carbamate) injected intraperitoneally. Initially a great deal of trouble was found in getting the birds to survive the 4 to 5 hour period necessary to complete the experimental readings. Eventually it was found that by giving urethane in this concentration

coupled with .5 cc of atropine sulphate to dry the respiratory tract, that the usual cause of death (choking due to excessive mucus in the respiratory tract) was prevented. Even so, only 2 birds in which a complete series of readings before and after the lesion, and which had the centrifugal tract completely sectioned, were available for analysis. Data on another six birds which had the centrifugal tract completely destroyed but on which readings at all levels of illumination were not obtained, were also used for comparison of possible centrifugal effects.

After injection the bird was placed in a stereotaxic instrument, the scalp opened and the bone overlying the optic tectum removed with a dental drill. The dura was covered with petroleum jelly to prevent drying and then the bone overlying the eye socket was removed enabling the indifferent electrode to be placed directly on the outside of the eye socket itself. The nictitating membrane was removed and the pupil dilated with a drop of tubocurarine chloride (since the pigeon's iris is striated, atropine is ineffective in inducing mydriasis). The bird's eyelids were held back with a pair of retractors and the bird was placed in the experimental apparatus and the eye positioned. The bird was then left for 40 minutes in the completely dark room to dark adapt and then the experimental session was begun. When the experimental session began a certain amount of illumination was present (from the oscilloscope and other instruments used and also from the torch that was necessary for the experimenter to adjust these instruments), and so the screened enclosure was completely covered with blackout material, and the optical apparatus was also carefully screened with similar material. After the initial series of readings were taken, beginning 2 log. units down from maximum intensity and working up, the amplifiers were switched off and a cut made through the optic tract and the anterior part of the optic tectum using a scalpel. Then the bird was left for a further 40 minutes to readapt before the second set of readings were taken. At the conclusion of the experiment the bird was removed from the apparatus and perfused through the carotid arteries first with 10% saline and then with 10% formalin. The brain was later removed from the skull and examined to make sure that the optic tract was completely destroyed.

In two birds (for which a complete set of data is not available) the centrifugal system was destroyed by implanting them with stainless steel electrodes aimed at the anterior section of the nucleus isthmo opticus and producing a lesion with radiofrequency current. These birds were treated identically to those used for the other procedure except that the brains were sectioned at 50 microns using a freezing microtome and stained with cresyl violet to ascertain that the lesion had in fact destroyed the centrifugal tract.

RESULTS

Examination of the E.R.G. to single 1 second flashes before and after destruction of the centrifugal tract (Figure 2.) shows that there is no apparent difference between the waveforms of the E.R.G's. obtained before and after the lesion. It should be noted in Figure 2 that the return to baseline of the negative potential that follows the b-wave is a function of the time constant of the amplifier and not a characteristic of the E.R.G. when it is recorded d.c.. The 'off' response of the pigeon's E.R.G. rises from a negative baseline when the waveform is accurately reproduced by the amplifier. There were slight changes in the total amplitude of the E.R.G. when pre and post lesion recordings were compared but these could be in either direction. In a subsequent experiment it was noticed that when the optic tract and anterior tectum was sectioned the pigeon produced a burst of eye movements, and this may well have resulted in either improved or impaired contact of the electrode.

When the waveform of the response to flicker is compared, again there is no detectable difference between the pre and post lesion recordings. It is difficult to be absolutely certain about this as the evaluation of the record is a fairly subjective process and there may be very slight differences that are not apparent to the present observer. Probably the only satisfactory way of analysing this type of E.R.G. record is by running a spectrum analysis of the wave form, but effects if they are present are obviously extremely slight (Fig.3 Page 71). The fall off in amplitude of the response of the E.R.G. above 5 cycles and the recovery in the region of 30 c.p.s. can be seen in Fig.3. This waning and recovery can be seen to occur both before and after the lesion.

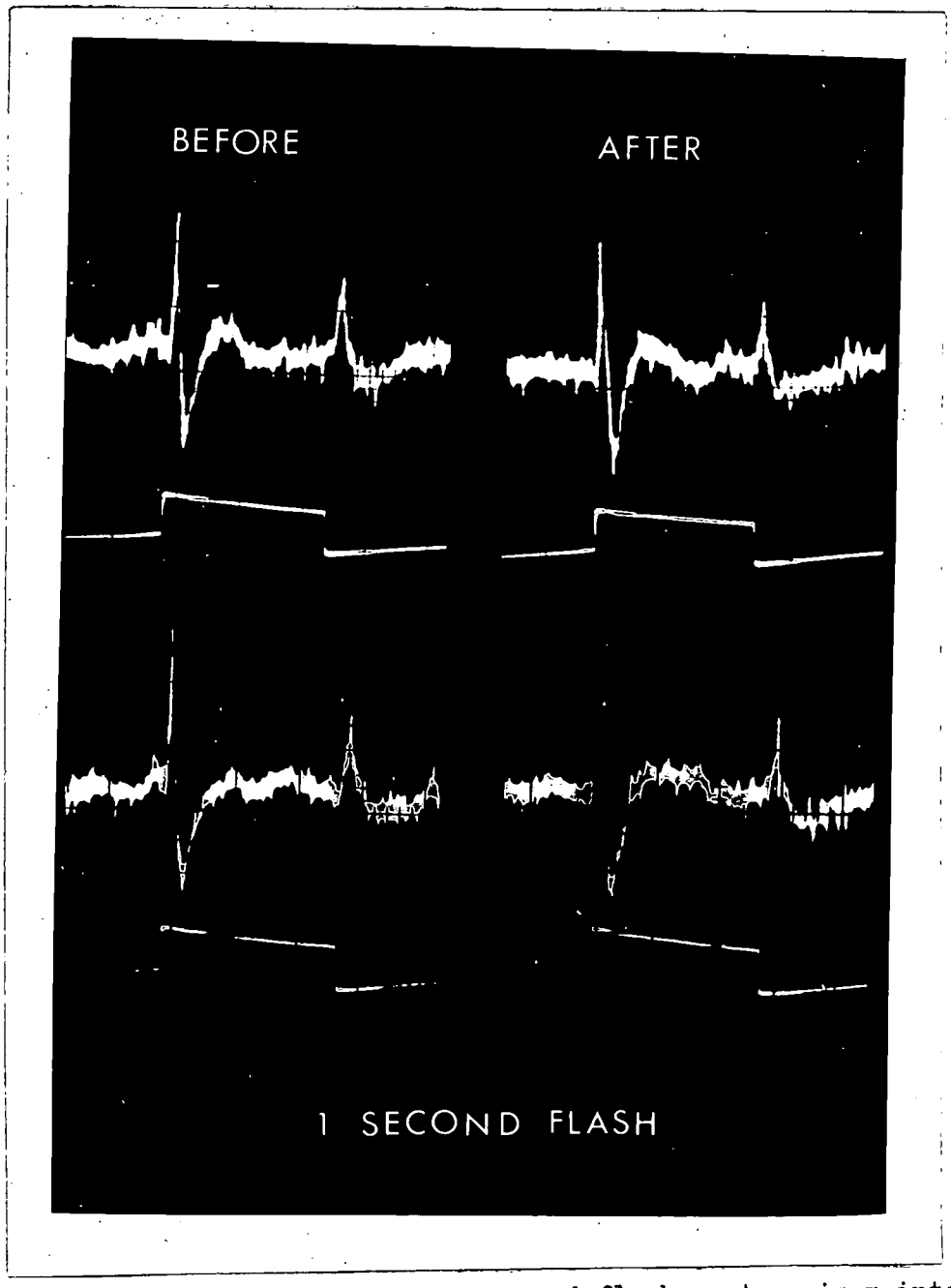


Figure 2. E.R.G. responses to one second flashes at maximum intensity (4.7 log. foot lamberts). Urethane anaesthesia. Storage oscilloscope photographs.

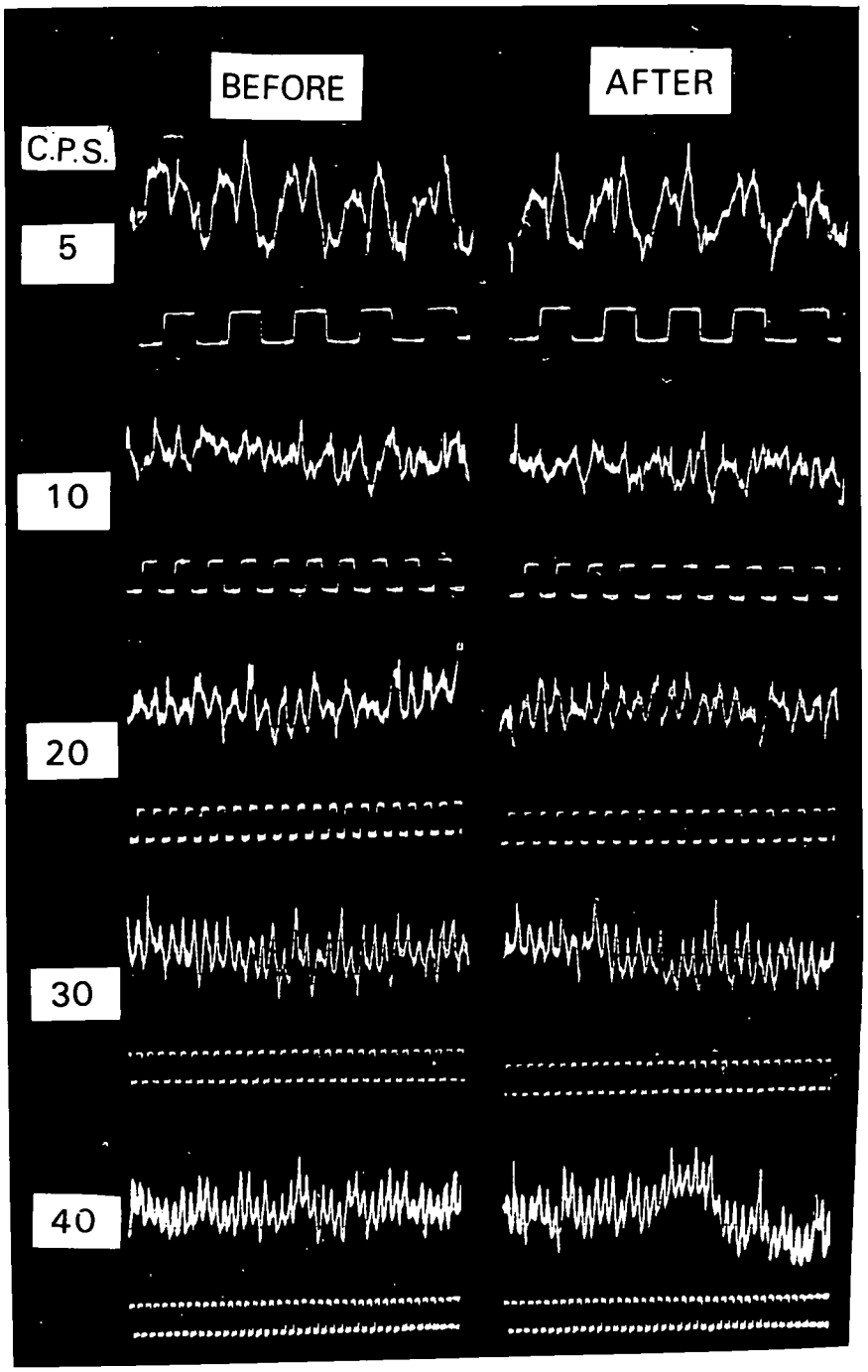


Figure 3. Responses of the E.R.G. to flickering light of different frequencies before and after destruction of the optic tract. Note the extremely variable waveform at 10 cycles per second and the recovery of a more regular response at higher frequencies.

When the curve of E.R.G. amplitude against flicker frequency is plotted before and after the lesion again no differences are apparent (Fig.4). The curves shown in Fig.4 were obtained by averaging 16 time periods of either 500 milliseconds or 250 milliseconds and plotting the height of the b-wave from the bottom of the a-wave for the low frequency flicker response, but above 15 cycles where the components of the E.R.G. disappear as distinct entities (Fig.3) the total amplitude of the response was taken. The increase in the amplitude of the E.R.G. in the region of 30 cycles is due to the sychronisation of the 'on' (b-wave) and the 'off' responses of the E.R.G.. As flicker frequency increases the 'on' and 'off' responses approach one another until they eventually fuse. The decay of this secondary peak in the E.R.G. with low levels of illumination may be due to the absence or fading of the cone response, and the consequent disappearance of the 'off' response which is a feature of cone responsiveness, and also to the inability of the rods to follow fast flicker rates.

DISCUSSION

The present experimental results strongly imply that centrifugal effects are not detectable in the E.R.G. of the pigeon. The response of the E.R.G. under a fairly wide set of conditions was examined and there appears to be no grounds for concluding that there is a difference between pre-and post-lesion waveforms. The increase in amplitude of the E.R.G. that has been noted by some authors following optic nerve section was not apparent in the present study (Abe 1962, Jacobsen and Gestring 1958). Jacobsen and Gestring (1958) did not quote values for the increase but Abe reported increases in the amplitude of the b-wave of between 200 and 300% following compression or section of the optic nerve. While these studies were carried out on unanaesthetised animals, the present experiments were carried out on animals that were fully anaesthetised. This difference may well account for the failure to detect such effects. Furthermr, it is known that urethane, the anaesthetic used in the present study exercises a marked depressive effect on certain areas of the brain. In the pulvinar of the cat, a nucleus that is responsive to visual stimuli

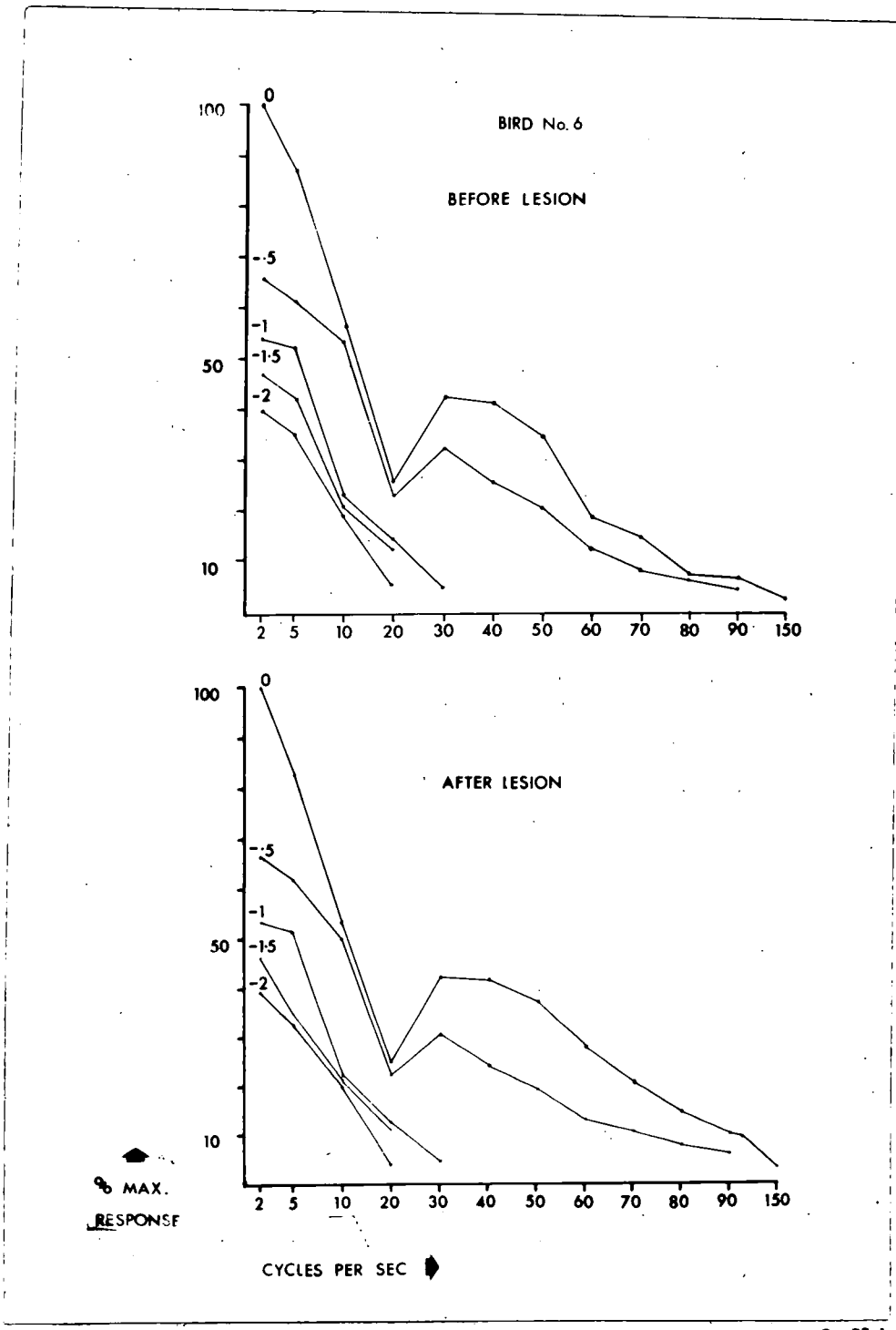


Figure 4. Graphs showing E.R.G. amplitudes as a function of flicker frequency before and after destruction of the optic tract. Figures above the origin point of the curves refer to the values of the neutral density filters used to attenuate the intensity of the stimulating beam. Both sets of curves obtained after 40 mins. dark adaptation. Each point is an average of 16 sweeps of the signal averager.

under barbiturate or chloralose anaesthesia, urethane completely supresses visual responsiveness (M. Wright 1969 personal communication). Despite the fact that there is a distinct possibility that centrifugal effects only appear in the E.R.G. when the animal is not anaesthetised, it seems worth examining the possibility of centrifugal control of the E.R.G. using an anaesthetic other than urethane.

Certain conclusions can however be drawn from the present experiment. The high flicker fusion frequency noted by previous workers on the pigeons E.R.G. (Dodt and Wirth 1953) was not measured directly in this experiment, but the clear response that was present in the E.R.G. at 150 cycles confirms that the fusion frequency was at least as high as this at maximum intensity. This response at high flicker frequencies was also present after destruction of the centrifugal tract and so it appears that even if the centrifugal system was depressed by the anaesthetic, the E.R.G. was in this respect functioning normally over quite a long time period (4-5 hours). The flicker fusion frequency found for the pigeon using behavioural threshold techniques have not been as high as those found using the electroretinogram. Powell (1967) found that with equal light dark intervals the fusion frequency in the pigeon was in the region of 120 c.p.s.. It is difficult to equate the conditions used in the behavioural and the electrophysiological experiments but both are in agreement that the fusion frequency of the pigeon is higher than that found in any other vertebrate measured. The present results strongly imply that this high fusion frequency is not a function of the centrifugal system. If this system was active, there was no change between the pre and post lesion readings. If it was not active then the high frequency flicker responses obviously do not depend on its functioning.

The response to single flashes and low frequencies of flicker are, however, a different case. If the action of the centrifugal system was completely depressed by the action of the anaesthetic, assuming of course that under normal circumstances effects of centrifugal action would be detectable, then no differences would be expected as a result

of destroying the centrifugal system. It was decided then to repeat the experiments on the E.R.G. response to single flashes and flickering light using a different anaesthetic.

EXPERIMENT 2. THE EFFECTS OF OPTIC TRACT SECTION ON THE RESPONSE OF THE PIGEONS E.R.G. TO SINGLE FLASHES AND FLICKERING LIGHT. (Equithesin anaesthesia).

Ogden (1969) in his studies on the effects of optic tract section on the electroretinogram of the pigeon, used Equithesin as the anaesthetic agent. While there is no certainty that this anaesthetic may not also exercise depressive effects on the E.R.G. or the centrifugal system, the fact that this was the anaesthetic used in the previous study, where visually evoked potentials were found in a wide range of sites within the forebrain, diencephalon and mesencephalon, at least suggests that the major part of the pigeon's visual system was active. However the use of this anaesthetic introduced certain new problems which made it necessary to modify the experimental design.

The advantage of using urethane as an anaesthetic is that it produces a stable preparation for a number of hours without the necessity of repeatedly injecting the animal and consequently altering the depth of anaesthesia. Drastic changes in the depth of anaesthesia is something to be avoided since it makes comparison between the pre and post lesion recordings difficult. The problem with equithesin is that it produces anaesthesia for only a relatively short time period; approximately one hour on initial injection and a further 30 minutes for each safe subsequent dose. There is as a consequence the difficulty that anaesthesia is lightening progressively during the course of the experiment and certain steps are necessary to try to minimise these fluctuations. Experience gained in the use of the anaesthetic during the experiments on visual evoked potentials was useful here. Equithesin consists of two major ingredients, pentobarital and chloral hydrate. Anaesthesia is induced by pentobarbital rapidly (15 minutes approximately, since the anaesthetic is injected into the pectoral muscles and not intravenously), but this anaesthetic does not continue to act for longer than about a further 30 minutes (Delius 1966). Chloral hydrate, while slower in

inducing anaesthesia, acts for a longer time period and it is this agent which keeps the bird anaesthetised when the effects of the pentobarbital are fading. Since the preparation of the bird took approximately 40 minutes the initial phase of the experiment could be run under the influence of chloral hydrate. By injecting the bird again at the end of the first phase of the experiment and allowing approximately 10 minutes to elapse before beginning the post lesion readings both parts of the experiment could be run under approximately the same conditions. The second injection was always 25% of the initial dose and so the effects of the pentobarital should not have been very marked. If clear differences between the pre and post lesion E.R.G's. did show up, then of course it would be appropriate to look for differences between birds under exactly similar conditions.

APPARATUS

The apparatus used was identical to that used in Experiment I, except for the fact that a variable band-width amplifier was used to clear up the high frequency interference in the records. This was set with a cut-off frequency of 50 cycles for the readings between 2 and 20 cycles and for higher frequencies was moved up to over 200 cycles. This results in a slight rounding of some of the peaks, but the record is much clearer and the components of flicker response easier to see.

PROCEDURE

The procedure followed was similar to that of Experiment I. The birds were injected with Equithesin (2.5 cc's per Kg.) and the bone overlying the tectum and the eye removed using a dental drill. The nictitating membrane was removed and the pupil dilated with curare. No birds were implanted with electrodes as in Experiment I. Readings were taken only at maximum intensity and only for a limited range of flicker frequencies 2 -40 c.p.s. except in the case of 2 birds where readings at 140 c.p.s. were also taken to see if the high frequency flicker response was also present. E.R.G's. to single flashes were taken as in Experiment I. The experimental session was therefore much shorter than the sessions required for the previous experiment. At the termination of the experiment the birds' brains were perfused and stored in formalin for examination at a later date. All results reported are for birds in which

the destruction of the optic tract had been complete. 6 pigeons were used.

RESULTS

Comparison of the E.R.G. responses to single flashes before and after destruction of the optic tract showed no reliable differences in amplitude of the electroretinogram's components (Fig.5). There were differences in the overall amplitude of the recordings but these were in both directions (increased or decreased amplitude in different birds). There was no evidence of an increase in the amplitude of the 'off' response or of a tendency for the E.R.G. to show any oscillation.

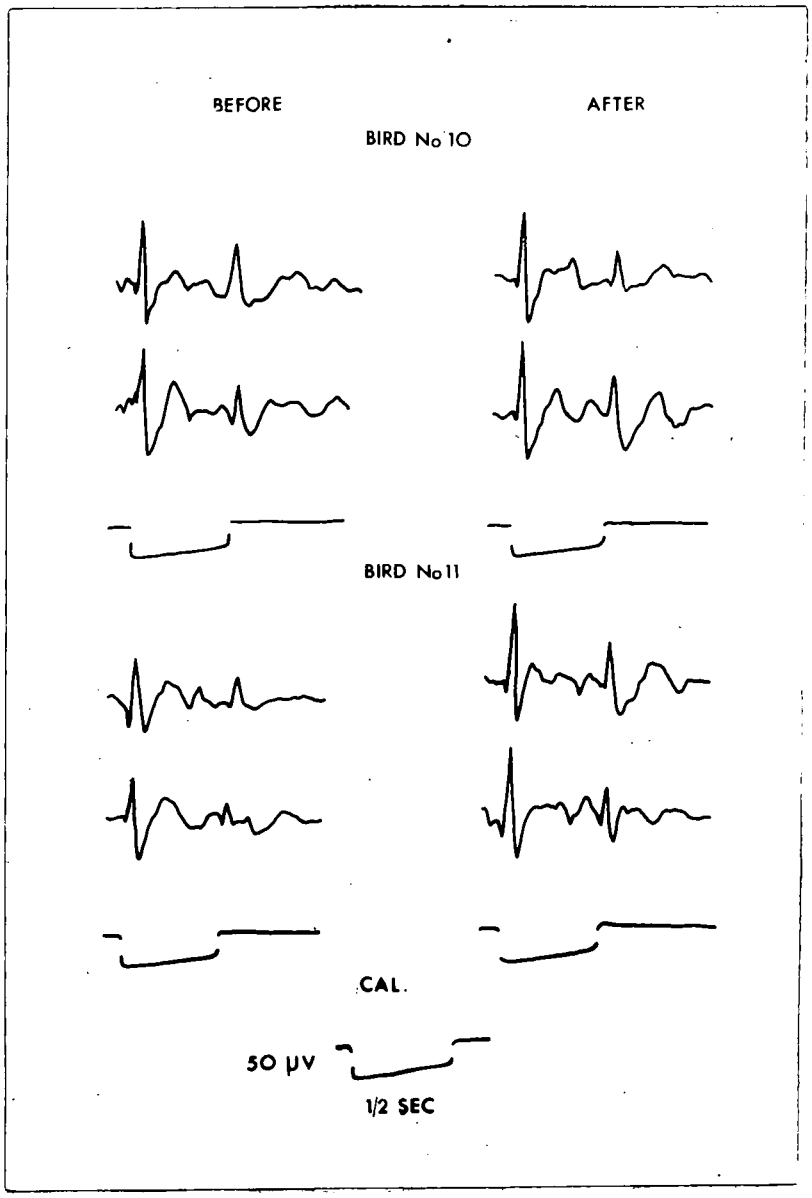


Figure 5. E.R.G. responses to single flashes for two experimental animals showing readings taken before and after destruction of the optic tract.

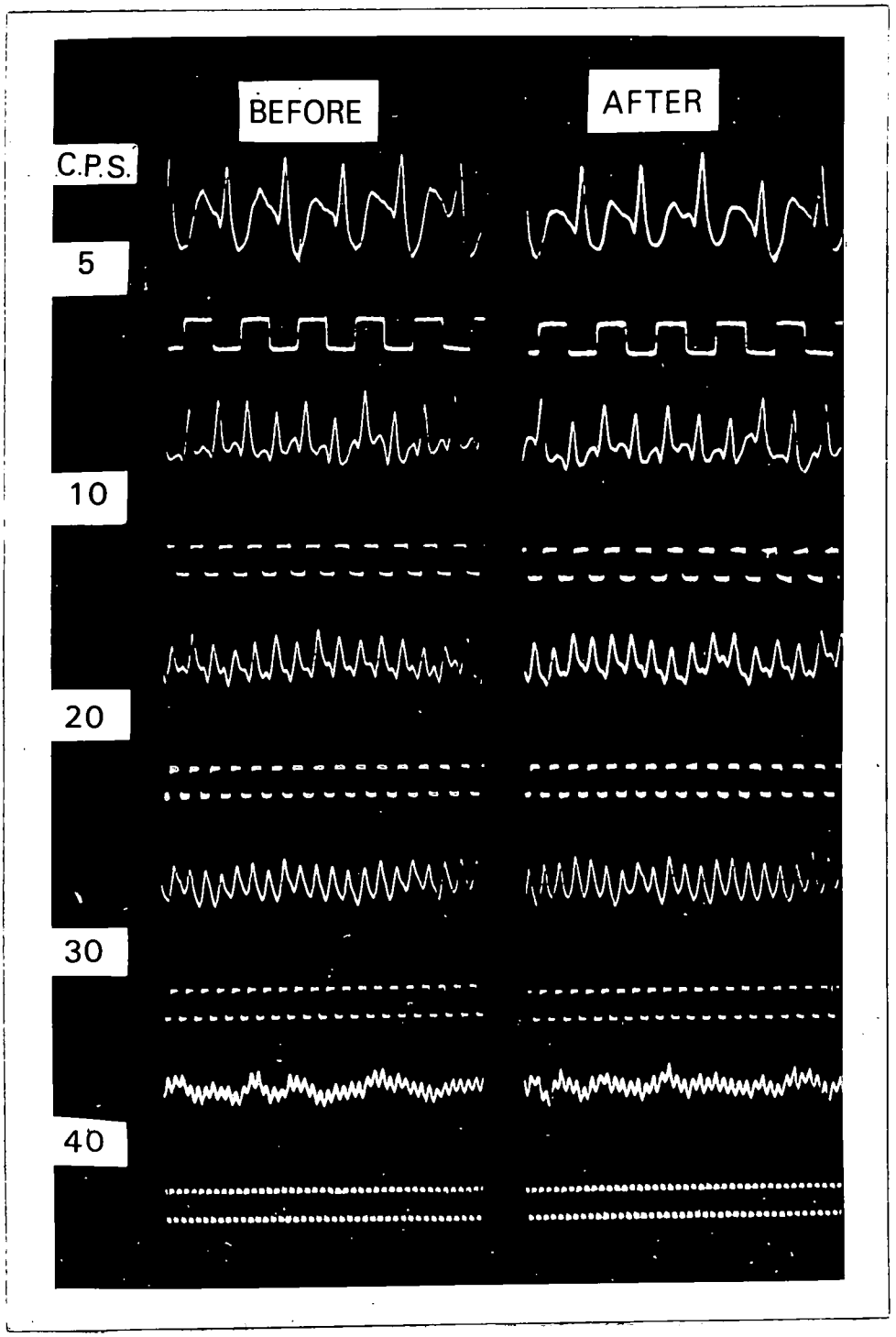


Figure 6. E.R.G. responses to flickering light of different frequencies before and after destruction of the optic tract. Note that the response at 10 cycles is not variable as it is under urethane anaesthesia.

Compared to the responses to single 1-second flashes found under Urethane, the present E.R.G's. were more variable. Increases in the absolute amplitude of the b-wave were seen in four of the six birds but the other two showed decreases. Since the optic tract was completely sectioned in all six birds, it would appear that this increased amplitude was due to improved electrode contact.

The response of the E.R.G. to low frequencies of flickering light was also almost identical before and after the lesion. No consistent differences could be detected either when raw data was compared (Fig.6) or when averaged data was examined (Fig.7). The E.R.G. was more variable under the conditions of the present experiment mainly due to the fact that eye movements were more common. One of the effects of Urethane compared with Equithesin is the tendency for the former to suppress eye movements. It was consequently extremely difficult to measure the response of the E.R.G. at high flicker frequencies since the amplitude of the signals from the birds eye movements were much greater than the amplitude of the E.R.G., and even when the averager was used, the 30 - 80 microvolt signals of the eye movements disrupted the record of the E.R.G. (in the region of 5 microvolts at 140 c.p.s.). It was possible to ascertain that a signal was present at 140 c.p.s. that followed the flicker frequency but it was impossible to compare the pre-and post-lesion amplitudes.

The decrease and recovery of the E.R.G. as frequency is increased under the conditions of the present experiment were not noted. The 'on' and the 'off' responses of the E.R.G. have almost fused by the time flicker frequency has reached 20 c.p.s. It is possible that the flicker frequencies used; 5, 10, 20 cycles per second, were not optimum for showing the effect. The flicker response at 50 c.p.s. is extremely regular while at 10 c.p.s. when Urethane is used the E.R.G. is extremely variable.

DISCUSSION

As with the previous experiment, the present experiment gave no evidence of any centrifugal effects on the E.R.G.. The E.R.G. was much the same under both anaesthetics, except for the tendency of the record to be much more variable under Equithesin an aesthesia. This tendency

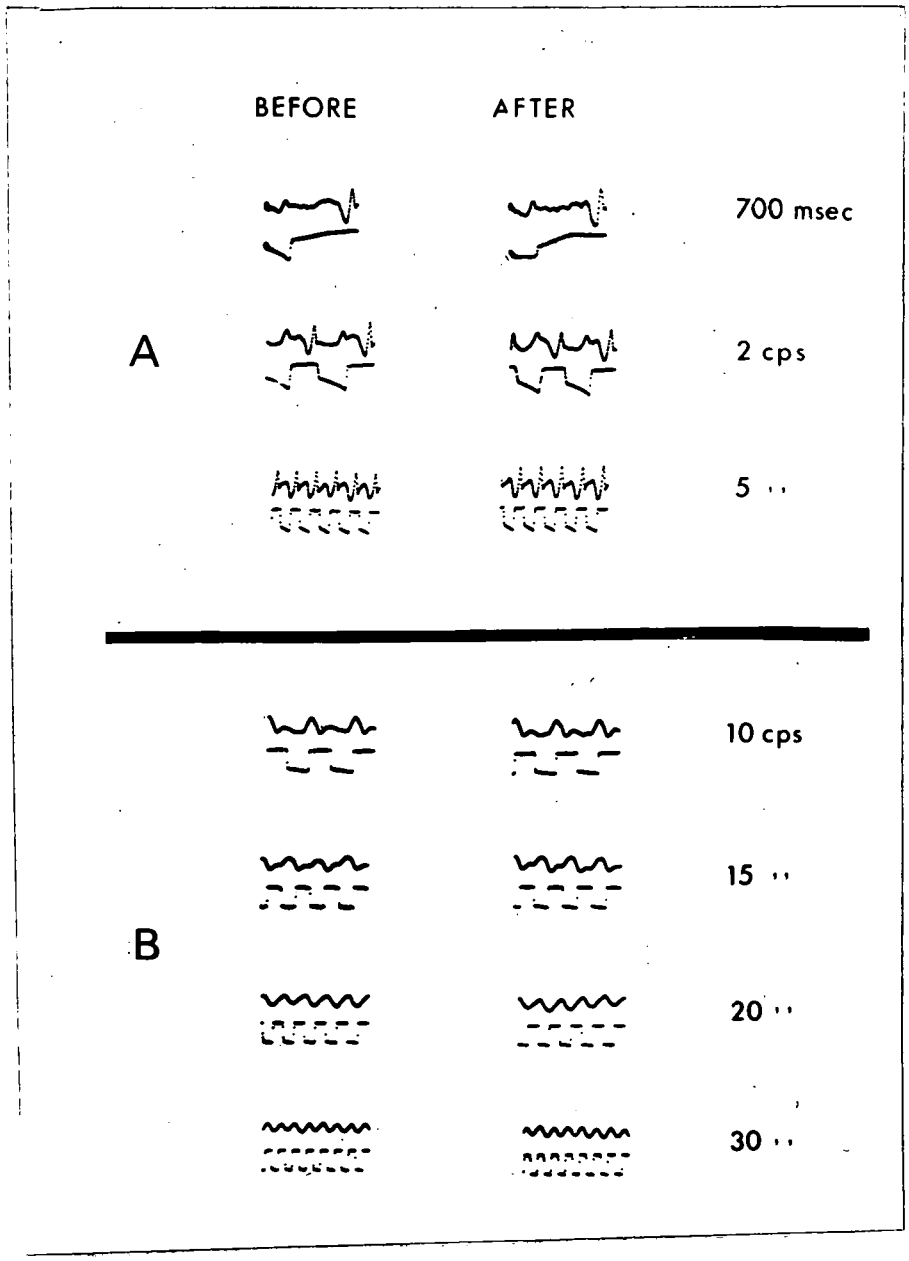


Figure 7. E.R.G. responses to single flash and flickering light. A - sweep duration 1 second. B - sweep duration 250 milliseconds. Stimulus onset is on the right of each record.

for the baseline to fluctuate, sometimes results in an apparent decrease in the 'off' response amplitude (see Fig.6), but this tendency was present to the same extent before and after the lesion.

While in the previous experiment E.R.G. responses over a wide range of illumination were recorded, in the present experiment only one light intensity was used. While there is a possibility that recordings at other intensities may have produced results that were positive, it seems unlikely. The pigeon's eye is principally a diurnal eye, and it seems reasonable to suppose that if effects are going to be apparent that they will show themselves at reasonably high levels of light adaptation. A feature common to both experiments however is the fact that the flicker frequencies chosen for comparison were arbitrary. If a flash of light does trigger the centrifugal system it may do so in two ways. Either the onset of light may trigger the system or the cessation of light may trigger it, quite aside from any specific parameters of stimulus. If the centrifugal volley follows the light pulse with a definite duration then the period after the triggering of the volley in which the subsequent activation of the retina falls is quite critical. The arbitrary flicker frequencies chosen may not have been suitable for detecting such an effect. Holden (1968) when stimulating the lateral tectum of the pigeon electrically found that the centrifugal wave at the optic nerve head followed the stimulation with a peak latency of 5 milliseconds. Allowing for the fact that when light is used as a stimulus the optic tectum evoked potential occurs approximately 16 - 17 milliseconds after the stimulus, then at the earliest one would expect the centrifugal volley to reach the retina 21 milliseconds after the effective stimulus. It seems clear from the data on single flashes that the onset of light does not produce effects on the E.R.G. or these would surely have shown up in the first two experiments where single flashes were used. If such effects are present then it seems worth while investigating the possibility that the 'off' response may trigger the centrifugal system, and the effects may be shown up in the response to the next flash of light. In order to test this possibility it was decided to carry out a further experiment.

EXPERIMENT 3. THE EFFECTS OF OPTIC TRACT SECTION ON THE DOUBLE FLASH RESPONSE OF THE PIGEON'S E.R.G. (Equithesin anaesthesia).

As stated in the previous discussion, it was decided to look at the effects of delivering a priming flash to the eye of the pigeon and varying the delay between the priming flash and the subsequent test flash. In order to facilitate the timing of the light flashes it was decided to use a stroboscope as the light source, in conjunction with a double pulse electrical stimulator in order to have accurate control of the interstimulus interval.

APPARATUS

The apparatus used for stimulation and recording is shown in Figure 8. Light from a Dawe model 1201E stroboscope was collected with a condensing lens. A small section of the beam was then focussed at the bird's eye to provide a field of approximately 15 degrees seen in Maxwellian view by the pigeon. The stroboscope was triggered by a Nuclear Chicago constant current stimulator. Data was amplified using an Electrophysiological Instrument's a/c preamplifier using a time constant of 1 second and a high frequency cut-off at 250 cycles per second.. A second amplification system was used to boost the signal to a level acceptable by the Biomac 500 signal averager. The display tube of the Biomac 500 was photographed to provide permanent records.

PROCEDURE.

The bird was prepared for the experiment in exactly the same way as in the previous experiment. The experimental room was illuminated by a single 60 watt bulb which gave a level of illumination in the vicinity of the bird of $0.03 cd/m^2$. The bird was never directly illuminated, all light in the region of the experimental apparatus being reflected from the walls of the experimental chamber. Sixteen readings were taken at each interflash interval. The delay between each first (priming) flash of the pair was approximately 5 seconds. Interflash intervals were 20, 25 and 30 milliseconds and then every 10 milliseconds up to a maximum of 180. After the completion of the first series of readings, the amplifiers were switched off and a cut made through the optic tract and anterior optic tectum. The extent of the lesion was subsequently checked in the way described in the previous

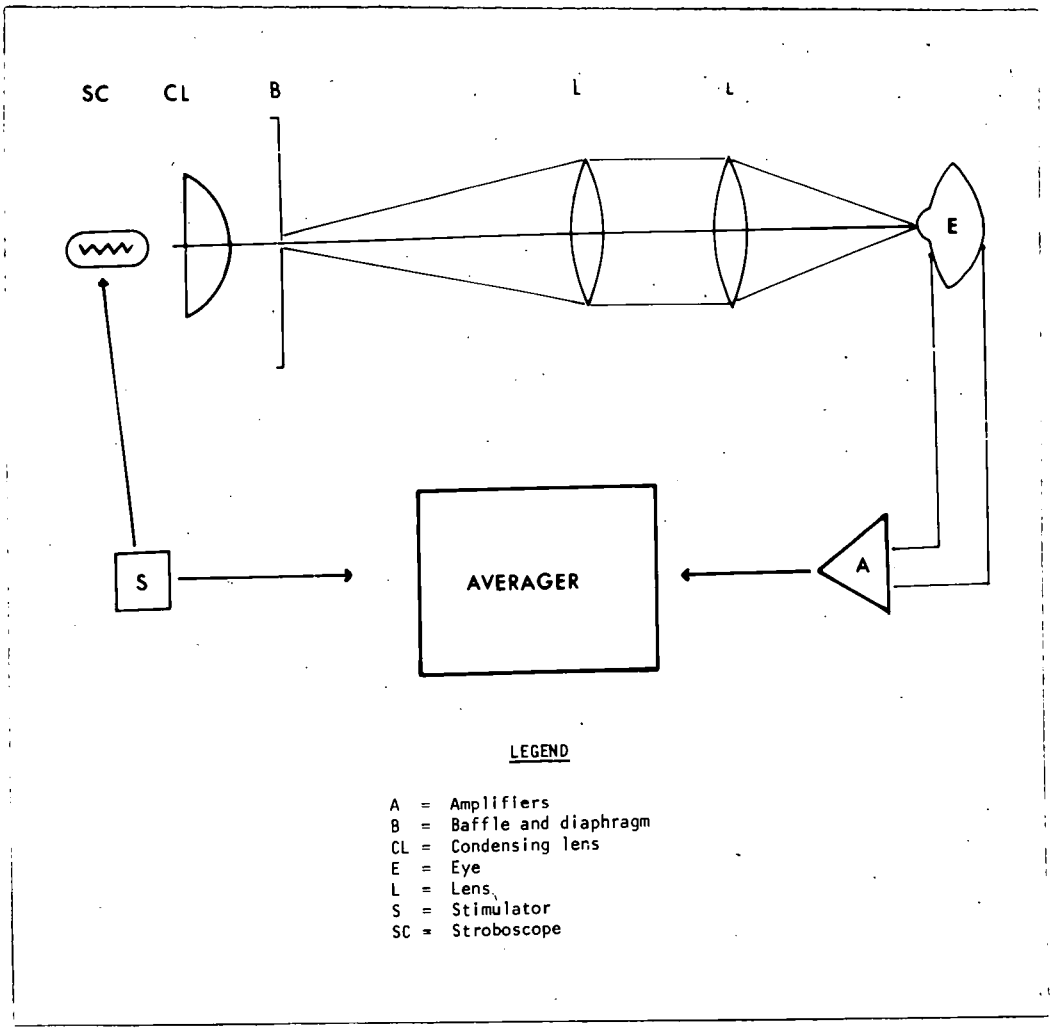


Figure 8. Shows the apparatus used for stimulating the eye and recording the E.R.G. in experiment 3 . The stimulus was a circular field of approximately 15° seen by the pigeon in Maxwellian view. Stimulus was a 40 microsecond 90 joule flash from a Dawe stroboscope.

experiments.

RESULTS

When the amplitude of the b-wave to the second flash is plotted it shows recovery from being delayed and markedly inhibited at 20 milliseconds to being almost fully recovered by the time that the interflash delay has reached 100 milliseconds (Figures 9 and 10).

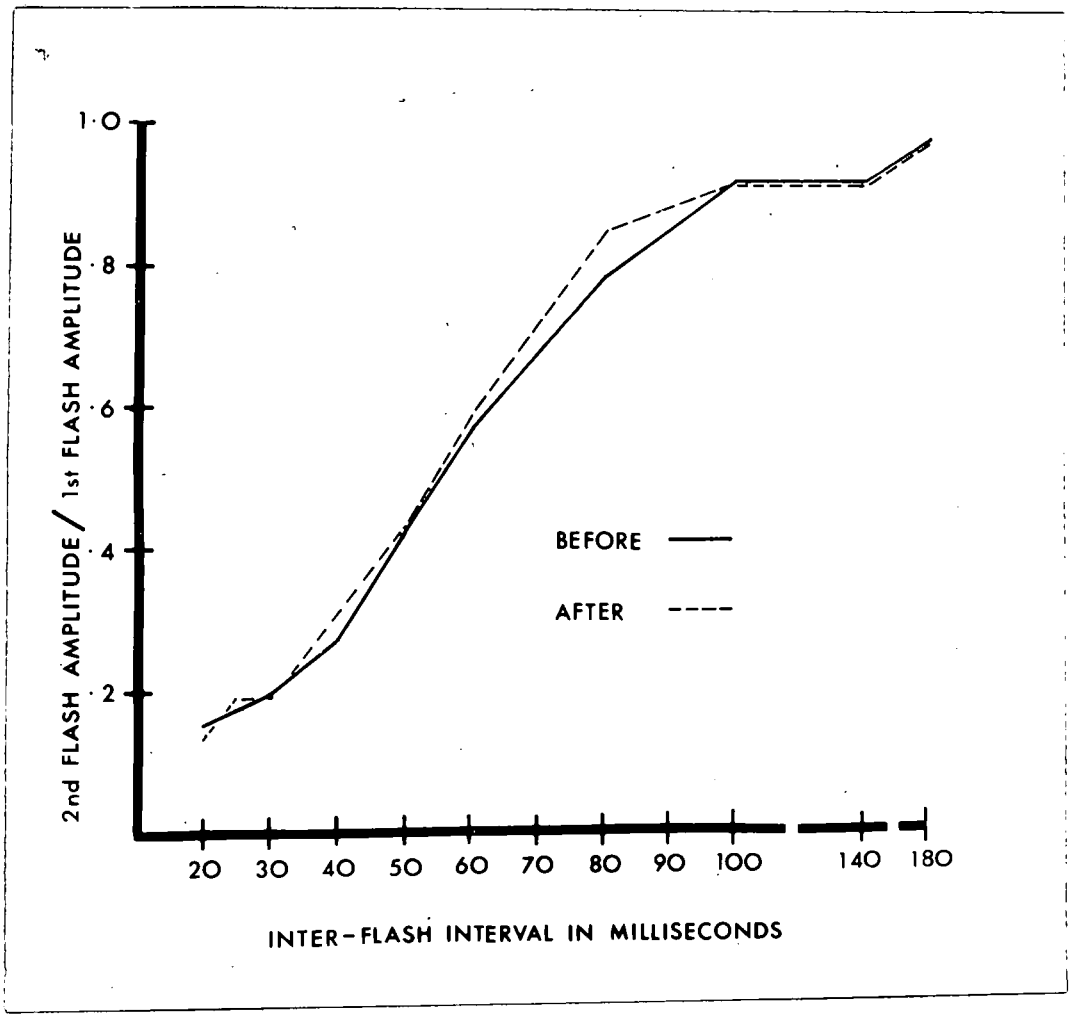


Figure 9. The recovery of the b-wave of the pigeons E.R.G. as a function of interflash delays. Average of 5 birds.

The waveform of the second b-wave was clearly very much effected by the first. In particular the peak of the second b-wave shows attenuation

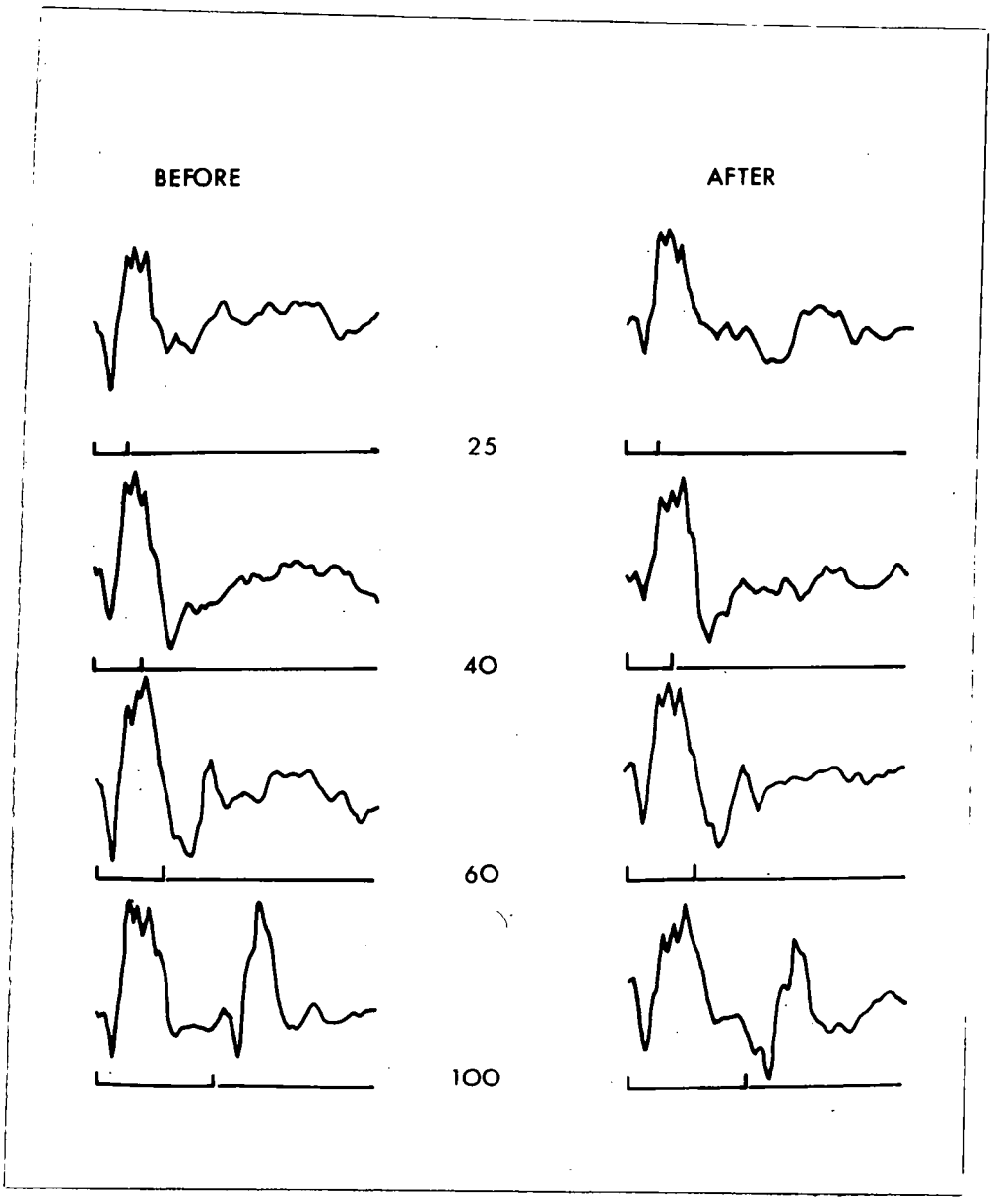


Figure 10. Tracings of E.R.G. responses to two flashes separated by short intervals before and after destruction of the optic tract. Figures given in the vertical meridian of the figure show the inter-flash delay in milliseconds. Upward deflection on baselines indicate occurrence of stimulus.

when compared to the waveform of the priming flash (Fig.10). The same effect is present both before and after the lesion and there seems no reason to conclude that the inhibitory after-period following the response to the first flash is in any way altered by the destruction of the centrifugal system. The slight divergence in the recovery curves is due to the influence of one bird and was not representative (see 80 millisecond point)Fig.9).

DISCUSSION

This experiment again produced no evidence of any centrifugal control of the E.R.G.. The recovery of the response to the second flash was regular both before and after the lesion. The inhibitory period that follows the retinal response to illumination is thus not effected by destruction of the centrifugal system, at least when the E.R.G. is recorded from an anaesthetised pigeon. Taken together with the previous two experiments the results are uniformly negative. However, in two birds in the present experiment the process of cutting the optic tract

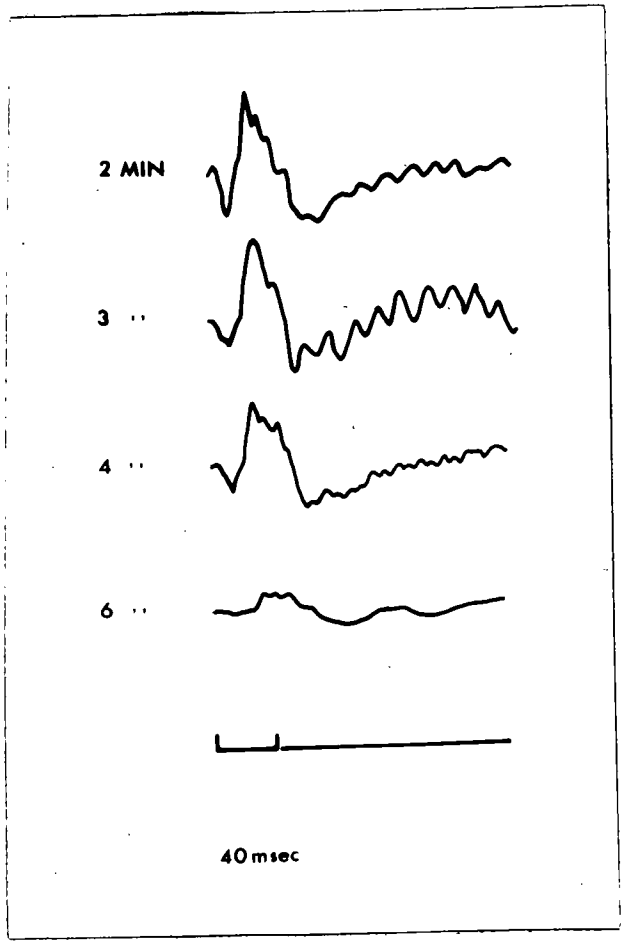


Figure 11. Responses of the E.R.G. of a pigeon in which the retina deteriorated over 10 minutes of recording. Recording began approximately 5 minutes after a cut made through the optic tract. Note the build up and decay of oscillations that are locked to the stimulus. The tracings are an average of 16 presentations of the stimulus. The interflash interval was 40 milliseconds when the effect was noticed.

resulted in damage to the internal carotid and opthalmic arteries which run under the anterior section of the optic tectum. This resulted in the slow death of the retina over a period of 10 minutes or so, but before the E.R.G. was abolished a series of oscillations appeared, grew in amplitude and then declined before the death of the retina (Fig.11). This clearly suggests that the oscillations were a direct consequence of damage to the retinal blood supply. While these results are not exactly similar to those reported by Ogden (1968), the appearance of oscillations when the retina is damaged appears to be more than coincidental. Oscillations were never seen during the course of the present series of experiments when the recordings were continued for as long as two hours following section of the optic tract (Experiment 1). It may be that when cells become damaged they become in some way hypersensitive and so oscillate in the way described by Ogden (1968). It should be noted that under normal conditions the E.R.G. of the pigeon may show a series of oscillatory beats when stimulated by bright light following adaptation to a low level of illumination (Nye 1968). In the present case the oscillations seen were induced by a very brief pulse of light and continued well beyond the period over which a normal E.R.G. response occurs following (compare with Figure 10). It should be noted however that these extremely brief flashes were much more effective in inducing complex b-waves than the more prolonged flashes used in experiment 2. Whether this effect of oscillations being produced as a result of retinal damage is peculiar to the pigeon or is a more general phenomenon is not known to the present author. Certainly Brown (1968) in his experiments on the effect of blocking the retinal circulation in the cat and cynomolgous monkey did not report any occurrences like those reported here. It should be noted that in Brown's studies however the clamping of the retinal circulation is much more like complete section of the arterial supply, which occurred several times during the course of the three experiments described above, but in all cases except the two described in this section the retina died very rapidly, the responses being almost completely abolished 1 minute after the cut. In the present case this plainly did not happen. By increasing the gain of

the amplification system a response could still be detected 10 minutes after section. This appears to be more akin to what may happen when the retina is disturbed for a long period of time, than when the response is abolished immediately. Whether or not the results reported by Ogden (1968) and the results reported here are in fact analagous can only be decided by reproducing more carefully the type of result reported above. Several attempts to repeat these results have failed because the damage done to the blood supply was too profound and the E.R.G. disappeared too rapidly to do anything with it.

This would have been the last experiment on the pigeon's E.R.G. but for the fact that a statement by Johnson, Riggs and Schick (1966) gave rise to fresh speculation. In measuring the spectral sensitivity of the human E.R.G. they noted that the response to a barred pattern was much larger than to an illuminated field of the same luminance. It is easy to understand why this might be the case, since the pattern of lateral inhibition in the retina might be expected to change when a striped pattern instead of an evenly illuminated field is used as the stimulus. If the centrifugal system affects the lateral spread of information within the eye, then it is possible that if differences in the response of the pigeon's E.R.G. to plain and patterned field could be detected, then it would be possible to continue and see if this differential response could be in any way modified by elimination of the influence of the centrifugal system.

EXPERIMENT 4. THE RESPONSE OF THE PIGEON'S E.R.G. TO PLAIN AND PATTERNED FIELDS

In the study of Johnson, Riggs and Schick (1966) the stimulus used was a barred vertical pattern with each bar subtending an angle of 1 degree 7 minutes. The stimulus for the E.R.G. response was a phase alternation of this pattern. In the present experiment it was decided to use a stationary stimulus that would be exposed for a given interval ($\frac{1}{2}$ sec.). While this stimulus is not the same as that used in the experiment by Johnson et al (1966) since it would not completely abolish the scotopic response that would result from the dark period between

each flash, it should still be possible to detect a change in the E.R.G. if this change was sufficiently large.

APPARATUS

The apparatus used in this study was the same as that used in experiment 1 except for some minor modifications. The size of the field seen by the bird was reduced to 10 degrees. A series of grating patterns were made by photographing a vertical striped pattern consisting of light dark intervals of equal period. The gratings produced stimuli of .3, 1, 1.8 and 4.8 cycles per degree respectively. A plain field .3 log. units below maximum intensity was used as a comparison stimulus. The responses were averaged on a Biomac 500 transient computer and the display tube photographed to provide permanent records.

PROCEDURE

The preparation of the animal was identical to that described in previous experiments. A series of readings were taken (32 at each spatial frequency and also with the plain field) before and after the lesion. The experimental room was not completely dark, the illumination of the lens in the absence of the stimulus being approx. 0.2 log. foot lamberts.

RESULTS

The results of this experiment showed no meaningful pattern (Fig.12). The amplitude of the b-wave and the 'off' response fluctuated wildly, often by as much as 30% when the same set of readings were repeated. Only 2 birds were used and it became clear that the fluctuations would completely mask any pattern that might have been present.

DISCUSSION

The wide variability present in the results of this pilot experiment made it impossible to continue even though the results shown (Fig.12) represent averages of 32 presentations of the stimulus. The impression gained by the experimenter was that the eye movements were responsible for the variability. If the eye movements occurred during the interflash interval then the E.R.G. was larger than if they failed to occur. The experiment is evidently deficient in several important respects. In the first place it would be necessary to stabilize the eye by using curare. In the second place the apparatus should be

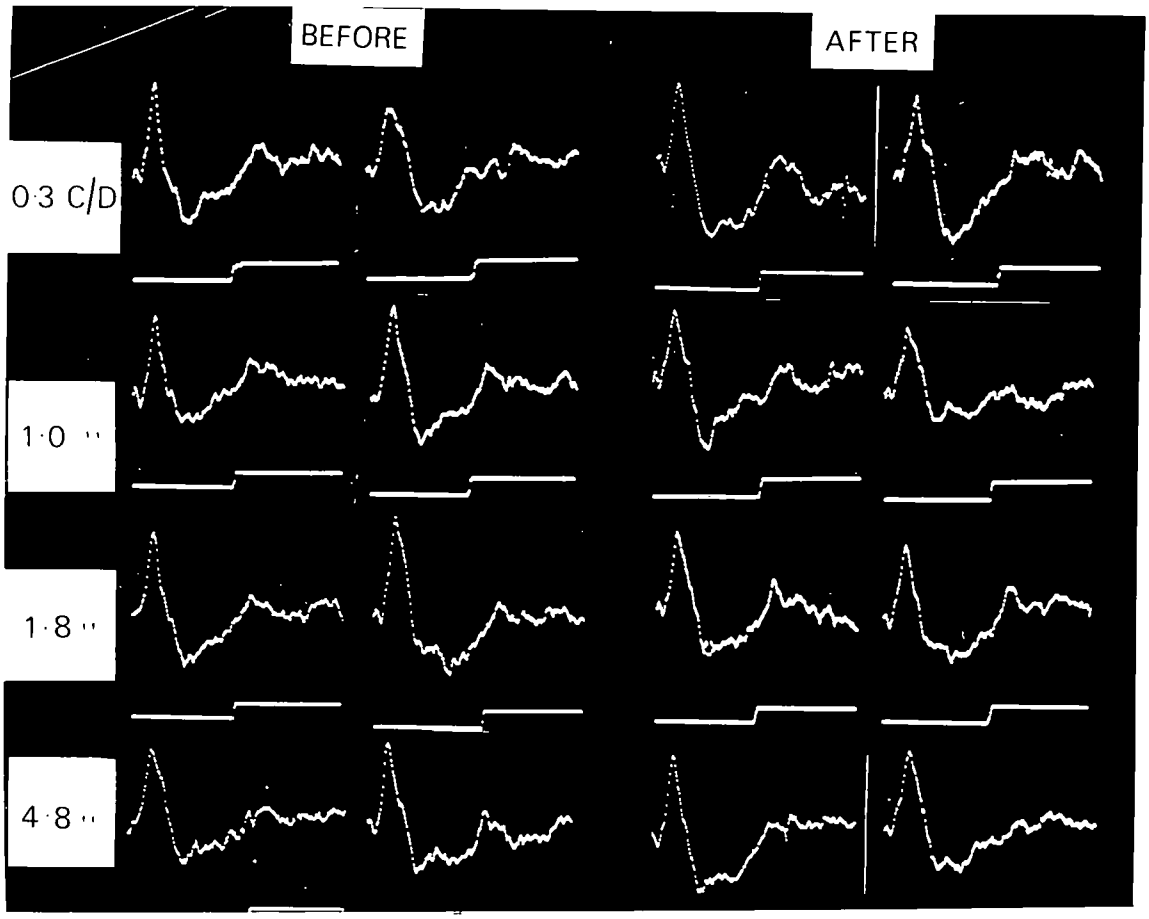


Figure 12. Shows the E.R.G's obtained when the spatial frequency of the stimulus field was varied. Each record is an average of 32 presentations of the stimulus. Note the wide variability in the response.

modified so that the stimulus could be presented in the same way as that of Johnson et al (1966) i.e. phase alternation. If these modifications were introduced the method would seem a promising one for the investigation of lateral inhibition mechanisms and the possible function of the centrifugal system in influencing them. It seems reasonable that

if the centrifugal system is not influencing the temporal structure of the E.R.G. wave form, then the next logical alternative is that it influences in some way the spatial interaction within the eye. The method used in experiment 4 was not a satisfactory means of investigating this hypothesis for the reasons given above, and also because the presence of a dark interval between presentations of the stimulus allowed some recovery of the rod process and this might well have masked any effect that would be attributable to the cones alone. The spatial summation effects in the rod dominated conditions of low illumination are much greater than under conditions of reasonably high light adaptation (Johnson et al 1966). Taken together then the faults present in this experiment and the wide variability found in the recordings do not allow any conclusions to be drawn about spatial interaction effects in the pigeons E.R.G.. It is hoped however that the construction of more suitable apparatus that meets the objections raised above will allow in the future the continuation of this line of research.

CONCLUSIONS

The experiments reported in this chapter were designed to investigate the possibility of finding centrifugal effects on the E.R.G. of the pigeon. Since the E.R.G. represents a summed activity of the retina, the possibility is always present that it is not a suitable recording method for detecting effects that may be highly specific. There is also the possibility that the basic assumption of these experiments, namely that the centrifugal system is exclusively or mainly a visual control mechanism, may be seriously in error. The points raised in chapter 2 concerning the likelihood that the optic tectum is not an exclusively visual centre raise the possibility that it is the interaction with other sensory systems that produces effects on the retina, since the centrifugal system receives its input exclusively from the tectum. However it can be said against the first point that the density of terminals within the retina of the centrifugal system is spread evenly (Maturana and Frenk 1965) and so effects might be expected on the massed retinal potential. On the second point, it can be said that even under the conditions of the present experiment there may have been sufficient stimuli from other

sensory modalities to have provided some intersensory interaction in the tectum, although if the system only responded on the basis of novelty or to transients then obviously effects would not be expected. In the absence of any clues however, the approach adopted in these experiments appears reasonable.

The absence of any positive effects in the experiments was however disappointing. The possible reasons for the negative findings have been mentioned in the discussions to the various experiments. Briefly these were that; A) the anaesthetics used might have exercised a depressive effect either on the E.R.G. itself or on either the optic tectum or the nucleus isthmo opticus itself. There is some reason to suppose that this might in fact be the case. Wright's (PERS. COM.) report on the central effects of urethane in the cat support such an interpretation at least as regards this anaesthetic, and Nye (1968) found that in his study of the pigeon E.R.G. Sodium Pentobarbital, urethane and equithesin suppressed the E.R.G. well below the levels found in the unanaesthetised bird. Of the anaesthtics he tried only the inhalation anaesthetics, Metofane and Halothane produced E.R.G's that were comparable to the concious animal. An attempt by the present experimenter to obtain these anaesthetics failed as the suppliers were only prepared to deliver them to registered anaesthetists. Aside from the difficulties of recording from unanaesthetised birds, the present experiments required that recording should begin immediately following surgical intervention and not after waiting for the animal to recover from the anaesthetic that would be required for surgery. Since no definite information is available which rules out the possibility that the centrifugal system may function adequately enough to allow some experiments to be carried out on it, it is reasonable to pursue, at least for the present, experiments which use anaesthetic agents. B) The experiments taken as a whole suggest that when evenly illuminated fields are used no effects are present on the E.R.G.. It should be mentioned that large (10 - 15 degree) fields are a rather unnatural means of stimulating an animal's eye, and it may well be that it is only when the field is not homogenous that the eye will function in a way that approaches the normal state. The inconclusive findings in experiment 4 do not allow any

definite statement to be made concerning this hypothesis. Experiments in which the lateral inhibition mechanisms of the retina are allowed to function in a near normal pattern do seem to be the next logical step in any experimental investigation of centrifugal control of retinal function. It is hoped to begin experiments along these lines in the near future.

CHAPTER 4. EFFECTS OF HYPERSTRIATAL LESIONS ON VISUAL LEARNING IN THE PIGEON

While serious deficits are produced on visual learning and orientation tasks among the majority of mammals when primary visual projection areas within the telencephalon are extensively damaged, the literature on inframmammalian forms does not allow similar conclusions. Thus in the rat (Lashley and Frank 1934), the cat (Smith 1938), and the primates (Kluver 1937, 1942), removal of the striate cortex produces severe impairment, on both retention and aquisition, of a range of visually guided tasks. Though this phenomenon is not uniform across mammalian species (Snyder et al 1966 found that removal of the striate cortex of the tree shrew made little difference to its visually guided behaviour) the situation found among mammals is in general in marked contrast to that found among those inframammalian species that have been subjected to experimentation. Thus Janzen (1933) found that in the goldfish removal of the entire forebrain made only a slight difference to the number of trials required to reach criterion on a colour discrimination task, and Bernstein (1962) found only a transitory loss in the retention of a hue discrimination (4 hours) which could easily be attributable to postoperative shock. Whether the forebrain in fish does or does not receive visual afferents is the subject of some dispute (Maliukina and Flerova 1960, Guselnikov 1964, Enger 1961). Guselnikov et al (1964) concluded that previous reports of visual projections to the forebrain of fish, were attributable to the investigator confusing potentials generated in the tectum and cerebellum with potentials generated within the forebrain. Potentials recorded on the surface of the forebrain had the same latency and waveform as those recorded from the optic tectum, and were distinguished only by having a much smaller amplitude than the recordings from the tectal surface. As far as information is available at present then, it may well be the case that the forebrain of fish does not receive a similar type of visual input to that found in mammals and birds, and so lesions here would not be expected to produce deficits in the analysis of visual information. So far as the present author is aware there has been no work carried out on the effects of

forebrain lesions on visual learning in either reptiles or amphibians.

When one considers the literature on the effects of lesions to the forebrain of birds the only strictly relevant experiments appear to be those of Layman (1936) on the effects of forebrain lesions on visual discrimination of chickens and Zeigler (1963) on the effects of forebrain lesions on visual discrimination in pigeons. Layman (1936) used a modified Yerkes' box for training her subjects and used a triangle and circle as the stimuli to be discriminated. Of the six animals, out of a total of 50, that failed to learn the discrimination all had extensiv e damage to the hyperstriatum and although on no subject was the hyperstriatum completely destroyed, bird No.45 closely approached complete destruction of the hyperstriatal layers. A large number of animals however showed a deficit in the number of trials required to reach criterion, some of these having extensive damage in the posterior pole of the neostriatum. However, a noticeable feature of Laymans (1936) results is the fact that those animals that took longer to learn than the controls, tended to have asymmetrical lesions. Of the six animals that failed to learn the discrimination, four had clearly asymmetrical lesions and there is a suggestion in the remaining two animals that this was also the case. Sprague (Sprague et al 1961, Sprague 1966) has emphasised that lesions involving unilateral damage to structures may produce more severe impairement than when bilateral damage is present. In the pigeon Bingelli et al (1963), and Patay & Tazartez (1957) have shown that where spatial tasks are involved the effects of unilateral damage may be overcome by producing damage in the contralateral side of the brain to the lesion. Sprague et al (1961) has suggested that the effects of unilateral damage may be to make the animal ignore stimuli on the contralateral side of the body. While it is difficult to be sure that asymmetry in the lesions may produce deficits on tasks that involve selecting between two stimuli differing in spatial location, the suspicion that this might be a relevant factor demands that lesions should be as nearly asymmetrical as possible if we are to draw conclusions about the function of the lesioned area.

Zeigler (1963) used a key pecking situation to study the effects of forebrain lesions on a triangle-circle discrimination in pigeons. He found that only lesions of the hyperstriatum or the paleostriatum consistently produced deficits in the acquisition and retention of the discrimination. The finding that damage to the paleostriatum produces decrements in performance is in no way surprising, as both the afferent and efferent tracts from the forebrain traverse this structure. There does appear to be agreement between this and Layman's study, in that lesions to the hyperstriatum produced deficits in the learning of a visual discrimination. The only other investigators that have studied the effects of forebrain lesions on the establishment of visual learning in birds are Tuge and Shima (1959). These investigators found that conditioned responses to a white (positive) and red (negative) stimuli could not be established in birds with extensive hyperstriatal damage. Taken together with the information presented in chapters 1 and 2, there appears to be good evidence that the hyperstriatal region of the pigeon's forebrain is in some way involved in visual discrimination, since there is anatomical and physiological evidence of this area receiving a visual projection, and lesions to this area produce deficits in the acquisition and retention of visual discriminations. There is little information available on the effects of lesions to other areas of the avian forebrain however. Destruction of parts of the paleostriatum cannot be taken as evidence of this area's involvement in the control of visually guided behaviour, since the afferent and efferent fibre tracts to other forebrain areas traverse this region and any deficits could be produced by these fibres of passage. Only Layman (1936) found any evidence of the posterior pole of the forebrain being involved in visual learning.

As a beginning to the investigation of the effects of forebrain lesions on visual discrimination in pigeons, it was decided to replicate the findings presented above, namely that lesions to the hyperstriatum of the pigeon produces deficits in colour (Tuge and Shima 1959) and pattern (Layman 1936, Zeigler 1963) discrimination. This was thought

necessary because the report of Tuge and Shima (1959) used a classical conditioning procedure and there is a possibility that a straightforward difference in excitability may be responsible for the failure of the classically conditioned response to differentiate. Since there were no control stimuli used, for example sound or vibration, it is not certain whether the failure of the response was a specific deficit or a quite general one. The study of Zeigler (1963) was in some sense similar to that of Tuge and Shima (1959) in that it involved a 'go-no-go' discrimination, and a difference in excitability between the experimental and control animals could well have produced an apparent decrement in their performance. Examination of the data from Zeigler's retention group supports this interpretation in that the scores were well above change on the first post operative day of testing in those animals that had been lesioned after learning the original discrimination. The data from Layman's (1936) study do not circumvent this difficulty (she used a two choice discrimination as opposed to a 'go-no-go') since in the animals which had extensive damage to the hyperstriatum there was also extensive damage to other areas, particularly the neostriatum, as well as a tendency for the lesions to be asymetrical. It seemed worthwhile to replicate the findings of deficits in colour and pattern discrimination using a two choice discrimination.

During the course of carrying out the experiment on colour discrimination, it was decided to try to gather some additional information. Colour is probably the dominant cue used by pigeons in the solution of problems, if it is available (Jones 1954). It is quite possible that the effects of a lesion may alter an attention bias in a hierarchy rather than abolishing the ability to discriminate along a dimension completely. The work of Bernstein (1961, 1962) suggests that this might be the case with forebrain lesioned goldfish. If stimuli differ along two dimensions rather than one, then it is possible to see how the animal chooses to solve the discrimination. It might learn about both dimensions, or only about one. In the present experiment it was decided to make the stimuli differ in both colour and brightness and to decide which dimension(s) the animals used by giving transfer trials. If the effects of the lesion were to alter the position of a cue in the

hierarchy or to make the animal less flexible (to attend to one cue rather than two) then by confounding the two cues during training, it should be possible to find out if this is the case. Under normal conditions a pigeon will choose to peck the brighter of two keys (personal observation). The positive stimulus was made both brighter (.8 log. units) and of a different wavelength (red) from the negative stimulus (blue). There were thus a number of alternative ways in which the discrimination could be learned:

1. colour alone
2. brightness alone
3. use both cues (colour and brightness)

The experimental and control animals could differ then in three possible ways, as well as showing an increased number of trials to reach criterion while still falling within one of the above categories.

EXPERIMENT 1. THE EFFECTS OF HYPERSTRIATAL LESION ON A COMPOUND COLOUR - BRIGHTNESS DISCRIMINATION IN THE PIGEON

Subjects and apparatus. The subjects were eight naive adult pigeons obtained from a commercial supplier. Following arrival in the laboratory, they were fed ad libitum for 14 days, then they were reduced to 80% of the ad libitum body weight before they were shaped to key peck. Following training to key peck the pigeons were allowed to regain full body weight.

The experimental chamber consisted of a standard two key Grason Stadler pigeon box. The keys were 1" in diameter and situated about 9" above the cage floor. The keys were approximately 6" apart. Stimuli were projected onto the keys using in-line digital display units, into which pieces of wratten colour and neutral density filter had been inserted. The positive stimulus was Wratten 25 (red) filter and the negative was Wratten 47b (blue) filter. It should be noted that while the photometric values quoted reflect the spectral sensitivity of the human eye, the difference between the sensitivity to red and blue for the pigeon is approximately the same as for the human (Blought 1957). Where the red and blue stimuli were equated for brightness they should also have been of approximately equivalent

brightness to the pigeon. The apparatus was controlled by a system of relays, timers and pulse formers. Choice latencies were measured with a print-out counter/timer.

Procedure

The pigeons were trained to key peck using the positive (red 25) stimulus. They were allowed 20 reinforcements after they had pecked the keys, 10 reinforcements on each key. The animals were then allowed to recover to 100% bodyweight before surgery. Four animals from the eight were randomly selected for the experimental group, the remainder serving as controls.

The four control birds were anaesthetised with Equithesin, placed in the stereotaxic instrument, the scalp opened and the bone overlying the hyperstriatum removed. No brain tissue was removed in these animals. The experimental animals were subjected to the same operative procedure but in addition the dura was lifted and cut, and the hyperstriatal tissue removed gently by suction using a vacuum pump and a fine glass capillary, the end of which had been left sharp. The aim was to destroy as much as possible of the hyperstriatum bi-laterally without damaging any other structures. Following the removal of the tissue the bone was plugged with sterispon (absorbable gelatine) soaked in thrombin, the skin was sutured and the animals returned to their home cages. They were allowed a week to recover on ad libitum food and water. They were then deprived of food and reduced to 80% body weight and the experiment begun.

The experimental situation was a discrete trial simultaneous discrimination. Both positive and negative stimuli were presented simultaneously on different keys. If the animal chose correctly (red), then the keys were blanked and the animal gained access to grain for 5 seconds. If the animal chose incorrectly the keys were simply blanked out. In the absence of intertrial pecking the next trial began 15 seconds after the stimuli presented on the previous trial had been blanked out. 30 trials were given per day. Pecking during the inter trial interval reset the time out so that the next trial began 15 seconds after the last response. When the animals reached the

+(Stimuli were switched randomely from side to side (Gellerman 1933)

criterion of nine out of ten correct responses in three consecutive blocks of ten trials they were given a further 60 trials to allow the response to the positive stimulus to become stable. They were then given transfer trials with the following pairs of stimuli. The brightness of the stimuli were measured relative to White using an S.E.I. photometer and are expressed in terms of log. units attenuation. The pairs of transfer stimuli were;

(1) White (0.0 log units) v Red (0.3 log. units)
(2) Blue (0.8 " ") v White (0.0 " ")
(3) Red (0.8 " ") v Blue (0.8 " ")
(4) Red (1.4 " ") v Blue (0.8 " ")
(5) Red (0.3 " ") v Red (0.8 " ")

Following twenty trials on the training stimuli Red (0.3 log. units) and Blue (0.8 log. units) the animals were given 10 trials on a pair of transfer stimuli in which no response was rewarded. The order of presentation of the pairs of transfer stimuli was not randomised. Beginning at (1) (above) ten presentations of each pair were given per day (1 through to 5) and then this sequence was repeated. If the animals had learned the discrimination on the basis of colour then their choice should be respectively (1) red, (2) white, (3) red, (4) red and (5) either. If the animals had learned on the basis of brightness then they should choose the brightest stimulus in each case. If the animals had learned about both cues then on (5) they should choose the brighter red and on pairs (1) and (4) the choice could be in either direction, but on (3) they should choose red.

Histology

Following the termination of this experiment and the subsequent experiment, the animals were injected with nembutal, the heads removed, and the brain perfused with 10% saline followed by 10% formalin by injection through the carotid arteries. The brains were then hardened in 10% formalin, impregnated and blocked in paraffin wax and cut at 20 microns, every tenth section being mounted and stained with cresyl violet. The extent of the lesions were drawn onto a series of standard drawings.

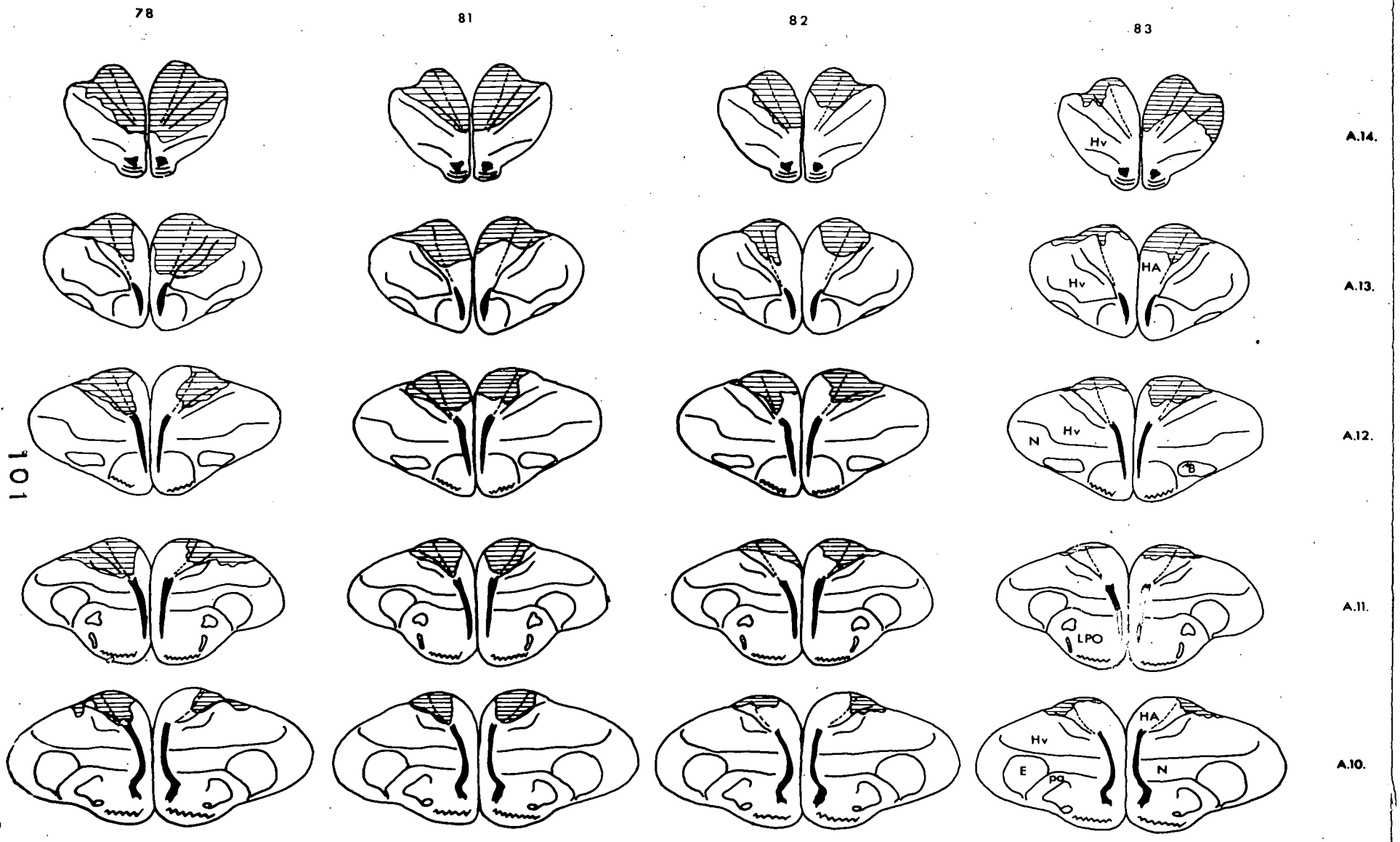


Plate 1. Shows the extent of tissue destruction in the hyperstriatal group. Numbers and letters on right refer to the plane of section in the atlas of Karten and Hodos (1967).

Results

The extent of the lesions in the four operated animals is shown in Plate 1 page 101. It can be seen that in all birds a considerable portion of the hyperstriatum ventrale has been left in-tact. Damage to the hyperstriatum is most severe in the case of birds 78 and 81. These birds showed considerable damage to the area which receives the major part of the visual projection from the dorsal thalamus (Karten and Nauta 1967, Revzin 1969 and Chapter 2 of this thesis). It should be noted however that Karten and Nauta 1967 do not report finding degeneration in the hyperstriatum ventrale following destruction of the dorsal thalamus. In the remaining two birds damage to the areas of most interest, hyperstriatum dorsale and hyperstriatum intercalatus superior is slight except in the most anterior part of the brain. Figure 1 shows the aquisition curve for the two groups of animals. It

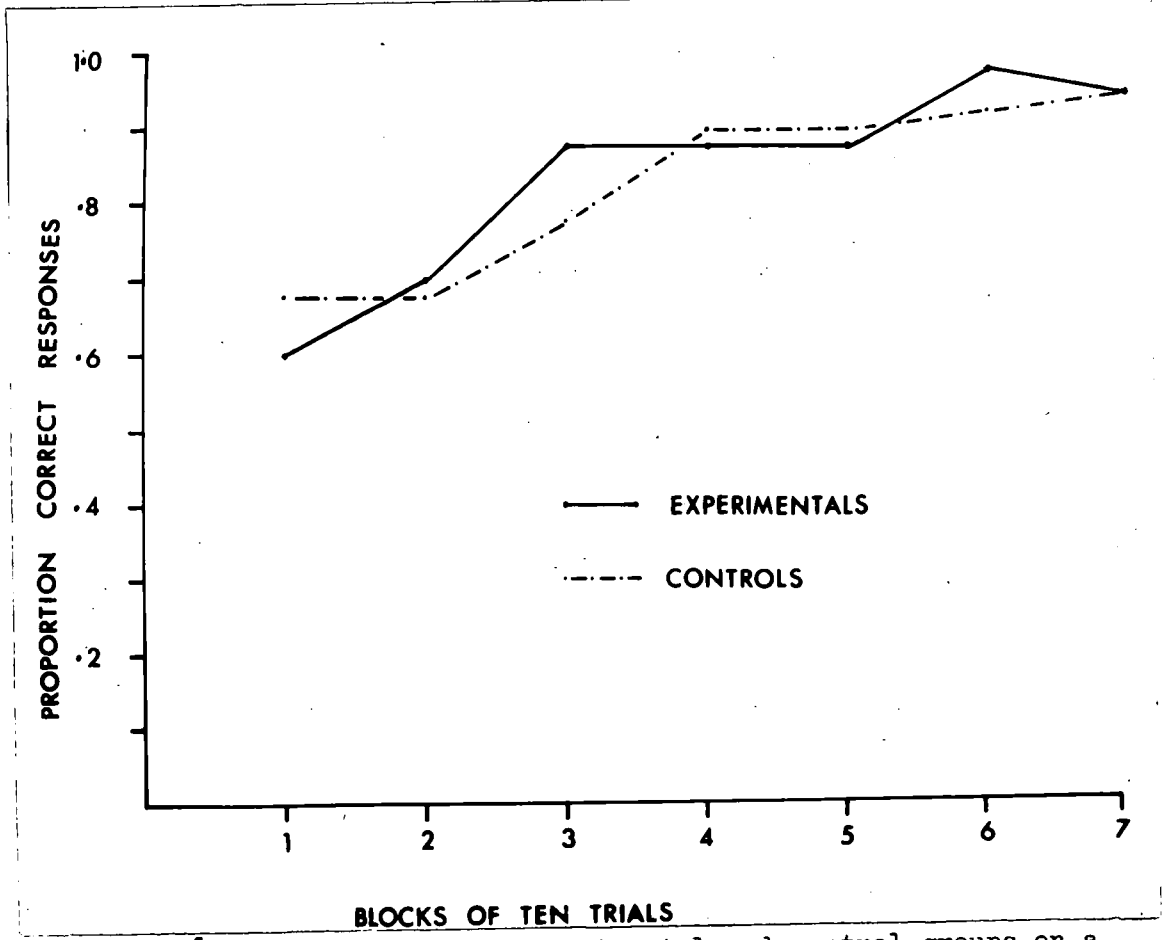


Figure 1. Aquisition data for experimental and control groups on a compound colour/brightness discrimination.

should be noted that all the animals were above chance on the first day of training which strongly implies that the difference in brightness of the positive and negative stimuli exercised quite an important effect. There is clearly no difference between the experimental and control group in terms of trials to criterion. When the choice latencies are compared however there is a difference between the groups (Fig.2). Early in training the latencies of the lesioned birds are much longer than those of the control group. The difference between the experimental

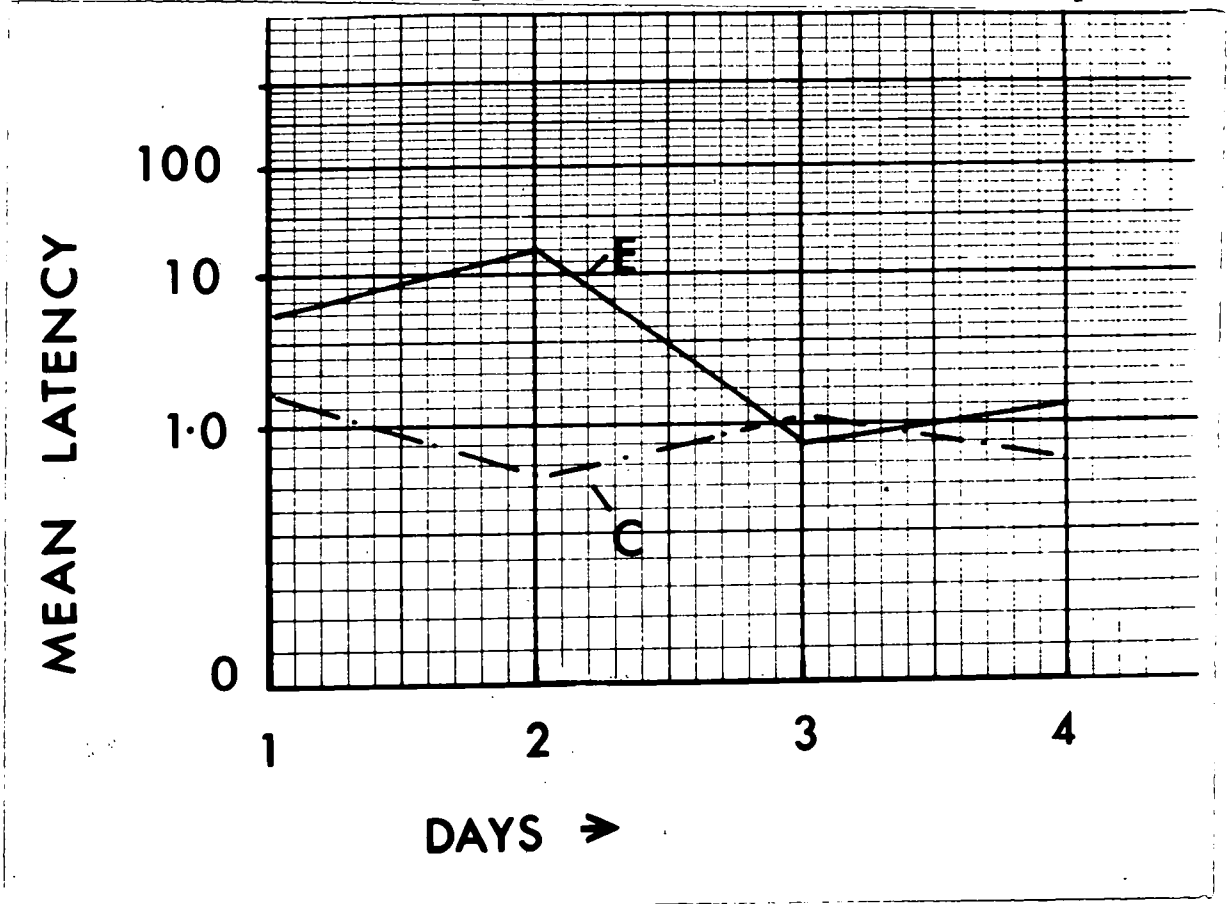


Figure 2. Mean choice latency for experimental (E) and control (C) groups over the first four days of training on a compound colour brightness discrimination.

and control group was due mainly to longer choice times occurring at the beginning of an experimental session on any one day. A statistical comparison between the (Table 1) means of the choice times over the

first four days shows the groups to be significantly different (Mann-Whitney U = 0, p = .028 two tailed test). So while there was no difference in trials to criterion the experimental group had longer choice times than the controls.

TABLE I

Experimental Group		Control Group	
Bird No. 78.	112.65	Bird No. 79.	5.01
" " 81.	17.83	" " 80.	7.59
" " 82.	12.98	" " 84.	2.25
" " 83.	14.31	" " 85.	4.125

Table 1. Shows mean choice times for experimental and control groups. Mann-Whitney U = 0 for n_2 = 4, p = 0.014.

The results of the transfer tests are given in Table 2 (page 105). It can be seen that on the choice of red versus white, only one bird, no.81, failed to choose the red stimulus a significant number of times from 20 choices. On the choices of blue versus white, red versus blue (equal brightness), and red against blue (red .3 log. units darker than blue) all birds in both groups chose in favour of having learned the discrimination on the basis of colour and not brightness. On the final test light red against dark red it can be seen that no bird showed any evidence of having learned anything about the difference in brightness of the positive and negative stimuli.

TABLE 2

BIRD NO.	RED v WHITE	WHITE v BLUE	RED (0.8) v BLUE (0.8)	RED (1.14) v BLUE (0.8)	RED (0.3) v RED (0.8)
78	15/20 (.05)	18/20 (.01)	18/20 (.01)	14/20 (N.S.)	10/20 (N.S.)
81	11/20 (N.S.)	17/20 (.01)	20/20 (.01)	17/20 (.01)	10/20 (N.S.)
82	17/20 (.01)	20/20 (.01)	20/20 (.01)	20/20 (.01)	12/20 (.N.S.)
83	19/20 (.01)	15/20 (.05)	19/20 (.01)	19/20 (.01)	9/20 (N.S.)
79	19/20 (.01)	18/20 (.01)	19/20 (.01)	14/20 (N.S.)	10/20 (N.S.)
80	20/20 (.01)	19/20 (.01)	19/20 (.01)	16/20 (.01)	11/20 (N.S.)
84	19/20 (.01)	16/20 (.01)	18/20 (.01)	15/20 (.05)	11/20 (N.S.)
85	19/20 (.01)	19/20 (.01)	19/20 (.01)	14/20 (N.S.)	8/20 (N.S.)

Table 2. Shows choices made to the stimulus shown at the top of the pair i.e. in column 1 red/v white 15/20 indicates red was chosen fifteen times out of 20. The figures shown underneath the number of choices indicates the level of significance on a twoltailed binomial test $Z = X-M\sqrt{npq}$. (N.S.) = Not significant.

Discussion

The fact that there is no difference in trials to criterion between the experimental and control groups is somewhat surprising since Zeigler (1962) reported deficits in brightness discrimination, and Tuge and Shima (1958) report deficits in colour discrimination in pigeons with hyperstriatal lesions. The latency differences between experimental and control groups may indicate that the group of lesioned birds found the discrimination slightly more difficult, but this difference could as well argue that the lesioned group found it more difficult to adapt to the situation. In the absence of any further data it is difficult to attatch any clear meaning to this difference. The lesions did not completely destroy the hyperstriatum (Plate 1, page 101); parts of the hyperstriatum ventrale in particular remained intact in all the lesioned animals. However the lesions in birds 78 and 81 are comparable in extent to those produced in the experimental animals of Zeigler (1962) in which he reported both brightness and pattern vision deficits. They are somewhat smaller than the lesions produced in the studies of Tuge and Shima (1958).

It is also somewhat surprising that in spite of the extremely rapid learning in both groups of animals there is no evidence of both cues (colour and brightness) being used. This may in fact be as much an indictment of the method of using transfer trials to ascertain whether an animal has learned about a given cue, as proof of the fact that they did not use that cue. There does seem to be some indication that the method used in testing for the $\overset{c}{\wedge}$quisition of stimulus control is important. Reynolds (1961) found that using a straightforward measure of response rate, evidence for stimulus control by only one component of a complex stimulus was found. Thomas, Scott Burr and Svinicki (1969) found that by using stimulus generalisation as the test of the $\overset{c}{\wedge}$quisition of stimulus control by the components of a compound stimulus, evidence was found for the control of behaviour by both cues. The results do however clearly show that pigeons with hyperstriatal damage can discriminate colour, at least when there is a substantial difference in wavelength.

The failure to find any evidence of a colour vision deficit in the present experiment when there was some evidence in the literature of this region being important in the control of visually guided behaviour made it necessary to continue and find whether the results of Zeigler (1962) concerning deficits in pattern vision could be replicated. Accordingly the birds used in the present experiment were not sacrificed but were run on a pattern discrimination task.

EXPERIMENT 2. THE EFFECT OF HYPERSTRIATAL LESIONS ON PATTERN DISCRIMINATION AND REVERSAL LEARNING IN THE PIGEON.

In view of the failure to find colour vision deficits in the animals with hyperstriatal lesions it was decided to run the animals on a pattern vision (triangle versus square) discrimination. The difference between the situations used by Tuge and Shima (1958) and Zeigler (1962), where a successive discrimination was used, and the present situation where the discrimination was simultaneous, might throw some light on the nature of the deficits found in the experiments of previous workers. It is easy to see that in the successive discrimination situation the inability to withold a response might result in the apparent failure of a discrimination, whereas another method may show no such failure. That such an interpretation is at least feasible is suggested by the results of some experiments on destruction of parts of the forebrain in mammals. The results of hippocampal lesions have frequently been interpreted as a failure to inhibit a learned approach response (Kimble 1968). The presence of the positive stimulus in a simultaneous discrimination situation means that the animal is always able to respond, so the interpretation of the nature of the deficit may be quite different when one uses this situation as opposed to a successive situation.

Subjects and Apparatus.

The subjects were the same as were used in the previous experiment. Training began one week after the termination of the last experiment. The apparatus was a two key pigeon chamber with grain feeder. The keys, situated nine inches above the grid floor were one inch in diameter. The inside of the box was painted mat black and was illuminated by a bulb placed behind a translucent panel on the wall opposite the keys.

The stimuli consisted of outline vertical triangle and square, both triangle and square being $\frac{3}{4}$ inches high. Responses to the triangle were rewarded by 5 seconds' access to grain. The apparatus was controlled in exactly the same way as that of the previous experiment. The animals were given 30 trials per day. The day following the session in which they attained criterion the positive stimulus was changed to the previously negative and the animals were run until they attained criterion. Five reversals of positive and negative stimuli were made in all.

Following the conclusion of the series of five reversals the animals were allowed three days (90 trials) for their performance to stabilise. Then on each day for the next 24 days they were given 20 trials on the training stimuli and then 10 transfer trials with new stimuli (see Table 4 in the results section) to determine whether there was any difference between the experimental and control group's reaction to the transfer stimuli. Each stimulus pair was presented twice (20 transfer trials in all) and the order of presentation was randomised.

Results

There was no difference between the groups in trials to criterion (Table 1), nor was there any significant difference in choice latency. (Table 2).

TABLE 1

Experimental Group				Control Group			
Bird No.	78.	270	Trials	Bird No.	79.	150	Trials
" "	81.	120	"	" "	80.	150	"
" "	82.	210	"	" "	84.	240	"
" "	83.	150	"	" "	85.	150	"

Table 1. Shows the number of trials to criterion for the experimental and control groups on a triangle (positive) square (negative) discrimination.

In terms of the severity of the lesion the bird with the most severe damage (78) took the greatest number of trials to criterion (270), while

TABLE 2

Experimental Group		Control Group	
Bird No. 78.	1.296.	Bird No. 79.	2.826
" " 81.	2.545	" " 80.	5.626
" " 82.	2.884	" " 84.	.890
" " 83.	1.521	" " 85.	1.963

Table 2. Shows mean choice latencies for experimental and control groups over the first four days of training, Triangle/square discrimination. Pecks to triangle rewarded.

the bird (81) with the next most severe damage learned the discrimination in 120 trials, which was less than any of the controls. The same situation was true of the 5 reversals (Figure P). Again bird No.78 took the greatest number of trials to complete the reversals (3900), while bird No.81 which was quite close in terms of amount of tissue destroyed completed the reversals in the least number of trials (870) (see Table 3).

TABLE 3

Experimental Group		Control Group	
Bird No. 78.	3900 Trials	Bird No. 79.	2070 Trials
" " 81.	870 "	" " 80.	2160 "
" " 82.	1590 "	" " 84.	1440 "
" " 83.	1710 "	" " 85.	1890 "

Table 3. Shows the number of trials required to attain criterion on 5 reversal of a triangle-square discrimination.

The results of the transfer tests are given in Table 4 (page III). It can be seen that the experimental and control group show no tendency to choose differently in the transfer tests except possibly in the choice between the + and x (Pair No.4), where three of the experimental animals failed to choose significantly in favour of the +, whereas all the controls did so.

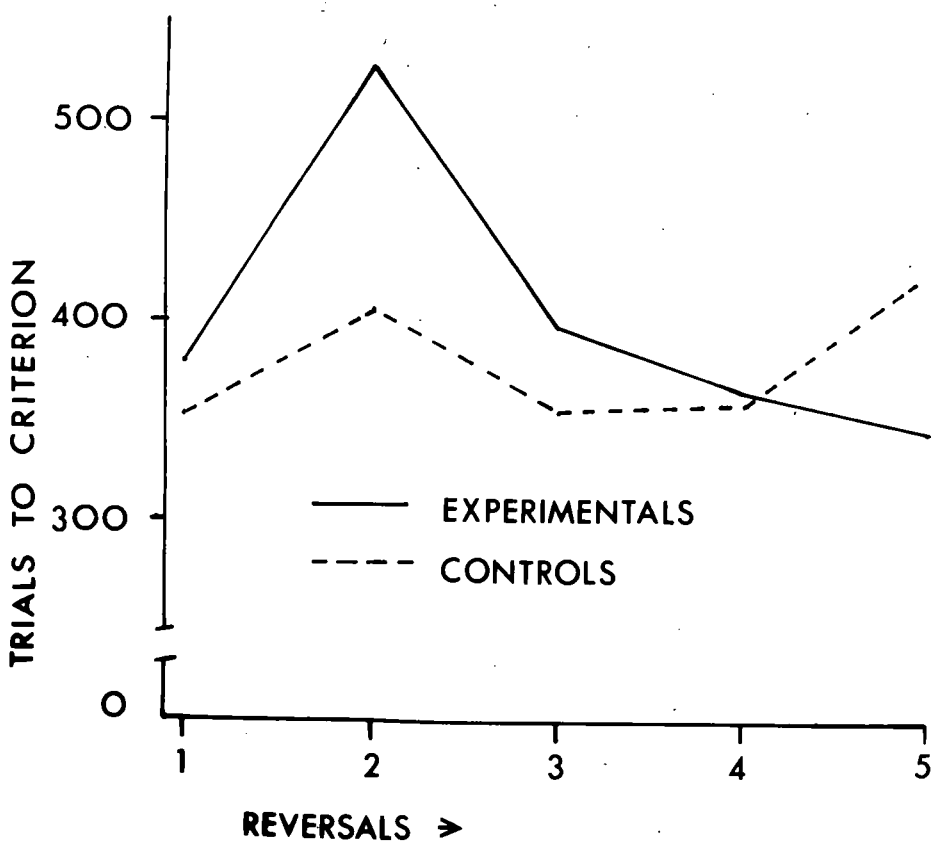


Figure 1. Shows mean No. of trials to criterion for experimental and control groups over 5 reversals of a triangle square discrimination.

Discussion

The present experiment like the previous one does not reveal any consistent differences between pigeons lesioned in the hyperstriatum and normal control animals. It has been argued by Karten (1970) that the projection from the dorsal thalamus to the hyperstriatum may be analagous to the geniculo-striate system of mammals. The present results tend to show that the similarity between the geniculo-striate system and the dorsal thalamic-hyperstriatal projection of the pigeon cannot be carried

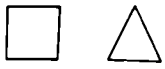
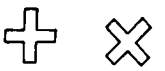
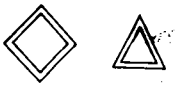
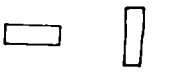
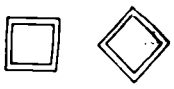
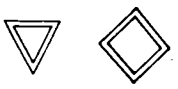
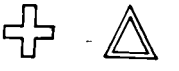
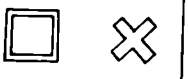
	BIRD No 78*	BIRD No 81*	BIRD No 82*	BIRD No 83*	BIRD No 79	BIRD No 80	BIRD No 84	BIRD No 85
	14	16	13	10	15	16	11	16
	14	11	10	11	10	12	11	11
	14	17	18	17	12	14	14	16
	15	9	12	10	18	15	15	17
	19	17	14	12	16	18	15	13
	10	12	10	10	10	10	11	12
	16	15	12	16	19	18	10	17
	14	15	18	13	18	20	19	18
	15	14	16	17	13	19	8	14
	20	17	16	18	16	16	16	14
	20	18	15	19	17	14	16	16
	15	17	19	16	18	17	18	15

Table 4. This table shows the number of times the stimulus shown in the left hand side of the columns showing the transfer shapes, was chosen from a total of twenty presentations of the pair. The training stimuli (outline triangle and square) are shown in the top left corner of the table. A score of 15 or above is statistically significant on a binomial test ($Z = X - M\sqrt{npq}$. two tailed test).

too far at the moment. While a considerable portion of tissue in the hyperstriatum was left intact in the present experiments the lesions in animals 78 and 81, which were the most severe of the group, involved considerable damage to the area of the hyperstriatum that appears to receive the major part of the visual projection (Revzin 1969, Chapter 2 of this thesis). It should also be mentioned that the area of the hyperstriatum that Karten (1970) considers may be analogous to the striate area of mammals (the granule cell layer which includes the hyperstriatum dorsale and hyperstriatum intercalatus superior) was extensively damaged in birds 78 and 81) and substantial amounts of tissue were removed from these areas in birds 82 and 83. The lesions in birds 78 and 81 involved damage as severe as that found in those animals in Zeigler's (1962) experiment which showed aquisition and retention deficits in learning a triangle-circle discrimination. The failure to find aquisition deficits in the present experiment may be due to a number of different causes. The fact that the present experiment was a simultaneous discrimination and not a successive one may have made a considerable difference. The fact that the animals in the present experiment had already had experience of a two choice discrimination situation, in which the stimuli differed along two dimensions that are easy for pigeons to discriminate, may have assisted the lesioned animals to overcome the initial difficulties of the situation. It may be inherently easier for a pigeon to learn to discriminate a triangle from a square, than from a circle, although this would appear to be the least likely of the alternatives. There are however no good reasons for picking one alternative instead of another as being the most likely.

The evidence from the transfer tests is difficult to interpret. While it shows that there is no consistent difference between the experimental and control groups, it should be remembered that these transfer tests were given after the animals had five reversals of the positive and negative stimuli and this may have resulted in any potential differences between the experimental and control groups being obscured. That such a situation is possible, or even likely is shown from an experiment by Sutherland (1966) in which rats learned eight reversals of stimuli differing both in orientation and brightness.

It was found that if on one reversal an animal used one cue (say brightness), when that animal was reversed it tended to learn the reversal in terms of the other cue (in this case orientation). In the present experiment it is possible that initially the experimentals and controls may have differed, in either the cue they used to solve the problem, or in the extent to which they could be distracted by the presentation of new stimuli, but in the course of reversal learning this difference disappeared, because the animals learned about different aspects of the stimulus during each reversal.

From the point of view of any hypothesis that the projection from the dorsal thalamus to the hyperstriatum is involved in the analysis of information about either colour or pattern the present experiments are decidedly negative. When one considers the two birds with the most severe damage of the hyperstriatal visual area (No's. 78 and 81), there is no evidence of an impairment in either colour or pattern vision. While bird 78 took the greatest number of trials to learn the triangle/square discrimination (270 trials) this figure is only 30 trials (one days training) longer than the slowest control. The data from the transfer trials also argues strongly for the fact that the visual processing capacities of these animals were essentially unimpaired. Even if the argument presented above for the fact that repeated reversal may overcome an attentional bias in the lesioned animals is true, the fact that the animals are not confused by the presentation of novel stimuli in opposition to the stimuli used during training, argues that the animals are perfectly capable of analysing the visual input. The ability to transfer from outline to filled in shapes is shown by both experimental and control groups, and the fact that neither group confused the triangle with the rotated square argues for the proposition that the visual analysis of the shapes was on a fairly sophisticated level. The equivocal behaviour of the animals in the choice of square versus inverted triangle, and the choice in favour of the inverted triangle when this was paired with the training triangle argues for the fact that the animals chose mainly in terms of the differences at the top of

the shapes. The choice of the rotated square when this was paired with the triangle shows that either the animals appreciated that the angle at the apex of the triangle was more acute than that of the square or else that in this choice they looked at other aspects of the shapes. In two pairs of transfer stimuli, the vertical and rotated cross and the horizontal and vertical bar, neither of the stimuli used in training were present. In the case of the horizontal, and vertical bar the choice behaviour of both groups was equivocal. In the case of the upright and rotated cross however all the controls chose significantly in favour of the upright cross while only one of the experimental animals did so. Since the experimental bird that did so however was the animal with the most severe lesion it does not seem worth while to speculate on the significance of this. It can be said, as Towe (1954) pointed out, that the analysis of patterns by pigeons is quite sophisticated and that this ability is not disrupted even by a fair degree of brain damage.

Chapter 5

The effects of forebrain lesions on orientation, size and brightness generalisation in pigeons

The failure to find any deficits in colour or pattern discrimination in pigeons with lesions of the hyperstriatum was disappointing but not too surprising, since Zeigler's (1962) experiment showed that on the first day of postoperative testing his retention group were above chance on both the brightness and pattern discrimination tasks. The results presented in the previous Chapter can be interpreted as evidence that factors other than a change in the capacity to analyse visual information were responsible for the failure of Zeigler's animals to keep pace with the control group on the acquisition and retention tests. While it may have been productive to continue from the results in the last Chapter and try to find out why animals comparable to those of Zeigler (1962), in so far as the extent of tissue destruction was concerned, did not show comparable deficits, this would have necessitated giving up the main point of the present investigation which was concerned with visual as opposed to learning deficits in pigeons. Accordingly it was decided to continue along the lines set out when the investigation began.

The method used by previous authors in the investigation of visual deficits in birds was the method of discrimination training (Layman 1936, Zeigler 1962). This method was also used by the present author in the experiments reported in the previous Chapter. This method, regardless of whether simultaneous or successive training tasks are used, may be insensitive to an organism's capabilities for a number of reasons. If a successive training procedure is used then an animal which is more exciteable than another, may tend to respond too soon before it has noticed which stimulus is present, or alternatively the animal may just find it difficult to withhold a response. Both of these response tendencies can be confused with the animal's capability to discriminate the difference between the stimuli. The simultaneous method of training, while it always allows

the animal to make a response may suffer from another source of error. This is the tendency of pigeons, when disturbed, to make consistent responses to a given position apparently ignoring the stimulus on the other key. This is also likely to be confused with the animal's ability to discriminate the stimuli, since normal animals adopt position preferences early in training and this drops out as training progresses (personal observations). Use of the method of generalisation testing to assess the degree of stimulus control seems potentially a more sensitive measure of whether an animal can discriminate stimuli or not. Evidence to support this view can be found in the results of different types of experiments carried out on pigeons and on other animals. Using stimulus generalisation as an indicator of stimulus control, Mello (1969) found no difficulty in showing that cats are quite capable of discriminating different wavelengths of comparable intensities. Previous investigators of colour vision in the cat had concluded that colour is a particularly difficult dimension for cats to discriminate (Meyer and Anderson 1965, Clayton and Kamback 1966), or had decided that cats are colour blind (Gunter 1954, Meyer et al 1954) when using choice discrimination techniques. In the pigeon evidence is available that, in normal animals at least, the method of taking generalisation gradients may be more sensitive in testing for stimulus control than other techniques. It was pointed out in the last Chapter that Thomas et al (1969) found evidence for control of behaviour by two elements of a compound stimulus when generalisation gradients were taken along the two dimensions, whereas it had been reported using a different method that pigeons only attend to one aspect of a complex stimulus (Reynolds 1961). Taking generalisation gradients of stimuli that were present during training promises to be a quite sensitive technique for assessing the effects of lesions on an animal's ability to react differentially to a variety of stimuli. This technique also has the advantage that it enables one to get some idea of which dimension an animal may be impaired on i.e. whether on size, orientation,

angularity, brightness etc. Failure to solve a conventional type of pattern discrimination could be due to the animals inability to use a particular cue. If destruction of a particular brain area fails to produce impairment on a discrimination task this may mean that there are alternative cues for an animal to use and the ability of the animal to analyse these cues is not affected by this particular lesion. If an animal shows a steep generalisation gradient to one stimulus, say size, but shows a flat gradient to another stimulus, say orientation, then this result would provide a more solid hypothesis about the function of a particular area. Given the result just mentioned, one could reasonably hypothesise that one would expect to find cells selectively responsive to orientation within the lesioned area. Bearing in mind the principal interest of the present investigator was whether or not areas in the forebrain that receive visual input were involved in the analysis of visual information, variables such as task difficulty which might produce apparent failure of discrimination were to be avoided as much as is possible.

Because of the advantages that appear to be present in using generalisation testing as opposed to discrimination learning in the assessment of lesions it was decided to use this method in the ensueing experiment. The plan of the experiment was to lesion the three main areas within the forebrain that were found in Chapter 2 to give consistent responses to visual stimulation. These areas were the hyperstriatum, the neostriatum caudale and the tissue around the ectostriatum. Following the lesions, the animals were trained on a 1 minute variable interval schedule in the presence of three stimuli, a vertical line, a square and an evenly illuminated key. Following stabilisation of the response, generalisation gradients were taken by varying the orientation of the line, the size of the square and the brightness of the key. For reasons to be reported in the results section only data from birds with lesions of the hyperstriatum, the neostriatum caudale and the control group will be presented.

The effects of lesions of the hyperstriatum and neostriatum caudale on orientation, size and brightness generalisation gradients in pigeons.

Subjects and Apparatus.

The subjects were 12 adult pigeons obtained from a commercial supplier. Following their arrival in the laboratory they were allowed ad libitum food for 14 days. They were then reduced to 80% of their free feeding body weight by withholding food. Water was available at all times in the home cage but not in the experimental chamber.

The experimental chamber was a Lehigh Valley two key pigeon box. The keys were situated about 9 inches above the floor. Only one key was used, the other remaining unilluminated and inoperative throughout the experiment. Stimuli were projected onto the key by an automated carousel projector (Lehigh Valley) which produced an image approximately 1:1. The stimulus patterns were a vertical bar (7 millimetres long and $1\frac{1}{2}$ wide), a square (7 millimetres wide) and an evenly illuminated key (0.9 log. foot lamberts). At the beginning and end of every session a red (wratten 25) filter was displayed so that the time out period was not associated with the presence of an unilluminated key, thus affecting the brightness generalisation gradient unduly. The stimulus patterns were changed on average once every minute and the order of presentation was quasi randomised. The apparatus was controlled automatically by a system of relays, counters and timers.

Procedure

When the birds were reduced to 80% of their free feeding body weight they were trained to key peck in the presence of the evenly illuminated key (0.9 log. ft. lambert). Once they had pecked the key they were allowed one reinforcement (5 seconds access to grain) for each of twenty responses on two consecutive days. They were then allowed to regain their full body weight before the operative procedures were performed. Operations were performed under Equithesin anaesthesia (2.5 cc per Kg.). The animals were placed in a Kopf stereotaxic

instrument with pigeon adaptor. The skin on the head cut and held with retractors and the bone overlying the relevant part of the forebrain removed with a dental drill. The dura was lifted and cut and the tissue aspirated using a glass capilary tube with a sharp end, and a vacuum pump. Following the removal of the tissue the bone was plugged with Sterispon (absorbable gelatin) soaked in thrombin. The control group were simply anaesthetised and no surgical procedure was performed. Following recovery from the anaesthetic the birds were allowed three days on ad lib food before they were again reduced to 80% of their body weight.

When the animals were again at 80% body weight they were replaced in the experimental chamber and given daily sessions of 30 minutes duration beginning with a variable interval 5 second schedule (reward on average once every five seconds) on the first postoperative day of training and then over the following days the reinforcement interval was gradually increased day by day until after 8 days the birds were pecking on a 1 minute variable interval schedule. They were given a further twelve daily 30 minute sessions on this schedule before generalisation gradients were taken. By this time responding in every bird was very stable.

The stimuli used for obtaining the generalisation gradients were for the vertical bar (90 degrees) bars at the following orientations, 80°, 70°, 60°, 30° and 0°. For the square (7 millimetres) the sizes of the generalisation stimuli were 6, 5, 4 and 3 millimetres. For the evenly illuminated key the stimuli were 1, 1.5, 2 and 2.5 log. units dimmer than the training stimulus. Three determinations of each point were made. On any given day of testing responses to one set of stimuli were taken only once. Each stimulus was presented for one minute. No generalisation test stimuli were presented during the first ten minutes of any session or in the last 5. Rewards were stopped for 20 seconds before, as well as during the presentation of any generalisation test timulus.

Histology

Following the termination of the experiment animals were given an

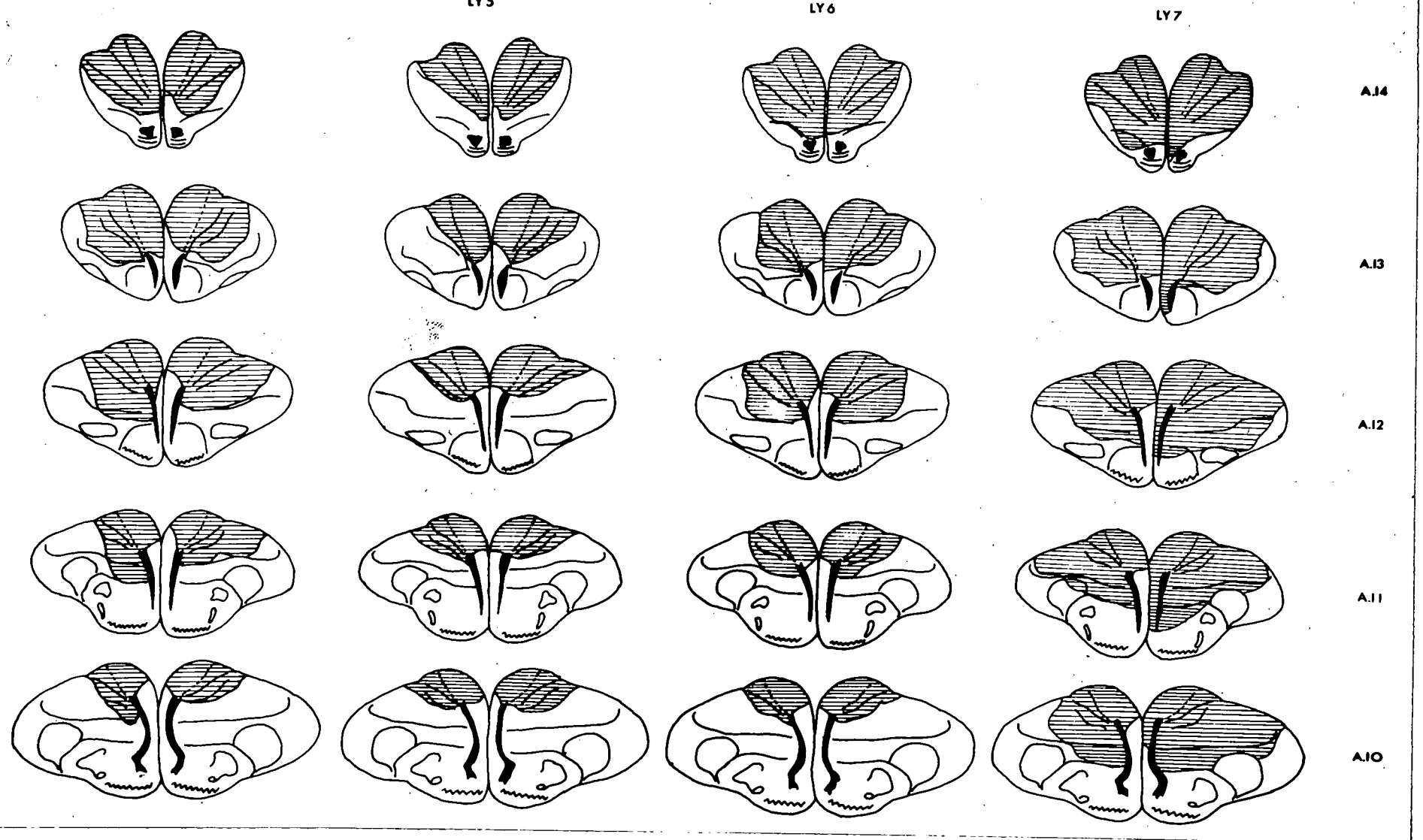


Plate 1. The extent of damage (shaded area represents total tissue loss) in the hyperstriate group. Letters and figures on the right of the plate refer to the levels of the section in the Atlas of Karten and Hodos (1967). Letters and figures at the top indicate individual animals.

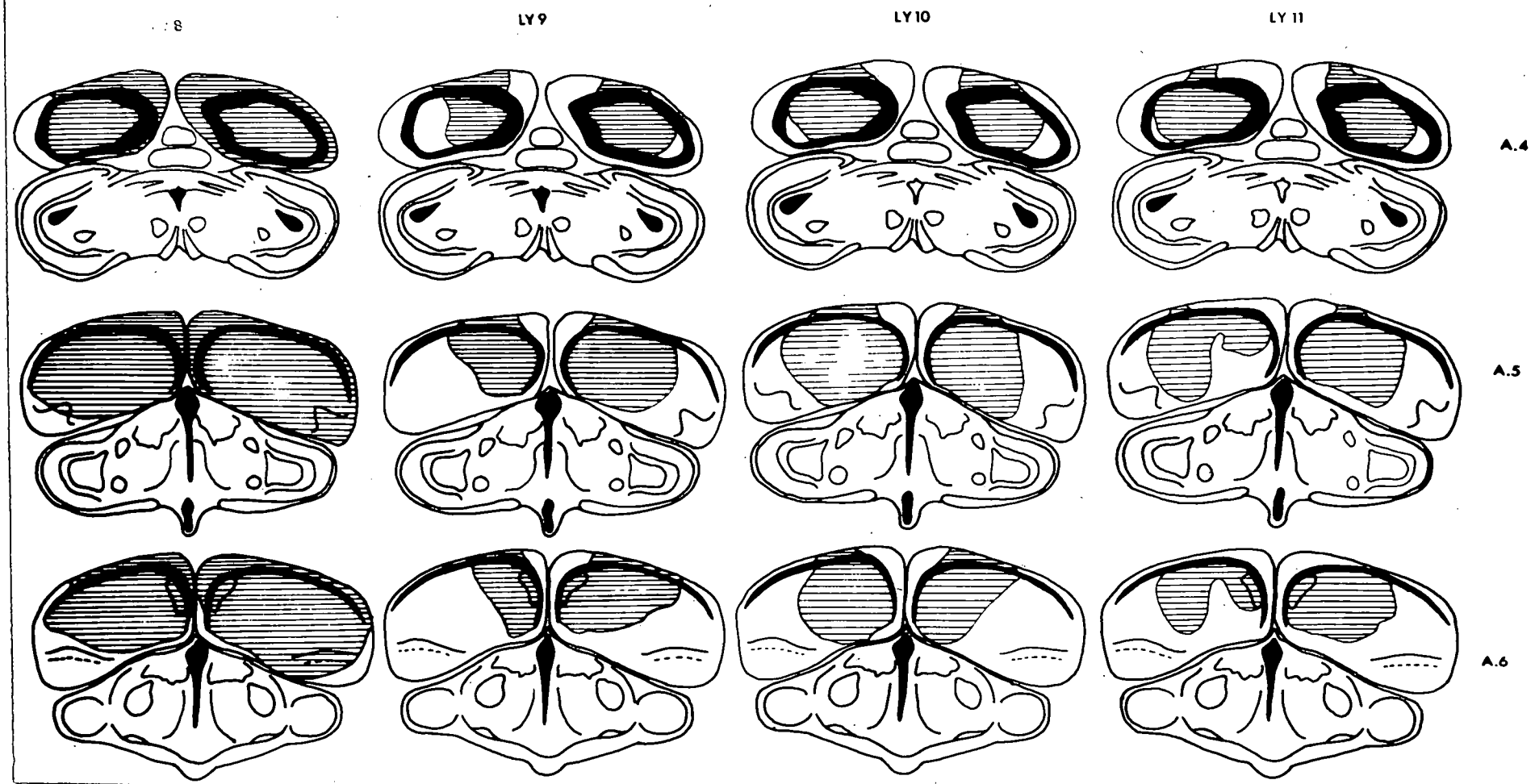


Plate 2. The extent of damage (shaded area represents total tissue destruction) to the neostriatum caudale group. Figures and letters at the right of the plate refer to the plane of section in the Atlas of Karten and Hodos (1967). Figures and letters at the top of the plate indicate individual animals.

overdose of nembutal and perfused first with saline and then 10% formalin through the carotid arteries. Because of the difficulty in obtaining frozen sections when so much tissue had been removed from the anterior and posterior sectors of the forebrain, the block of tissue was frozen on the stage of the freezing microtome and the extent of the lesions were drawn directly onto a series of standard drawings of sections through the pigeons forebrain, as the tissue was removed with the microtome knife.

Results

The extent of the lesions are shown in plates 1 and 2 (pages 120 and 121). It can be seen that the extent of the lesions in the hyperstriatal group (Plate 1) was large. Almost the complete hyperstriatum was destroyed in bird LY7 (Hyperstriatum accessorium, hyperstriatum intercalatus superior, hyperstriatum dorsale and hyperstriatum ventrale, taking the layers in order from top to bottom). Bird LY4 shows the next most severe damage, showing almost complete destruction of the hyperstriatum as far as the hyperstriatum ventrale in the anterior area (A14 and A13), but in the more posterior areas (A12 to A10) more of the hyperstriatum ventrale is left intact. In the remaining two birds considerable portions of the hyperstriatum ventrale are left intact. In all four birds however the whole of the upper three hyperstriatal layers were completely destroyed (hyperstriatum accessorium, hyperstriatum intercalatus superior and hyperstriatum dorsale). The lesions to the neostriatum caudale group (Plate 2) were also fairly substantial. Bird LY4 had the neostriatum caudale completely destroyed but in the remaining three birds parts of the lateral area of the neostriatum caudale were left intact. This is not so distressing as it might at first appear since recent evidence collected by Delius and Bennetto (PERS. COM.) suggests that the focal area for the visual projection to the neostriatum caudale is a medial sector of the neostriatum caudale just lateral and posterior t o Karten's L area (Karten 1968). If this is true then the lesions in these birds completely destroyed the visual projection to the

neostriatum caudale. In any case the damage to this caudal forebrain area is fairly substantial and would be expected to produce a deficit if the task involved the function of the neostriatum caudale.

Results of the generalisation gradients to orientation (Figure 1, page 124), size (Figure 2, page 125) and brightness (Figure 3, page 126) for the hyperstriatal group indicate that birds with lesions in this area are still able to respond selectively to these three dimensions. Figures 4, 5 and 6 (pages 127, 128, and 129) show the results of the neostriatum caudale group. In this case there is also evidence that they can selectively respond to the stimuli used in training. Data from the control group are shown in Figure 7, 8 and 9 (pages 130, 131, and 132) and these figures show the expected generalisation gradients found in normal animals.

In order to see if any difference between the experimental and control animals was apparent, best fit straight lines were fitted by eye to the data from individual animals. Only the data from the size generalisation gradients showed itself to be promising for analysis, and this difference is apparent to the unaided eye in the comparisons of the group mean gradients (Figures 10, 11 and 12 pages 133, 134, 135). Slope coefficients for the animals in all three groups were computed for the size generalisation data, using the method of least squares. The resulting coefficients were subjected to an analysis of variance (Table 1, page 136). The analysis showed a significant F ($F = 39.33$ for 2 and 9 df. $p < .05$). The other results did not show themselves as being worth testing as there was too much overlap in the slopes of the regression lines.

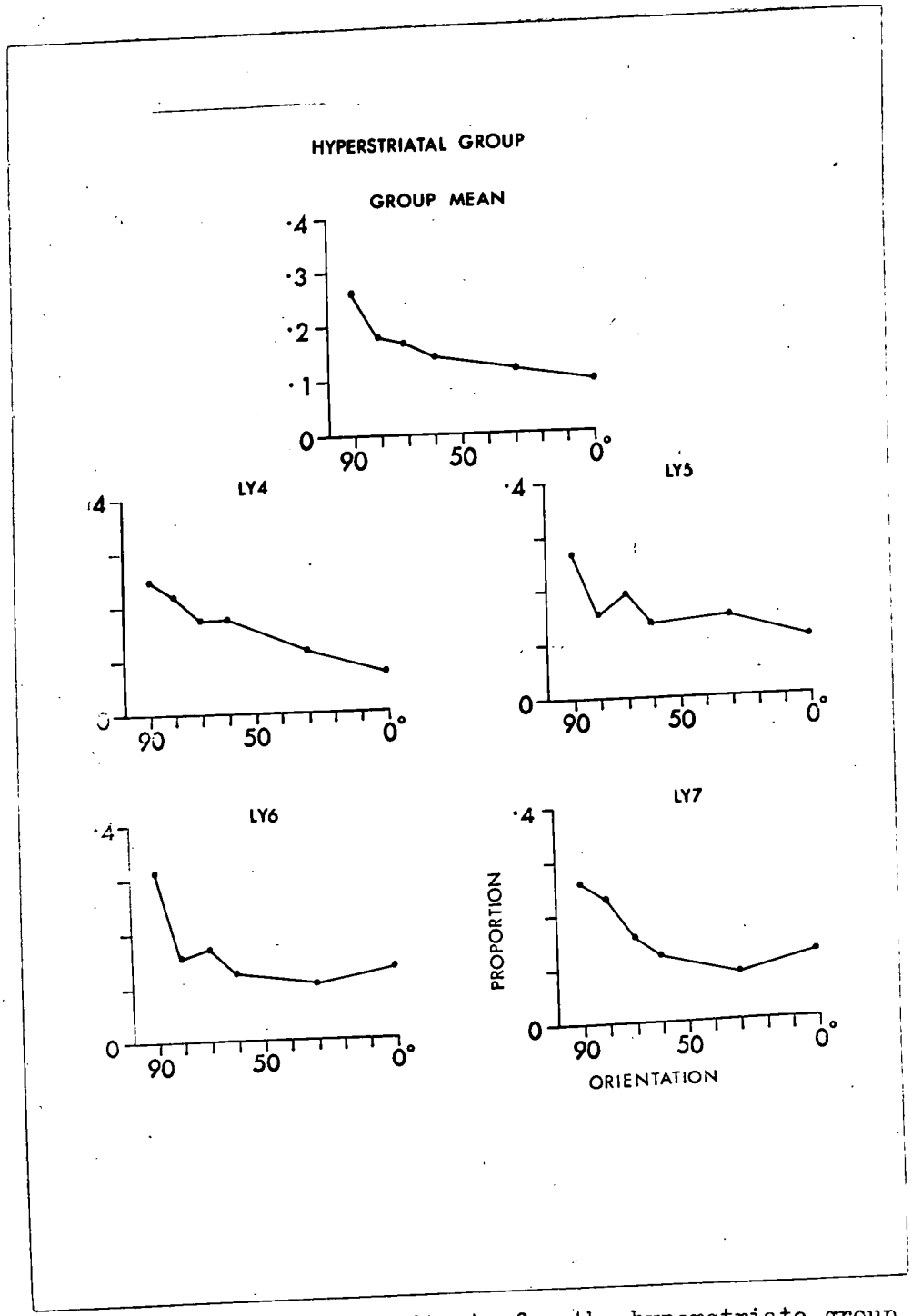


Figure 1. Generalisation gradients for the hyperstriate group to stimuli differing in orientation from the training stimulus (90°). Individual gradients and the group mean gradient are shown. The ordinate gives the proportion of the total number of responses made in the presence of the stimuli of different orientation shown along the abscissa. Each point on individual birds gradients is the mean of 3 determinations.

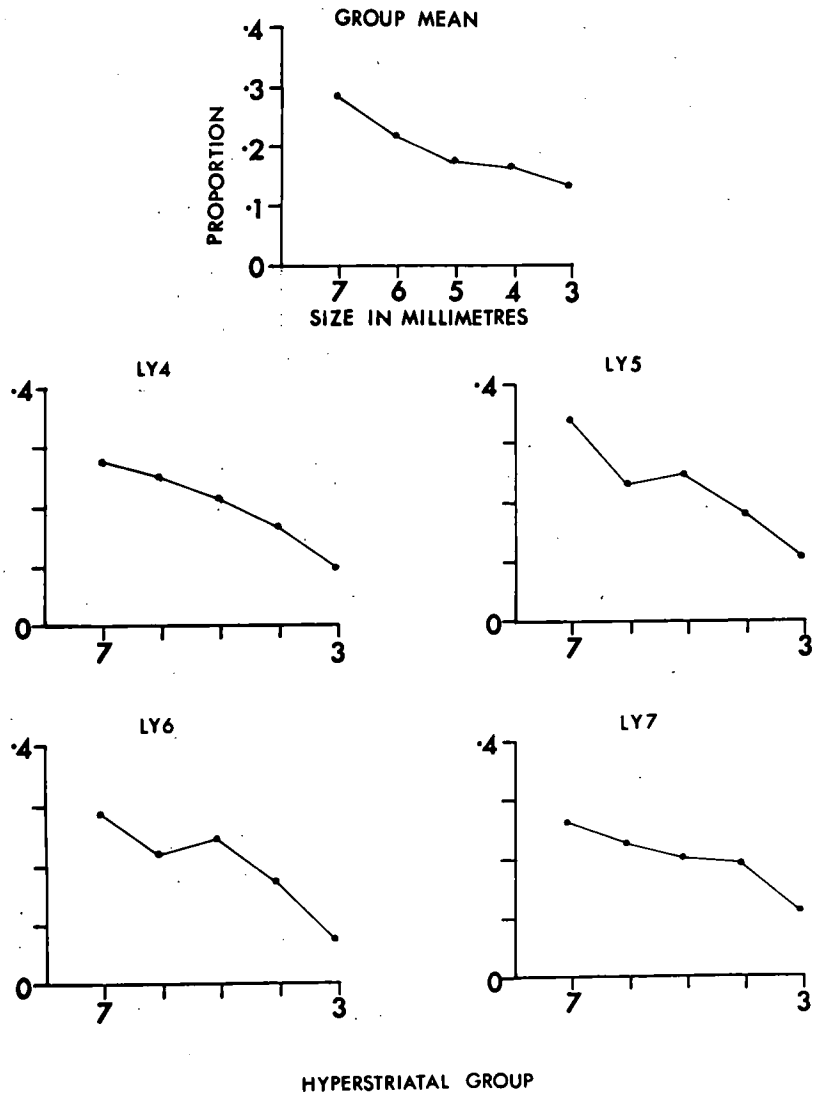


Figure 2. Generalisation gradients for the hyperstriate group to stimuli differing in size from the training stimulus (7mm) individual gradients and the group mean gradient are shown. The ordinate gives the proportion of the total number of responses made in the presence of the stimuli of different size shown along the abscissa. Each point on individual birds gradients is the mean of 3 determinations.

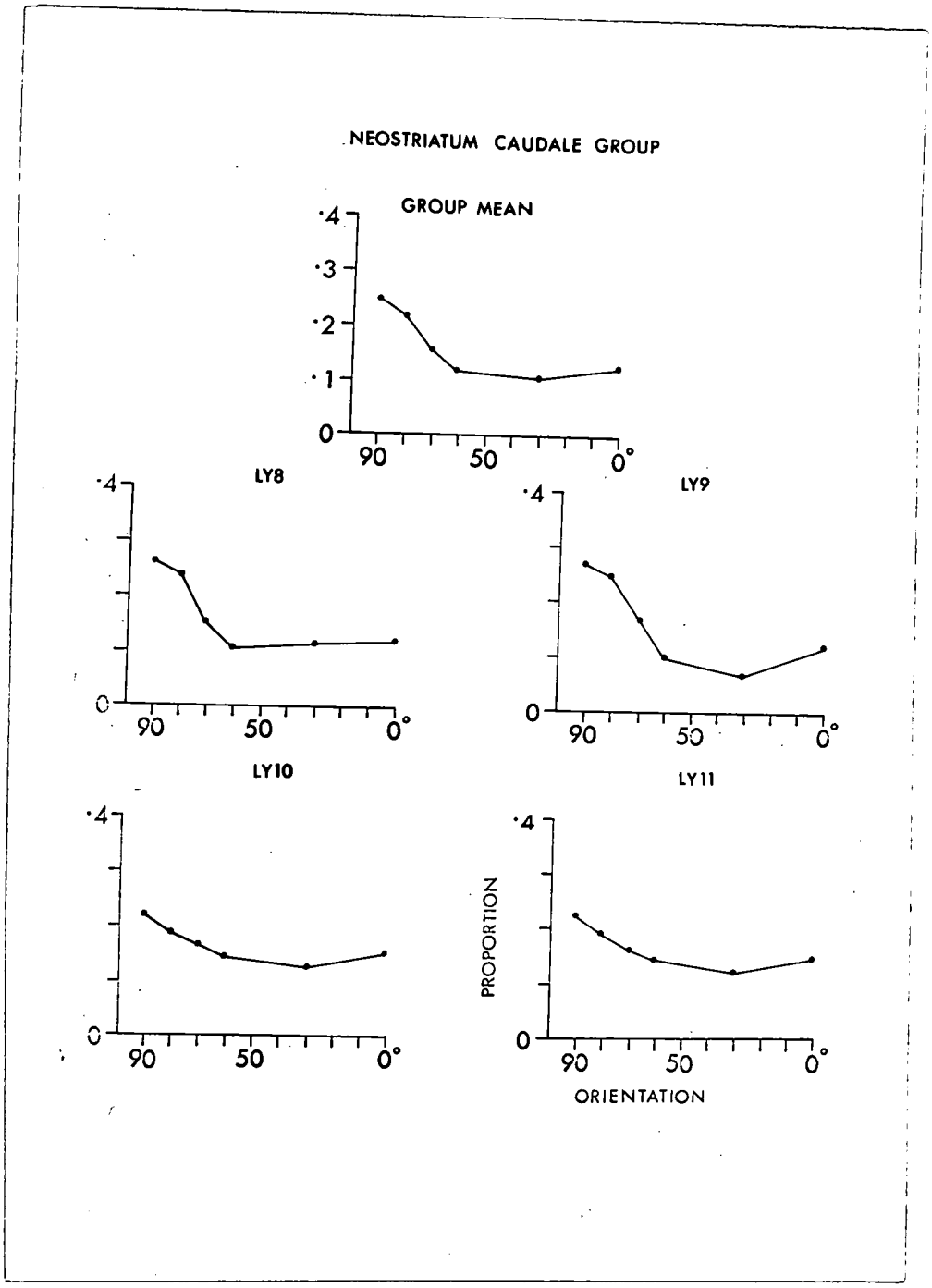


Figure 4. Generalisation gradients for the neostriatum caudale group to stimulus differing in orientation from the training stimulus (90°). Individual gradients and the group mean gradient are shown. The ordinate gives the proportion of the total number of responses made in the presence of stimuli of different orientations shown along the abscissa. Each point on individual birds gradients is the mean of 3 determinations.

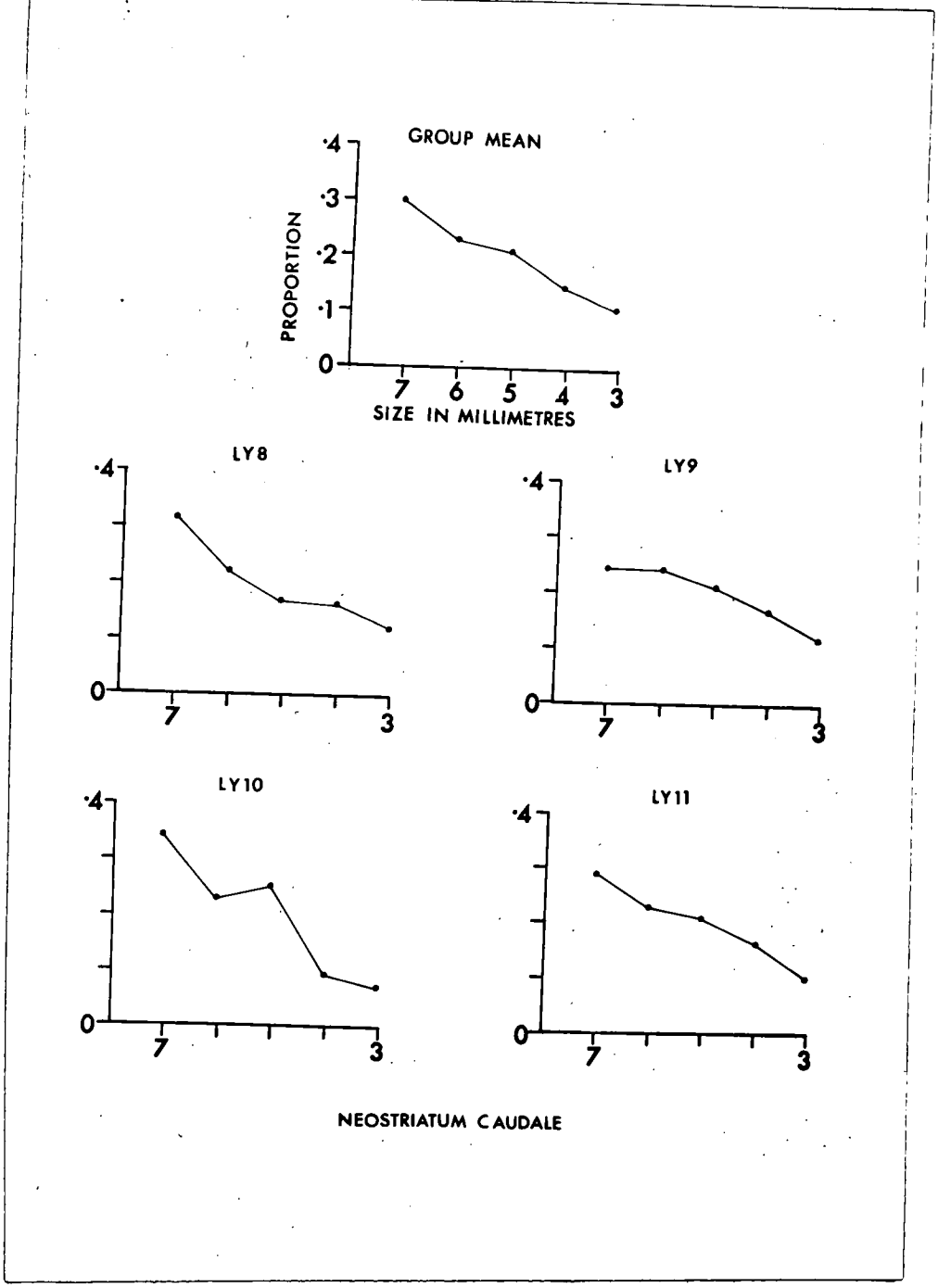


Figure 5. Generalisation gradients for the neostriatum caudale group to stimuli differing in size from the training stimulus (7mm). Individual gradients and the group mean gradient are shown. The ordinate gives the proportion of the total number of responses made on the presence of stimuli of different size shown along the abscissa. Each point on individual birds gradients is the mena of 3 determinations.

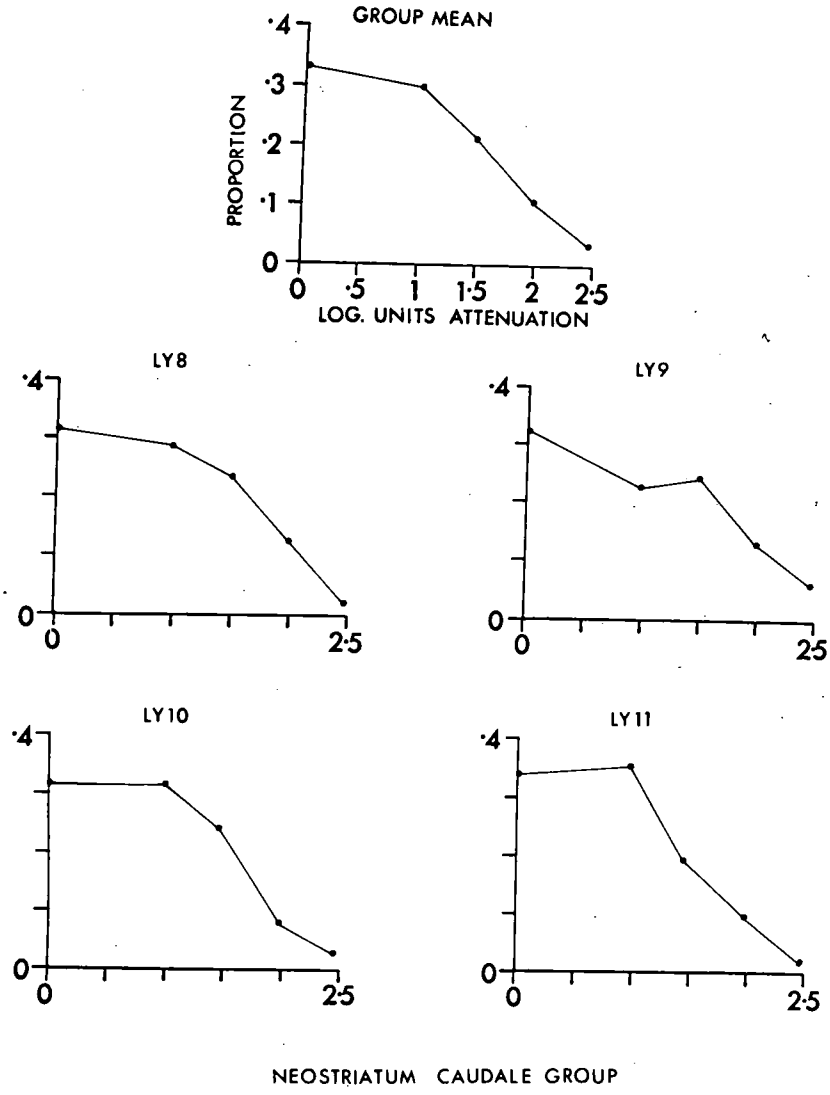


Figure 6. Generalisation gradients for the neostriatum caudale group to stimuli differing in brightness from the training stimulus (0 log units). Individual gradients and group mean gradient are shown. The ordinate gives the proportion of the total number of responses made in the presence of stimuli of different brightness shown along the abscissa. Each point on individual birds gradients is the mean of 3 determinations.

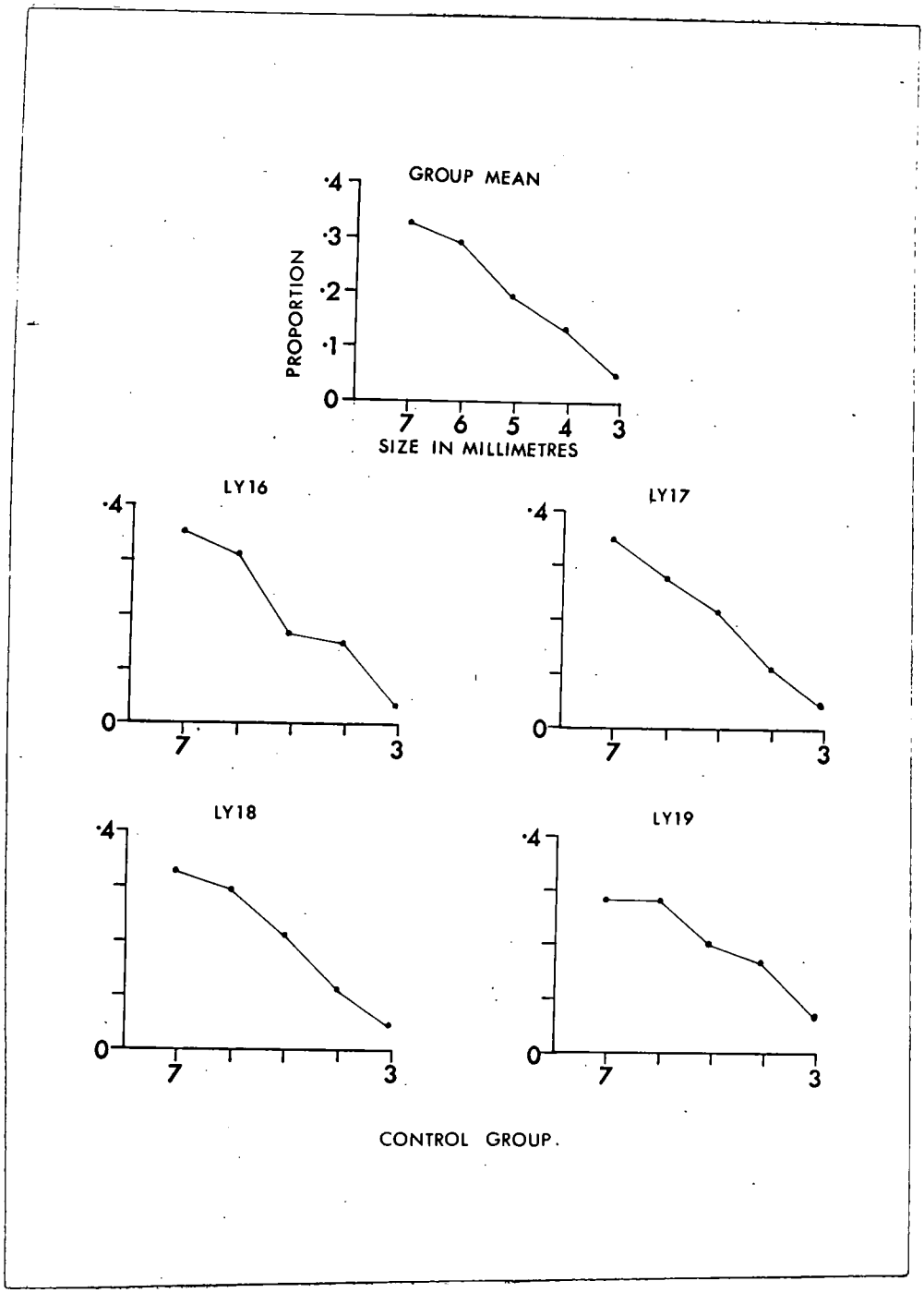


Figure 8: Generalisation gradients for the control group to stimuli differing in size from the training stimulus (7mm). Individual gradients and group mean gradients are shown. The ordinate gives the proportion of the total number of responses made in the presence of stimuli of different size shown along the abscissa. Each point on individual birds gradients is the mean of 3 determinations.

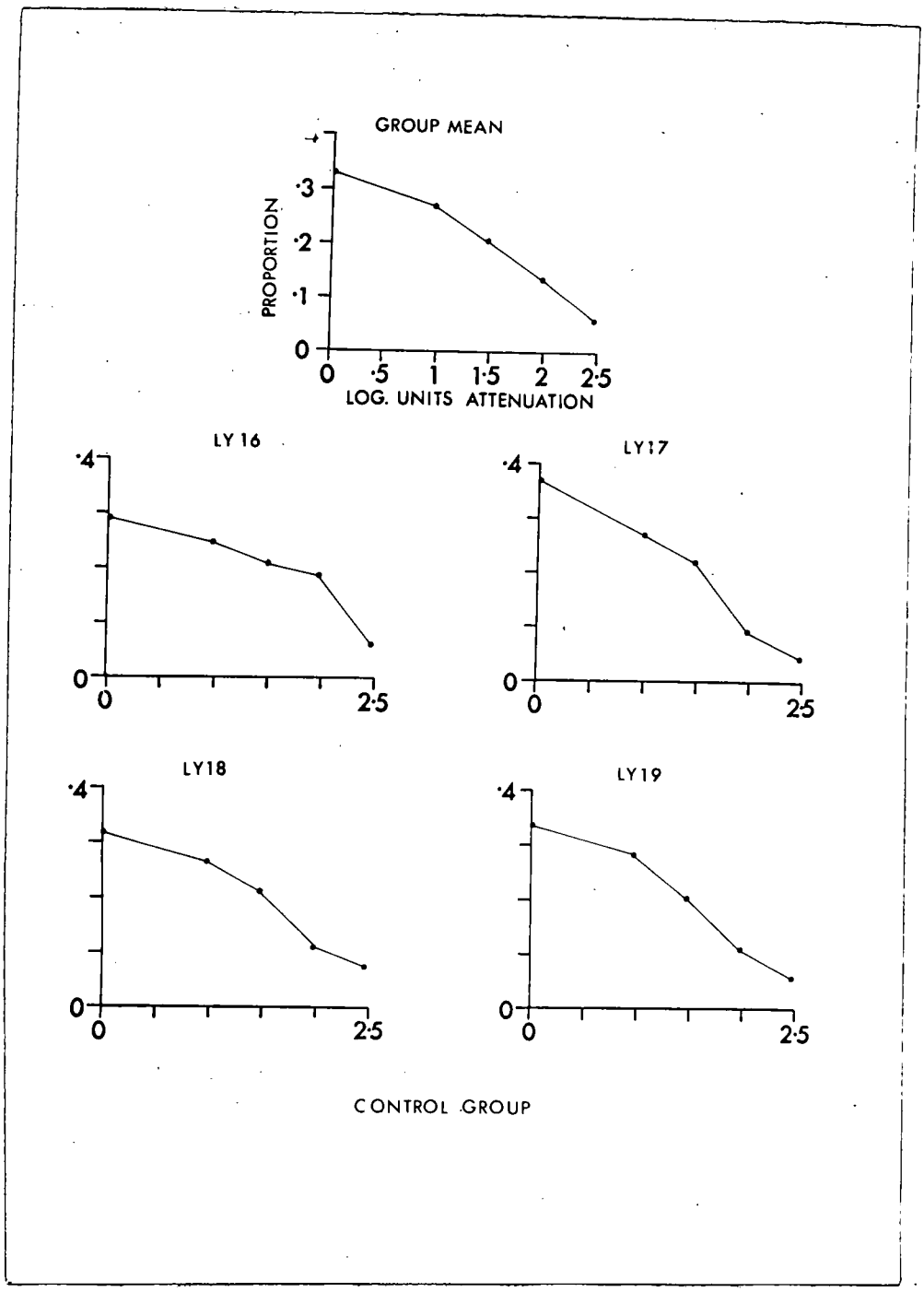


Figure 9. Generalisation gradients for the control group to stimuli differing in brightness from the training stimulus (0 log. units). Individual gradients and the group mean gradient are shown. The ordinate gives the proportion of the total number of responses made in the presence of stimuli of different brightness shown along the abscissa. Each point on individual birds gradients is the mean of 3 determinations.

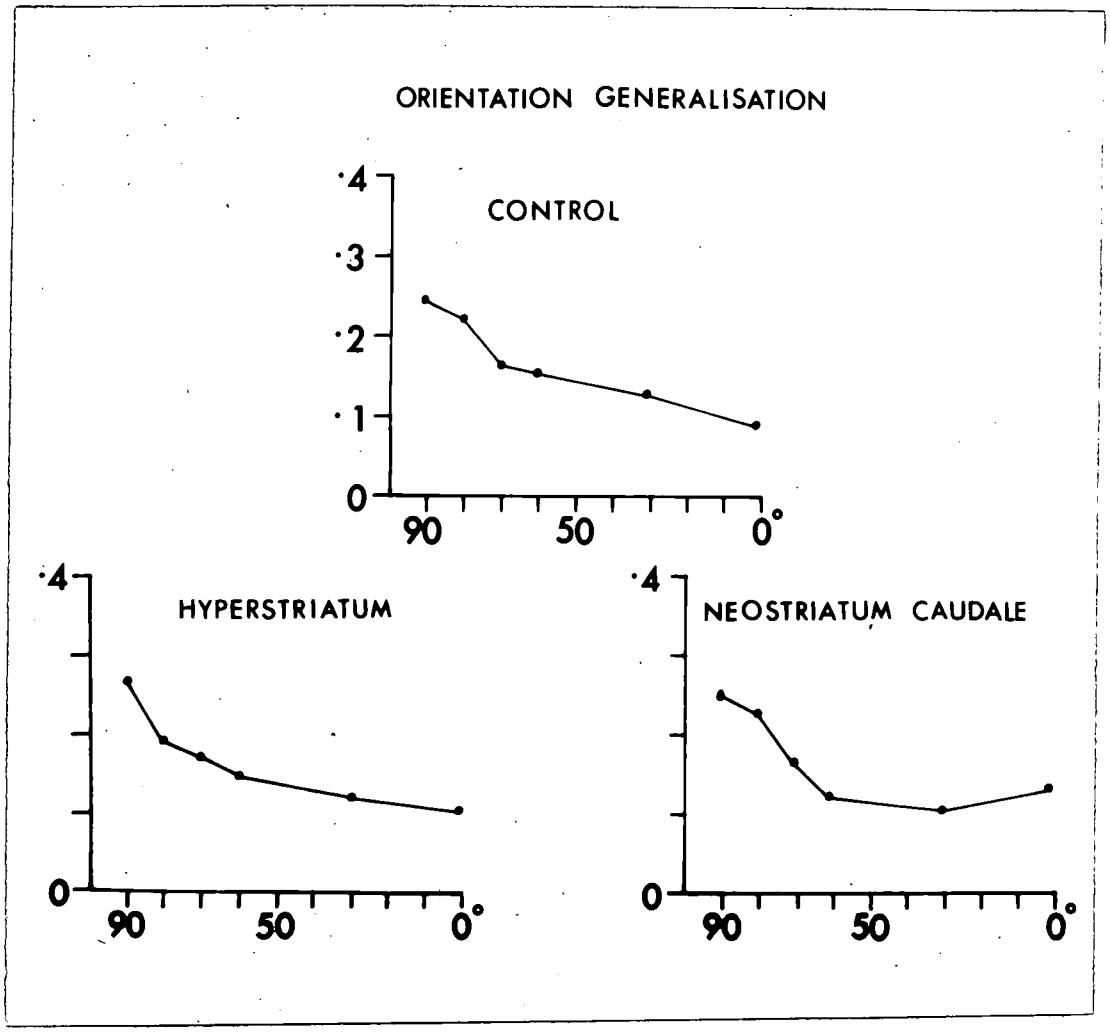


Figure 10. A comparison of the group mean generalisation gradients for the control, hyperstriate and neostriatum caudale groups for stimuli differing in orientation.

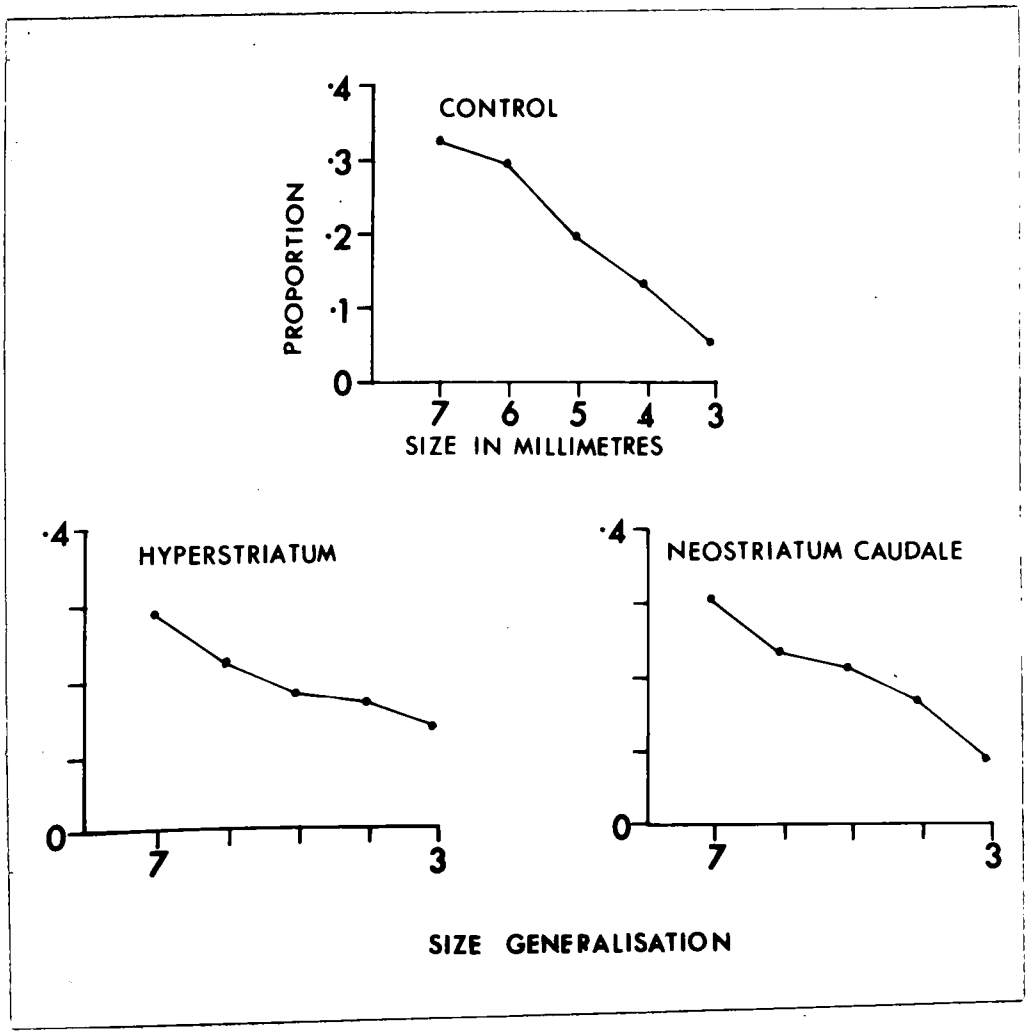


Figure 11. A comparison of the group mean generalisation gradients for the control, hyperstriate and neostriatum caudale groups for stimuli differing in size. An analysis of variance of the slope coefficients shows that the slopes of the generalisation gradients for the control group are significantly steeper ($p < .05$) than those for the two experimental groups (see Table 1).

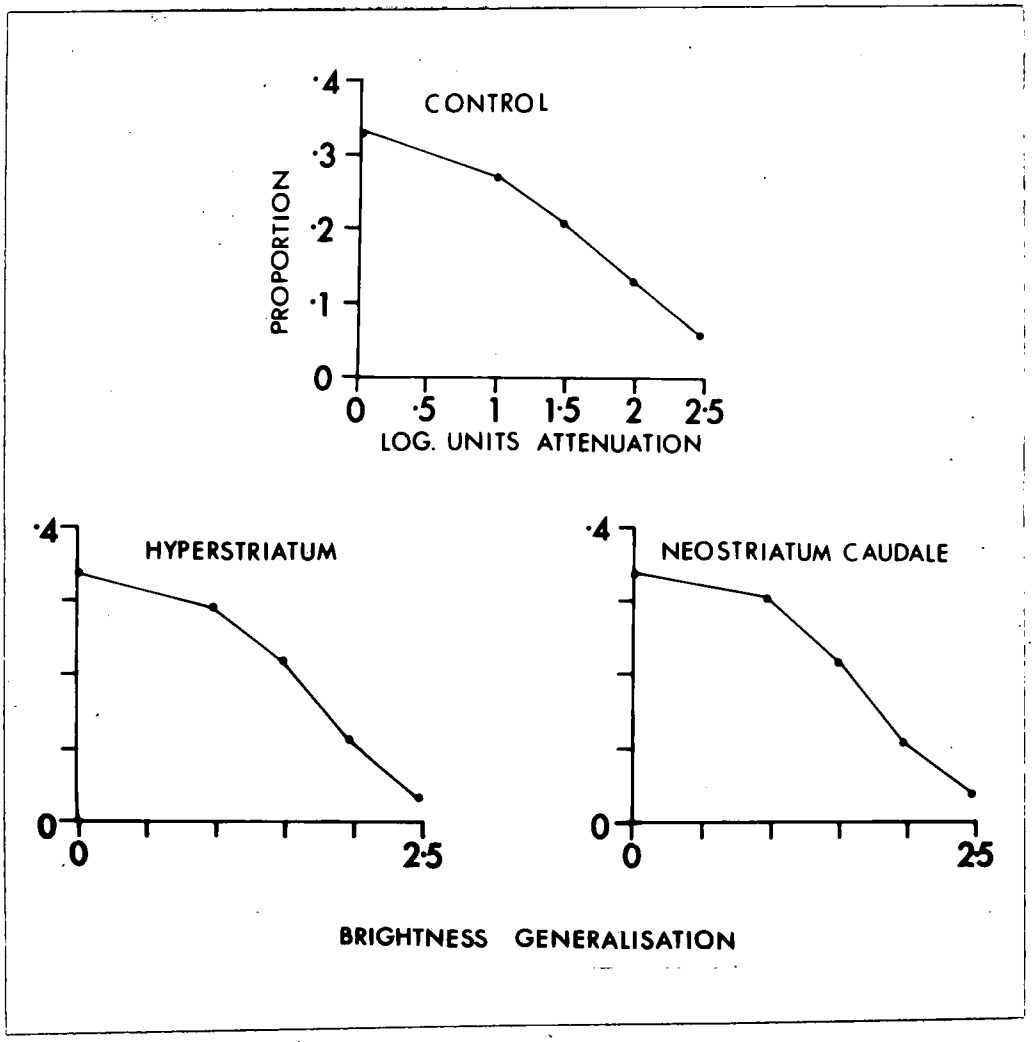


Figure 12. A comparison of the group mean generalisation gradients for the control, hyperstriate and neostriatum caudale group for stimuli differing in brightness.

TABLE 1

	Hyperstriatal Group	Neostriatum Caudale Group	Control Group
	4.30	4.53	8.14
	4.69	3.22	7.86
	4.66	6.87	7.51
	3.26	4.45	5.53
MEAN =	4.227	4.77	7.26

Total sums of Squares	121.496			
Between groups squares.	109.023	df 2	54.51	39.33
Within groups squares.	12.474	df 9	1.38	

F = 39.33 for 2 and 9 degrees of freedom. $p < .05$.

Table 1. shows the gradients of the regression lines of size against responses, X 100. Comparison of the means of the hyperstriatal group and the neostriatum caudale group with that of the control mean shows that they are significantly different (Dunnet's test for comparing treatments with a control. Dunnet 1955). Critical difference (two tailed test) between the means for significance at .05 level is 2.173.

Discussion

The results of this experiment are quite clear in that they indicate on the three dimensions used in the test for stimulus generalisation, orientation, size and brightness, the experimental animals all show evidence of being able to discriminate the training stimuli from the novel stimuli. Only on the size generalisation test is there any evidence of a difference between the experimental and control groups. However even here there is clear evidence of discrimination. Precisely what meaning can be attached to the flatter gradients shown by the experimental animals is not clear. It may be that these animals genuinely found the discrimination of stimuli differing on size more difficult, but it is surprising that both lesioned groups should show the same tendency. If the effect had been differential, the neostriatum caudale group showing flatter gradients than the controls on size generalisation, while the hyperstriatal group showed flatter gradients on orientation, then the temptation to believe that it was in fact a detection difficulty would be stronger. It may be however that size was the least salient cue to the animals and the effect of the lesion may have been to make the animals less responsive to cues that are not so obvious.

Taken in conjunction with the results from the previous chapter the present results tend to suggest that forebrain visual areas in the pigeon are not similar in function to the cortex in mammalian vision. It is unfortunate that the lesions of the ectostriatal surround area were not successful as the picture would have been a little more complete. However these lesions were markedly asymmetrical and destroyed more of the lateral neostriatum than the ectostriatal surround. These birds however also showed generalisation gradients to the three dimensions used in this study, so in this case also there was no evidence of a sensory deficit. In so far as forebrain visual areas are concerned then it seems that birds are more similar to fish than to mammals. In fish, ablation of the forebrain makes little difference to colour discrimination, and the results from studies

of forebrain ablation in teleosts (Kaplan and Aronson 1969) suggests, that the visual orientation of these animals is essentially normal. While birds without forebrain are markedly less responsive than fish, they do show a surprising amount of complex behaviour considering the severity of the damage. Birds in which the telencephalon is completely isolated are able to fly avoiding obstacles and land apparently normally. They are also able to avoid obstacles while walking, although spontaneous behaviour completely disappeared (Akerman et al 1962). This survival of quite complex visually guided behaviour after total destruction of the telencephalon suggests that a great deal of the analysis of visual information occurs at the thalamic and mesencephalic levels in the pigeon. This may lead one to expect that lesions to the visual areas of the forebrain may have effects that are more subtle than can be detected by simple pattern or colour discriminations. Alternatively it may be that there is an enormous amount of parallel processing in the visual system of the pigeon and lesions to one area leave others intact which are still capable of analysing the same visual information. Damage to the thalamus does produce deficits in both pattern brightness and colour discrimination (Hodos and Karten 1966, Hodos 1969). These studies both involved lesions to the nucleus rotundus of the pigeon and the effects of these lesions on previously acquired discriminations were studied. However it is by no means clear that the deficits were deficits in the ability to analyse visual information or whether some other ability was involved. As was mentioned in Chapter 1, the nucleus rotundus receives its input from the optic tectum which in mammals at least appears to be more concerned with spatial orientation than with the analysis of colour, brightness or pattern information (Schneider 1969, Humphrey and Weiskrantz 1967). It is interesting that in both experiments involving lesions to the nucleus rotundus of the pigeon (Hodos and Karten 1966, Hodos 1969), the birds were required to make a spatial choice. In one case this involved simply choosing the appropriate key (Hodos and Karten 1966) in the other case

(Hodos 1969) this involved choosing either the right or left key depending on which colour was shown on a centrally located key. If the animals did find it difficult to locate the position of stimuli in space relative to their own bodies, then this could produce an apparent deficit in visual analysis. The proper experiment to be carried out to determine if the animals are still capable of discriminating pattern and colour, is a go-no-go discrimination in which the animals are not required to make a spatial choice.

There are a large number of nuclei in the diencephalon and mesencephalon of the pigeon which receive direct input from the optic tract (see Chapter 1) and these may well mediate colour and pattern vision without the involvement of the telencephalon. Such a conclusion is not strictly warranted by the information presented in this thesis, and information available elsewhere, because not every area within the forebrain that receives visual input has been lesioned. The two areas of major importance that have not been studied are the ectostriatal surround (the attempts to produce lesions of this area were not successful) and the ectostriatum itself. While no evidence was found in the evoked potential study reported in Chapter 2 of a visual projection to the ectostriatum, Revzin and Karten (1967) have reported a projection from the nucleus rotundus to this area. Evidence available from my own attempts to produce bilateral lesions in this area did show that following unilateral destruction of the ectostriatum the ipsilateral nucleus rotundus undergoes degeneration. There is still a possibility that lesions to one or other of these areas will produce visual deficits in pigeons. What is surprising is that two areas within the forebrain that receive a visual input of relatively short latency (hyperstriatum and neostriatum caudale) do not produce severe deficits in visual learning. This is particularly surprising if one accepts Karten's (1970) proposition that the projection from dorsal thalamus to the hyperstriatum is homologous to the geniculo-striate pathway of mammals. Clearly from the results

of studies reported in this thesis as well as the results of previous authors (Layman 1936, Zeigler 1962) the deficits produced by lesioning the hyperstriatum are slight in so far as visual tasks are concerned. It is noteworthy that studies involving the electrical stimulation of the avian forebrain have failed to locate any area within it that is homologous to the motor cortex of mammals (Delius, personal communication). Taken together with the evidence for lack of visual deficits in pigeons with forebrain lesions, this may point to a fundamental difference in the organisation of the avian and mammalian telencephalon. Anatomically this is certainly true (Jones and Levi - Montalcini 1958, Kuhlenbeck 1938) since the avian telencephalon lacks any clearly defined neocortex. Incidental observation on the birds involved in the present study suggested that no major deficits in feeding, drinking or escape behaviour were present following the lesions, except in the case of bird LY8 in which there was damage to the posterior portion of the archistriatum, which produced a deficit in escape behaviour (this taming effect of archistriatal destruction has been reported by Phillips 1964). Observations by Harwood and Vowles (1967) on the effects of electrical stimulation of the forebrain in birds show that electrical stimulation does not elicit behaviour patterns with any high probability. It may be that the avian telencephalon is similar to the teleost telencephalon which appears to serve as a facilitator of behaviour whose substructure lies at the diencephalic and mesencephalic levels of the brain (Kaplan and Aronson 1969).

Chapter 6. CONCLUSIONS

The diencephalic and mesencephalic ramifications of the pigeon's visual system are extensive. No less than ten structures receive a direct input from the optic tract. These structures are the nucleus lateralis anterior, n. geniculatus lateralis pars ventralis, n. geniculatus pars dorsalis principalis, n. lentiformis mesencephali pars magnocellularis and pars parvocellularis, n. ectomammilaris, n. pretectalis, n. dosolateralis anterior pars lateralis and pars magnocellularis and the optic tectum (chapter 1, part 2). Indirect projections within the diencephalon and the mesencephalon are also extensive. Apart from to the oculomotor nuclei, there are substantial inputs from the tectum to the nucleus rotundus, n. isthmi pars parvocellularis, pars magnocellularis and pars semilunaris as well as the nucleus isthmo opticus (chapter 1, part 2). The latter nucleus is particularly interesting because it is the nucleus of origin of the centrifugal fibres to the retina (Cowan 1970). Whether these secondary projections can be seen as exclusively or even mainly visual is of course a debatable matter. It has already been pointed out (chapter 1, part 2) that in the reptilian and avian brain there is a convergence of somatic and auditory system fibres on the stratum griseum et fibrosum superficiale (Huber and Crosby 1933, Kappers, Huber and Crosby 1936, Karten 1963, Baker-Cohen 1968). Consequently the interpretation of fibre systems that arise from the tectum as visual must remain tentative until other sensory systems have been positively excluded.

Experimental investigations of the functional role of visual structures in the pigeon's diencephalon and mesencephalon have been relatively few, and at least in the present state of knowledge results are ambiguous in a number of cases: Cohen (1967) has reported deficits in the acquisition of a brightness discrimination in pigeons following unilateral and bilateral tectal lesions. The animals also however show a greater number of trials to extinction, a result which may imply that factors other than sensory deficits are involved.

Bingelli, Tschirgi and Wenzel (1963) have found that unilateral tectal ablation facilitates aquisition of complex visual discriminations, a finding which is difficult to reconcile with any simple view of tectal function in the pigeon. The same problem of interpretation arises when we go on to consider the ascending and descending projections from the optic tectum. It is established that lesions to the nucleus rotundus produce deficits in visual discrimination learning (Hodos 1969, Hodos and Karten 1966). Whether these deficits can be interpreted as showing an involvement of this nucleus in the analysis of visual information per se is not clear however. Wenzel and Salzman (1968) have shown that damage to the olfactory bulb produces retarded visual discrimination learning in pigeons. Under the present state of knowledge it would be quite reasonable to interpret these deficits as learning and not sensory deficits, since the deficits firstly have not been shown to be specific to the visual system, and secondly the variables of task complexity has not been taken into account. In the first instance there is suggestive evidence that other sensory systems may be involved in the projection to the nucleus rotundus. Revzin and Karten (1967) found that electrical stimulation of the nucleus mesencephalicus lateralis pars dorsalis, a nucleus of the ascending auditory system (Karten 1967) produced potentials in the rotundus whose amplitudes were equivalent to those produced by stimulation of the marginal optic tract. In the second instance compared to tasks that have usually been used to confirm sensory deficits in animals (Blake 1959, Kluver 1933, Lashley 1931, Snyder et al 1966, Wing 1946, Winans 1968), where simple spatial or successive tasks involved the presentation of no more than one pair of stimuli during the aquisition of the response, the tasks used by Hodos (1969) and Hodos and Karten (1966) were rather complex. Hodos and Karten (1966) used a simultaneous discrimination situation in which four pairs of stimuli were presented in a random order during aquisition and postoperative testing. Hodos (1969) used a matching to sample task in which three pairs of colours were present during aquisition and postoperative retesting. The

complexity of the task may thus well be an important variable in determining the deficit. These objections appear to be sufficient to hold in reserve any conclusions on the functional role of the nucleus rotundus of the pigeon.

When one considers the descending projections of the optic tectum to the isthmi complex, again strong objections can be raised against any definite conclusions being made on the functional role of structures in this group. These nuclei which form the descending tectal projection system of Karten (1969a) are the isthmi nuclei, pars parvocellularis, pars magnocellularis and pars semilunaris together with the nucleus isthmo opticus. The projection from the optic tectum to these nuclei is topographical and, in the case of the former three nuclei, a columnar organisation pattern is apparent with the tectal efferents terminating within a narrow column of cells (Karten 1969b). Hodos (1969b) has suggested that lesions to the descending tectal projections may produce effects that are more severe than when the ascending tectal and thalamic system are destroyed simultaneously. What meaning can be attached to these findings is not as yet clear. It may imply that the organisation of the avian visual system is so unusual that the major part of the sensory analysis and interpretation is performed at the mesencephalic level. If this were true then it would surely be expected that the input to these nuclei i.e. the output from the optic tectum, would be different in birds and mammals. The evidence which we have however suggests a remarkable similarity. Thus experiments by Jassik-Gerschenfeld (1971) indicate that unit responses in the optic tectum of the pigeon show the same properties as those found in the homologous structure in mammals (Michael 1967, Hill 1966, McIlwain and Buser 1968, Humphrey 1968). Alternatively it might be expected that mesencephalic lesions will always have more profound effects on behaviour than thalamic lesions if they are relatively large, because of the convergence of afferent and efferent pathways from all sensory systems at this level of the brain.

That the latter interpretation is the more likely one, is supported to some extent by the work of Sprague and associates (Sprague et al 1963, Sprague et al 1961) on collicular and sub-collicular lesions in the cat, They found a wide variety of deficits following such lesions. Of particular note in these studies was the effect lesions to the leminiscal system (which runs beneath the colliculi in the cat) had on the visual behaviour of the animals. Visual placing disappeared, and there was a total failure to respond to visual stimuli. Sprague et al (1961) interpreted the deficits as being a failure to appreciate the significance of the stimuli together with the impairment of the ability to make adaptive responses to the environment, rather than being a deficit in the analysis of sensory information. That lesions in auditory, vestibular and somatic pathways can produce profound effects in the visual behaviour of animals should make us wary of interpreting the effects of lesions at this level of the brain in an oversimple way.

Of particular interest among the nuclei in this region of the brain is the nucleus isthmo opticus. This nucleus sends fibres to the inner nuclear layer of the retina where they synapse on amacrine and displaced ganglion cells (chapter 3). Previous work (Ogden 1968) has claimed to show that this nucleus exercises a tonic inhibitory effect on the retina, since section of the optic tract results in the appearance of oscillations on the electroretinogram and an increase in the amplitude of the 'off' response. However these responses do not appear until about three hours after the optic tract has been sectioned and after 18 hours the conditions of light/darkness under which they appear are reversed, (the oscillations appearing at 18 hours post-op in the dark being inhibited by light). If the centrifugal system does exercise a tonic inhibitory effect on retinal function it is difficult to see why the removal of its influence should take so long to show itself. The experiments reported in chapter 3 on the results of cutting the optic tract found no evidence for the centrifugal system exercising any influence on the normal E.R.G. of the pigeon. No evidence of an increase in the amplitude

of the 'off' response was found immediately following the section of the optic tract under conditions where two different anaesthetics were used. Nor was any evidence found of the appearance of oscillations during 2 hours of postoperative recording. In two birds where the optic tract was cut and the retina subsequently died, oscillations did appear. It is probable that these oscillations were indicative of metabolic abnormality which occured as a consequence of circulatory disturbance. In this connection it should be noted that Abe (1962) suggested that the changes he observed in the E.R.G. of the rabbit following section or compression of the optic nerve could have been due to retinal metabolic abnormalities induced by optic nerve damage. Certainly in Ogden's case there is some evidence that the same hypothesis could explain his findings. He reports that ganglion cell activity followed the oscillatory waves and disappeared at the same time. From intraretinal recordings and injection of procaine into the vitreous Ogden proposed that the oscillatory mechanism was located in the inner plexiform layer of the retina. This would be a most unexpected finding if the centrifugal system was normally responsible for supressing this oscillatory mechanism, since the synapses of the centrifugal system occur not in the inner plexiform layer but in the inner nuclear layer, and on any conventional neurophysiological criteria the effects of destruction of the centrifugal system should have been most apparent here. It thus seems safest to attribute Ogden's findings to other sources than the removal of the inhibitory effects of the centrifugal system.

In the experiments reported in chapter 2, particular attention was paid to the possibility that the centrifugal system may be in part responsible for the high flicker fusion frequency found in the E.R.G. of the pigeon (Dodt and Wirth 1953). Such a hypothesis about the function of the centrifugal system in the retinas of invertebrates was proposed by Autrum (1958) who claimed that the presence of centrifugal fibres in some species was correlated with high flicker fusion frequencies. Autrum's findings were not confirmed by Ruck

(1958, 1961), but, despite this, the hypothesis that the centrifugal system may play a role in the production of a high flicker fusion frequency in vertebrates cannot be discounted. When the magnitude of the E.R.G. amplitude is plotted against flicker frequency before and after section of the optic tract, no differential effects were detectable, nor could any differential effects in the temporal interactions of the E.R.G. components be detected. While flicker amplitude was plotted systematically at high frequencies only under the condition where urethane anaesthesia was used, the fact that flicker was still discernable in the E.R.G. at a stimulation frequency of 150 c.p.s. would appear to be sound evidence that the centrifugal system is not involved in the maintenance of this response. Even if the anaesthetic (urethane) resulted in the suppression of the normal functioning of the centrifugal system, so that it was inoperative before the tract was sectioned, then the presence of a flicker response at high stimulation frequencies implies that the flicker mechanism is independant of the centrifugal system. Examination of the effects of a priming flash on the response to a test flash also failed to reveal any difference in the response before and after section of the optic tract.

Since these experiments were completed, a number of papers have appeared in the literature concerned with the centrifugal system; Van Hasselt (1969) has reported centrifugal effects on the E.R.G. of rabbits. There are a number of reasons however why this report should be treated with caution. In the first place the animals were totally blinded by coagulation of the optic chiasma and the experiments were not performed until 10 days later. The major effect found was an increase in the amplitude of the a-wave response to a priming flash and a decrease in the amplitude of the a-wave to a second flash occuring 500 milliseconds later. It is unfortunate that a delay of ten days occurred between the operative procedure and the test procedure, when it is known that the optic nerve is undergoing degeneration

throughout this period and that this degeneration may produce metabolic abnormalities in the retina. It is also somewhat obscure why one should expect changes to occur in the a-wave when the only information we have concerning centrifugal fibres to the retina indicates that they terminate within the inner nuclear layer (Cowan 1970), even in the rabbit when they have been reported (Cragg 1962). Since the a-wave of the E.R.G. is generated in or close to the inner segments of the rods and cones (Brown 1968) or perhaps even more distally (Penn and Hagins 1969), it is difficult to see why the centrifugal system should affect it. Since in mammals the subdivisions of the internal carotid artery that supply the eye, lie close to the chiasma, disruption of any of these could have unpredictable consequences on the normal response and recovery cycle of the eye when stimulated. There is also the added criticism of studies that involve effectively blinding the experimental animal, which also applies to the design of the present thesis' E.R.G. experiments, which is the possibility that such a procedure may prevent any indirect responses to visual stimulation, mediated by the autonomic nervous system. For example, exposure to a flash of light will normally produce an orienting reflex (Sokolov 1963), which will have autonomic components (vasoconstriction or vasodilation, changes in heart rate etc) which may alter the response of the retina to light and the recovery cycle after stimulation. Destroying the optic nerve or optic tract will prevent such nonspecific changes and may lead the experimenter to draw erroneous conclusions about centrifugal affects in the retina.

Recent investigations of the centrifugal system in the pigeon (Holden 1970) and the chick (Miles 1970, 1971) are more promising. Miles (1970) found that stimulation of the centrifugal tract in the unanaesthetised decerebrate chick produced facilitation of ganglion cell firing, probably by depressing the surround inhibition of the retinal receptive fields. Thus the first clear functional evidence available on the centrifugal system indicates that its effects are facilitatory rather than inhibitory as other authors have concluded (Autrum 1958,

Van Hassalt 1969, Jacobsen and Gestring 1958, Ogden 1968). Cells in the centrifugal system (Holden 1970, Miles 1971) like cells in the optic tectum (Jassik-Gerschenfeld 1971) appear to be strongly movement sensitive and Miles (1971) has proposed that they receive their input via the tectum, from movement sensitive 'on-off' cells in the optic nerve. While these results are extremely interesting and suggestive, they do not help as yet to answer one of the central questions surrounding the existence of the centrifugal system: that if a visual feedback system is necessary why should it occur in the brain and not in the retina? Except for Spinelli and Weingarten (1966) most investigators have assumed that the centrifugal system is a visual feedback loop. Bearing in mind what has been said previously about the multisensory inputs to the tectum, it would not be surprising if the reason for the nucleus isthmo opticus receiving input from the tectum were due to the necessity for altering the outputs of retinal ganglion cells to make them more compatible with the information from other senses. The pigeon does a great deal of its visual information processing at the retinal level (Maturana 1961). In particular, movement and orientation information are abstracted at this level. It is clear such information only has relevance when the movement and orientation of the body are already known. The only mammal in which evidence is available concerning centrifugal fibres to the retina which will stand the test of criticism is the rabbit (Dodt 1956, Cragg 1962) and this animal also has orientation and movement detectors at the retinal level (Levick 1967). It may be that the centrifugal system is a means of compensating for head and body movements so that the retinal output remains directly relevant and the advantages of early visual processing are not lost.

When one turns to the direct thalamic visual projection even less is known about these nuclei than about the projections of the tectal system. Galifret (1961) has recorded colour sensitive units in the nucleus lentiformis mesencephali pars parvocellularis (the nucleus that Kuhlenbeck 1937 thought formed part of the dorsal lateral geniculate nucleus). The function of the visual input to the dorsal

thalamus remains obscure although the discussion (below) on the possible function of the hyperstriatum is relevant here because these nuclei send a projection to this forebrain region. The visual input to this sub-group of nuclei within the nucleus dorsolateralis anterior is independant of the tectum (Galifret 1966, Rougeul 1957) and chapter 2 of this thesis). The units within the lateral geniculate nucleus pars ventralis show strong 'on' but weak 'off' responses and show spectral sensitivity curves similar to the photopic spectrum of the pigeon as obtained by Galifret (1966) according to King-Smith (1970), although nothing is known of any particular features that they respond to.

The visual thalamus of birds (accepting Karten's 1969a meaning of the term visual i.e. including the nucleus rotundus) projects to several areas within the forebrain. From the nucleus rotundus a system ascends through tractus thalamo-frontalis pars lateralis to the ectostriatum (Revzin and Karten 1967). The existence of this system was established by Kondo (1933) and has been confirmed by Revzin and Karten (1967) using electrophysiological techniques and by Karten (1970) using anatomical techniques. Recently Hodos and Karten (1970) have shown that lesions to this area results in retention deficits on brightness and pattern vision tasks. Aside from the issue of task complexity which has been discussed previously in connection with rotundal lesions, the interpretation of the deficits produced by lesions of the ectostriatum are complicated by other factors. Revzin and Karten (1967) reported the latency of responses to visual stimuli following photic stimulation of the eye as being about 30 milliseconds. This is in strong dissagreement with Revzin's (1967) determination of the latency of rotundal neurons to a light flash as being between 60 and 80 milliseconds, a figure that agrees with the evoked potential data presented in chapter 2. I have not been able to record evoked potentials to visual stimuli within the ectostriatum. There is also the problem that most of the lesions additionally involved the paleostriatum and the area surrounding the ectostriatum as well as the ectostriatum proper. In view of the evidence presented in chapter

2 of a visual projection to the region surrounding the ectostriatum it is difficult to interpret Hodos and Karten's (1970) deficits as being due to ectostriatal damage. That the defects might have been produced by damage to structures around the ectostriatum is supported in part by evidence provided in their own paper. Correlations between the extent of damage to the centre or periphery of the ectostriatum and the extent of the deficit shows a slightly higher correlation for the periphery (0.44 Kendall rank difference partial correlation) than for the centre (0.33). It thus seems premature to conclude that the ectostriatum is involved in visual sensory processes of the pigeon.

The fact that the pigeon has a visual projection to the hyperstriatal region of it's forebrain has been known for some time (Rougeul and Buser 1953, Rougeul 1957, Adamo and King 1967) and suspected for some time before that (Layman 1936). The evoked potential data presented confirm the existence of this projection, and also suggest that there might be further successive projections within the hyperstriatum, since the potentials found in the most superficial region is more complex than those found as the penetration of the electrode proceeds ventralward (chapter 2). What function this area has in the control of the pigeon's behaviour is more difficult to interpret. Layman (1936) established that chickens with lesions in this area take longer to acquire a triangle-circle discrimination. Zeigler (1963) also found deficits in the acquisition and retention of a triangle-circle discrimination although in his retention group the lesioned animals were all above chance on the first post-operative day of testing. Lesions of this same area have been found to produce deficits in activity (Zeigler 1963) and mating behaviour (Beach 1951). Lesions in this area however also produce deficits in orientation to auditory stimuli (Adamo and Bennett 1967) and there is evidence that this region of the brain receives projections from auditory and somatic senses as well as from the visual one (Adamo and King 1967, Delius and Bennetto in prep). Cohen (1967) has reported that hyperstriatal lesions in pigeons produce deficits in escape behaviour, reduce spontaneous flight, and lower

general responsiveness to exteroceptive stimulation. When this region is stimulated electrically (Cohen and Pitts 1967) there is evidence of a topographical relationship between site of stimulation and the body azimuth position that the animal responds to by appropriate movements of head, neck and body. Taken together then the evidence points to the hyperstriatum being involved in arousal and orientation to exteroceptive stimuli. Zeigler (quoted in Cohen 1967) has observed that under normal conditions a sequence of approach behaviour in the pigeon begins with head orientation to the stimulus and if this does not occur then the ensuing behaviour will also fail to occur. These results may begin to explain the failure to secure deficits in the compound colour-brightness discrimination study (chapter 4). Colour is known to be a powerful attention-getter in birds and, other things being equal, this dimension will be chosen most readily in the solution of discrimination problems (Jones 1954). Providing the most obvious cue (colour) probably helped to overcome any differences in terms of arousal properties of the stimulus between experimentals and controls. Differences between the two groups were however apparent in terms of latency measures, a result that might be expected if the above hypothesis is correct. The proposal that hyperstriatal lesions reduce orientation to external stimuli cannot be accepted unreservedly however, since Phillips (1968) found that lesions in this area in peach-faced love-birds produced an increase in mobbing behaviour.

If however, an arousal deficit is produced by lesions of the hyperstriatal region of the pigeon brain then the results of the experiments on generalisation gradients to size, brightness and orientation are not too surprising. That the animals can discriminate along these three dimensions after lesions to the hyperstriatum can be seen clearly from the results (chapter 5) and this bolsters the argument that the deficit is not sensory. The only difference that is apparent between the hyperstriatally lesioned animals and the controls is the difference in the slope of the generalisation gradients that is apparent when the stimuli of varying size were presented. This difference was however shared by the animals with lesions of the

neostriatum caudale, a fact which does not make for clear differentiation of the functional differences between the projections to the two areas. It has been proposed by Akerman et al (1962) that the pigeon's forebrain in general acts as an arousal system for stimuli controlling instinctive action patterns. Even if this were true however it would still not help to explain why two different visual projection areas should be separate in location if they are not functionally different. It seems that too much cannot be made of this difference however until further information is available on more general types of deficit produced by lesions of the neostriatum caudale (approach-avoidance behaviour, sexual and feeding behaviour etc).

The finding of a visual projection to the neostriatum caudale (chapter 2) confirms the results of Bremer, Dow and Morruzi (1939). It may confirm the results of Rougeul (1957) who recorded potentials somewhere in this region of the brain but it is difficult to know whether she was recording from the posterior edge of the paleostriatum augmentatum or from the neostriatum caudale. Similarly, the failure to use other than very vague and general terminology has done much to undermine the value of the Russian work on the forebrain of the pigeon (Gusel'Nikov 1958, 1959, Vasilevskii 1966, Belekova 1966). It is difficult to be sure which areas of the brain they are referring to e.g. which part of the forebrain corresponds to their cortex. It can be established however that the posterior medial region of the pigeons forebrain may be similar in several important respects to the anterior region (hyperstriatum). As well as containing a visual projection area this region of the brain also contains an auditory (Karten 1968) and a somatic sensory area (Delius and Bennetto in prep.). Stimulation of the posterior area of the pigeon's brain results in orienting reactions that may have certain features in common with the results of hyperstriatal stimulation, (Bremer et al 1939). However little can be said about the normal stimuli that release this behaviour, or about the role of vision in its arousal and control.

In many respects recent research on the function of the avian forebrain has tended to confuse rather than enlighten. Behavioural studies seldom give the clear cut results that are apparent from anatomical and electrophysiological studies, and this is particularly true of the studies that involve lesions to the avian forebrain. Perhaps this is not too surprising: the vast amount of work on the mammalian brain using anatomical and physiological techniques has helped to delineate the areas of the brain that are functionally related, and has stimulated the investigation of functional systems by physiological psychologists. The view of the mammalian brain that has gained ground in recent years, a system of sensory analysers and motor control systems that are a least in several important respects functionally separate, may have hampered rather than helped those of us who began an investigation of some aspects of the avian brain. Perhaps investigators have expected the same functional systems as those found in mammals but located in areas that 'looked' different anatomically and were called by different names (see Karten 1969a). The attempt to find areas within the avian hypothalamus that were functionally similar to those found in the mammalian hypothalamus and the evident failure thereof (Akerman, 1960, Wright 1968) may be a warning. Zeigler's (1969) description of the feeding system of the pigeon suggests that it may be organised functionally in a very different way from that of mammals in that it does not appear to involve the hypothalamus. Perhaps motivation as we know it is a concept that applies only to mammals, since the deficits produced by destruction of different parts of the feeding system appear to relate to seizing and mandibulation difficulties rather than to a loss of the desire to eat (Zeigler 1969). The same change may be necessary to the way in which sensory systems of birds are viewed, and the view gained from mammalian studies of a hierarchical organisation of analysis may be irrelevant. As was suggested by Maturana (1961), if the avian visual system is geared to the requirements of a more stable environment then it may well turn out to operate on different principles. The large number of diencephalic and mesencephalic nuclei involved in

the processing of visual information amy be an indication that much analysis may be carried out without any telencephalic involvement.

APPENDIX 1

The Measurement of Visual Acuity in the Pigeon in Terms of the Modulation Transfer Function

The usual method of measuring visual acuity in animals is to determine the threshold (50% correct choice) in terms of the minimum discriminable width of light and dark bars. This method has been employed in studies of visual acuity in a number of species (Chapter 1). Recently a new method of measuring visual acuity has been developed by Campbell and associates (Campbell 1968, Campbell et al 1969, Campbell and Robson 1968). This method involves determining the sensitivity of the eye to gratings of different spatial frequency. The gratings are produced on an oscilloscope screen in which the z axis (electron beam) is modulated sinusoidally as it sweeps across the screen, on which a uniformly bright area has previously been produced. This method produces gratings where the spatial variation in illumination is sinusoidal, and not square as is the case in the usual grating patterns used in the study of visual acuity. The sensitivity of the visual system is plotted by taking the reciprocal of the threshold contrast at a number of x different spatial frequencies. Contrast can be varied by simply altering the amplitude of the sinusoidal voltage fed through the z axis of the oscilloscope. As the voltage of the input falls the contrast of the grating steadily decreases until when the voltage is zero, the stimulus consists of an evenly illuminated field of the same space average luminance of the grating. The resulting plot of sensitivity against spatial frequency is known as a modulation transfer function (MTF). Using this method Campbell (1968) has determined the MTF for both the optics of the human eye and the eye brain channel. Electrophysiological work on both humans and animals has indicated that across species the variation in visual acuity can be explained in terms of the spatially selective nature of the cells in the retina and lateral geniculate body. Thus in the cat, cells in the lateral geniculate body show a range of spatial

selectivity lying between 0.2 and 2.5 cycles per degree of visual angle (spatial selectivity refers to the spatial frequency that produces maximum responses in the cells). In the squirrel monkey the range for lateral geniculate cells is between 0.5 and 8 cycles per degree, a similar range to that of the cat (about $3\frac{1}{2}$ octaves) but the sensitivity is somewhat higher up the frequency spectrum, the resolving power of the primate's visual system should be about three times that of the cat. This physiologically predicted difference in visual acuity is paralleled by the known behavioural difference in acuity that exists between cats and primates.

The advantages of this method of measuring visual acuity are two fold. Firstly it gives a much fuller description of the performance of the eye at different spatial frequencies. Secondly it enables one to determine whether an animal's visual system is sensitive to higher spatial frequencies than another without actually having to take measures at very high spatial frequencies. Thus if one animal shows the peak sensitivity of its MFT at 8 cycles per degree while another animal shows a peak at 6 cycles, then the former animal will have a better minimum separably acuity than the latter. In taking the measurements it does not matter whether an animal has a higher response criterion than another since the method is relative. As long as the assumption can be made that its criterion remains the same across a range of spatial frequencies then the measurement will not be biased. This method of measuring the visual acuity of animals has been employed by Nye (1968) in the measurement of the binocular acuity of pigeon. Nye (1968) found that the peak of the pigeons MFT occured at 4.2 cycles per degree, as against the peak of the transfer function for the human which occurs at 6 cycles per degree. This means that the acuity of humans is 1.4 times the acuity of pigeons. Conventional measurements of pigeon's acuity have usually concluded that it is much poorer relative to humans than Nye's estimate. If the measurements of Chard (1939) are accepted, then the pigeon's acuity is 5 times worse than humans at high spatial frequencies. However Nye (1968) measured the binocular acuity of the pigeon, and the binocular

field does not contain the fovea. If a comparison of the pigeons visual acuity with that of primates is to be meaningful, then it is the foveal acuity of the pigeon that should be used for comparison. For this reason it was decided to make an attempt to measure the visual acuity of the lateral field of the pigeon (that area of visual space which projects onto the area of the retina which contains the fovea).

8 pigeons were selected for the task, the intention being to select the best birds from this number. The apparatus is shown in Figure 1, (page 158). The apparatus had two keys, one above the other so that whichever key the animal pecked it would be the same distance from the stimulus screen. The stimulus was the screen of a model 502 Tektronix oscilloscope. The pigeon had to discriminate between a grating pattern and an evenly illuminated field of the same space average luminance. The evenly illuminated screen was produced by feeding a 1 megacycle sawtooth voltage to the Y axis of the oscilloscope and arranging for the sweep speed of the oscilloscope to be too low to resolve it. This produces an evenly illuminated field. The sine wave grating was produced by feeding the output from a since wave generator to the Z axis of the oscilloscope. This modulates the intensity of the beam as it sweeps across the screen. The display could be sychronised by taking a second output from the sine wave generator to the external trigger of the oscilloscope. The display could be alternated by switching a relay controlled by a film-strip timer. The voltage of the input to the Z axis was arranged so that it produced 100% modulation of the beam so that the illumination of the screen was zero at the centre of the dark bars. This was the condition to be used in training. The modulation of the beam could be altered from 100% to zero so that when the animals reached criterion on the discrimination its threshold for discriminating the grating pattern from the evenly illuminated field could be determined at a range of spatial frequencies. The threshold would be determined by reducing the modulation of the Z axis thus reducing the contrast of the grating.

The birds were trained to peck the upper key in the presence of the grating and the lower key in the presence of the plain field.

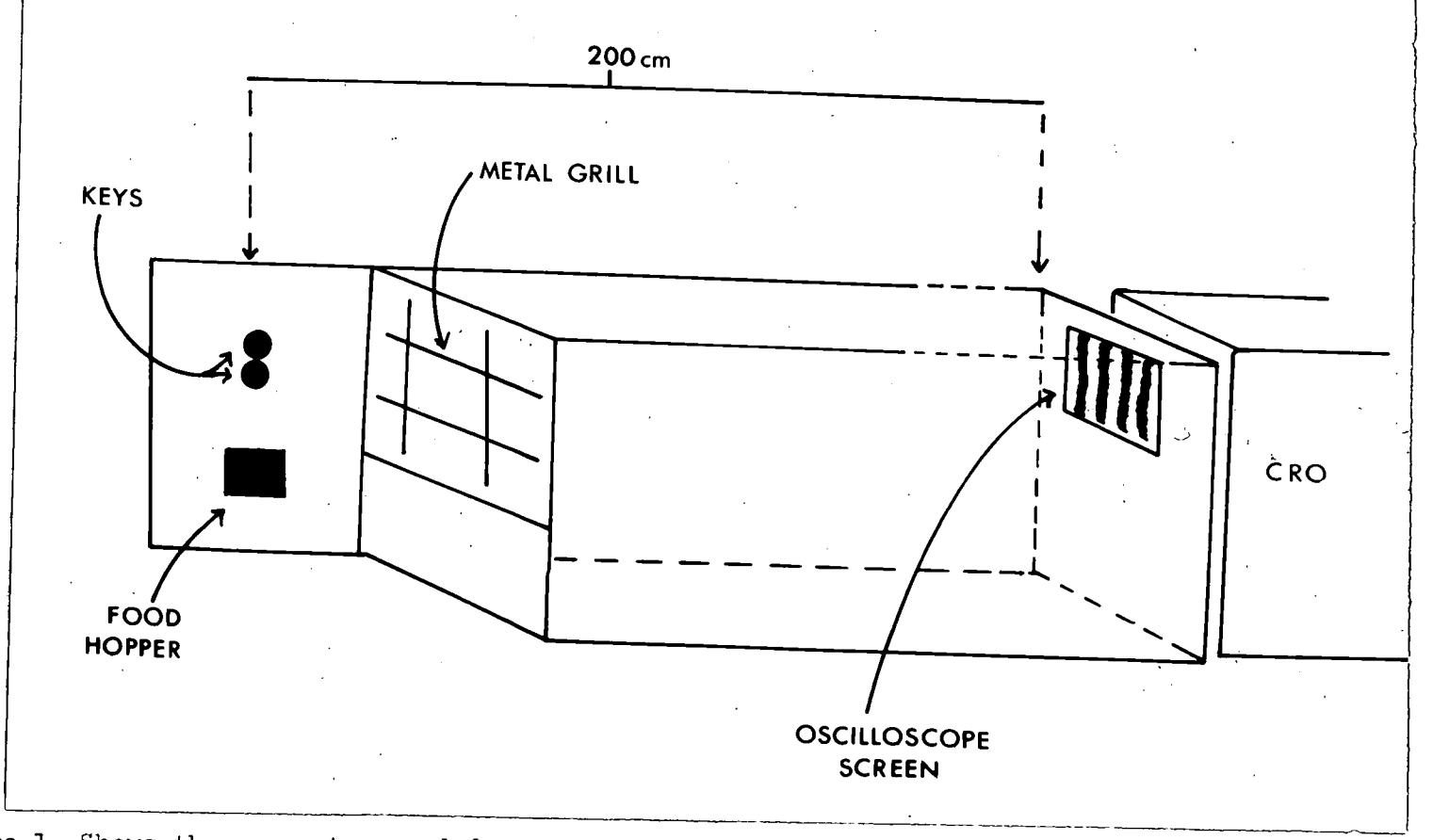


Figure 1. Shows the apparatus used for training pigeons to discriminate a sinusoidal grating pattern from a plain field of the same space average luminance. C.R.O. - oscilloscope. Keys were placed above one-another so that regardless of whch one the animal pecked it remained the same distance from the oscilloscope screen. The grill, which prevented the animal entering the alley which contained the oscilloscope, was of large guage so that the birds view of the screen was not impaired.

In order to make the stimulus more noticeable, the grating display was not synchronised i.e. it drifted across the screen slowly. It was thought that a moving stimulus would be more easily noticed by the bird since the response area (the keys) were in a completely different spatial location to the stimulus. Training began by using only the upper key which the birds pecked in the presence of the grating. Pecks in the presence of the plain field were not rewarded. Four birds rapidly rose above chance on this task and the remaining four were discarded. The second key was now introduced and pecks on this key were rewarded in the presence of the plain field. The bird had to peck the correct key 5 times to get 4 seconds access to grain. If four pecks were made on the incorrect key then the light behind the keys was extinguished and 10 seconds of time out ensued during which both keys were inoperative. After four weeks of training on this schedule one bird was pecking randomly while the other three were showing gradual improvement. This former bird was discarded and training continued with the other three. The number of pecks required to get a reward was raised to eight. Over the next four months the three remaining birds at times showed improvements but at other times their performance fell to chance. Only one bird ever came near to attaining the usual criterion of 90% correct.

At this time it became apparent that the training situation would have to be changed. The birds were taken back to the original one key situation and were trained on a 1 minute variable interval schedule in the presence of the grating. The grating was again allowed to drift across the screen to make the stimulus more obvious. Over the next two months the three birds showed very gradual improvement on this task but still did not reach the criterion of 90% correct although they were all above chance. Introducing the second key at this point resulted in the birds returning to chance performance so the training on the one key situation was continued for another three months. During this time several attempts were made to introduce the second key but each time this resulted in a return to chance performance, so it was decided to abandon the experiment.

The reason why the birds failed to reach criterion while they were being trained on the ratio schedule was probably because they could obtain a large number of rewards relatively easily even though they made a substantial number of errors. Training on the ratio schedule could not have been continued indefinitly as it was eventually necessary to get the birds performing on a variable schedule in order to obtain the thresholds under conditions of extinction. Probably the inherent difficulty of the task as well as the previous experience on the ratio schedule hampered the development of reliable discrimination when training was begun with the variable interval schedule. There was also the added complicating factor that the oscilloscope was placed closer to the birds at the start of training and gradually moved away from the birds as training progressed. The number of variables that operated during training probably contributed to the lack of success of the experiment. When the experiment is repeated care will be taken to train the birds to criterion on a variable interval schedule, then to move the oscilloscope to the maximum distance from the bird before introducing the second key. Rather than have the second key produce reward it would probably be an advantage to have pecks on the second key secure the return of the rewarded stimulus (the grating pattern). This might have the advantage of making the animal more attentive to the stimulus. The fact that animals can rise above chance on this type of problem even when the training procedure had many faults shows there is a strong possibility of obtaining an MFT for the lateral visual field of pigeons.

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