# THE EFFECT OF VISUAL DISCONNECTION OF THE CEREBELLUM UPON VISUAL PAVLOVIAN CONDITIONING AND THE FAILURE OF INTEROCULAR TRANSFER IN THE RABBIT.

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# ABSTRACT

This thesis was concerned with examining the differential role of the ipsilateral and contralateral optic fibre systems in: (a) oculomotor control, and (b) interocular transfer in the rabbit.

The first experiment was concerned to test the notion that the ipsilaterally projecting ganglion cell fibres constitute a retino-geniculo-striate system that is mainly concerned with pattern vision; and that the contralateral fibre system is both concerned with vision and oculomotor control. Transection of the contralateral optic fibre system was used to visually disconnect the cerebellum and examine the effect of this on both optokinetic nystagmus (OKN) responding and on Pavlovian conditioning of the nictitating membrane (NM) response. The results showed that both OKN and NM conditioning were lost following chiasma section.

The second experiment was concerned to examine the role of oculomotor scanning strategies in interocular transfer (IOT) in the rabbit. A comparison was made of the amount of IOT found for monocular learning of a two choice visual discrimination compared

with monocular learning of visual NM conditioning. The first task involves extensive oculomotor scanning and is believed to be mediated mainly by the ipsilateral optic fibre system; whereas the second entails no oculomotor scanning and depends entirely on the contralateral optic fibre system. The results showed there was a complete absence of IOT in the rabbit using either procedure.

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# CONTENTS

Pages

## Chapter I

Pages

Chapter II

Pages

Pages

Chapter III

Pages

# FIGURES AND TABLES

Pages

Chapter I

Chapter II

Chapter III

Pages

Pages

Appendix

# CHAPTER I

## INTRODUCTION

The origins of research on interhemispheric relations arises from partly philosophical and partly medical concerns with the problem of the unity of perception and consciousness. The various theories have essentially focused on principal structures in the brain. In the periphery the optic chiasma was early considered as a mechanism of visual integration. The earliest description of the optic chiasma and its connections with the brain in fish was provided by Aristotle, (384-322 B.C.). Subsequently the Alexandrian School of anatomy and medicine, identified the visual role of the optic chiasma. The nerves, believed to be hollow tubes were described as emerging from the base of the brain and meeting in the chiasma, and then bifurcating laterally to enter both eyes.

Galen's (A.D. 129-199) views on the optic chiasma were obscure. Its principal function was to ensure a proper distribution of information from the brain to both eyes. During monocular vision it acted to redeploy all of the information to the open eye. thus to compensate for the loss of one eye by doubling the power of the other. At the same time the chiasma served to prevent diplopia.

Alhazen (A.D.965-1039), believed the chiasma to be an association nerve where the contents of the two hollow optic nerves came together and were mixed to result in visual unity.

Avicenna (A.D. 980-1037), believed the optic nerves in the chiasma to be completely crossed such that the separate visual representations from the eyes are conveyed to the opposite cerebral hemispheres, where they were united in the ventricular system. This scheme was in essence taken over by Descartes in the 17th century who proposed that the pineal gland in the third ventricle was the site of sensory unification (sensu communis). Russell & Russell (1979); Polyak (1957).

Newton (1704) was the first to propose that where the optic nerves cross in the optic chiasma there is a division of fibres. An early concept of this. called partial decussation, showed how the fibres came together to carry information from corresponding parts of each eye. Newton's proposal, unlike that of Galen or Descartes, has been verified by modern research.

In lower vertebrates, all of the optic fibres from one eye cross over in the chiasma to form the optic tract of the other side, so that each eye is connected only with the opposite half of the brain. This is called total decussation.

In mammals, the decussation of the optic nerves is partial; some of the afferent fibres from each retina fail to cross over, and hence enter the optic tract on the same side. These fibres arise from the temporal half of each retina, and are called ipsilateral fibres. The fibres from the nasal half of each retina are the only ones which decussate and they are called contralateral fibres.

In all mammals, the relative number of uncrossed fibres is closely proportional to the degree of frontality. It is about 5% in the rat and rabbit, 40% in the cat and 50% in the higher primates and man (Walls, 1942).

The number of uncrossed fibres in the optic chiasma thus depends on the amount of overlap of the two visual fields, and this number tended to increase as animals evolved with eyes occupying a more frontal position (see Fig.I,1). The rabbit for example, has an extreme lateral siting of the eye in the skull, and there will be a small amount of overlap and a small proportion of ipsilateral or uncrossed fibres in the optic chiasma. Thus each of its cerebral hemispheres is heavily dominated by contralateral, or crossed, fibres from the opposite side. As the amount of binocular overlap increases from animal to animal, so does the number of ipsilateral fibres. In man there is almost complete overlap and 50% of the fibres of the optic nerve are uncrossed (Pettigrew, 1972).

## Interocular Transfer (IOT) in Rabbit & Rat

When an animal such as a cat or monkey is presented with a visual input to one of its eyes, it will usually be able to respond appropriately on the basis of the received information when using the other eye. The same, holds true for human subjects. This is called Interocular transfer (IOT) (Russell, Bookman & Mohn, 1979). The process is essential for the integration of visual input received through the two separate eyes, and for the appropriate organisation of responses to the visual environment. The last 25 years have seen a great number of experimental studies of IOT in a variety of different animals. The main

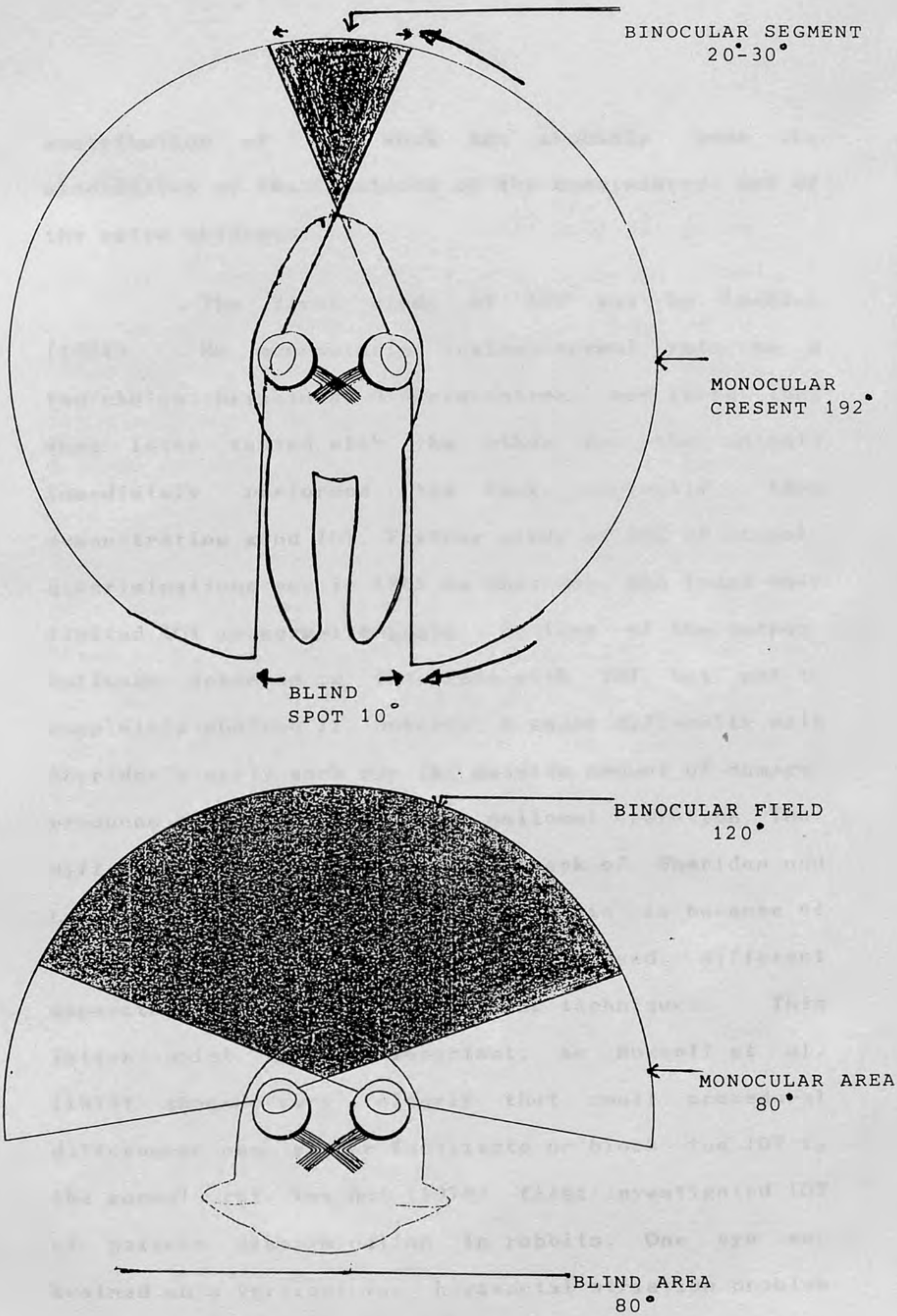


**Figure (1). The visual fields of the rabbit and cat eyes.**

contribution of the work has probably been the elucidation of the functions of the commissures, and of the optic chiasma.

The first study of IOT was by Lashley (1924). He monocularly trained normal rats on a two-choice brightness discrimination, and found that when later tested with the other eye, the animals immediately performed the task correctly, thus demonstrating good IOT. Further study of IOT of visual discriminations was in 1965 by Sheridan, who found only limited IOT in normal animals. Section of the corpus callosum appeared to interfere with IOT, but not to completely abolish it. However, a major difficulty with Sheridan's early work was the massive amount of damage produced in his animals by the callosal operation. The differences in IOT between the work of Sheridan and Lashley are difficult to explain. This is because of the different strains of animal used, different apparatus and different training techniques. This latter point is most important, as Russell et al. (1979) showed very clearly that small procedural differences can either facilitate or block the IOT in the normal rat. Van Hof (1970) first investigated IOT of pattern discrimination in rabbits. One eye was trained on a vertical vs. horizontal striation problem and the other eye was trained on a 45° vs. 135°

striation task. After the 90% correct choice level was reached by each eye the IOT was tested. The left eye was exposed to the training problem of the right eye and vice versa. He found little or no IOT exists in rabbits. This strongly argued that the ipsilateral fibres in the chiasma (some 10% of the total number) do not contribute substantially to memory trace formation during monocular training and that in some way interhemispheric communication via the intercerebral commissures is either absent or actively blocked. He concluded that IOT is poorly developed in most rabbits. Since then, many studies have examined IOT in the rat, cat and monkey. The results have been surprisingly variable. However, for the rabbit there is as yet no evidence of IOT.

Failure to demonstrate IOT in rabbits could stem, at least partly, from a somewhat unclear or simplistic concept of the process of IOT, and a neglect of the possible influences of certain experimental variables on this transfer. Before considering the available experimental evidence, it is therefore perhaps useful to outline both the behavioural factors and neural structures which may play a role in IOT in the rabbit.

Considering first the apparent absence of IOT in the normal rabbit, it becomes evident that what is involved is not simply the transfer of the specific visual information on which the animals have been trained. Whilst learning a visual discrimination, a rabbit clearly also acquires general information about the training procedures and the apparatus used, and learns to make the appropriate required response. If the animal is trained with only one eye, the usually extensive panoramic visual field is considerably reduced, and covers quite a different angle from that experienced by the contralateral eye. In addition, the animal may adapt its responses to the monocular condition experienced during training. Thus when tested with the untrained eye, the rabbit not only has to remember the visual discrimination, but must also recognize the apparatus when viewed with the other, different, visual field. The rabbit also has to re-adapt its response patterns or oculomotor strategies of visual scanning, in order to be able to perform correctly the required choice response. While this often presents no great difficulty for the animal, it has been shown (Russell et al.,1979) that under certain experimental conditions, normal rats fail to show IOT because these oculomotor strategies do not transfer. It now appears that monocular training affects a number of peripheral aspects of behaviour, and this may seriously interfere with IOT.

The third important aspect of IOT concerns the neural route via which the information is transferred interocularly. The corpus callosum, optic chiasma and several other pathways may be involved in IOT in rabbits and rats. When a rabbit uses monocular vision, most of the information perceived with the eye will be transmitted to the contralateral half of the brain, since the great majority (90%) of retinal fibres cross the optic chiasma. However, a small proportion (10%) of optic fibres project ipsilaterally. Information may therefore be conveyed to both hemispheres simultaneously,independently of commissural transmission, where there is binocular convergence of information on the border areas 17 and 18 of the visual cortex (Hughes, 1971).

In addition to the ipsilateral optic fibre system, the rabbit possesses a number of commissures, the largest being the corpus callosum which is probably the main intercortical connection. However, other commissures also interconnect the visual areas of the brain, usually subcortical ones such the as anterior, posterior and tectal commissures. Powell (1976) has described a projection from visual areas 17, 18 and 19 to the superficial layers of the contralateral superior colliculus from the ipsilateral superior colliculus via the collicular commissure. The other decussating projections go to tegmental structures and a zone of the central gray matter directly above the oculomotor complex. Edwards (1977) suggested that the commissural fibres are involved more in the visuomotor functions of the superior colliculus than in strictly sensory functions. In the following pages, a brief description of anatomical and functional aspects of the rabbit's visual and commissural system will be given to provide a background for a further review of the behavioural evidence.

## The Visual System

The present account will emphasise those aspects of the rabbit's visual system which would appear of immediate relevance to the phenomenon of interocular transfer. Thus the description will include a consideration of the visual field and eye movements, as well as outlining the anatomical projections of the visual system.

### Visual Field

A diagrammatic representation of the visual field of the rabbit is shown in Fig.I,1 A. The panoramic visual field measures roughly 360° (Hughes, 1971) whereas in the rat it is 320°. The binocular field, in which the visual field of the two eyes overlap is 20-30° and the rat it is 80-85°. Both rabbits and rats have a maximum of 10% of ipsilateral fibres and a minimum of 90% of contralateral fibres. Furthermore, rabbits have the eyes sited laterally in the skull. Comparing that with other species such as the monkey and cat, the panoramic field in the monkey is 180° whereas, in cat it is 160° (see Fig.I.1 B). The binocular field, in monkey is 130° whereas in cat is 120°. Both animals have frontally positioned eyes in the skull.

Because of the lateral siting of the eye in the rabbit's head, the animal has a large visual field which is almost a complete sphere. This is shown in Fig.I.2 where Hughes (1971) has schematised the topography of the optical axis and the visual field. His observations were taken with rabbits in the freezing position (Fig.I.3) where they crouch motionless with the nasal bone about 35° away from the vertical. In this freeze position, the optical axis of each eye is directed about 2° anterior to the transverse plane. The monocular visual field extends 90° lateral to and 102° nasally from the optical axis, thus the total extension is 192° in the horizontal

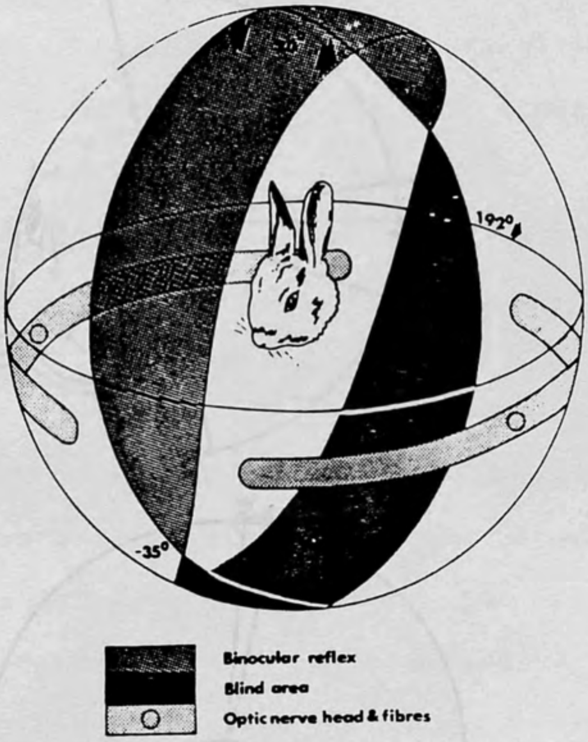


**Figure (2). The visual field of the rabbit divided into its respective binocular, monocular and blind regions.**
**Binocular area 20°-30°.**
**Blind area 10°.**
**Monocular area 192°.**

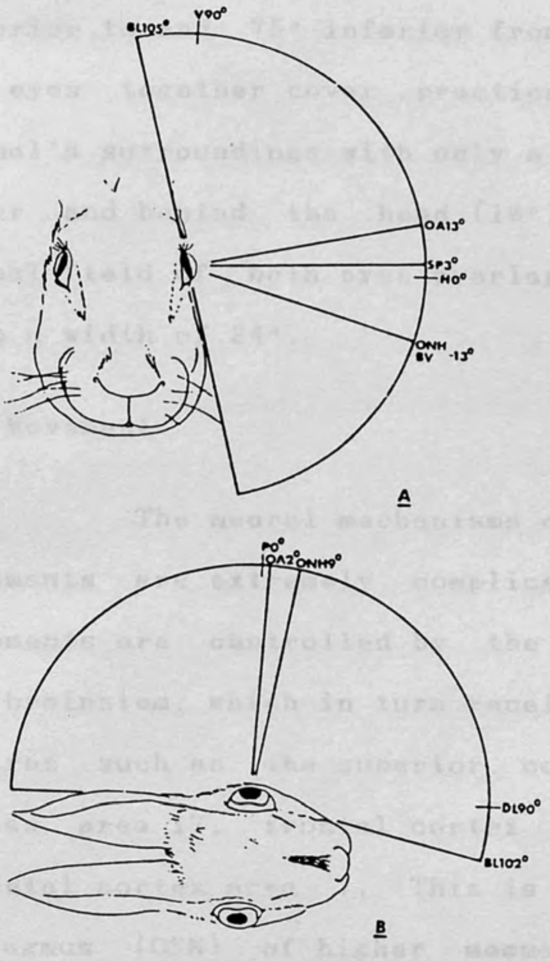


**Figure (I,3).** **Projection of retinal landmarks in the visual field of the rabbit in the freeze position: A in the vertical plane, B in the horizontal plane. BL binocular limit; V vertical; OA optic axis; SP streak peak ganglion cell count; H horizontal parallel; ONH and BV optic nerve head and blood vessels; DL presumed projection of the decussation line; P perpendicular to long axis of head (Hughes, 1971).**

plane. Vertically, the visual field extends about 105° superior to and 75° inferior from the axis. Thus, the two eyes together cover practically the whole of the animal's surroundings with only a negligible blind zone under and behind the head (10°). Frontally the two visual field of both eyes overlap in a binocular zone with a width of 24°.

## Eye Movement

The neural mechanisms of the control of eye movements are extremely complicated. Basically, eye movements are controlled by the oculomotor nuclei of the brainstem, which in turn receive input from visual centres such as the superior colliculus, and visual cortex area 17, frontal cortex eye-field area 8 and parietal cortex area 7. This is true for optokinetic nystagmus (OKN) of higher mammals such as man and monkey, but in lower mammals such as the rabbit and the rat there is no cortical control of OKN (Russell et al., 1987).

Eye movements are defined as rotations of the eye in the orbit, effected by the six extraocular muscles. The eye movements can be defined as the displacements of the eye with respect to the world (Collewijn, 1981). Unlike species with foveal vision such as man and monkeys, cats and rabbits do not show eye movements of the fixation type when presented with some object that should arouse their interest, such as food or other animals. Actually one can hardly observe any eye movements in a rabbit, unless the animal is actively moving around. Thus the rabbit's oculomotor system was considered to be insensitive to optical stimuli. Ter Braak (1936) demonstrated that optokinetic reactions could be elicited in the rabbit only by using an adequate stimulus. The stimulus consisted of rotation of the visual surroundings as a whole (a striped drum 120 cm diameter, 100 cm height). He concluded that OKN or spontaneous eye movement are found very rarely in the rabbit (Collewijn, 1971). The nearly panoramic visual field and lack of afovea make the gaze stabilisation of the rabbit difficult to define and accommodation of the eye is hardly, if at all, present (Zuidam & Collewijn, 1979).

In this regard, a major part of the rabbit's oculomotor repertoire consists of elementary gaze stabilisation by OKN and vestibulo-ocular reflexes (VOR) (Collewijn, 1981). Selective stimulation of retinal areas has shown that OKN is controlled predominantly by the lateral visual fields which stimulate central regions of the visual streak (see appendix, 6); whereas the frontal part of the visual field exerts only a weak influence (Russell et al., 1987). The eye movements have been described in the rabbit using panoramic field of OKN stimulation. Although such results show that vergence movements in the rabbit are technically possible (Collewijn & Noorduin, 1972) the magnitude of the convergence varied widely between trials and animals. Pure vergence responses without a conjugate component have been observed. Since the experimental situation did not specifically constrain locomotor strategies, the results strongly suggested that convergence will occur in any freely behaving rabbit during the active approach of a target (Zuidam & Collewijn, 1979).

## The Visual Pathways

A comprehensive review of the projections and morphology of the visual system of the rabbit was provided by Hughes (1971). Approximately 90% of the optic fibres arising from the retina of the rabbit cross to the contralateral side in the optic chiasm, while roughly 10% project ipsilaterally. It has been estimated that the optic nerve and tract of the rabbit contain approximately 395,000 fibres, most, if not all of which are myelinated (Rose & Malis, 1964). From the chiasma, the fibres run towards the thalamus, where most and possibly all of them give off collaterals.

These either innervate the dorsal and ventral lateral geniculate nuclei (LGNd,LGNv), or pass through to the pretectal nucleus and lateral nucleus of the optic tract in the pretectal area. The pretectal projection is mainly contralateral, with only a very sparse ipsilateral component (Edwards, 1977). The LGN receives both contralateral and ipsilateral fibres but again (Russell et al., 1987) the contralateral projection is considerably larger. In the LGNd, fibres terminate in a precisely retinotopic fashion,i.e. fibres originating from a specific retinal location always project to a specific area of the LGNd. Retinotopic mapping is present also in the LGNv, but appears to be less precise (Hughes, 1971;1977).

The main branch of the tract, after coursing over the LGN, forms the brachium of the superior colliculus. It terminates in the superficial layers of the superior colliculus which also receives an input from the LGNv. The superficial layers of the superior colliculus receive contralateral optic fibres. Contralateral projecting ganglion cells are found throughout the retina, whereas ipsilateral projecting cells are restricted to a very narrow strip on the margin of the temporal retina (Provis & Watson, 1981). As usual, the ipsilateral projection is smaller than the contralateral one, but that ipsilateral retinal ganglion cell projection in the optic chiasma plays a greater role in vision than is suggested by the small proportional anatomical representation in the optic tract (Russell et al., 1987). Efferent fibres from the superficial layers project back to the posterior lateral nucleus of the thalamus, which is the equivalent of the pulvinar of higher mammals.

In addition, there are decussating fibres in the deep layers of the superior colliculus, which in turn send efferent fibres to the brainstem, and in particular to areas involved in the coordination of head and eye movements. The deep layers of the superior colliculus also project to the contralateral superior colliculus via the tectal, posterior and supraoptic commissures (see Fig.I.4).

Considering the efferent projections of the lateral geniculate nuclei (LGN), the ventral nucleus has two dorsomedial projections going to the superior colliculus, the ipsilateral pretectal area, and the contralateral pretectal area (decussating tract fibres) via the posterior commissure. Three additional ventromedial projections send fibres to the pons and ipsilateral zona incerta, and to ipsilateral and contralateral brainstem areas. The efferent projection of the LGNd is the optic radiation, projecting mainly

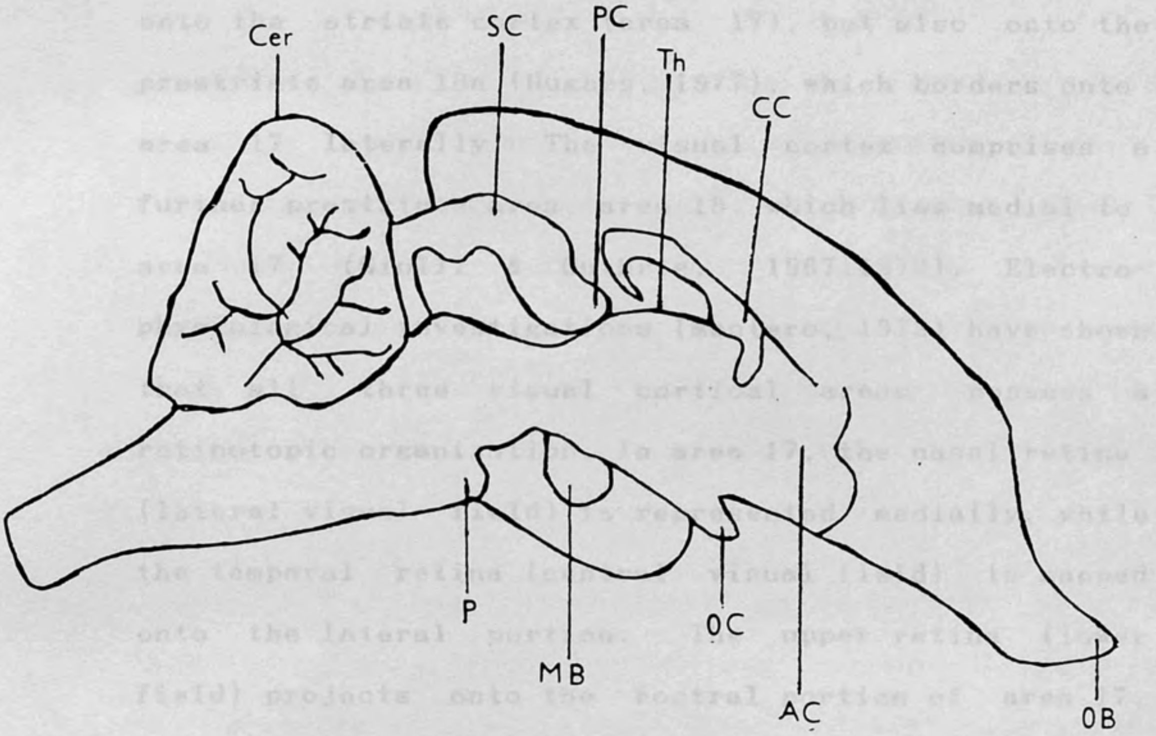


**Figure (I,4). Parasagittal section through the rabbit's brain, showing the position of the commissures. AC- anterior commissure, OC- optic chiasma, CC- corpus callosum, Th- thalamus, PC- posterior commissure, SC- superior colliculus, Cer- cerebellum, OB- olfactory bulbs, P- pons, MB- mammillary body.**

onto the striate cortex (area 17), but also onto the prestriate area 18a (Hughes, 1977), which borders onto area 17 laterally. The visual cortex comprises a further prestriate area, area 18, which lies medial to area 17 (Giolli & Guthrie, 1967;1970). Electrophysiological investigations (Montero, 1973) have shown that all three visual cortical areas possess a retinotopic organisation. In area 17, the nasal retina (lateral visual field) is represented medially, while the temporal retina (central visual field) is mapped onto the lateral portion. The upper retina (lower field) projects onto the rostral portion of area 17, the lower retina (upper field) onto the caudal part. The retinotopic maps in the prestriate areas are mirror images of that seen in area 17.

Area 17 receives both ipsilateral and contralateral input. Binocular cells are found over almost half of the striate cortex, moving medially from the lateral border (Adams & Forrester, 1968; Montero, 1973). Apart from the afferent projection from the ipsilateral LGNd, the striate cortex also receives fibres from the contralateral visual cortex via the corpus callosum, as well as a very sparse projection from the principal and posterior lateral thalamic nuclei.

Area 17 sends association fibres to both areas 18 and 18a. Area 18 furthermore has an afferent projection from the principal and posterior lateral thalamic nuclei, and possibly from the anterior thalamic nuclei. Area 18a, in addition to the input from the LGNd and area 17, receives fibres from the posterior lateral thalamic nucleus (Giolli & Guthrie, 1970).

Callosal connections exist in both area 18 and 18a. Two efferent projections from area 17, namely to prestriate areas and the contralateral visual cortex, have already been mentioned. In addition, there are extracortical projections to both dorsal and ventral LGN, to the superficial layers of the superior colliculus, and to pretectal and subthalamic areas.

## The Effect of Monocular Occlusion

The most obvious result of completely covering one eye of an animal is the reduction in the size of the total visual field. In the rabbit, this would amount to a restriction of between 180° to 190°, in the contralateral temporal field. Because of the small binocular overlap of the two monocular fields, vision in the central area of the visual field (i.e.

visual input to binocular cells in the cortex), is not in fact greatly affected. Nevertheless, observations of monocularly occluded rabbit show that they do tend to adapt their motor behaviour to the monocular condition (Russell et al., 1979).

A second consequence of monocular occlusion in the rabbit is that it probably introduces an asymmetry into the visuomotor behaviour of the animals. Monocularly elicited optokinetic nystagmus (OKN) responses in the rabbit are asymmetrical. Rotation of a large pattern in the nasal direction elicits a vigorous nystagmus with the slow phase in the same direction, whereas motion of the stimulus in the temporal direction is relatively ineffective (Ter Braak, 1936; Collewijn, 1969). The rabbit shares this preference with most afoveate species (Tauber & Atkin, 1968), with lateral eyes. In contrast to the cat (Montarolo et al., 1981), and monkey (Pasik & Pasik, 1964), transcortical or geniculo-striate routes are insignificant for OKN in the rabbit, which is mediated subcortically by the nucleus of the optic tract (NOT). The NOT receives many retinal afferents (Giolli & Guthrie, 1969), whereas the projections it receives from the superior colliculus and visual cortex are very weak or absent. Electrical stimulation of the NOT causes a vigorous nystagmus with the slow componant towards the stimulated side (Collewijn, 1975). These suggest that the preferred OKN to nasal motion is mediated through a purely contralateral connection of each eye to the NOT.

In the recent findings of functional adaptive processes in basic oculomotor reflexes such as the vestibulo-ocular reflex (VOR) and OKN in the rabbit (Ito et al., 1979; Collewijn & Grootendorst, 1979) it is of interest whether the rabbit is capable of regaining asymmetric OKN after the permanent loss of one eye (Collewijn & Holstege, 1984). These observations suggest that OKN responses involve a cortical loop in mammals with frontally sited eyes; whereas there may be no cortical control of OKN in animals with laterally sited eyes, where the OKN is organised only subcortically (Russell et al., 1987).

Rabbits would therefore be expected to show an asymmetrical type of response. This might well affect the monocular visuomotor responses of the animals in a visual discrimination situation. In a typical IOT experiment, in which rabbits are tested with their two eyes separately in succession, such asymmetrical visuomotor responses might interfere with the animal's ability to generalise from one monocular condition to the other.

## Investigations of Interocular Transfer (IOT)

### IOT in normal rats and rabbits

From the preceding anatomical description it is evident that both the ipsilateral optic projection and a variety of commissures may provide pathways for the interocular transfer of visual information in the rat and rabbit. The study of IOT in the normal animal is clearly a prerequisite for assessing the effects of the surgical disconnections on this process. Furthermore, observations on normal animals may provide a certain amount of information about the capacity and characteristics of the neural structures involved. Thus a comparison of the amount of IOT found for different visual stimuli, for example, may give insight into the type and amount of information that can be conveyed. Similarly, observations on normal animals presented with conflicting discriminations to their two eyes may give information about the integrative capacity of the nervous structures concerned with IOT. In addition, a detailed investigation into the role of the experimental procedure and apparatus, combined with a careful behavioural analysis, may lead to insight into the contribution of peripheral, or behavioural factors to the process of IOT. This in turn should allow a more accurate assessment of the effects of surgical interventions.

The great majority of studies on IOT in the rat have found that normal rats show fairly efficient transfer. Lashley (1924) was the first to report good IOT of brightness discrimination in normal rats. Similar findings have been reported by a number of workers, using a variety of simultaneous two-choice visual discriminations. Apart from brightness discrimination, efficient IOT has been shown to occur for orientation discrimination of striations inclined at 45° vs.135° (Sheridan, 1965a; Levinson & Sheridan, 1969), and horizontal vs. vertical stripes (Creel & Sheridan, 1966; Buresova & Bures, 1971; Cowey & Parkinson, 1973), as well as shape discrimination of a triangle vs. a square (Levinson & Sheridan, 1969). However, no stimulus control tests were done, which were important due to the poor learning criterion used by Sheridan. Russell et al. (1979) showed that poor IOT occurs when the detail of the visual information is increased, i.e. vertical versus horizontal is low in detail, but oblique striation discriminations require a lot of training; and also show poor IOT. Most studies utilised shock reinforcement, but Cowey & Parkinson (1973) found successful IOT when a food reward was employed. Mohn & Russell (1980) found equally high levels of transfer in two strains of rat (albino and pigmented). Using brightness and pattern discrimination their results indicated that IOT in the pigmented rat depends on the uncrossed optic fibres, and that the commissures of the rat's brain are also capable of efficient transfer.

Interocular transfer of orientation discrimination tasks is poorly developed or absent in most rabbits (van Hof, 1970). The results showed that the normal rabbit behaves to some extent like a split-brain cat. The untrained eye of the intact rabbit has little or no access to the memory trace formed during monocular training. The similarity with the split-brain cat at first sight suggests that the rabbit's behaviour is caused by a combination of a memory trace localised on one side of the brain and an insufficiency of the interhemispheral commissures. However, observations made while the animal is choosing the target show that, also with one eye occluded by a mask, the nose is more or less pointing in the direction of the targets. This implies that mainly the posterior part of the retina is used during training. As described by Thompson, Woolsey & Talbot (1950), the retina of each eye projects onto both hemispheres; the first 20° from the sagittal plane of the nasal part of the visual field is represented ipsilaterally.

The ipsilateral and contralateral projections, which converge on the border of areas 17 and 18 are connected interhemispherically by callosal fibres. Because of this projection onto both hemispheres from the posterior part of the retina, the memory trace built up during training is not necessarily localised on one side of the brain. It would mean that the ipsilateral fibres in the chiasma (10% of total number) do not contribute substantially to memory trace formation during monocular training and that in some way interhemispheric communication via the intercerebral commissures is either absent or actively blocked. Therefore, the fact that little or no IOT exists could well be due to a lack of intrahemispheric rather than interhemispheric communication (van Hof, 1979). Since that time further research has clearly established the fact that the ipsilateral pathway plays a crucial role in pattern vision (Russell et al., 1984; Russell & van Hof 1987, Russell et al., 1987). Further section of the corpus callosum in rabbit has been found to have no detectable effect on interhemispheric communication during proximal binocular vision (Russell et al., 1978; Russell et al., 1983) although it does alter the cortical control of the optical when tested for vision in depth (Russell et al., 1983). If binocular integration is presented then it is most unclear why there is a lack of IOT in the rabbit. The apparent differences in IOT reported for the rat and rabbit may be partly related to the different methods used for assessment of IOT by different investigators.

Interocular transfer has been measured by some as the savings seen on retraining of the second eye in comparison to initial acquisition, while others compare initial performance with the untrained eye to the final performance level seen with the trained eye. Finally, some workers have retrained the first eye to obtain a measure of normal fluctuations in performance, and have related the performance of the untrained eye both to initial acquisition and retraining of the first eye. All of these measures usually indicate that IOT is not quite perfect in rats and rabbits, since the untrained eye usually requires some training before reaching the adopted criterion. Furthermore, retraining of the first eye generally proceeds faster than training of the second eye. However, the differences in methods of IOT assessment do not seem sufficient to explain the differences in the amount of IOT reported. It is likely that the experimental conditions of the different experiments influenced transfer to some extent. It has been suggested that the imperfect IOT generally observed is: (a) due to the animals' difficulties in generalising from one monocular condition to the other, because of the differences between the two monocular visual fields, and (b) the training methods. Animals which had learnt a two-choice discrimination show perfect IOT, whereas animals with a three-choice discrimination, had a considerable impairment of IOT (Russell, Bookman & Mohn, 1979). Also IOT may vary with the spatial aspects of the experimental apparatus used, and may thus also contribute to the variable results obtained. In addition, Sheridan (1965) found that in rats IOT improved if the first eye was trained to criterion twice before the second eye was tested for transfer. Thus the general stability of performance appears to affect levels of IOT. These considerations argue for the importance of peripheral factors in determining the extent of IOT, factors which are not necessarily related to the transfer of information about the visual discrimination.

Failure of IOT

(1) Conflicting Discrimination

This becomes more evident when one considers cases in which IOT is severely impaired, or even completely absent. In studies with a simple experimental situation, such as a two-choice discrimination, rats show good IOT if the second eye is asked to perform the same discrimination as that previously learned with the first eye. Rabbits showed very poor savings even in a simple experimental situation.

Sheridan (1965) and Levinson & Sheridan (1969), Mohn & Russell (1980) trained rats and rabbits on an interocular reversal paradigm, using a horizontal/vertical or 45°/135° orientation discrimination. When the first eye was tested for retention of the original discrimination after second eye reversal training, there was some evidence of interfering transfer effects from the second eye. All the studies indicate that rats are capable of using their two eyes quite independently, and that interocular integration can be disrupted.

It can be seen when visual scanning involving efficient or detailed oculomotor integration is required, then IOT deteriorates (Russell et al., 1979). It would appear as if the monocular visual guidance system used by the animal in the discrimination performance becomes highly dependent upon or tied to these visuomotor mechanisms. When the monocular occlusion is changed to the opposite eye then there will be a lateral inversion of such oculomotor patterns. When the animal's performance is tightly coupled to such visuomotor integrations then reversed eye patching will produce a profound disorganisation of its visual guidance system and block IOT (Russell et al., 1979).

Studies on interocular conflict have been undertaken also in a variety of animals other than the rat and rabbit, including fish (Shapiro, 1965; Ingle, 1968), birds (Levine, 1945; Catania, 1965; Graves & Goodale, 1977), cat (Myers, 1962) and monkey (Trevarthen, 1962).

Particularly, the experiments on birds and fish have provided useful insight into the factors influencing the animals' ability to learn conflicting discriminations. Although the visual system of both fish and birds differs from the mammalian system in the complete crossing of optic fibres at the optic chiasma, many of the conclusions or suggestions derived from the work on lower vertebrates are clearly applicable also to the rat and rabbit. The findings are pertinent not only to the acquisition of conflicting discriminations, but also to the general process of IOT, even when non-conflicting tasks are used.

Two mechanisms have been proposed which would allow animals to perform conflicting discriminations without significant interference between the two eyes (Ingle, 1968; Graves & Goodale, 1977) these are:

(a) The first suggestion is that the information from each eye is confined to one hemisphere of the brain, and that commissural interaction of the two memory traces is suppressed, or interrupted by the stronger direct visual input. This clearly depends on a strict separation of the optic projections from each eye, present in fish and birds. Mammals always have bilateral optic projections. However, it could be argued that the small ipsilateral projection of lower mammals such as the rat and rabbit may still allow sufficient lateralisation in the brain. The hypothesis also assumes that direct visual input to the visual cortex via the LGN is stronger than the indirect commissural information to the subcortical projection, perhaps because the latter involves transmission across at least one more synapse.

(b) The second hypothesis suggests that perceived differences between the two monocular conditions enable animals to form conditional discriminations, where performance of the discriminations becomes conditional on the use of a particular eye. This notion is clearly related to the concept of state-dependency, which argues that the performance of a task can become dependent on the behavioural state of the animal. When a different state is induced, the performance is abolished. It would be predicted that the establishment of conflicting discriminations would be easier in animals with completely decussated optic fibres, and laterally implanted eyes, such as bird and fish.

This would arise because the overlap of the two monocular visual fields is usually smaller in these animals than in animals with bilateral optic projections. In general, the interocularly conflicting discriminations are more easily acquired by lower vertebrates, while such tasks pose great difficulties for higher mammals like the cat and monkey (Myers, 1962; Trevarthen, 1962).

In rabbit, where IOT is poorly developed, conflicting discriminations can be learned. In other words, the two halves of the rabbit's visual system appear to function more or less independently (van Hof, van der Mark, 1976) and it can solve an interocular reversal task without any apparent difficulty (van Hof, Russell, 1977).

The results have pointed to a number of experimental factors which may affect performance on conflicting discriminations and more generally, interocular transfer. One important variable is the part of the visual field in which the stimuli are presented. This may affect both the behavioural response and the central projection of the stimuli.

When the stimuli are situated in the central field of vision, the differences experienced between the two monocular conditions, when looking at the stimuli, will be quite small, thus making conditional discrimination learning more difficult. In addition, the stimuli may be projected to area of the brain concerned with binocular integration, since they lie near the vertical midline. Lateral presentation of the stimuli would both increase the perceived differences, and result in projection of the stimuli to areas lacking direct binocular input.

This would make for strong interactions between the two monocular conditions. It is thus clear that the ability to perform conflicting tasks is related not only to the extent of bilateral optic projection and the binocular visual field, but also to a variety of peripheral experimental factors both peripheral behavioural and central processes. The rabbit has a relatively narrow binocular field, mainly from the temporal part of the retina (Hughes & Vaney, 1982). At the behavioural level, observations have shown that rabbits use the temporal region of the retina during visual discrimination learning (van Hof & Lagers van Haselen, 1974).

(2) The role of peripheral factors

Direct evidence for the involvement of peripheral factors in the process of IOT in the rat comes from experiments by Russell et al. (1979). It was found that under certain experimental conditions, normal rats fail to show the usual level of IOT with the conventional transfer paradigm. Modification of the training box to provide a simultaneous three-choice situation, for example, resulted in a severe IOT impairment. Even in the two-choice apparatus, little IOT was seen when a shock-escape procedure was used rather an avoidance paradigm. Finally, IOT in the two-choice box failed even under avoidance conditions when the visual angle between the stimuli was increased to be similar to that in the three-choice box. It seemed that IOT was impaired when the animals had to organise their responses very efficiently in order to minimize the amount of foot-shock received. This is clearly the case under escape conditions, but also when a greater number of stimuli has to be inspected, or a greater angle must be scanned.

Further experiments indicated that the impairment was related to the characteristics of the particular visual stimuli employed. It was found that the transfer deficit in the three-choice apparatus was greater for more complex discriminations, such as a horizontal/ vertical orientation task and a pattern discrimination, than for a simple brightness discrimination. The authors therefore suggested that during initial acquisition, performance of the task becomes linked to visual search responses, such as scanning movements, directed towards the visual display. Such responses would be more complex for pattern discriminations than for a brightness discrimination. If the temporal or spatial aspects of the task require a very efficient organisation of the scanning movements, the animals actually become dependent on using the eye efficiently.

It is possible to break the dependency on the originally used eye by giving the animals a few trials on a completely novel discrimination with the untrained eye before testing for transfer of the original discriminations. This enabled the animals to learn to use their eye for a visual discrimination, and they then showed good transfer of the original task. Thus the observed IOT impairment was apparently due to an inability to perform the appropriate oculomotor responses, which was strong enough to completely obscure the underlying transfer of information about the specific discrimination which has clearly occurred.

These experiments demonstrate the importance of the experimental conditions to the success or failure of IOT. Furthermore they show that peripheral, behavioural factors such as oculomotor scanning responses, are an integral part of the process of IOT. These conditions are important for the assessment of the effects of surgical disconnections on IOT.

# CHAPTER II

## EXPERIMENT 1

## THE EFFECT OF VISUAL DISCONNECTION OF THE CEREBELLUM ON RETENTION OF PAVLOVIAN CONDITIONING IN THE RABBIT.

### INTRODUCTION

The essential basis of Pavlovian conditioning involves the temporally successive presentation of two different stimuli. It is important that one of these, the unconditioned stimulus (US) should reliably produce a reflex which is called the unconditioned respose (UR). The other stimulus, which is presented first, is behaviourally neutral with respect to the UR, although it must be able to produce a general orienting response. This stimulus is known as the conditional stimulus (CS). After repeated paired presentations of the CS followed by US, the animal typically changes its reaction to the CS by replacing the orienting response with a conditioned response (CR), which is similar to the UR.

Pavlovian conditioning of the nictitating membrane (NM) response in the rabbit was first demonstrated by Gormezano et al. (1962) who argued that this preparation was an ideal model system for studying associative learning. A large body of behavioural research supports this position. The true associative nature of the conditioning was convincingly demonstrated by Schneiderman et al. (1962) who showed that it was only when the CS and the US were sequentially paired that learning occurred and that the preparation was uncontaminated by alpha responding or sensitisation effects.

Furthermore, the absence of any pseudo-conditioning was demonstrated by Smith et al. (1969) who showed that there was an optimal interstimulus interval (ISI) of 400 ms separating the CS and US for conditioning to occur. Learning was dramatically attenuated when either shorter (100 ms) or longer (800 ms) ISI values were used. Furthermore no learning was found when either simultaneous or backward (CS-US) presentations were used. The amount of conditioning or speed of acquisition has also been found to be directly related to the length of the intertrial interval (ITI), Leventhal & Papsdorf (1970); Kehoe & Gormezano (1974). Subsequent research has shown that not only are the major quantitative parameters of NM conditioning known, but they are impressively constant across different laboratories. It is this last feature of the NM preparation that makes this type of associative learning such a powerful model for studying neural mechanisms of conditioning.

The first study of the underlying neural mechanisms of Pavlovian eyelid conditioning were made by Hilgard & Marquis (1936). Using a visual CS they demonstrated that lesions of visual cortex had no effect on conditioning in the dog. Oakley & Russell (1967) were the first to continue this using the NM preparation in the rabbit. They showed that large cortical lesions did not effect such learning to either visual or auditory conditioning. Subsequent research by Oakley & Russell has convincingly excluded any role of the cerebral cortex in associative learning and has provided powerful evidence for the existance of a subcortical memory trace. Total removal of the neocortex did not impair either the de novo acquisition or the subsequent retention of both single stimulus and differential Pavlovian delayed conditioning (Oakley & Russell, 1972,1974,1975,1977; Russell 1971,1980). Similar results were also found for trace conditioning (Yeo et al. 1984) and NM inhibitory conditioning (Moore et al. 1980; Yeo et al. 1983).

Single unit recordings during NM conditioning have shown that some type of memory changes do occur in the hippocampus during conditioning. However the hippocampal circuit is not essential for learning (Berger & Thompson, 1978). Extensive brain lesions including the neocortex, the dorsal hippocampus and parts of basal ganglia can impair, but they neither abolish nor do they prevent, NM conditioning (Enser, 1976). However Weisz et al. (1980) have argued that the role of the hippocampus in associative learning is to establish a model of the CS rather than to store the association. If this is true then such hippocampal model-making would be a critical mechanism in trace conditioning, where the US is paired with a memory of the CS. In support of this Weisz et al. (1980) showed that hippocampal lesions severely impaired trace conditioning but did not affect normal delayed conditioning of the NM.

In contrast large cerebellar lesions in the rabbit have been reported to abolish completely a previously learned NM response to an auditory CS, as well as blocking its re-acquisition (McCormick et al. 1982). Similar lesions also prevented NM conditioning in naive rabbits (Lincoln et al., 1982). Such lesions only abolish the CR and are without effect on the UR, indicating the impairment of conditioning was not due to a simple loss of motor control over the NM response.

However it should be noted that such lesions do not totally destroy all signs of conditioning. They blocked or attenuated only the conditioned response ipsilateral to the cerebellar lesion. If the air puff US is transferred to the other eye then retention of conditioning was found in terms of significant savings to relearn. These findings have been interpreted by Thompson (1986) as clear evidence for associative memory storage in the cerebellum. Such a claim however is not without precedent. Brindley (1964) originally proposed that the cerebellum acts as a learning machine, and this has subsequently been elaborated by Eccles (1967); Marr (1969) & Albus (1971) who claim that the cerebellar cortex functions as a site for motor memory. The basis of this position can best understood when we consider the role of motor learning in regulating the oculomotor reflexes that are concerned with gaze stabilisation. There the point of optimal performance is to ensure a minimal amount of retinal image slip when the animal moves arround. Such compensatory control entails complex information processing from several sensory systems, for example including interactions between canal-ocular, maculo-ocular, (in the case of the rabbit that has an afoveate eye the information would be concerned with integrating streak-ocular translations) optokinetic and cervico-ocular responses.

Even if genetic programming could be perfect these systems, identified above, could not possibly meet the requirement of visual behaviour without the need for environmental adjustment or re-calibration. It is in this theoretical context that the cerebellum has been traditionally regarded as the source of such plastic adaptation or motor learning mechanisms. These mechanisms have been studied by:

(A) Recovery of motor control following unilateral labyrinthectomy.

This causes an imbalance in vestibular control due to unilateral deafferentation. Within 7-21 days a remarkable degree of equilibration returns and normal motor coordination is possible.

(B) Effects of neonatal dark-rearing on the development of oculomotor control.

Compensatory eye movement such as the vestibulo-ocular response (VOR) and the optokinetic nystagmus (OKN) response are made to ensure stable vision. In complete darkness, the VOR is elicited but is without functional significance, due to the lack of visual feedback which normally regulates its efficiency. Similarly the OKN is never produced in darkness. Thus animals reared in darkness subsequently show profound and irreversible deficit of both VOR and OKN.

(C) Adaptation of the VOR during reversal of left-right relations of the visual field by the wearing dove prisms.

Essentially with such optical reversal gaze control during body movement is lost, but is recovered within a few days to be within normal limits.

(D) A final example of motor adaptation is that of Pavlovian learning.

The first claim that the cerebellum was involved in such learning comes from the report by Karamian et al. (1969) who found decerebellate cats had impaired classical conditioning. Subsequent work by Thompson et al. (1983) has confirmed and extended these earlier claims. Using the Marr-Albus models, he has suggested that the CS information is relayed by the mossy fibres to the cerebellar cortex, and that the US information goes via the climbing fibres. Conditioning occurs when the mossy fibres input to the Purkinje cell is modified by climbing fibres activity (see Fig.II,1).

Taking these separate sources of evidence together Robinson, (1975) proposed that the cerebellum could be considered as the centre controlling the acquisition of new motor patterns. Here, the specialized nature of the synaptic organisation of the cerebellar cortex is a major factor drawn upon to support this view point. This concerns the nature of the afferent fibre innervation of the Purkinje cells, where both the climbing fibre and the mossy fibre granule systems have distinct and different morphological connections on the dendrite of Purkinje cells (see Fig.II,2(A)).

In essence it is held that the climbing fibre with its wide spread innervation with the dendritic tree has the specific function of modifying synaptic efficiency of the mossy fibre input (see Fig.II,2(B)). This modification is believed to be long lasting and to be the cellular substrate of motor learning. The same mechanism was also believed by Robinson (1975) to be responsible for motor compensation following either peripheral or central neural damage where functional re-adjustment was

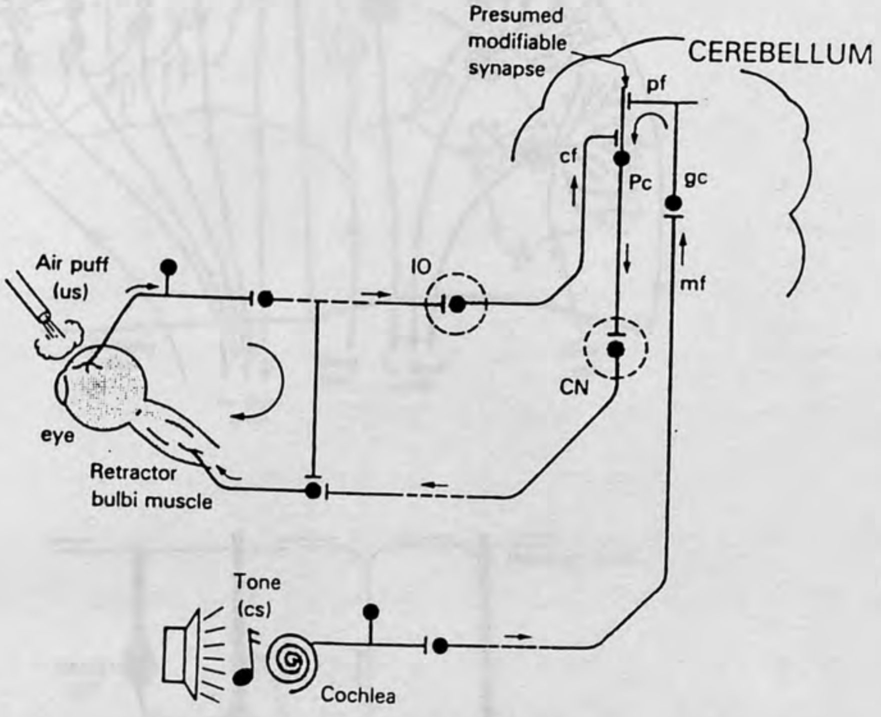


Figure (II,1). The sketch, based on the Marr-Albus hypothesis, shows the putative circuitry for generating both the unconditioned response and the conditioned response. An air puff to the eye - the unconditioned stimulus - leads to the activation of motor neurons innervating the retractor bulbi muscle, which is one element of the NM response. Presence of the unconditioned stimulus is also signalled to the Purkinje cells in the cerebellar cortex via the climbing fibres whose cell bodies all reside in the inferior olive. The Purkinje cells also receive information about the tone - the conditioned stimulus - via a multi-synaptic pathway that includes mossy fibres and granule cells giving rise to the parallel fibres. The hypothesised plastic site is the synapse between the parallel fibre and the Purkinje cell, and its modification is assumed to depend upon concurrent activity in the climbing fibre and the parallel fibre. The Purkinje cells project to the cerebellar nuclei, and thence to the motor neurons mediating the NM response. Only minimal circuitry essential to the model is shown. Broken lines indicate pathways of unspecified connectivity.

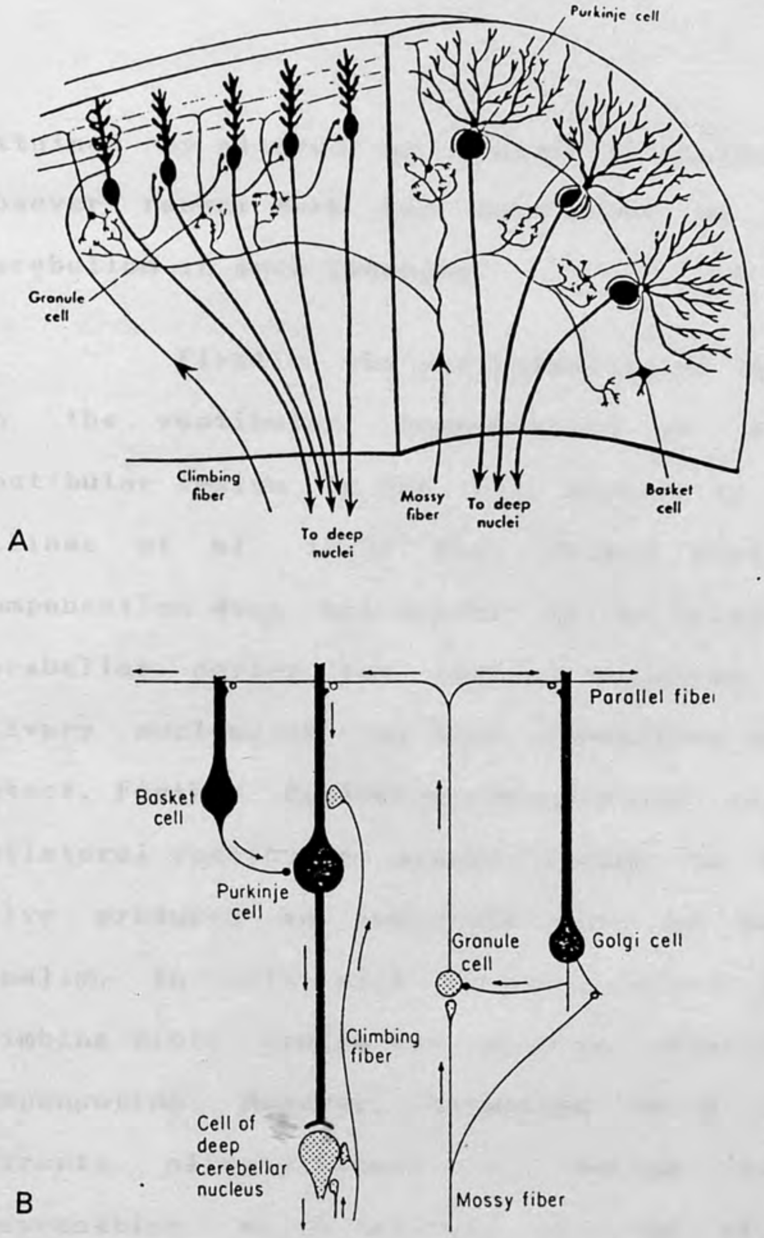


Figure (II,2). A: Diagram of cells in the cerebellum. The Purkinje cells have a large dendritic tree. Mossy fibres synapse with many granule cells. The axons of granule cells enter the molecular layer and divide, each branch running lengthwise as a parallel fibre, synapsing with Purkinje cells and basket cells. Climbing fibres synapse directly with Purkinje cells. Axons of Purkinje cells have recurrent branches to adjacent Purkinje cells. B: Also illustrates the principal synaptic connections within the cerebellum. Inhibitory cells shown in black; excitatory cells and synapses are stippled. (Eccles, 1973).

attained by altered or plastic cerebellar circuits. However recent work has cast doubt on the role of cerebellum in such learning.

Firstly, the participation of the cerebellum in the vestibular compensation to a unilateral vestibular lesion in the rats appears to be doubtful (Llinas et al. 1975). They showed that vestibular compensation does not depend on the integrity of the cerebellar cortex but instead requires either the olivary nucleus or the deep cerebellar nuclei to be intact. Further following compensatory recovery after unilateral vestibular damage, damage to the inferior olive produced an immediate loss of compensation. Finally, in rats with partial olive lesions the climbing fibre system was able to support vestibular compensation. However, harmoline which specifically disrupts olivary functions, caused the loss of compensation, which returned when the effect of the drug wore off. This suggests that the inferior olive has an important role in both the acquisition and maintenance of motor compensatory adaptation. It raises doubts concerning the cerebellar cortex as the site of motor learning.

Second, similar findings have been found for VOR compensation following hemilabyrinthectomy (HLE).

Compensation was spared following ablation of the flocculus, modulus and the uvula in the cat (Haddad et al., 1977). Further, Courjon et al. (1982) have shown that flocculectomy prior to HLE markedly delayed VOR compensation in the cat. Removal of the flocculus after VOR compensation to HLE did not have any effect. Thus at best it would appear that the cerebellar cortex could have a role initiating compensatory processes, but is not itself the site of adaptive learning.

Third, investigations of cerebellar mechanisms involved in neonatal dark-rearing deficits are few. It is likely that the effects are due to the superior colliculus and not the cerebellum (Flandrin & Jeannerod (1980). Harris & Cynader (1981) found that dark-reared kittens lost both VOR adaptation and rebalancing. In contrast, chiasma sectioned cats (which are deprived of their retino-tectal projections) maintained VOR adaptation and re-balancing. Thus taking these results together it suggests that in higher mammals, such as cat and monkey, the cerebellum is not the site of developmental oculomotor plasticity. Such animals have both a cortical and a brain stem system for oculomotor control. There is the ipsilateral retino-geniculo-striate pathway; as well as the contralateral retino-NOT-cerebellar connection. It is only ipsilateral control system which is subject to developmental modulation. In rabbits there is no cortical contribution to oculomotor control; section of the optic chiasma thus results in a permanent impairment of the VOR, OKN response and drift (Russell et al., 1987).

Finally, with regard to the role of the cerebellum in Pavlovian conditioning there is a similar development. Clear evidence has been provided that conditioned NM responses are blocked when the deep cerebellar nuclei are damaged (Lincoln et al., 1982; McCormick et al., 1982). Such reponses are also blocked by lesions restricted to the dentate and interpositus nuclei alone (Yeo et al., 1985), to the red nucleus (Rosenfield & Moore, 1983) and to the dorsal lateral pons (Desmond & Moore, 1982). There is still controversy regarding the extent of the involvement of the cerebellum in learning. In general, it is clear that the effect of the cerebellar cortex lesions appears to be less and not as permanent as first claimed. The Thompson group was the first to report deficits in conditioning due to cortical lesions. This has a recently been extended by Yeo et al. (1985) to suggest cortical localisation for NM conditioning in the lobus simplex, where lesions produce CR loss to the ipsilateral eye. However no deficits were seen when the input was switched to the contralateral eye. However Woodruff-Pak et al. (1985) have shown that lesions of the loblus simplex do not always impair NM conditioning, and that when deficits are found they are transient, not lasting than more 10-15 days.

This indicates that the cerebellum may not be the brain structure where the neural programme for associative learning is generated or stored. It is more likely that the cerebellum deals with information coordination solely concerned with motor expression of all motor reflexes and also those involved in this type of learning.

The major problem with the use of lesions to investigate the role of the cerebellum in Pavlovian conditioning, is that such procedures can produce motor deficits which are indistinguishable from a learning impairment, i.e. the lesion could block the motor expression of the learning without affecting the learning itself.

This point becomes more clear when the inherently temporal nature of Pavlovian conditioning is considered. The essential change that is observed is the movement of the CR forward in time as part of its attachment to the prior CS presentation. A salient feature of cerebellar function is to anticipate motor requirements ahead of time. Thus damage to the cerebellum could well affect Pavlovian conditioning due to a disruption of this temporal modulation of motor control. The conditioning would no longer be detectable in terms of an anticipatory CR to the CS by an on-line measure, but the learning could nonetheless still be preserved.

The solution to this potential confounding is to avoid damage to the cerebellar modulation of motor control, and to substitute instead section of the optic chiasma for a cerebellar lesion. This will have the effect of disconnecting all retinal input to the oculomotor pathways including the cerebellum, but it would leave cerebellar control intact for the timing of all motor activities (Russell, van Hof, van der Steen & Collewijn, 1987). Thus conditioning of the NM response to an auditory signal should be intact, but impossible to a visual one (see Fig.II,1), where the auditory CS pathways are shown. When using a visual CS, the sole input to the cerebellum would be via the contralateral optic nerve projections.

If true, this would strongly argue that the effect of visual disconnection of the cerebellum leading to a loss only of visual nictitating membrane

(NM) response conditioning is due to an interference with the motor expression of the learning and not with the interference with the memory storage mechanism itself. Thus damage by cerebellar lesions in the past has produced the loss of visual as well as auditory NM conditioning because both types of memory required common motor output machinery.

Russell et al. (1987) in their study of the effect of chiasma section on visual and oculomotor function in the rabbit clearly showed that: (a) the ipsilateral projection was capable of supporting normal pattern vision, (b) the contralateral fibre system was the sole source of projections to the nucleus of the optic tract, (c) only the contralateral retinal projections play a crucial role in the initiation of the optokinetic reflex and a major role in the vestibulocular reflex.

Taken together these observations strongly argue that the role of the ipsilateral projection in the rabbit is a complete retino-geniculo-striate pathway to the borders of visual areas 17 and 18. This would appear to be a purely visual system. In contrast, the contralateral projection is anatomically mixed i.e. projecting equally to the cortex, tectum and brain stem centres. The function of this pathway is both visual and also it is the sole source of visual oculomotor control.

The purpose of the present experiment is to test the effect of midsagittal section of the optic chiasma on retention of visual conditioning of the NM response. It will directly explore the notion that lesions of the cerebellum impair NM conditioning by a loss of motor control as opposed to disruption of any memory trace. Further, it will extend the observation of Russell et al. (1987) by examining the effect of removal of all contralateral retinal projections on a third type of oculomotor reflex, which is the visual control of the NM response.

## MATERIAL AND METHODS

### II.1. ANIMALS

The animals used were 15 dutch belted rabbits, roughly six months of age at the beginning of the experiment. An approximately equal number of male and female animals were used. Those that were involved in the behavioural testing of the experiment were maintained at 90% of body weight throughout such training, with a daily ration of food pellets being given after each daily training session.

## II.2. SURGICAL PROCEDURES

The animals were anaesthetised with a gaseous mixture of 30% oxygen, 70% nitrous oxide and 2% halothane. In order to both harden and shrink the brain 10 ml/kg b.w. of 20% mannitol was injected via the ear vein at a rate of 10 ml per minute. The skull was then exposed and a 7 mm diameter trephine hole was made just posterior to the bregma and to the left of the sagittal suture.

A small dental elevator was used to detach the dura adhesion to the ventral surface of the skull. The bone defect was then extended towards the frontonasal suture to expose the medial aspect of both hemispheres as far as the extreme tip of the frontal pole, and subsequently laterally over the dorsal surface of the left hemisphere to permit retraction of this hemisphere with minimal risk of compression. A longitudinal incision was made in the dura mater 1 mm to the left of the sagittal sinus extending from bregma to the frontal pole. The dura mater was carefully draped over the margin of the right hemisphere to expose the sagittal sinus. Using a miniature pair of flat bladed falx retractors, the two hemispheres were cautiously separated starting at the frontal pole. There access between them was facilitated by the bifurcation of the sagittal sinus. In this way it was possible to preserve the integrity of the vascular supply of the entire medial wall of both hemispheres.

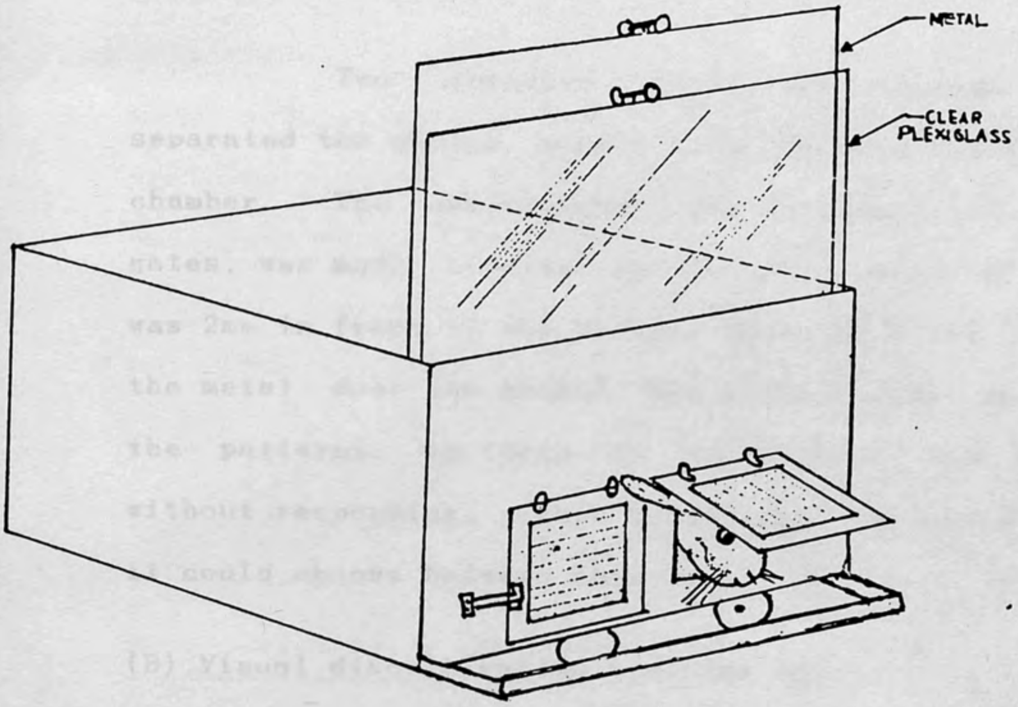
Using the microretractors the hemispheres were gradually displaced until the anterior spheniod bone was visualised. Care was taken to avoid damaging either the ethmoidal anastomotic vessels or the anterior cerebral artery when displacing them to access the anterior arch of the chiasma. The entire optic chiasma was then sectioned midsagittally with a microknife taking pains to avoid damage both to the ventral hypothalamic regions adjacent to the posterior chiasma and the pituitary gland.

Extreme precautions were taken when dissecting around the midline vessels, as such vascular damage invaribly compromised the procedure and the animal's viability. After section of the chiasma the entire area was irrigated with warm sterile saline at 35°C to check for any vascular seepage. Following this the retracted hemisphere was gently returned to its midline position. The dura was replaced and the scalp closed with silk sutures. To maintain hydration 50 ml of warm Ringer's solution were injected subcutaneously after the procedure and before the animal recovered consciousness. Following recovery from anaesthesia all animals were maintained under intensive care until they regained normal weight regulation.

## II.3. APPARATUS

### (A) Pretraining shaping box:

This consisted of an aluminium box 50 cm long, 50 cm wide, and 35 cm high. One wall had two top-hinged panels, each giving access to a separate rear mounted food well. Light entering the box came through the two panels (each 10x10 cm) in the wall. The separation between these two was 2.5 cm wide. Each panel was made of transparent perspex to enable rear-mounted visual displays to be attached. These consisted of either a striated pattern consisting of parallel black stripes on white translucent perspex. (both the black and white stripes 12.5 mm wide) or a simple black or white card could be fitted for a brightness or intensity problem. To reach the food pellet behind the panel, the animal had to lift the panel with its head to gain access to the food well (see Fig.II.3).



Figure(II,3). The pretraining shaping box. An aluminium box, 50 cm long, 50 cm wide, and 35 cm high. Two guillotine screen doors separated the choice panels from the test chamber, one made of clear perspex, the other of metal. To reach the food pellet behind the panel, the animal had to lift the panel with its head to get access to the food well.

Two separate guillotine screen doors separated the choice panels from the rest of the test chamber. The one closest, 2mm in the front of the gates, was made of clear perspex. The other of metal, was 2mm in front of the perspex door. By first opening the metal door the animal was given visual access to the patterns, to force it to look at the choices without responding. Then by lifting the perspex door it could choose between them.

(B) Visual discrimination training box:

An automatic control system was used. The apparatus essentially consisted of a test chamber (46 cm wide, 45.5 cm long, 36 cm high) with one wall having two top-hinged panels on to which visual displays could be back-projected. These consisted of visual patterns projected onto a 10cm diameter translucent circular window in each panel (distance between centres was 17 cm). To make a correct choice the animal was required to press the panel on which the correct display (S+) was projected. This response was automatically rewarded by the delivery of a 100mg food pellet directly behind the door with the correct display. After 3s the displays were turned off and the trial ended. Responses made to the panel with the incorrect display (S-) produced no reward and terminated the trial immediately as a noncorrection procedure was used. A 6s intertrial interval was made throughout all training trials. The position of the correct and incorrect displays was randomised by a computer with the main constraint that no one position would recur more than 3 times consecutively (see Fig.II.4).

For the brightness test the ratio between intensity level was 100:1. The patterns that were used. were composed of alternating 12.5 mm wide black and white vertical vs. horizontal striations.

### (C) Nictitating Membrane (NM) Response:

The nictitating membrane of the rabbit (third eyelid) at rest, is drawn into the anteromedial canthus of the eye. On stimulation of the cornea or the skin around the eye with a noxious stimulus such as an electric shock or an air blast, the membrane is reflexly moved and passes laterally across the eye towards the temporal canthus, maintaining its intimate contact with the cornea as it does so. The rabbit nictitans in common with that of other mammals is conjunctival in origin and as in many grazing species it has a supporting sheet of cartilage reaching almost to its lateral margin. Outward movement of the NM in

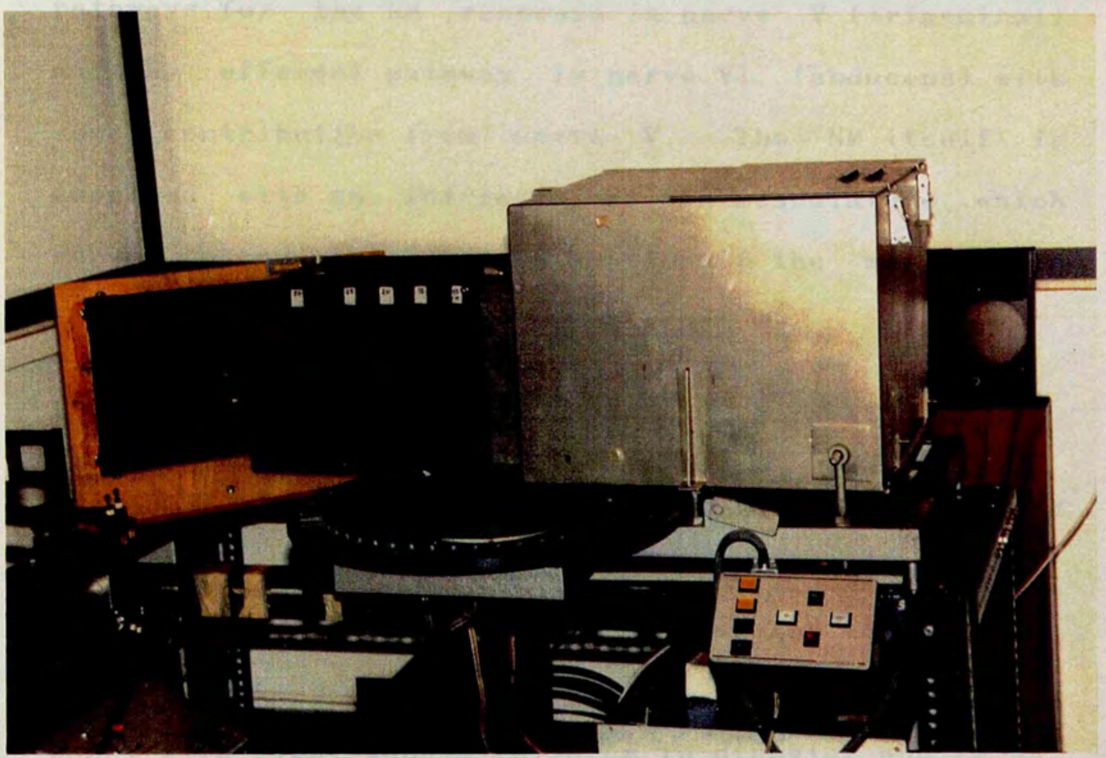


Figure (II,4). An automatic control training box, consisting of a test chamber, with one wall having top-hinged panels on to which visual displays could be back-projected. To make a correct choice the animal is required to press the panel on which the correct display is projected. This response is automatically rewarded by the delivery of a 100 mg food pellet directly behind the door with the correct display. Incorrect displays produce no reward and turn off the trial immediately.

the rabbit is dependent on passive protrusion as a consequence of eyeball retraction. The afferent pathways for the NM response is nerve V (trigeminal) and the efferent pathway is nerve VI (abducens) with some contribution from nerve V. The NM itself is supplied with an intrinsic smooth musculature which serves to maintain the retraction of the membrane in the medial canthus when it is at rest.

(D) Nictitating Membrane Conditioning Apparatus:

The animals were run individually in a sound and light insulated test cabinets with internal dimensions of 37.5 cm wide, 55 cm long and 29 cm high. These contained a restraining stock and an intelligence panel with light panels (6.36 cm in diameter and 20.35 cm the distance between centres), audio-speakers, and plugs for shock leads and the NM response transducer (Fig.II.5). Ventilation blowers provided a continuous masking noise of 85 dB (ref. 20 $\mu N/m^2$). The light of CS consisted of illumination of the chamber by two incandescent lamps located behind milk glass screens with a measured intensity of 0.3 log foot lamberts (1.3 lux). The auditory CS was a 1200 Hz sinusoidal tone 85 dB (Moore et al., 1980).

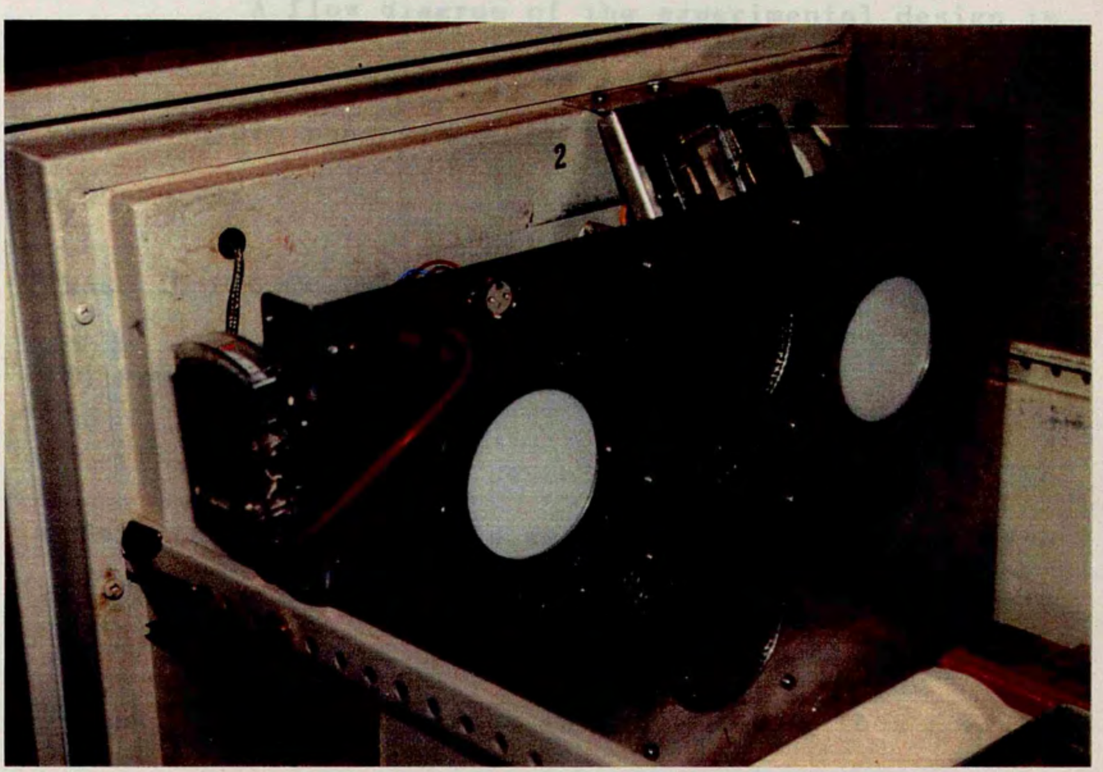


Figure (II,5). Individual test cabinet with internal dimensions of 37.5 cm wide, 55 cm long and 29 cm high. These contained a restraining stock and an intelligence panel with light panels, audio-speakers, and plugs for shock leads and the NM response transducer. The light illuminated the chamber by two incandescent lamps located behind milk glass screens to an intensity of 0.3 log foot lamberts (1.3 lux). The auditory stimulus was a 1200 Hz sinusoidal tone at 85 dB.

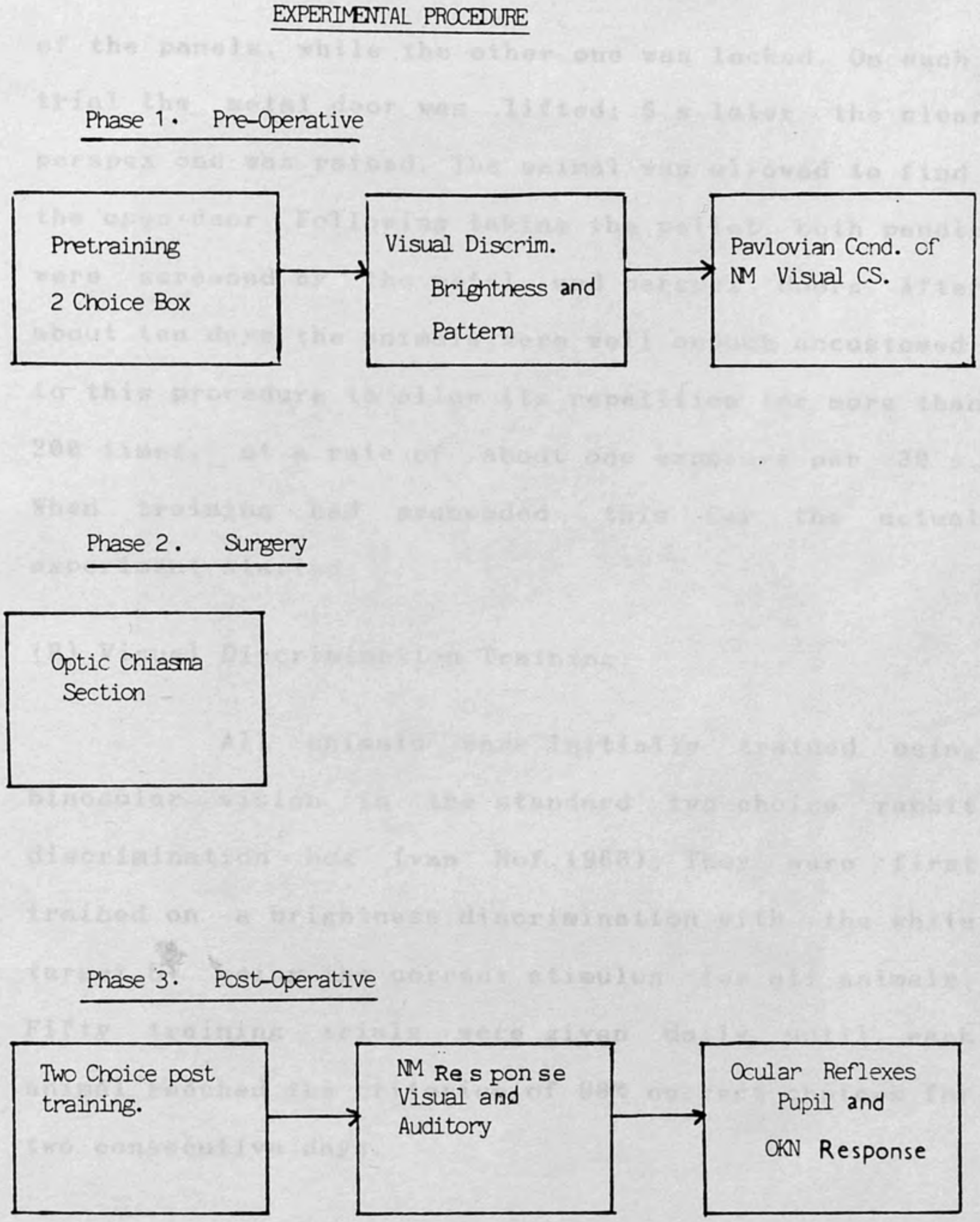
## II.4. TRAINING METHODS

A flow diagram of the experimental design is given in Schematic II.I which summarises both the main experimental phases and the sequence of experimental procedures.

### Phase 1. Pre-Operative.

(A) Pretraining:

A group of seven rabbits was used in the experiment. The animals were exposed to four to five days of food restriction i.e fed once daily, such that any loss of weight would not exceed 90% normal body weight. They were placed in the training box for 1-2 hr per day. At first, both the metal and perspex screens were left permanently open, and food pellets were placed behind both panels. No visual cues were present as the food could not be seen through the two white translucent perspex plates which covered the panels. Within two or three days the animal learned to push open the panels and eat the pellets. The procedure was then changed: the screen doors covering both panels, were opened only for short periods at frequent intervals and the amount of food was gradually reduced. Finally only one pellet was placed behind one



**Schematic (II,I). The main phases in the training methods. NM, nictitating membrane; CS, conditioned stimulus; OKN, optokinetic nystagmus.**

of the panels, while the other one was locked. On each trial the metal door was lifted; 5 s later the clear perspex one was raised. The animal was allowed to find the open door. Following taking the pellet, both panels were screened by the metal and perspex doors. After about ten days the animals were well enough accustomed to this procedure to allow its repetition for more than 200 times, at a rate of about one exposure per 30 s. When training had proceeded this far the actual experiment started.

### (B) Visual Discrimination Training:

All animals were initially trained using binocular vision in the standard two-choice rabbit discrimination box (van Hof,1966). They were first trained on a brightness discrimination with the white target S+ being the correct stimulus for all animals. Fifty training trials were given daily until each animal reached the criterion of 90% correct choices for two consecutive days.

Following this they were then tested for ocular symmetry. Monocular viewing was possible by the use of a light-weight cloth mask, which covered the rabbit face as can be seen in Fig.(II,6). The mask fitted over the animal's face and under its chin.

Figure (II,6). Cloth mask, which covers the rabbit's face, leaving one eye and the mouth free. Draw-tapes are tied behind the ears.

leaving one eye and the mouth free. It was secured by draw-tapes being gently tied behind the ears. Rabbits adapt spontaneously and immediately to use of this mask. No adaptation or pretraining in wearing of the mask was necessary. On alternate days the animals were trained monocularly using each eye (e.g. the left eye on even-numbered days and the right eye on odd days) with the brightness task. This was continued until both eyes gave criterion performance of 90% correct choices. During this procedure a daily record of each animal's number of correct choices was made.

After completion of this procedure the animals were then trained on a pattern discrimination (horizontal vs. vertical striations) with binocular vision, the vertical display as the S+. They were given the same number of daily trials as on the previous task until the same criterion was reached. After reaching criterion they were also tested for ocular symmetry with the pattern task. For both the training as well as the ocular symmetry testing the same, procedures were used as in the first task.

(C) Pavlovian Visual Conditioning:

The Pavlovian conditioning procedure chosen was that involving the NM of the rabbit (Gormezano, 1966).

On the day prior to the beginning of training, the animals were anaesthetised with halothane. A silk suture was placed in the right NM. Gentle pressure was exerted on the eyeball through the external lids and the leading edge of the NM was grasped with a fine rat-tooth forceps as it moved out from the median canthus of the eye. The suture (Ethicon mesuture, 10 mm reverse cutting, braided silk) was placed in the membrane approximately 2 mm below the angle in its leading edge and 4 mm away from the margin (see Fig.II,7). The needle was brought out again slightly less than 2 mm away from the edge of the membrane and tied loosely with as small a loop as possible. Once the suture was in place, the eyeball was flooded with ophthalmic choramphenicol solution (cloromycetin, Parke-Davis). Before the rabbit was returned to its home cage the fur was shaved from the side of its head with standard small animal clippers behind both above and below its tested eye. Wound clip electrodes (Clay-Adams 9mm) were attached paraorbitally to the tested eye. The usual procedure following preparation of the animal was to allow one day for recovery from anaesthestic or other effects, to allow the eye to be checked for possible infection and to ensure that the membrane suture was correctly and

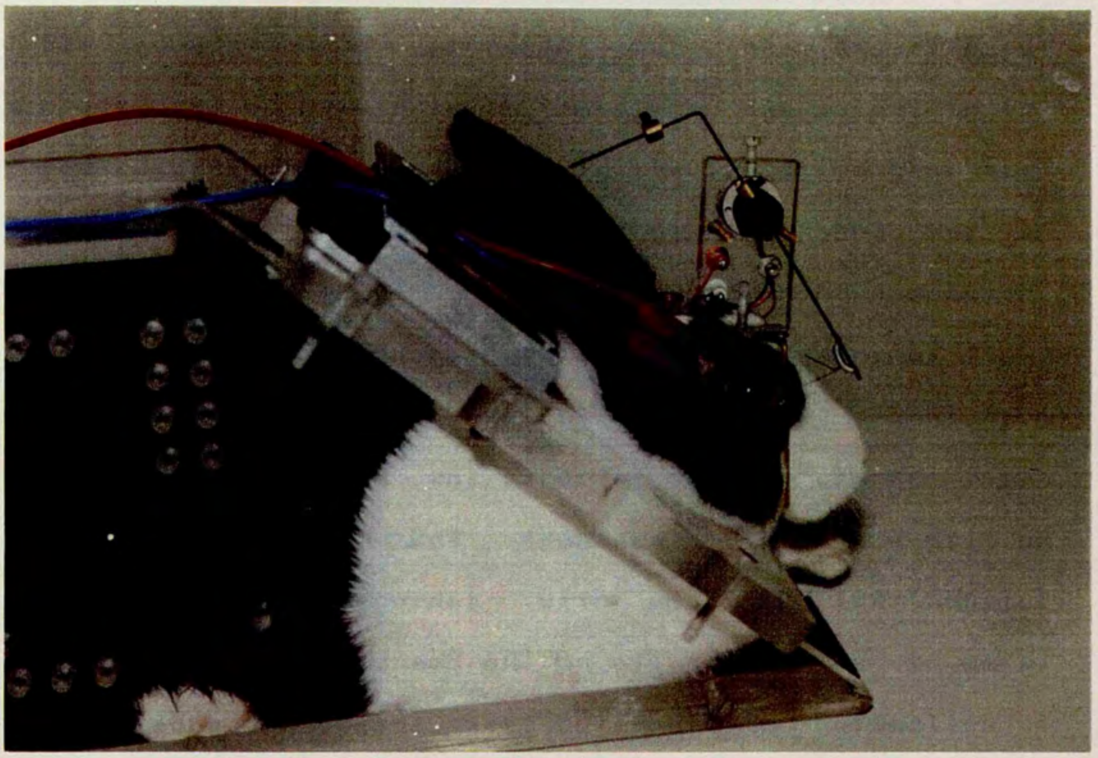


Figure (II,7). The rabbit in the restraining stock with the suture is placed in the nictitating membrane 4 mm away from the margin. Two wound clip electrodes are attached behind both above and below its test eye. The response transducer consists of a mechanical link to a low-torque rotary potentiometer. The signal from movement of the NM is recorded on one channel of an oscillographic recording pen.

securely in place (Moore & Desmond, 1982).

On the second day, the animal was placed in the conditioning apparatus for the experimental procedures associated with training. The animal in the restraining stock was placed in the isolation chamber, the leads attached, and the box was shut for an adaptation period of 50 min, the duration of a session. The response transducer consisted of a mechanical link to a low-torque rotary potentiometer. The signal from movement of the NM was recorded on one channel of a Washington 400 Md4 4-channel direct writing oscillographic recorder with model FC 100 coupler units. The paper speed on on all trials was 25 mm/s. Conditioned responses were defined as a deflection of the oscillographic recording pen of at least 1mm after CS onset but before US onset. All sessions lasted 50 ms. With trials (i.e. CS-US presentations) occurring either every 15 s or 30 s. A delayed paradigm was used with each CS being 450 ms in duration, and a 50 Hz AC shock was applied paraorbitally ipsilateral to the eye during the last 100 ms of the trial.The shock consisted of a single 100 ms shock train duration given at an intensity just above threshold to produce a NM movement on every trial. For three animals (Group I) 100 trials were given each daily session with an intertrial interval(ITI) of 15 s. For the four animals in Group II

50 trials per day were given with an ITI of 30 s.

Phase 2. Surgery

Optic Chiasma-Section:

Following the completion of the first phase of normal training, all animals had the optic chiasma sectioned midsagittally using the dorsal approach via the frontal pole. Postoperative recovery of between 2-4 weeks was then allowed before any postoperative testing.

Phase 3. Post-Operative

(A) Retention Tests:

All the chiasma sectioned animals were retrained on both the brightness and pattern discrimination apparatus. As before 50 trials daily sessions were given until either the animals reached criterion or a maximum of 15 sessions were given on each problem.

After completion of this retention test sequence, all animals were again tested for monocular retention with either the brightness or the vertical vs. horizontal orientation task using the same procedure as in the first phase of the experiment. This phase was to establish if the animals could see following division of the optic chiasma. Therefore, any deficits obtained to the visual CS with Pavlovian conditioning could not be due to blindness, if normal visual discrimination behaviour is obtained in this phase. For this reason the monocular retention test used the same eye that was trained later in the NM response re-conditioning phase.

### (B) Pavlovian Re-Conditioning:

### B.1. Nictitating Membrane Visual Response

The animals were retested on the identical procedure as that before the operation. A maximum of five days Pavlovian training is given with the light CS.

### B.2. Nictitating Membrane Auditory Response

They are finally trained with an auditory CS using a 1200 Hz sinusoidal tone at 80 dB. In all other respects the training procedure was unchanged and the animals are trained to criterion. If there is no conditioning after chiasma section to the light CS, but there is a normal acquisition to the tone CS, then the visual deficit cannot be due to motor problems caused by transection of the optic chiasma.

(C) Ocular Reflexes:

Post-operatively the animals were first examined for a change in pupillary diameter, as well as pupillary reflexes to bright light. This was done by examining the size of pupil and iris using a Zeiss operating microscope with a graticule in one eye piece. The size of the pupillary dilation following chiasma section was readly observable by this means, as was the speed of contraction when the eye was illuminate by bright light.

Optokinetic responses were visually recorded in the rabbits to monocular stimulation. Each animal was placed in a large, 1.5 meter diameter by 1 meter high circular drum. The sides of the drum were covered with a black and white Julesz display, where each square was 1 cm in size. This was rotated at a speed of 12°/s either clockwise or counter-clockwise to the eye being stimulated. The number of optokinetic nystagmus (OKN) responses per minute were visually counted for each eye successively.

## II.5. HISTOLOGICAL PROCEDURE

The animals were deeply anaesthetized with a lethal injection of pentobarbitone (40 mg/kg) and were perfused intracardially with physiological saline (9% sodium chloride) and neutral buffered 10% formalin. The brains were removed from the skull and fixed in formal-sucrose until they sank. Then they were washed for 24 hours in running water and embedded in gelatin (see appendix, (2)Embedded technique) and were cut in 30u sections using a freezing microtome. Every 5th section was mounted on subbed slides and kept overnight to dry them. They were then stained with Cresyl violet, and examined microscopically.

## II.6.THE RESULTS

### II.6.1. Visual Behaviour

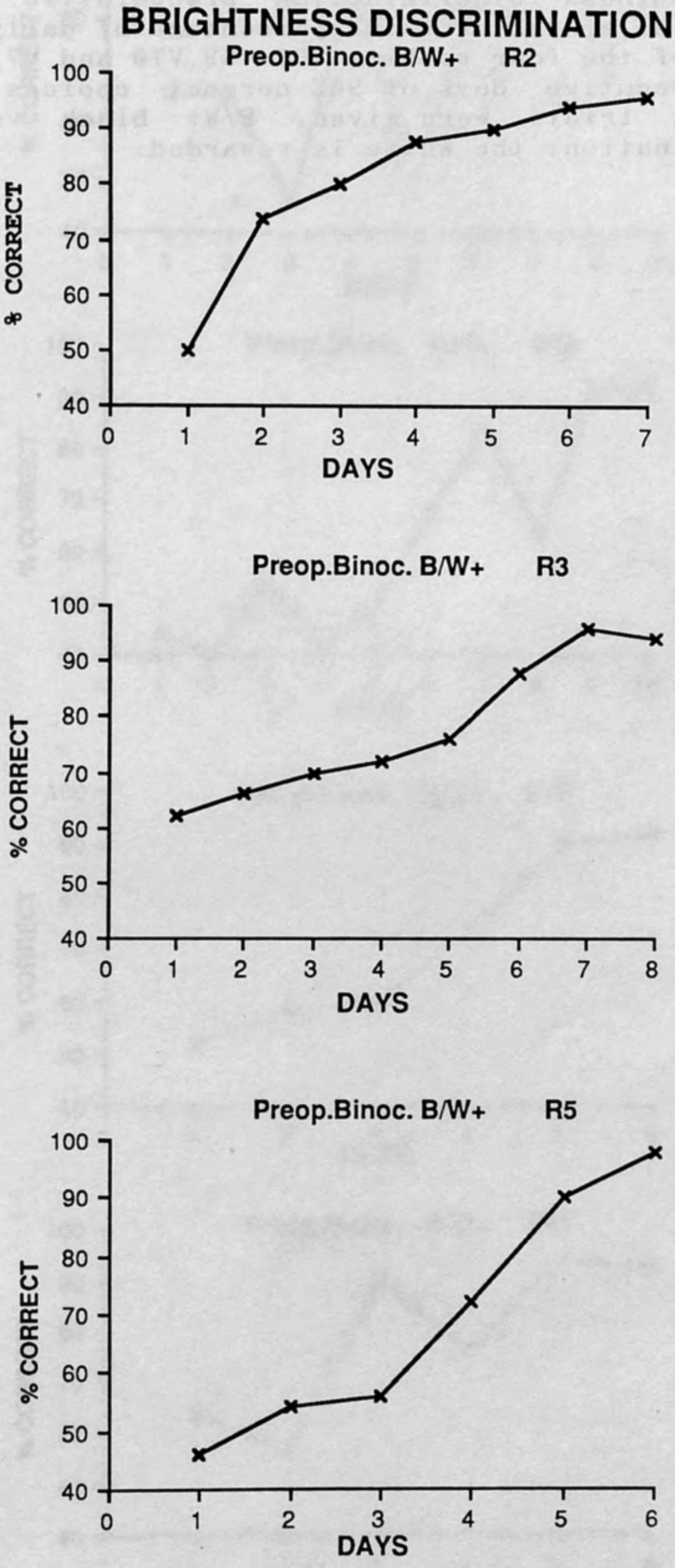
Figures II,8; II,9; II,10 and II,11 show the performance of the seven different animals on brightness discrimination learning. It is clear that although there were individual differences, in general the acquisition was similar for all animals.

In Table II,1 it can be seen that the animals take an average of 371 trials ± SEM= 31 to learn the brightness discrimination with a mean of 99 ± 17 errors.

Opposite:

Figure (II,8). Learning performance of normal rabbits on brightness discrimination preoperative binocular tasks. The graphs show the percentage of daily correct trials of the three rabbits R2,R3 and R5 to reach two consecutive days of 90% correct choices. 50 daily training trials were given. B/W+ black vs. white discrimination; the white is rewarded.

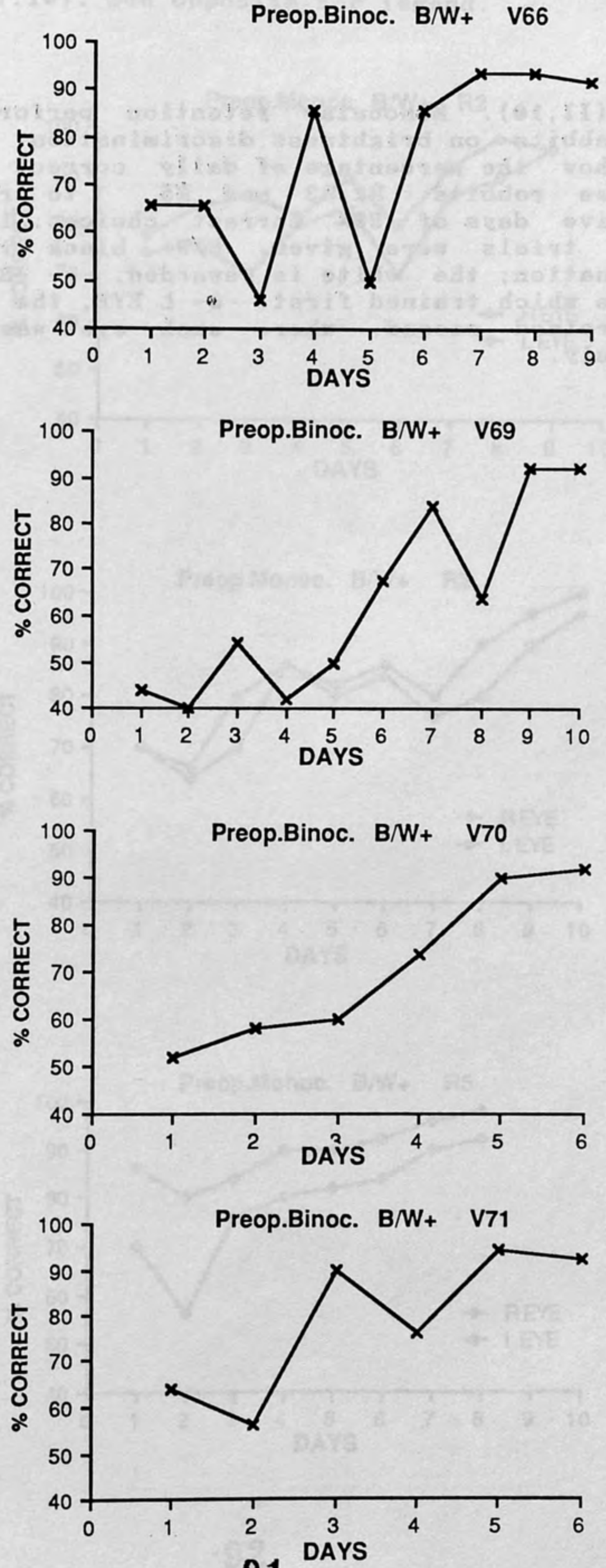
Figure (II,8). See opposite for legend.



Opposite:

Figure (II,9). Learning performance of normal rabbits on brightness discrimination preoperative binocular tasks. The graphs show the percentage of daily correct trials of the four rabbits V66,V69,V70 and V71 to reach two consecutive days of 90% correct choices. 50 daily training trials were given. B/W+ black vs. white discrimination; the white is rewarded.

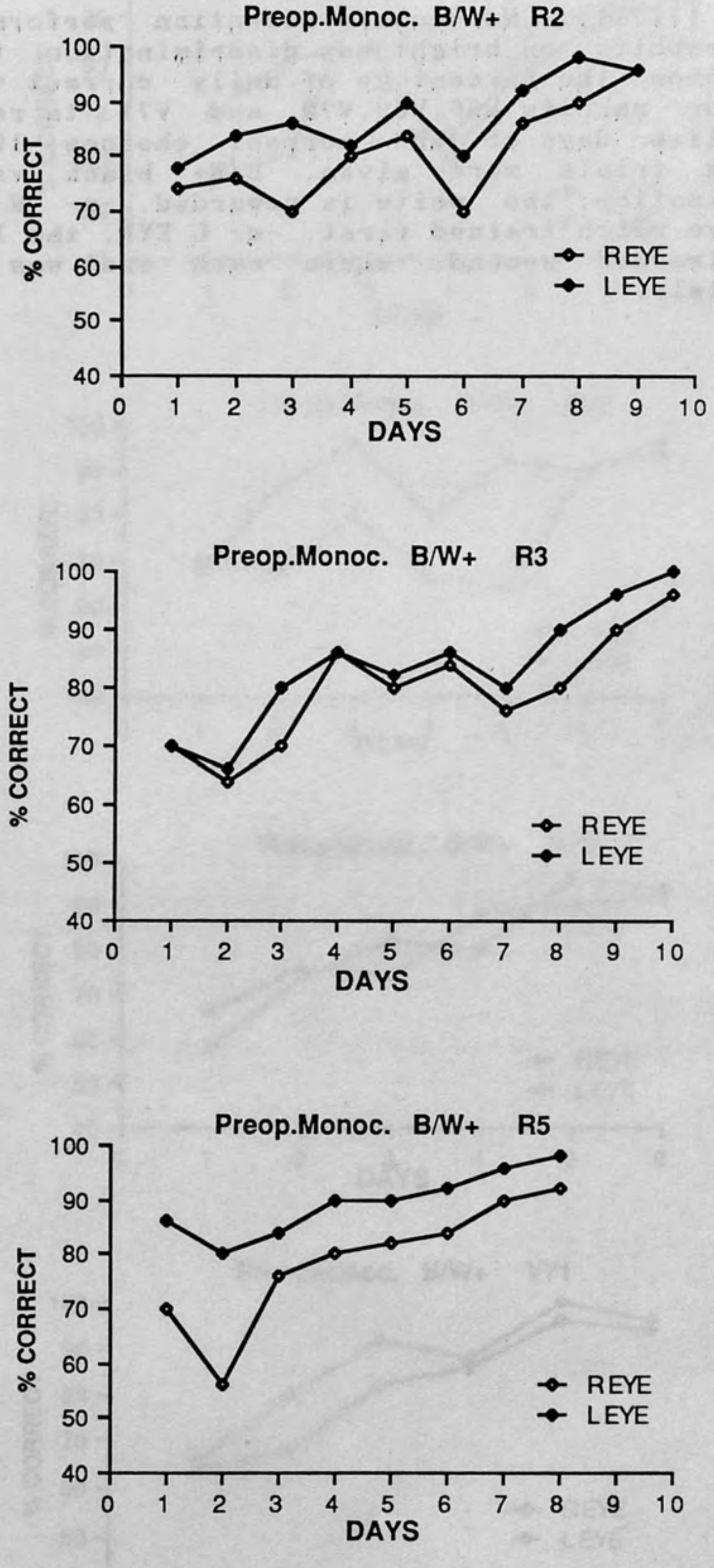
Figure (II,9). See opposite for legend.



Opposit:

Figure (II,10). Monocular retention performance of normal rabbits on brightness discrimination task. The graphs show the percentage of daily correct trials of the three rabbits R2,R3 and R5 to reach two consecutive days of 90% correct choices. 100 daily training trials were given. B/W+ black vs. white discrimination; the white is rewarded. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second, where each eye was trained alternately.

Figure (II,10). See opposite for legend.



Opposit:

Figure (II,11). Monocular retention performance of normal rabbits on brightness discrimination task. The graphs show the percentage of daily correct trials of the four rabbits V66,V69,V70 and V71 to reach two consecutive days of 90% correct choices. 100 daily training trials were given. B/W+ black vs. white discrimination; the white is rewarded. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second, where each eye was trained alternately.

Figure (II,11). See opposite for legend.

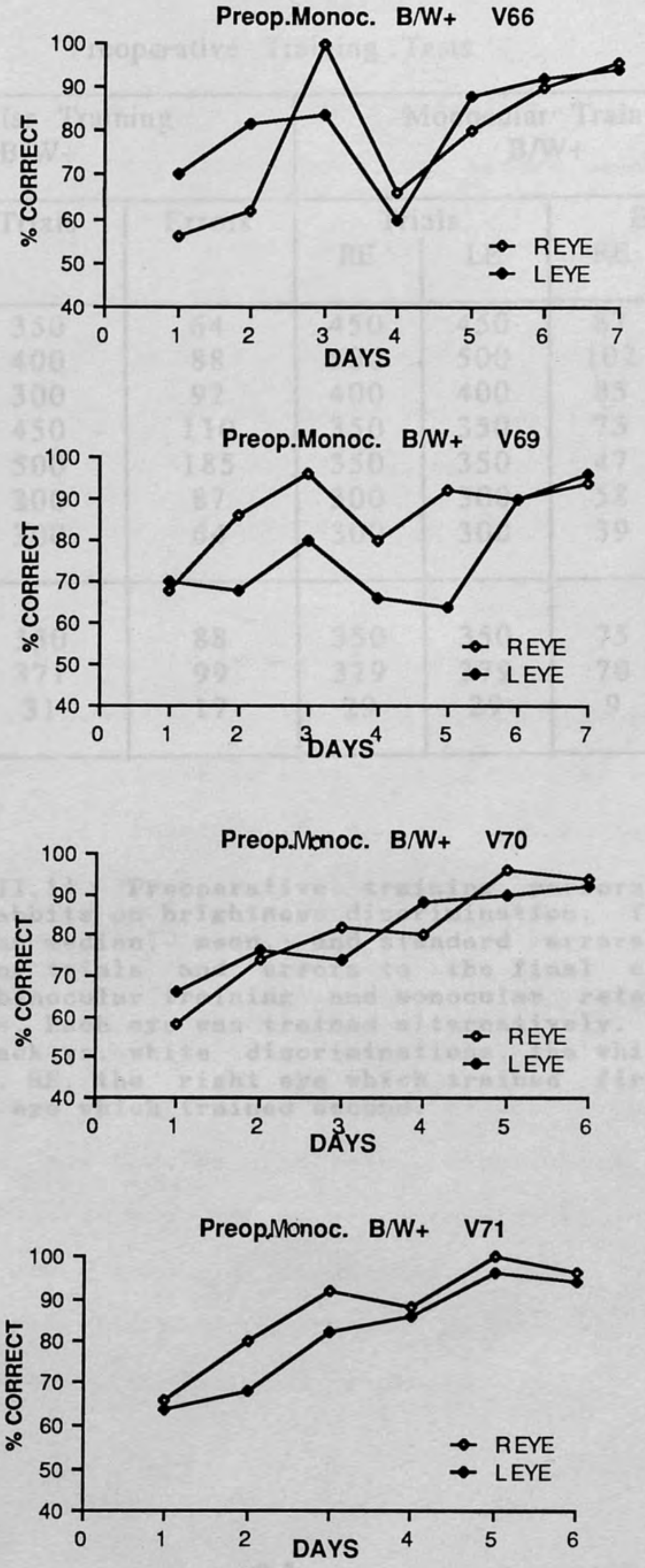


Table II,1

Preoperative Training Tests

| Binocular Training B/W+ | | | Monocular Training B/W+ | | | |
|---|---|---|---|---|---|---|
| Animal | Trials | Errors | Trials | | Errors | |
| | | | RE | LE | RE | LE |
| R2 | 350 | 64 | 450 | 450 | 87 | 57 |
| R3 | 400 | 88 | 500 | 500 | 102 | 82 |
| R5 | 300 | 92 | 400 | 400 | 85 | 40 |
| V66 | 450 | 110 | 350 | 350 | 75 | 65 |
| V69 | 500 | 185 | 350 | 350 | 47 | 82 |
| V70 | 300 | 87 | 300 | 300 | 58 | 57 |
| V71 | 300 | 64 | 300 | 300 | 39 | 55 |
| Mdn | 350 | 88 | 350 | 350 | 75 | 57 |
| Mean | 371 | 99 | 379 | 379 | 70 | 63 |
| SEM | 31 | 17 | 29 | 29 | 9 | 6 |

Table (II,1). Preoperative training performance of normal rabbits on brightness discrimination. The table gives the median, mean, and standard errors of the number of trials and errors to the final criterion during binocular training and monocular retention of both eyes. Each eye was trained alternatively.
B/W+, black vs. white discriminations, the white was rewarded. RE, the right eye which trained first. LE, the left eye which trained second.

Similarly, the ocular symmetry test following brightness acquisition clearly establishes that all animals had learned this visual task binocularly.

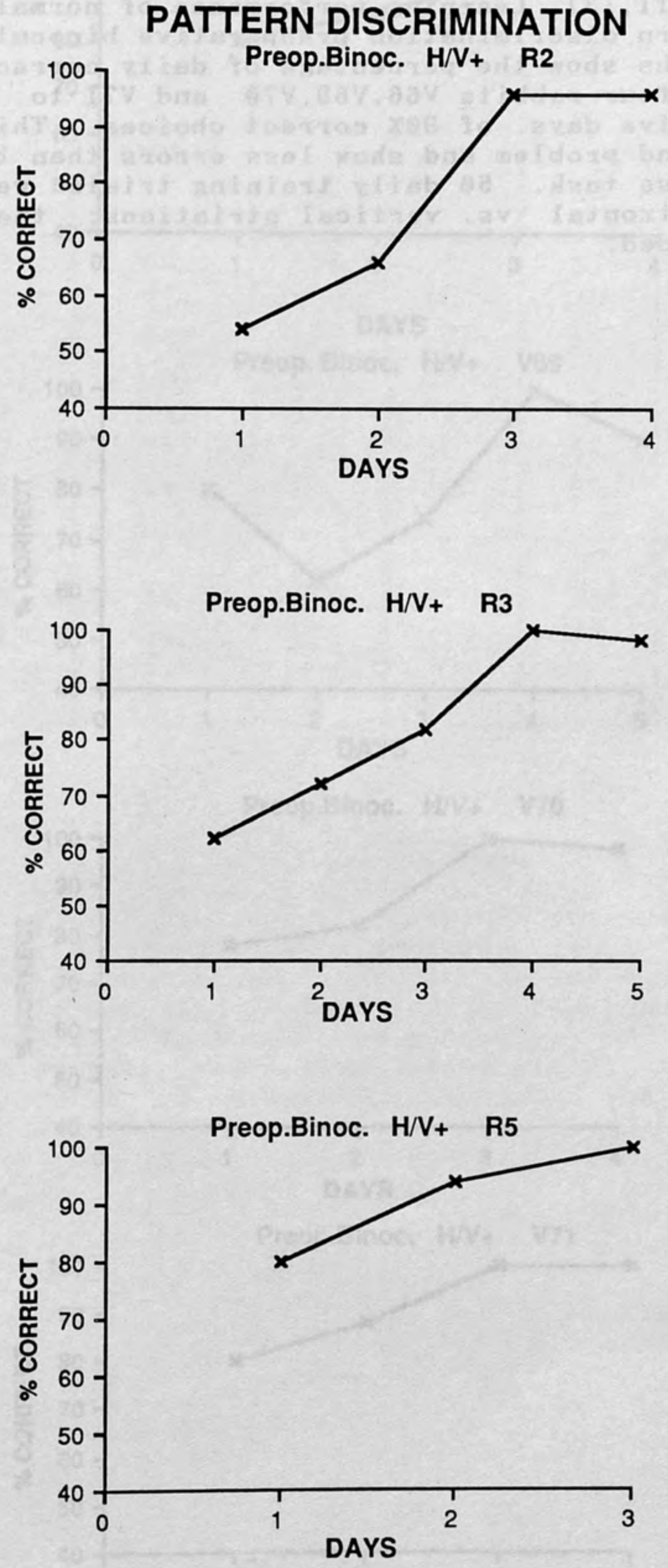
Retention under monocular conditions in all cases required some retraining to reach criterion, but this was equal for either the left or the right eye. In Table II,1 it can be seen that the right eye on average made of 70 ± 9 errors compared to the left eye performance of 63 ± 6 errors. This difference was not significant, (t= 0.73).

Figures II,12 and II,13 show the individual acquisition curves for all animals on the pattern task. From Table II,2 it can be seen that on average animals took 207 ± 13 trials with 29 ± 5 errors to reach criterion. Individual differences are clearly seen in Figs.II,12 and II,13, but these were not excessive. The ocular symmetry tests following acquisition of the pattern discrimination (see Figs.II,14 and II,15) show that similar results were found for monocular retention of pattern and for the brightness discrimination. All animals required some degree of retraining to maintain criterion under monocular conditions. However it should be noted that this monocular retention loss was smaller than was seen for brightness retention.

Opposite:

Figure (II,12). Learning performance of normal rabbits on pattern discrimination preoperative binocular task. The graphs show the percentage of daily correct trials of the three rabbits R2,R3 and R5 to reach two consecutive days of 90% correct choices. This task is the second problem and show less errors than the first brightness task. 50 daily training trials were given. H/V+ horizontal vs. vertical striations; the vertical is rewarded.

**Figure (II,12). See opposite for legend.**



Opposite:

Figure (II,13). Learning performance of normal rabbits on pattern discrimination preoperative binocular task. The graphs show the percentage of daily correct trials of the four rabbits V66,V69,V70 and V71 to reach two consecutive days of 90% correct choices. This task is the second problem and show less errors than the first brightness task. 50 daily training trials were given. H/V+ horizontal vs. vertical striations; the vertical is rewarded.

Figure (II,13). See opposite for legend.

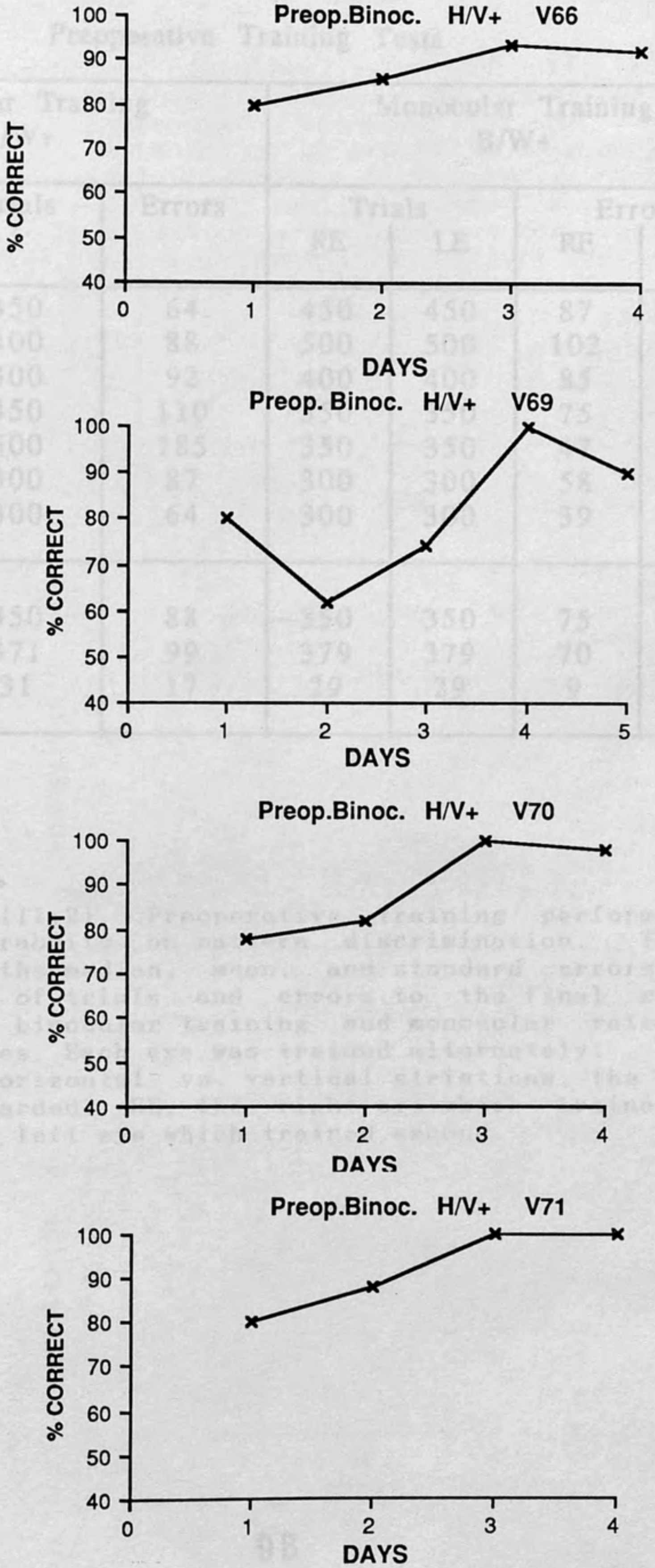


Table II,1

Preoperative Training Tests

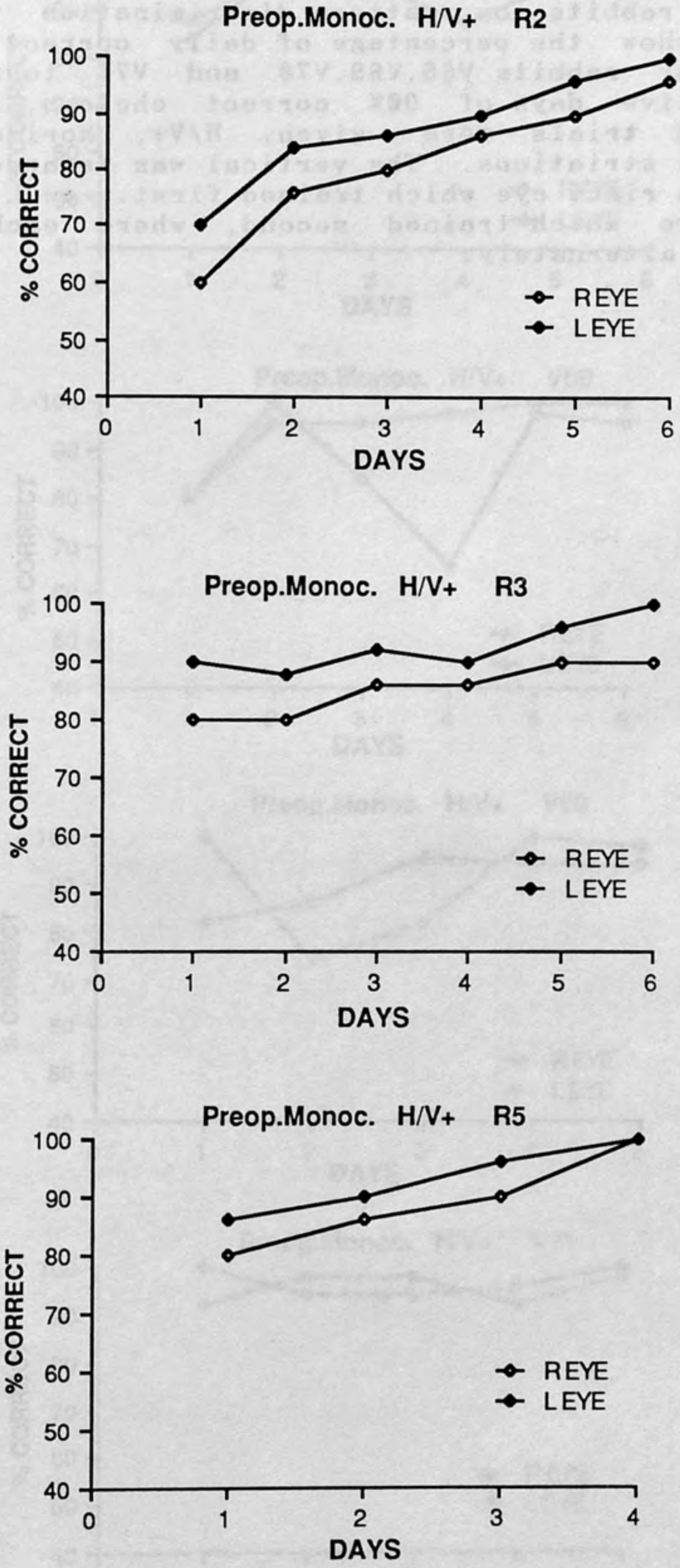
| | Binocular Training B/W+ | | Monocular Training B/W+ | | | |
|---|---|---|---|---|---|---|
| Animal | Trials | Errors | Trials | | Errors | |
| | | | RE | LE | RE | LE |
| R2 | 350 | 64 | 450 | 450 | 87 | 57 |
| R3 | 400 | 88 | 500 | 500 | 102 | 82 |
| R5 | 300 | 92 | 400 | 400 | 85 | 40 |
| V66 | 450 | 110 | 350 | 350 | 75 | 65 |
| V69 | 500 | 185 | 350 | 350 | 47 | 82 |
| V70 | 300 | 87 | 300 | 300 | 58 | 57 |
| V71 | 300 | 64 | 300 | 300 | 39 | 55 |
| Mdn | 350 | 88 | 350 | 350 | 75 | 57 |
| Mean | 371 | 99 | 379 | 379 | 70 | 63 |
| S.E. | 31 | 17 | 29 | 29 | 9 | 6 |

Table (II,2). Preoperative training performance of normal rabbits on pattern discrimination. The table gives the median, mean, and standard errors of the number of trials and errors to the final criterion during binocular training and monocular retention of both eyes. Each eye was trained alternately.
H/V+, horizontal vs. vertical striations, the vertical was rewarded. RE, the right eye which trained first. LE, the left eye which trained second.

Opposite:

Figure (II,14). Monocular retention performance of normal rabbits on pattern discrimination task. The graphs show the percentage of daily correct trials of the three rabbits R2,R3 and R5 to reach two consecutive days of 90% correct choices. 100 daily training trials were given. H/V+, horizontal vs. vertical striations. The vertical was rewarded. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second, where each eye was trained alternately.

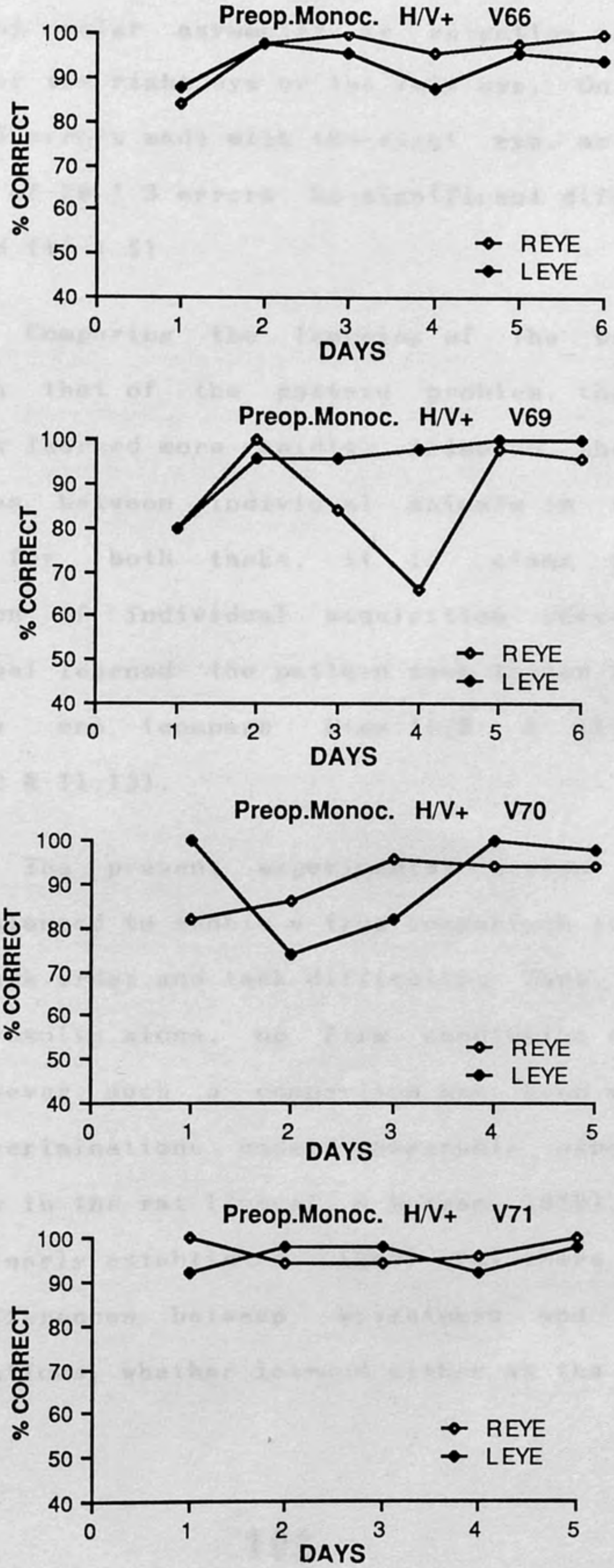
Figure (II,14). See opposite for legend.



Opposite:

Figure (II,15). Monocular retention performance of normal rabbits on pattern discrimination task. The graphs show the percentage of daily correct trials of the four rabbits V66,V69,V70 and V71 to reach two consecutive days of 90% correct choices. 100 daily training trials were given. H/V+, horizontal vs. vertical striations. The vertical was rewarded. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second, where each eye was trained alternately.

Figure (II,15). See opposite for legend.



The important point was that no animals showed any ocular asymmetry, as retention was equal with either the right eye or the left eye. On average of 29 ± 5 errors made with the right eye, as compared to a mean of 20 ± 3 errors. No significant differences were found (t= 1.5).

Comparing the learning of the brightness task with that of the pattern problem, the second problem is learned more rapidly. Although, there were differences between individual animals in rates of learning for both tasks, it is clear from the examination of individual acquisition curves, that every animal learned the pattern task faster than the brightness one (compare Figs.II,8 & II,9 with Figs.II,12 & II,13).

The present experimental design was not counter-balanced to enable a true comparison to be made between task order and task difficulty. Thus, from the present results alone, no firm conclusion could be made. However, such a comparison has been made for these discriminations under comparable experimental conditions in the rat (Russell & Morgan, 1979). There it was clearly established that: (a) there were no task differences between brightness and pattern discriminations, whether learned either as the first or the second task. (b) there was a very large and significant difference between learning for the first as compared with the second problem. The first problem always took longer then the second, independent of the type of visual stimuli. Similar observations have been made on rabbits by van Hof, (1989 personal communication). From this independent evidence it is therefore reasonable to assume that the present finding of faster learning on the pattern task were due to task order and not task difficulty.

The present results show that preoperatively all animals had normal brightness and pattern vision before section of the optic chiasma. Furthermore, no animal showed any preoperative ocular asymmetry for either task. This means that it was appropriate to decide randomly which eye should be used for NM conditioning. Had any animal showed ocular preference (van Hof & van der Mark, 1974), then the dominant eye would have had to be used for subsequent eye NM response training.

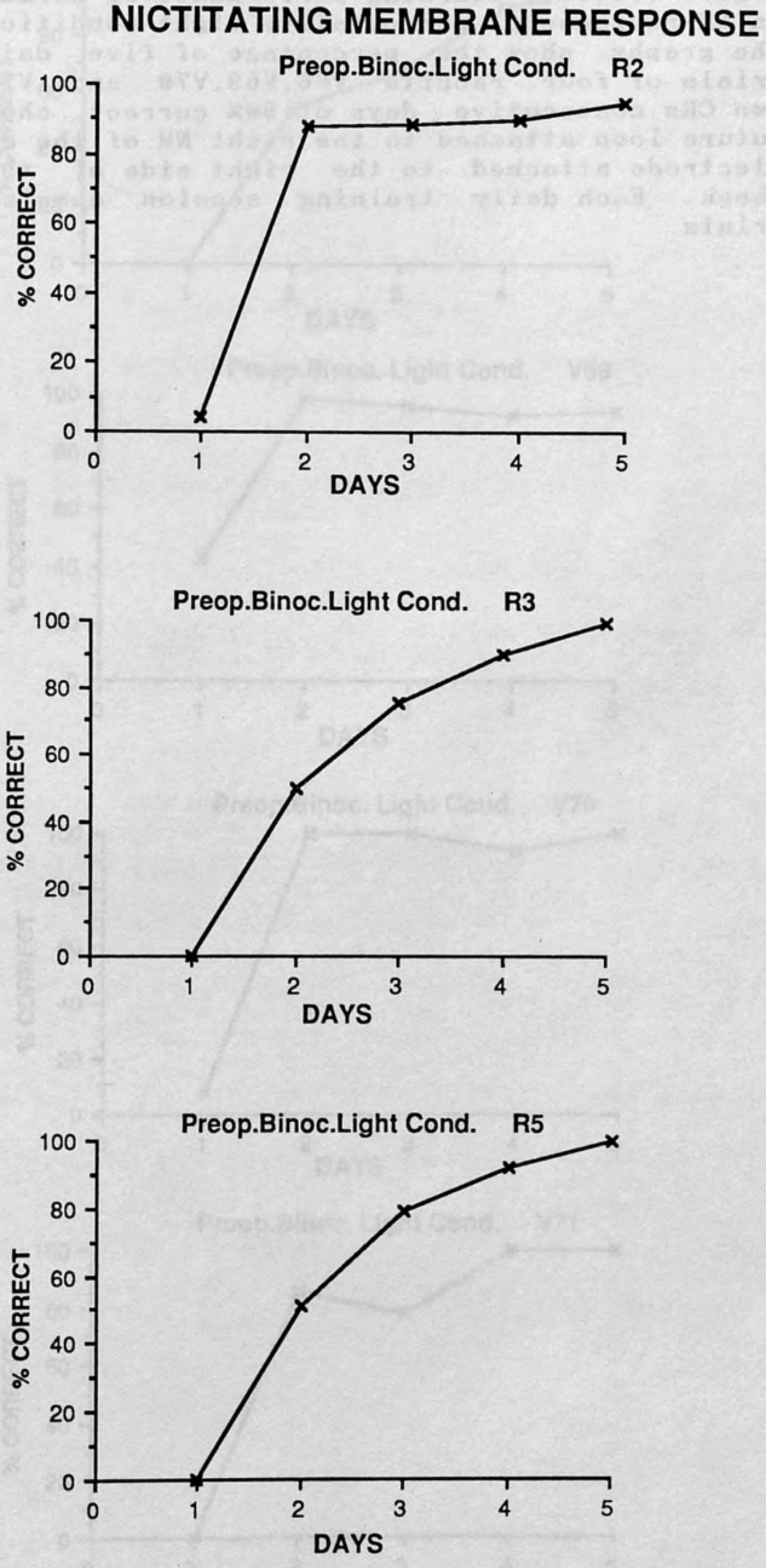
### II.6.2. Nictitating Membrane Response Training

The results for individual animals are given for Group I (n= 3) in Fig. II,16 and for Group II (n= 4) in Fig. II,17. In both it can be seen that

Opposite:

Figure (II,16). Learning performance of normal rabbits on NM response of preoperative light conditioning task. The graphs show the percentage of five daily correct trials of three rabbits R2,R3 and R3 to reach two CRs consecutive days of 90% correct choices. The suture loop attached to the right NM of the eye and the electrode attached to the right side of the rabbit's cheek. Each daily training session consisted of 100 trials.

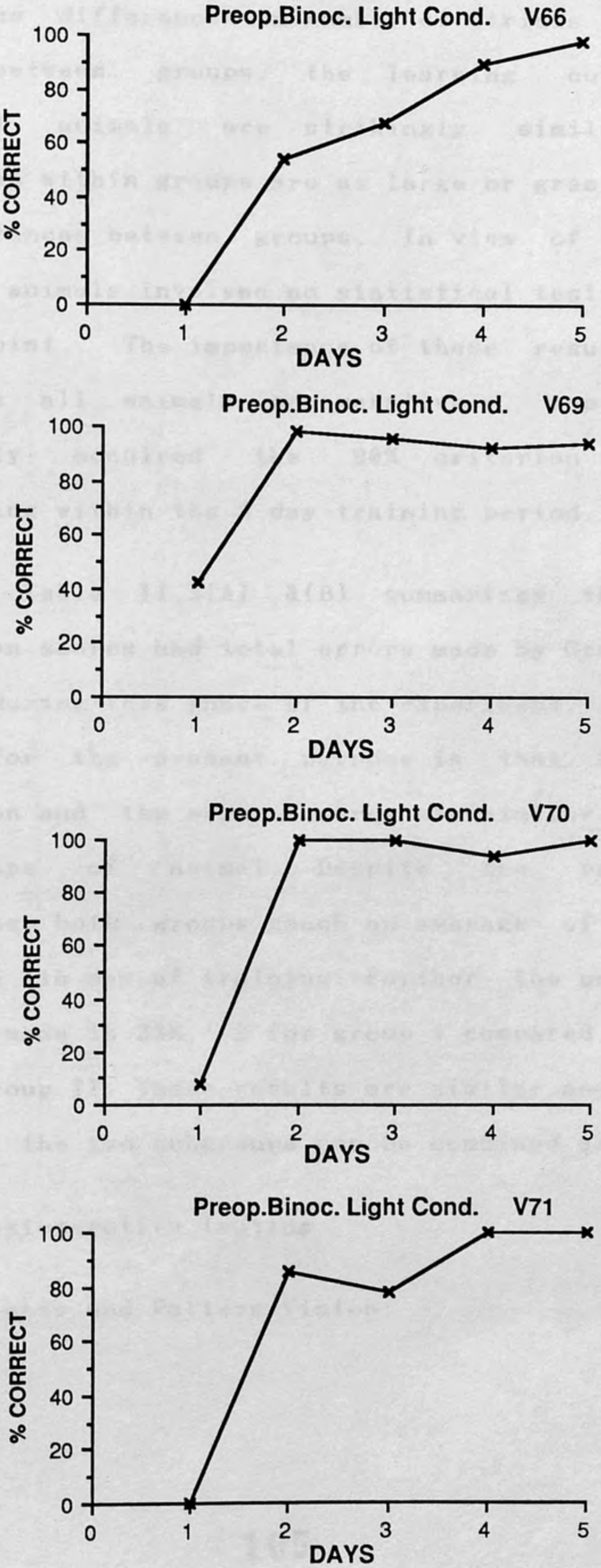
Figure (II,16). See opposite for legend.



Opposite:

Figure (II,17). Learning performance of normal rabbits on NM response of preoperative light conditioning task. The graphs show the percentage of five daily correct trials of four rabbits V66,V69,V70 and V71 to reach two CRs consecutive days of 90% correct choices. The suture loop attached to the right NM of the eye and the electrode attached to the right side of the rabbit's cheek. Each daily training session consisted of 50 trials.

Figure (II,17). See opposite for legend.



despite the differences in number of trials per daily session between groups, the learning curves for individual animals are strikingly similar. The differences within groups are as large or greater than the differences between groups. In view of the small number of animals involved no statistical test was made of this point. The importance of these results is to show that all animals preoperatively, rapidly and efficiently acquired the 90% criterion of NM conditioning within the 5 day-training period.

Table II,3(A) &(B) summarises the daily acquisition scores and total errors made by Group I and Group II during this phase of the experiment. The main concern for the present purpose is that both the acquisition and the error scores are similar for the two groups of animal. Despite the procedural differences, both groups reach an average of over 90% CRs on the 4th day of training. Further, the proportion of errors made is 33% ' 2 for group I compared with 26% ' 6 for group II. These results are similar and make it clear that the two subgroups can be combined as one.

### II.6.3. Postoperative Testing

#### (A) Brightness and Pattern Vision:

Table II,3

Preoperative NM Response
3(A) Group (I) Percentage CRs (100 trials/day)

| | Sessions | | | | | | |
|---|---|---|---|---|---|---|---|
| Animal | 1 | 2 | 3 | 4 | 5 | Errors | % |
| R2 | 4 | 88 | 89 | 90 | 95 | 134 | 27 |
| R3 | 0 | 50 | 75 | 90 | 99 | 186 | 37 |
| R5 | 0 | 51 | 79 | 92 | 100 | 178 | 36 |
| Mdn | 0 | 51 | 79 | 90 | 99 | 178 | 36 |
| Mean | 1.3 | 63 | 81 | 91 | 98 | 166 | 33 |
| SEM | 1 | 13 | 4 | 1 | 2 | 16 | 2 |

3(B) Group (II) Percentage CRs (50 trials/day)

| | Sessions | | | | | | |
|---|---|---|---|---|---|---|---|
| Animal | 1 | 2 | 3 | 4 | 5 | Errors | % |
| V66 | 0 | 54 | 68 | 90 | 98 | 105 | 42 |
| V69 | 42 | 98 | 98 | 92 | 94 | 38 | 15 |
| V70 | 8 | 100 | 100 | 94 | 100 | 49 | 20 |
| V71 | 0 | 86 | 78 | 100 | 100 | 68 | 27 |
| Mdn | 4 | 92 | 88 | 93 | 99 | 59 | 24 |
| Mean | 13 | 85 | 86 | 94 | 98 | 65 | 26 |
| SEM | 9 | 11 | 8 | 2 | 1 | 16 | 6 |

Table (II,3). Postoperative daily acquisition of normal rabbits on NM response test for two groups. 3(A) is group I (R2,R3 and R5), they have 100 trials per day and 3(B) is group II (V66,V69,V70 and V71), they have 50 trials per day. The tables give the median,mean and standard errors of the number of daily session errors and percentage for one eye (right eye), of CRs, conditioned responses.

The effect of chiasma section on individual retention of visual ability is seen in Figs.II.18; II,19; II,20 and II,21. Following recovery from the operation, all animals were first retrained binocularly on the brightness discrimination.

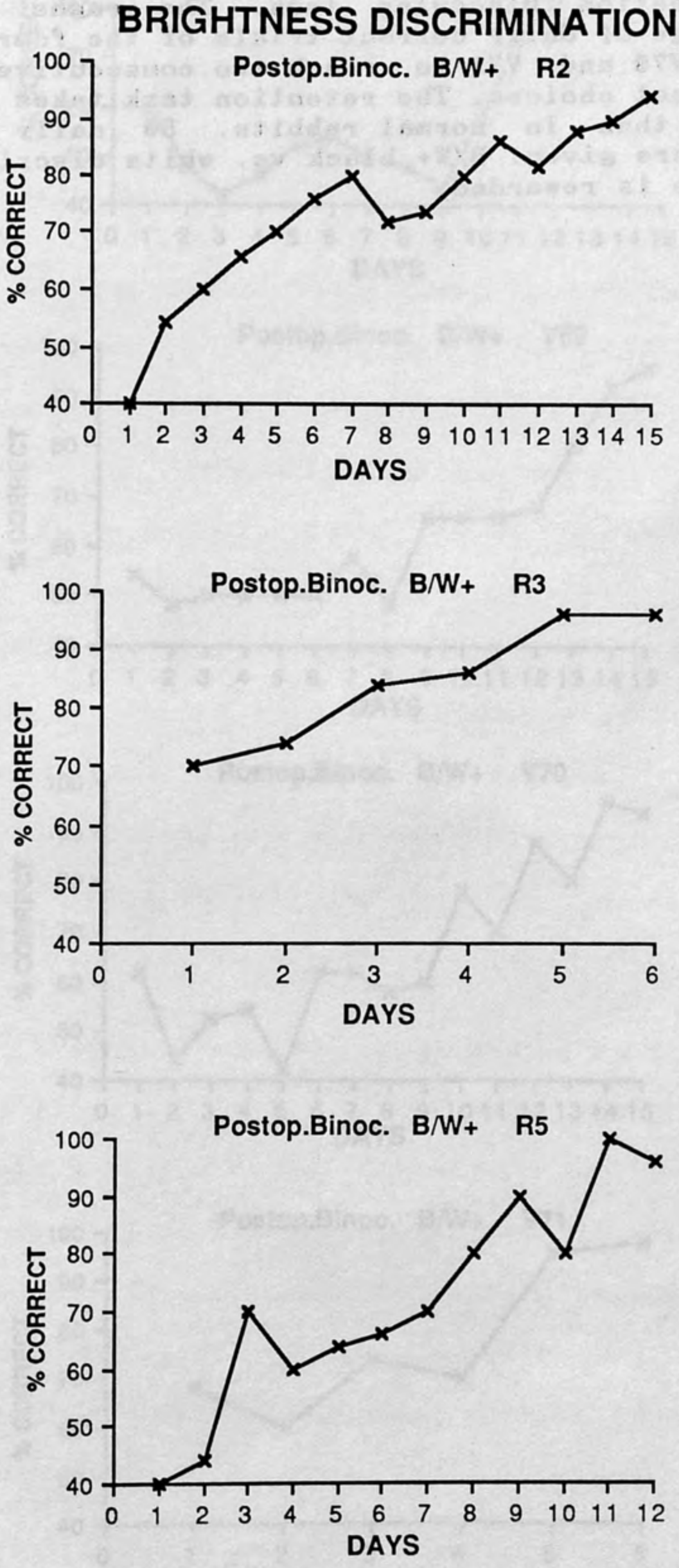
The re-acquisition curves for individual animals are given in Figs.II,18 and II,19. Great variability was shown in the retention of the intensity discrimination. The majority of animals started at chance level in the immediate postoperative testing period. Thereafter, the relearning showed a gradual, and in most cases lengthy recovery period. Two animals reached criterion within 6 days of retraining whereas the remainder required 12 to 15 days. Nonetheless, at the end of training all met the same criterion of 90% correct for two consecutive days.

In contrast, after learning the brightness task, acquisition of the pattern task was, with two exceptions, enormously facilitated. Only animals R2 and V69, required the same number of trials to relearn both problems following the chiasma section (see Figs.II,20 & II,21). In Table II,4(A) the average trials for all animals to relearn the brightness discrimination was 600 ± 80 with a mean of 184 ' 37 errors. This compares Table II,4(B) with an average

Opposite:

Figure (II,18). Retention performance of the optic chiasma section rabbits on post-operative brightness discrimination binocular task. The graphs show the percentage of daily correct trials of the three rabbit R2,R3 and R5 to reach two consecutive days of 90% correct choices. The retention task takes longer to acquire than in normal rabbits. 50 daily training trials were given. B/W+ black vs. white discrimination; the white is rewarded.

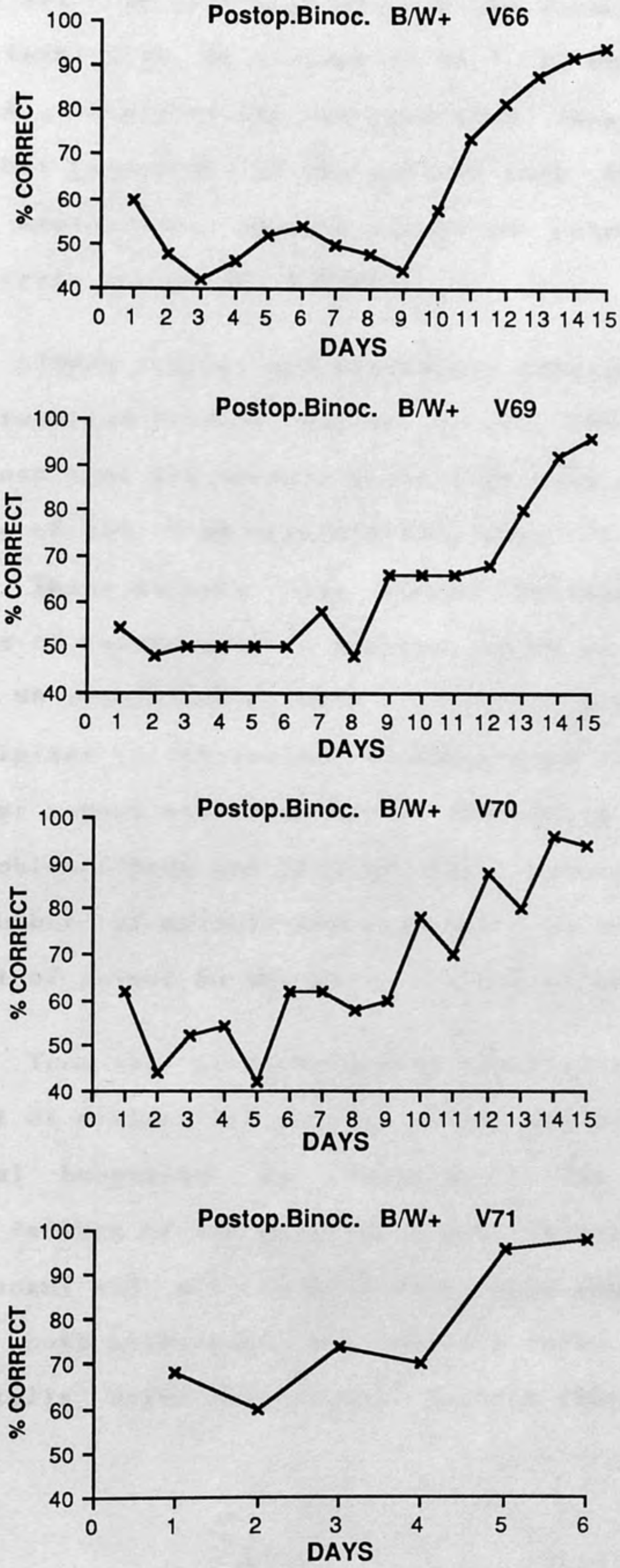
Figure (II,18). See opposite for legend.



Opposite:

Figure (II,19). Retention performance of the optic chiasma section rabbits on post-operative brightness discrimination binocular task. The graphs show the percentage of daily correct trials of the four rabbit V66,V69,V70 and V71 to reach two consecutive days of 90% correct choices. The retention task takes longer to acquire than in normal rabbits. 50 daily training trials were given. B/W+ black vs. white discrimination; the white is rewarded.

Figure (II,19). See opposite for legend.



number of 271 ± 96 trials to relearn the second problem (patpern task) with an average of 56 ± 32 errors (see Table II,4). There it can be seen that three animals show perfect retention of the pattern task (R3, V66 & V71) and another two require almost no retraining in terms of error scores (R5 & V70).

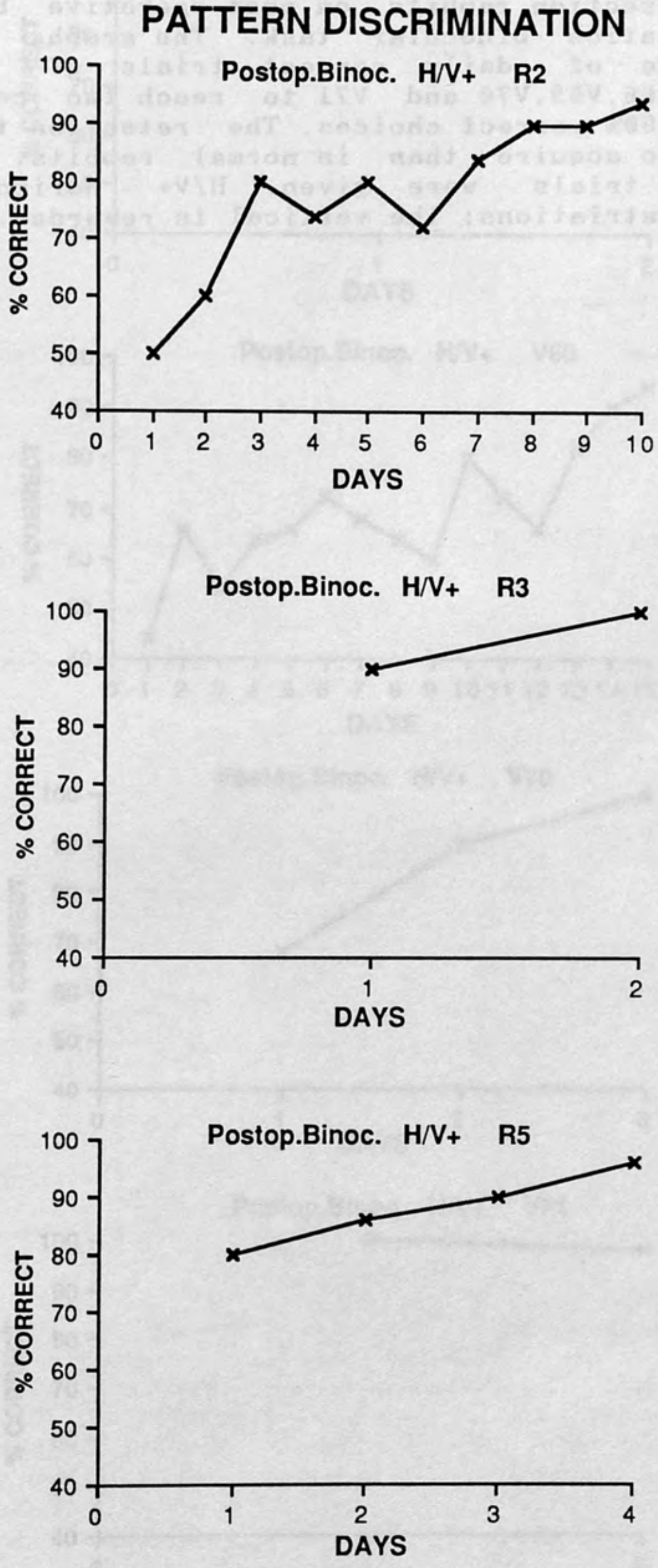
These results are strikingly similar to the previous reported finding (Russell et al., 1987), where it was shown that six animals postoperatively required an average of 633 ± 60 trials with a mean of 236 ± 37 errors. These animals also showed savings in the relearning of second pattern problem, where an average of 200 ± 98 trials and a mean of 47 ± 32 errors were taken. Similar to the present finding, many animals in the earlier report also required no retraining for the second problem (three out of six). This compares with a similar number of animals who required no retraining (three out of seven) in the present group of animals.

Thus the present results clearly show that the effect of midsagittal section of the optic chiasma on visual behaviour is transitory. The initial retention failure of the brightness discrimination was not permanent and all animals were able rapidly to reacquire both brightness and pattern tasks. Unlike experimentally naive chiasma-cut rabbits (Russell et

Opposite:

Figure (II,20). Retention performance of the optic chiasma section rabbits on post-operative brightness discrimination binocular task. The graphs show the percentage of daily correct trials of the three rabbit R2,R3 and R5 to reach two consecutive days of 90% correct choices. The retention task takes longer to acquire than in normal rabbits. 50 daily training trials were given. H/V+ horizontal vs. vertical striations; the vertical is rewarded.

Figure (II,20). See opposite for legend.



Opposite:

Figure (II,21). Retention performance of the optic chiasma section rabbits on post-operative brightness discrimination binocular task. The graphs show the percentage of daily correct trials of the four rabbit V66,V69,V70 and V71 to reach two consecutive days of 90% correct choices. The retention task takes longer to acquire than in normal rabbits. 50 daily training trials were given. H/V+ horizontal vs. vertical striations; the vertical is rewarded.

Figure (II,21). See opposite for legend.

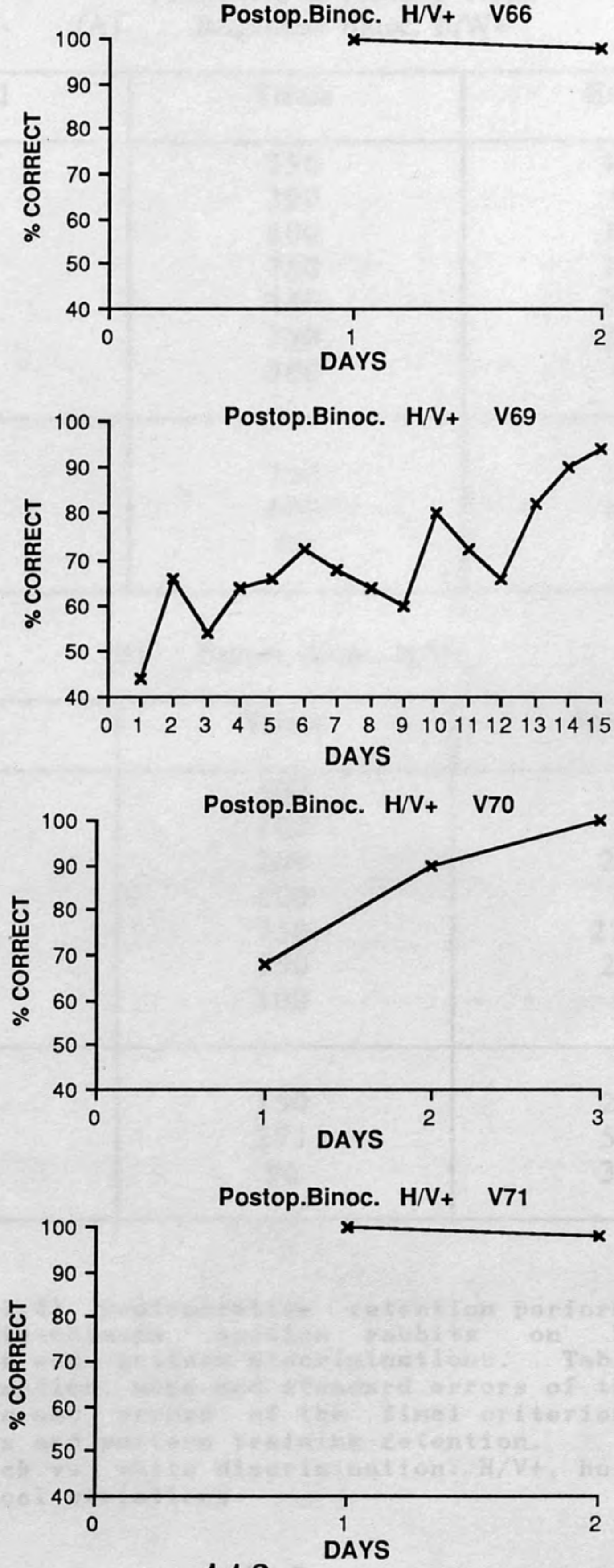


Table II,4

Postoperative Training Tests.

(A) Brightness Binoc. B/W+

| Animal | Trials | Errors |
|---|---|---|
| R2 | 750 | 194 |
| R3 | 300 | 47 |
| R5 | 600 | 170 |
| V66 | 750 | 284 |
| V69 | 750 | 279 |
| V70 | 750 | 250 |
| V71 | 300 | 67 |
| Mdn | 750 | 194 |
| Mean | 600 | 184 |
| SEM | 80 | 37 |

(B) Pattern Binoc. H/V+

| Animal | Trials | Errors |
|---|---|---|
| R2 | 500 | 113 |
| R3 | 100 | 5 |
| R5 | 200 | 24 |
| V66 | 100 | 1 |
| V69 | 750 | 229 |
| V70 | 150 | 21 |
| V71 | 100 | 1 |
| Mdn | 150 | 21 |
| Mean | 271 | 56 |
| SEM | 96 | 32 |

Table (II,4). Postoperative retention performance of the optic-chiasma section rabbits on binocular brightness and pattern discriminations. Tables (A&b) give the median, mean and standard errors of the number of trials and errors of the final criterion during brightness and pattern training retention.
B/W+, black vs. white discrimination. H/V+, horizontal vs. vertical striations.

al., 1984) they were able to reacquire rapidly visual skills postoperatively. Indeed, it would appear that all that was required for five of the animals, was to learn how to maximise the use of their restricted visual fields in the two-choice visual discrimination situation. When they had acquired this skill with the intensity task, it is significant that no difficulty was found with the subsequent orientation problem.

Table II,5 gives the individual results of monocular retention testing after section of the optic chiasma. Half of the animals were tested for visual function with the right eye using the pattern task, and the other half were tested with the same eye using the brightness problem. The purpose of this test was to establish the visual capability of all rabbits using the eye which would be subsequently tested for NM conditioning. An additional purpose of this test was to demonstrate that if any NM deficit were obtained, it could not be due to ocular blindness. Due to the lack of time available for further testing of these animals it was only possible to test one eye monocularly in this phase of the experiment.

From Table II,5, it can be seen that all animals were able to reach the criterion of monocular retention within six to ten days retraining. Despite

Table II,5

Postoperative Retention Test.

(A) Brightness Monoc. B/W+

| Animal | Trials<br>RE | Errors<br>RE |
|---|---|---|
| V66 | 450 | 243 |
| V69 | 500 | 249 |
| V70 | 450 | 209 |
| V71 | 300 | 141 |
| Mdn | 450 | 226 |
| Mean | 425 | 211 |
| SEM | 43 | 25 |

(B) Pattern Monoc. H/V+

| Animal | Trials<br>RE | Errors<br>RE |
|---|---|---|
| R2 | 500 | 95 |
| R3 | 350 | 65 |
| R5 | 450 | 105 |
| Mdn | 450 | 95 |
| Mean | 433 | 88 |
| SEM | 44 | 12 |

**Table (II,5). Postoperative retention performance of the optic-chiasma section rabbits on binocular brightness (V66,V69,V70 and V71) and pattern (R2,R3 and R5) discriminations. Tables (A&b) give the median, mean and standard errors of the number of trials and errors of the final criterion during brightness and pattern training retention.**

**B/W+, black vs. white discrimination. H/V+, horizontal vs. vertical striations. RE, the right eye which only trained.**

considerable, individual differences, retention for pattern or brightness vision showed no obvious differences. Examination of individual training curves in Fig. II,22 and II,23 established beyond doubt that every animal had good visual capability following section of the optic chiasma.

## (B) Oculomotor Reflexes

### B.1. Pupil Reflexes:

The pupil reflex was examined postoperative in all animals one hour after recovery from anaesthesia. Every animal showed a large dilation of the pupil of both eyes (Behr's sign). Despite this, sustained and permanent mydriasis, positive pupil reflexes were produced from either eye by bright light stimulation. No recovery of this condition was seen throughout the experiment.

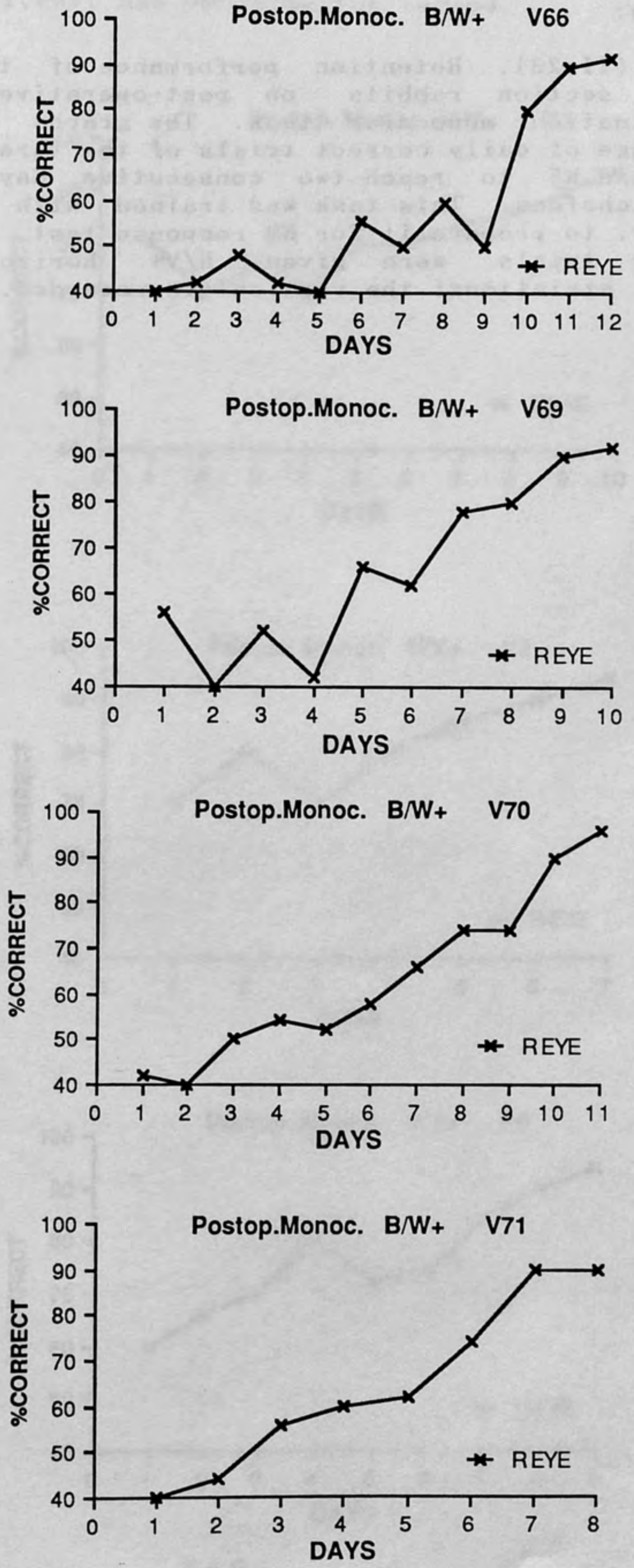
### B.2. Nictitating Membrane (NM) Response:

Postoperatively all animals were tested for NM conditioning either to the previously trained light CS, as well as a novel auditory CS.

Opposite:

Figure (II,22). Retention performance of the optic chiasma section rabbits on post-operative pattern discrimination monocular task. The graphs show the percentage of daily correct trials of the four rabbits V66,V69,V70 and V71 to reach two consecutive days of 90% correct choices. This task was trained with the right eye only, to prepare it for NM response test. 50 daily training trials were given. B/W+ black vs. white discrimination; the white is rewarded.

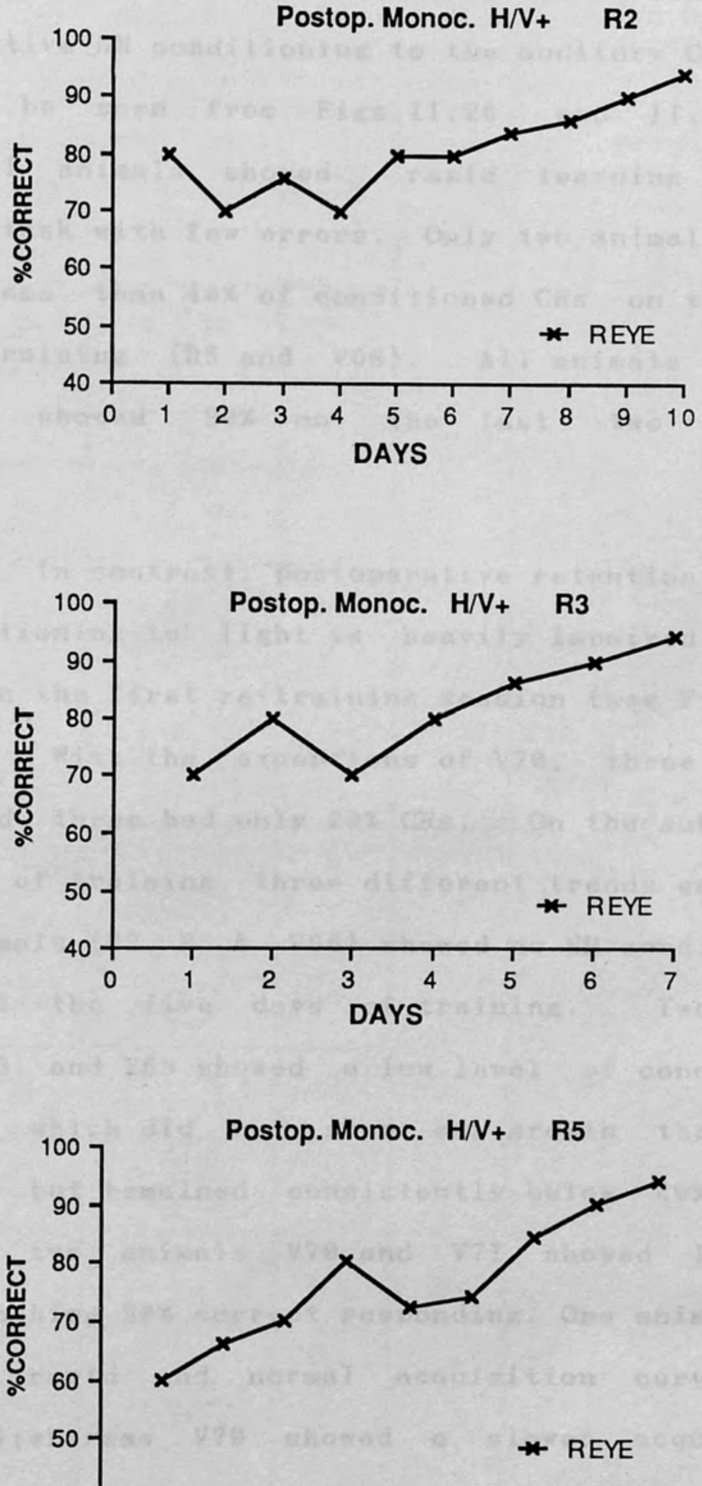
Figure (II,22). See opposite for legend.



Opposite:

Figure (II,23). Retention performance of the optic chiasma section rabbits on post-operative pattern discrimination monocular task. The graphs show the percentage of daily correct trials of the three rabbits R2,R3 and R5 to reach two consecutive days of 90% correct choices. This task was trained with the right eye only, to prepare it for NM response test. 50 daily training trials were given. H/V+ horizontal vs. vertical striations; the vertical is rewarded.

Figure (II,23). See opposite for legend.



Opposite:

Figure (II.22). Retention performance of the optic chiasma section rabbits on post operative pattern discrimination. The graphs show the percentage of daily correct trials of the three rabbits R2,R3 and R5 to reach two consecutive days of 90% correct choices. This task was trained with the right eye only, to groups II for RE response 100%, 50 daily training trials were given H/V horizontal vs. vertical striations, the striations as described.

Tables II,6.a and II,6.b give the results of all animals of Group I and Group II. Considering postoperative NM conditioning to the auditory CS first, it can be seen from Figs.II,26 and II,27 that individual animals showed rapid learning of the auditory task with few errors. Only two animals failed to show less than 40% of conditioned CRs on the first day of training (R5 and V66). All animals without exception showed 90% on the last two training sessions.

In contrast, postoperative retention of the NM conditioning to light is heavily impaired in all animals on the first re-training session (see Fig.II,24 & II,25). With the exceptions of V70, three animals had 0% and three had only 20% CRs. On the subsequent four days of training, three different trends emerged. Three animals (R2, R5 & V66) showed no NM conditioning throughout the five days of training. Two other animals R3 and V69 showed a low level of conditioned responses which did not show any growth throughout training, but remained consistently below 40%. The remaining two animals V70 and V71 showed learning curves reaching 90% correct responding. One animal V71 showed a rapid and normal acquisition curve (see Fig.II,23);whereas V70 showed a slower acquisition pattern.

Opposite:

Table (II,6). Postoperative daily retention of optic chiasma sectioned rabbits on NM response light and tone conditioning test for two groups. 6(A) is group I (R2,R3 and R5), they have 100 trials per day and 6(B) is group II (V66,V69,V70 and V71), they have 50 trials per day. The tables give the median,mean and standard errors of the number of daily session errors and percentage for one eye (right eye). CRs, conditioned responses. CS, conditioned stimulus.

Table II,6. See opposite for legned

Postoperative NM Response
6(A) Group I Percentage CRs (100 trials/day)

| | Light CS | | | | | | | Auditory CS | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sessions | | | | | | | Sessions | | | | | | |
| Animal | 1 | 2 | 3 | 4 | 5 | Errors | % | 1 | 2 | 3 | 4 | 5 | Errors | % |
| R2 | 0 | 0 | 0 | 0 | 0 | 500 | 100 | 77 | 94 | 92 | 97 | 99 | 41 | 8 |
| R3 | 17 | 40 | 35 | 37 | 40 | 331 | 66 | 87 | 98 | 81 | 100 | 97 | 37 | 7 |
| R5 | 0 | 0 | 0 | 0 | 0 | 500 | 100 | 32 | 100 | 97 | 90 | 96 | 85 | 17 |
| Mdn | 0 | 0 | 0 | 0 | 0 | 500 | 100 | 77 | 98 | 92 | 97 | 97 | 41 | 8 |
| Mean | 6 | 13 | 12 | 12 | 13 | 444 | 89 | 65 | 97 | 90 | 96 | 97 | 54 | 11 |
| SEM | 5 | 11 | 9 | 10 | 11 | 56 | 11 | 17 | 2 | 5 | 3 | 1 | 15 | 3 |

Postoperative NM Response

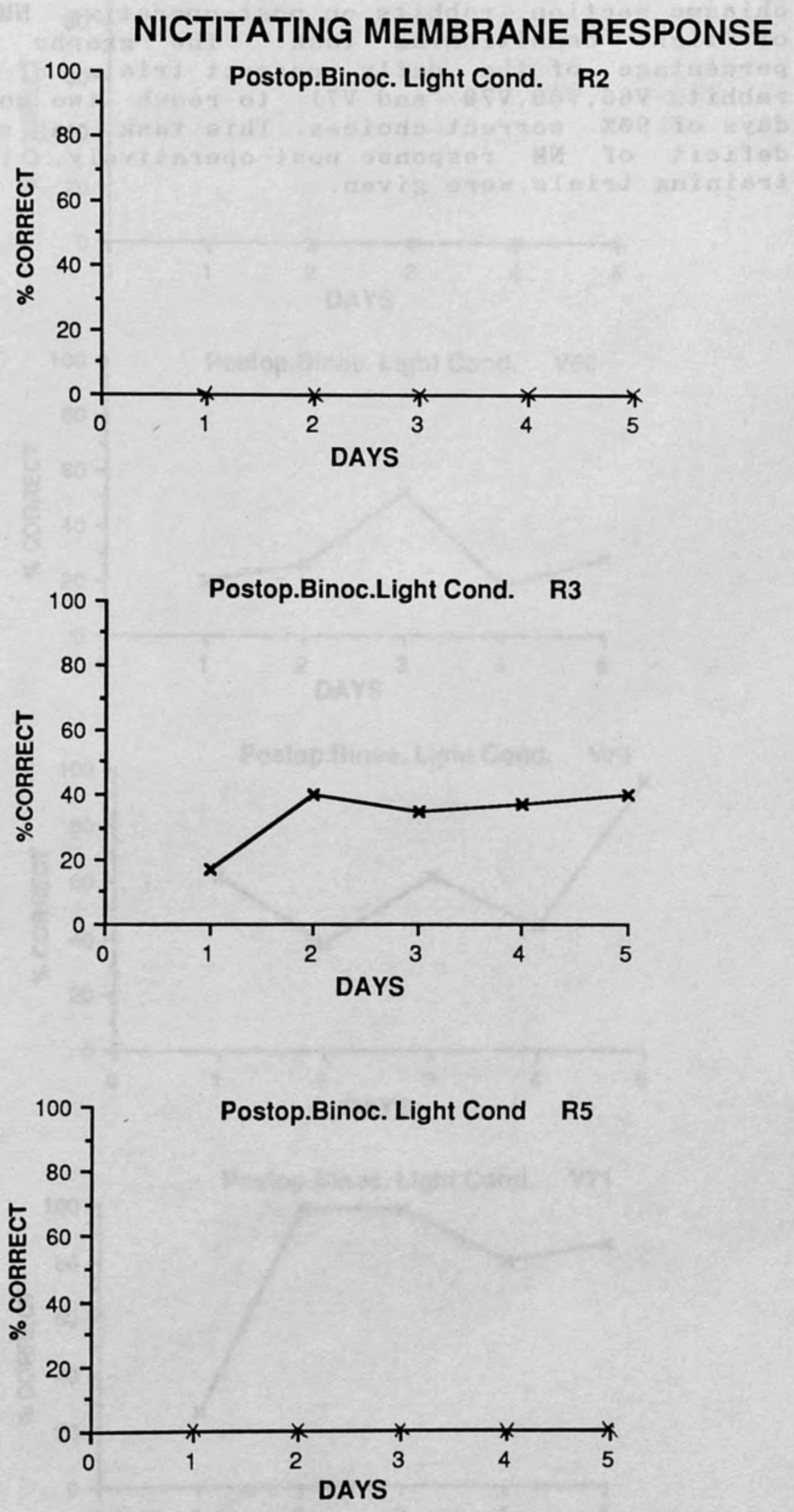
6(B) Group II Percentage CRs (50 trials/day)

| | Light CS | | | | | | | Auditory CS | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Sessions | | | | | | | Sessions | | | | | | |
| Animal | 1 | 2 | 3 | 4 | 5 | Errors | % | 1 | 2 | 3 | 4 | 5 | Errors | % |
| V66 | 0 | 0 | 0 | 0 | 0 | 250 | 100 | 26 | 76 | 60 | 98 | 96 | 72 | 29 |
| V69 | 20 | 26 | 52 | 18 | 28 | 178 | 71 | 92 | 96 | 94 | 100 | 94 | 12 | 5 |
| V70 | 62 | 38 | 62 | 44 | 96 | 99 | 40 | 84 | 100 | 94 | 96 | 100 | 13 | 5 |
| V71 | 26 | 98 | 98 | 80 | 86 | 56 | 66 | 74 | 88 | 96 | 90 | 96 | 28 | 11 |
| Mdn | 23 | 32 | 57 | 31 | 57 | 139 | 56 | 79 | 82 | 94 | 97 | 95 | 21 | 8 |
| Mean | 27 | 41 | 53 | 36 | 53 | 146 | 58 | 69 | 90 | 86 | 96 | 97 | 31 | 13 |
| SEM | 10 | 17 | 16 | 14 | 17 | 43 | 17 | 15 | 5 | 9 | 2 | 1 | 14 | 6 |

Opposite:

Figure (II,24). Retention performance of the optic chiasma section rabbits on post-operative NM response of light conditioning task. The graphs show the percentage of the daily correct trials of the three rabbits R2,R3 and R5 to reach two consecutive days of 90% correct choices. This task was showed the deficit of NM response post-operatively. 100 daily training trials were given.

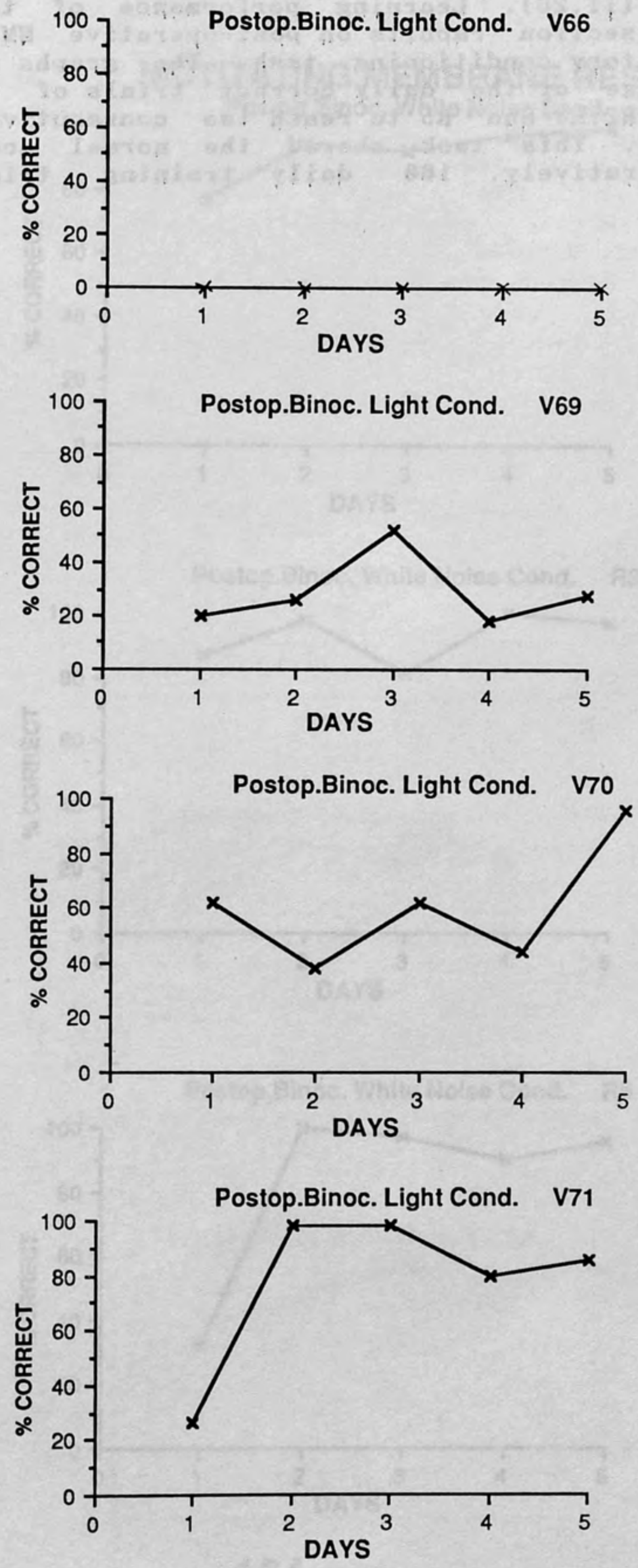
Figure (II,24). See opposite for legend



Opposite:

Figure (II,25). Retention performance of the optic chiasma section rabbits on post-operative NM response of light conditioning task. The graphs show the percentage of the daily correct trials of the four rabbits V66,V69,V70 and V71 to reach two consecutive days of 90% correct choices. This task was showed the deficit of NM response post-operatively. 100 daily training trials were given.

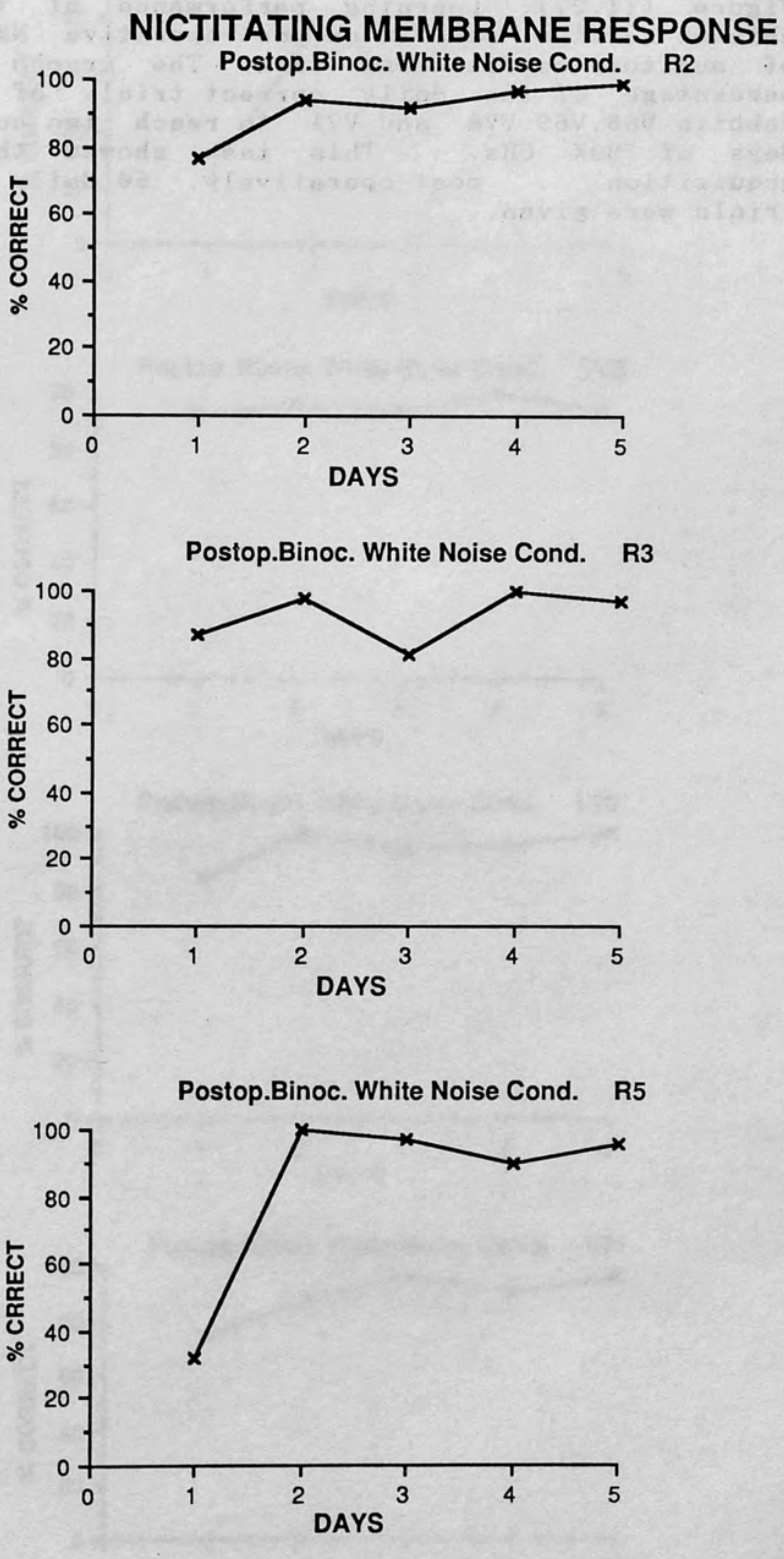
Figure (II,25). See opposite for legend.



Opposite:

Figure (II,26). Learning performance of the optic chiasma section rabbits on post-operative NM response of auditory conditioning task. The graphs show the percentage of the daily correct trials of the three rabbits R2,R3 and R5 to reach two consecutive days of 90% CRs. This task showed the normal acquisition post-operatively. 100 daily training trials were given.

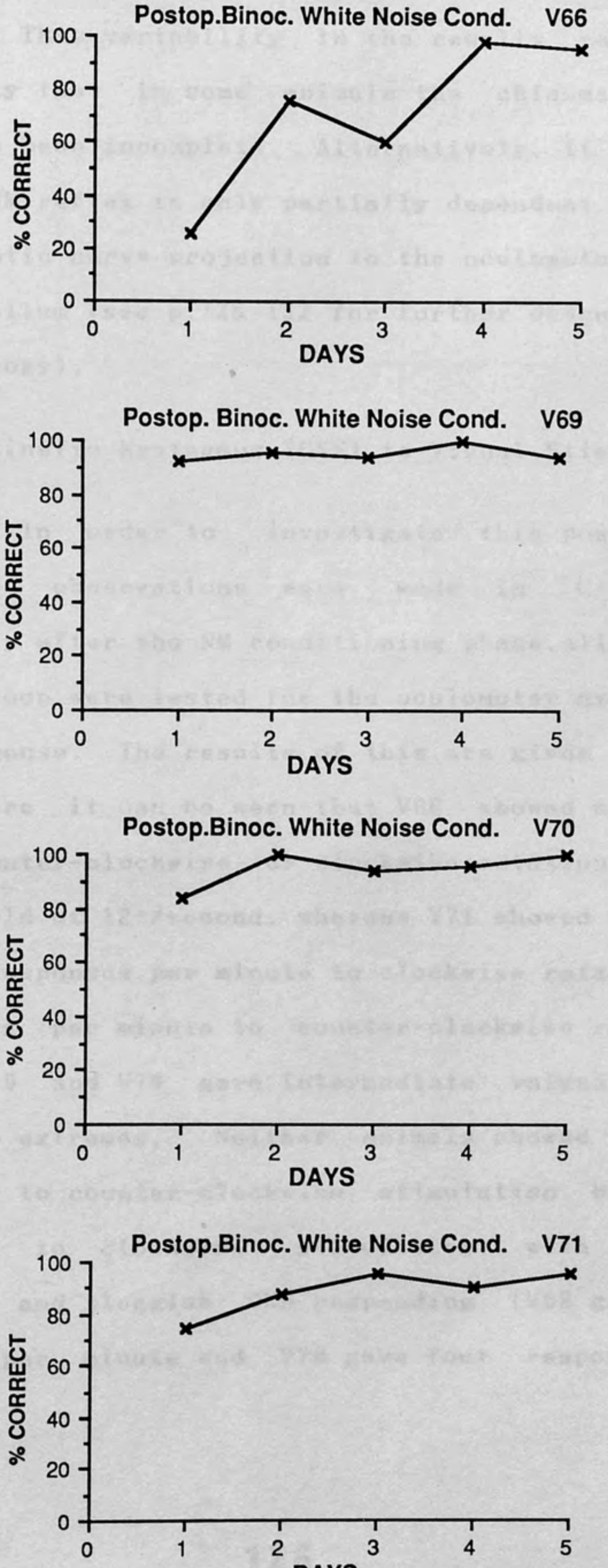
Figure (II,26). See opposite for legend.



Opposite:

Figure (II,27). Learning performance of the optic chiasma section rabbits on post-operative NM response of auditory conditioning task. The graphs show the percentage of the daily correct trials of the four rabbits V66,V69,V70 and V71 to reach two consecutive days of 90% CRs. This task showed the normal acquisition post-operatively. 50 daily training trials were given.

Figure (II,27). See opposite for legend.



This variability in the results raises the possibility that in some animals the chiasma section could have been incomplete. Alternatively, it could be that the NM reflex is only partially dependent upon the crossed optic nerve projection to the oculomotor nuclei and cerebellum (see p.128-132 for further discussion of the histology).

### B.3. Optokinetic Nystagmus (OKN) to Visual Stimulation:

In order to investigate this possibility additional observations were made in Group II. Immediately after the NM conditioning phase,all animals in this group were tested for the oculomotor nystagmus (OKN) response. The results of this are given in Table II,7. There it can be seen that V66 showed no OKN to either counter-clockwise or clockwise rotation of the visual field at 12°/second, whereas V71 showed a normal i.e. 12 responses per minute to clockwise rotation and 0 responses per minute to counter-clockwise rotation. Animals V69 and V70 gave intermediate values between these two extremes. Neither animals showed any OKN responses to counter-clockwise stimulation, but both responded to clockwise stimulation, with a low frequency and sluggish OKN responding (V69 gave six responses per minute and V70 gave four responses per

Table II,7

Postoperative OKN Test
12 /second

| Animal | Clockwise Rotation | Counterclockwise Rotation |
|---|---|---|
| V66 | 0 | 0 |
| V69 | 6 | 0 |
| V70 | 4 | 0 |
| V71 | 12 | 0 |

Table(II,7). Optokinetic nystagmus performance of the optic-chiasma section rabbits. The table show the clockwise rotation and the counter-clockwise rotation of the visual field at 12°/ second. Only V71 showed a normal response.

minute).

These results are in striking agreement with NM conditioning. Animal V66 showed neither any NM nor OKN responses; whereas V71 gave a normal pattern for both NM and OKN oculomotor reflexes. V69 and V70 showed a severe impairment equally for NM and OKN reflex system. Russell et al. (1987) have clearly demonstrated that when the optic chiasma was completely sectioned, there was a loss of both OKN responses as well as an anatomical denervation of the visual input to the oculomotor nuclei.

The present results therefore strongly argue that where both the OKN and NM reflexes are spared to such a extent, this is due to some crossed optic nerves surviving from the operative procedure.

### (C) Anatomical Observations

The postoperative recovery period lasted for 26 months. Consequently, the postoperative degeneration must have been virtually complete.

The animals were anaesthetised by intravenous injection with sodium-pentobarbitone administered via the ear vein. Both the carotid artery and the jugular vein were canulated bilaterally. The animals were then bilaterally perfused by the carotid arterial system, first by physiological saline to remove all blood from the cerebral vascular tree. This was immediately followed by a second perfusion with 10% formal-saline. The brains were then removed from the skull taking care to preserve the optic nerves.

However, due to the prolonged postoperative recovery period this was very difficult, due to the very thin and highly degenerated nerves. Examining the brains microscopically, it was found in two of the three animals the optic nerves had been lost from the slide. In the case of R2 the optic nerves were preserved and the sections were seen to be complete from optic nerves to optic tracts, as can be seen in Fig.II,28.

For R3 and R5 examination of the optic nerves were not possible to verify the completeness of the optic chiasma. It was possible anatomically to examine the size of the optic tracts. In both of these animals the tracts were seen to be massively reduced in size due to the large amount of fibre degeneration as a consequence of the optic chiasma section. In both cases the optic tracts appeared to be symmetrical in size. Unfortunately, in the absence of direct histological

Figure (II,28). Above, the optic chiasma (OC) was completely sectioned. Below, the optic chiasma was intact.

examination of the sectioned optic nerves in the chiasma it is impossible to know whether or not the section was either complete or symmetrical. This last point is important in that it is possible that when the chiasma was cut that the line of section could deviate either horizontally or vertically from the midline. This could only checked for by examination of a complete serial section of the chiasma. In the rabbit, the caudal part of the chiasma frequently is slightly elevated in the midline above the level of the trunk of the chiasma. This means that the section of the last fraction of the chiasma is not always under direct visual control. Thus, it is possible that some contralaterally projecting optic fibres could have been spared from the lesion (see Fig.II,29).

Histological examination of the optic chiasma for animals V66,V69,V70 and V71 revealed that in the case of V66 the section was complete. In the remaining animals there was a failure to cut completely the posterior part of the chiasma. V71 showed the greatest amount of sparing where approximately 15% of the chiasma was intact. For V69 and V70, although only a small amount of the posterior chiasma remained intact, the sections were also to a lesser extent incomplete (see Fig.III in appendix).

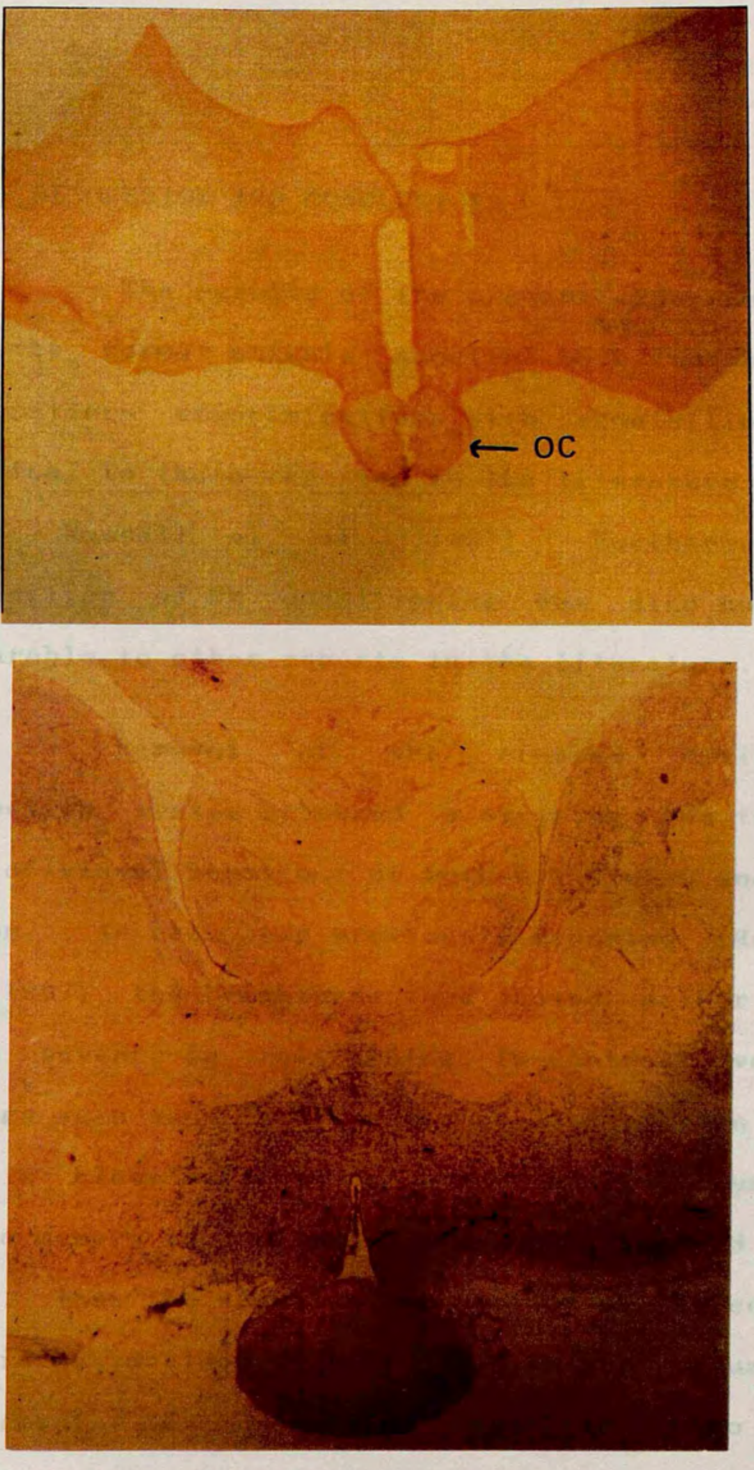


Figure (II,29). Above, the optic chiasma (OC) was not completely sectioned. Some optic nerves were spared from the lesion. Below, the optic chiasma was intact.

## II.7. DISCUSSION AND CONCLUSIONS

The results of the present experiment showed that the normal animals acquired both the brightness and pattern discriminations with acquisition curves identical to those reported in the literature (van Hof, 1975; Russell et al., 1987). Furthermore their acquisition of NM conditioning was also normal and comparable to other reports in the literature.

Removal of the crossed optic fibre projection system produced a striking but transitory loss of visual behaviour of both brightness and pattern vision. As has been previously reported (Russell et al., 1987) the brightness task showed either negative or no savings in re-training. In contrast very large savings were seen in all cases for the pattern task. This is clear evidence of a retrieval failure rather than a memory loss of those previously learned visual tasks. Thus the visual disconnection of the cerebellum by chiasma section did not lead to any visual memory impairment for learning in the two choice discrimination situation.

Furthermore, the fact that all chiasma sectioned animals were able to relearn both the brightness as well as the pattern discrimination tasks, demonstrates that none of the animals were blind. This is further emphasized by the fact that postoperatively all animals were also retrained monocularly on either the brightness or the pattern problem. The fact that this monocular learning was very slow following prior binocular training further attests to the genuine nature of the binocular visual learning. The loss of binocularity would be expected to show such a deficit only if the learning was purely visual and not due to the use of non-visual cues, as can happen in rats (Russell et al., 1978).

The effect of section of the optic chiasma was dramatically different on oculomotor reflexes. All animals showed a permanent and large Behr's pupil sign. Furthermore all animals showed an initial total lack of retention of the NM conditioning. In 5 animals the deficit was permanent and unchanging throughout the retraining period. Of these, three made no conditioned responses, and the remaining two made a small number of CRs which were of very small amplitude and did not become consistent during successive training days. At no point did they ever rise above the level of 20% to 40%. Two other animals showed normal learning or acquisition curves.

Half of the animals were also tested for OKN responding, which showed exactly parallel results to those found for the NM response. That is where there was retention of NM conditioning there was also retention of OKN. Where there was a low level of NM responses with small amplitude longs latency responses, there was also a similar OKN effect with low frequency and sluggish responding. Finally, where there was a complete lack of NM response, the OKN was also absent. Despite the impairments seen for visual conditioning, the NM conditioning to auditory stimuli was rapid and showed facilitation compared with NM response learning to light before the chiasma section. This clearly showed that the effect of chiasma section was specific solely to visual associative learning and did not produce any motor output deficit on conditioning.

These results both confirm and extend earlier findings on the effect of chiasma section on visual and oculomotor behaviour. They show clearly that the loss of the crossed fibre projection system, which is 90% of the total retinal output, does not abolish either brightness or pattern vision. Its principal effect appeared to be on oculomotor control of brain stem reflexes by visual inputs. Thus the present work shows that impairment of the crossed fibre projection in varying degrees produces either a total loss of the OKN, or if there is some sparing of the crossed fibre system, then there is partial and rudimentary optokinetic nystagmus present. As has been previously mentioned this agrees with the earlier finding of Russell et al. (1987). It also extends these observations by noting that incomplete lesions of the crossed fibre system produce a graded loss of optokinetic responses.

Furthermore the observations on the effect of chiasma section on the visual control of the NM response showed strikingly similar findings. This clearly establishes the fact that the NM response and OKN depend on similar neural circuitS. Caloric nystagmus responses can be obtained in the normal rabbit when the ear is irrigated with warm water, and similar observations have been made on chiasma sectioned rabbits (Russell, personal communication).

These observations in addition to the fact that the present results showed normal, or facilitated, NM conditioning to an auditory CS, clearly indicate that the crossed optic fibre system served only as the visual input route for the visual control of oculomotor reflexes. The loss of such reflexes are due to sensory disconnection from either the cerebellum or the brain stem oculomotor centres. They are not a result of any motor impairment. Nor can they be due to any visual deficit such as blindness, because all animals were trained successfully to criterion for both brightness and pattern vision. Thus the deficit for both OKN and NM conditioning is a specific visual one.

It further suggests that lesions of the cerebellum which have been reported to produce a deficit in NM conditioning (Thompson et al., 1982) could be due to a loss of a cerebellar oculomotor system and are not necessary due to the loss of a learning mechanism per se.

The effect of section of the optic chiasma on visual behaviour was seen to produce a profound initial performance deficit. This was not due to any memory loss, but to a memory retrieval impairment. When the brightness task was relearned, by acquiring a new oculomotor strategy, there was automatic access to the pattern memory. Thus the retinal loss due to chiasma section gave the superficial impression of memory loss.

It is therefore possible that cerebellar lesions which produce loss of NM conditioning, do so by a similar effect. This would not be a memory loss (trace disruption), but instead a subtle disturbance of motor control, where the timing is gone. Thus after cerebellar damage, animals cannot anticipate motor movement requirements, although they can make normal motor reactions. Thus the UR would remain and the CR would be lost. The present findings in showing that both NM response and the OKN are dependent on the same oculomotor circuits would suggest this argument should be taken seriously.

# CHAPTER III

## EXPERIMENT 2

## THE ROLE OF STATE-DEPENDENT LEARNING STRATEGIES IN INTEROCULAR TRANSFER IN THE RABBIT. ATTEMPTS TO PREVENT THIS AS A SOURCE OF INFORMATION-RETRIEVAL FAILURE.

### INTRODUCTION

In the rabbit the literature of interocular transfer (IOT) is entirely consistent in finding that there is a complete lack of IOT. This is independent of whether monocular training methods are used (van Hof, 1970), or binocular training methods (De Vos Korthals and van Hof, 1983), or even reversal training (van Hof, 1981). Several explanations have been used to explain this finding.

The first theory is that in rabbit there is a very small proportion of retinal fibres which is uncrossed. This ipsilateral projection is less than 10% of total retinal output, and has been frequently regarded as too small a projection system to be significant in visual behaviour (van Hof, 1979).

However, recent evidence has clearly shown that chiasma sectioned rabbits with only the ipsilateral projection system, have no obvious loss of their visual capacity for pattern discrimination learning (Russell et al., 1987). This observation and similar ones in rats (Cowey & Franzini, 1979; Russell, van Hof & Al-Hamdan, 1987) argue that although the ipsilateral projection may be small it nonetheless plays a crucial role in vision.

A second possibility to explain the lack of IOT in the rabbit has been the argument that monocular eye occlusion results in a dramatic reduction in neural activity of the contralateral hemisphere due to the removal of the retinal input to that hemisphere. This reduction in activity in the contralateral hemisphere, in turn triggers inhibitory processes via the corpus callosum from the active hemisphere receiving retinal input (see Fig.III.1). This inhibition of the hemisphere contralateral to the eye patch, is the reason why the ipsilateral input is ineffective. Thus the side effect of monocular occlusion is to produce direct callosal inhibition of the contralateral hemisphere. Furthermore, it is this inhibition which prevents any IOT in the normal rabbit (De Vos Korthals & van Hof, 1983). If this mechanism were true then

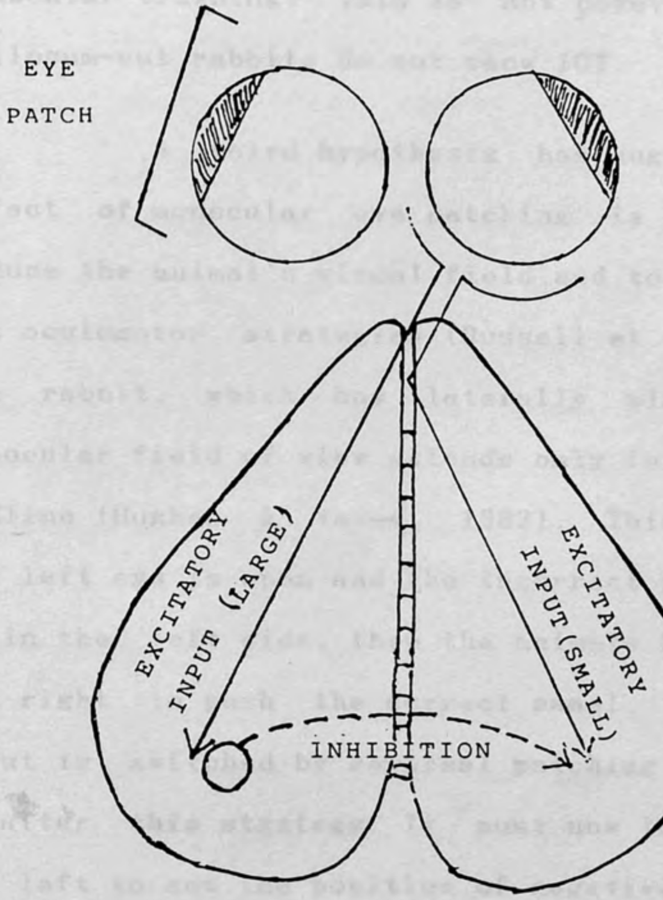


Figure (III,1). Monocular eye occlusion produces a reduction in neural activity of the contralateral hemisphere due to the removal of the retinal input to that hemisphere. This reduction in activity in the contralateral hemisphere, in turn triggers inhibitory processes via the corpus callosum from the active hemisphere receiving retinal input. This is inhibition of the hemisphere contralateral to the eye patch.

section of corpus callosum should abolish interhemispheric inhibition and produce IOT following monocular training. This is not however the case, as callosum-cut rabbits do not show IOT.

A third hypothesis has suggested that the effect of monocular eye patching is to dramatically reduce the animal's visual field and to also influence its oculomotor strategies (Russell et al., 1979). In the rabbit, which has laterally placed eyes, its monocular field of view extends only for 12° across the midline (Hughes & Vaney, 1982). This means that if the left eye is open and the incorrect pattern, the S- is in the left side, then the animals have to move to the right to push the correct panel. If the visual input is switched by reversal patching the animal has to alter this strategy. It must now turn its head to the left to see the position of negative stimulus, and then move to the right to find the reward panel. In this "motor strategy" theory, relearning via the second eye is not a relearning of the pattern identification but a simple learning to disconnect the previous monocular strategy from an oculomotor"state-dependency" (Russell, Bookman & Mohn, 1979).

A fourth hypothesis relates to the role of the ipsilateral fibres in frontal vision of the rabbit (van Hof & Lagers van Haselen, 1973), and the retinal distribution of the cells of the origin of these fibres (Provis, 1981). It has been shown that unlike the rat where the ipsilateral fibres originate from the ventro-temporal retinal region of approximately 25% of the total retina, in the rabbit the retinal origin of the ipsilateral projection derives from a small area on the horizontal meridian of the extreme temporal margin of the retina. This is less than 5% of total retina. Under binocular vision the rabbit uses this small temporal region of the retina for pattern vision. When this area is occluded, pattern recognition is severely impaired (van Hof & Lager van Haselen, 1973). The importance of the ipsilateral projection for IOT is that it is only those projections from the retina which go to the binocular cellular units in the visual cortex. Thus when the rabbit uses this part of the retina for visual analysis, it is the ipsilateral fibres which convey the visual information to the binocular cells in the visual cortex. These cells are connected interhemispherically by callosal fibres, and should therefore provide a neural mechanism for IOT.

Zuidam & Collewijn (1979) first reported vergence eye movements in the rabbit during visual discrimination behaviour. They observed that the rabbit during a visual discrimination task uses frontal vision and was able to converge its eyes up to 8°. They also noted that monocular occlusion produced a drift in the optical axes of approximately 8°. This suggests that monocular occlusion in the rabbit would seriously affect the alignment of the retina such that the information from the single temporal retina (ipsilateral projection) could no longer be efficiently projected to either the appropriate binocular units or even to monocular units in the cortex.

In addition to monocular eye patching misaligning the ipsilateral projection to monocular cortical units, it is also responsible for other errors of information storage. During monocular training, due to the lack of binocular vision and the reduction in the central visual field, the animal is forced into making a large number of scanning movements in order to view the information in the contralateral half field, this will mean that the role of the crossed fibre projection in pattern vision is enormously enhanced. As the contralateral projection is 95% of the total retinal area, its "image capture" under such monocular viewing will be predominant, with the consequence that its output almost is exclusively to monocular visual cells. By definition they are incapable of interhemispheric communication. As a consequence learning under such monocular conditions is registered by a visual system which is inaccessible to the other eye. Hence, IOT under such input conditions is impossible.

The present experiment undertook to test these last two theories in two ways:

(1) It examined the effect of procedures which were designed to minimize the effect of state-dependent monocular strategies developing during monocular training, on IOT.

(2) It examined the effect of monocular NM conditioning on IOT. As NM conditioning did not involve any scanning strategies optimum stimulation of the ipsilateral projection could be possible, and therefore good IOT might be obtained.

## MATERIALS AND METHODS

### III.1. ANIMALS

The animals used were 16 dutch belted rabbits, roughly six months of age with an equal number of males and females. The animals were maintained at 90% of body weight and allowed free access to water. They weighed between 2.30 and 2.60 kg, at the beginning of the experiment.

## III.2. APPARATUS

The same preshaping box, visual discrimination training box and nictitating conditioning apparatus were used as described in experiment 1.

## III.3. TRAINING METHODS

Group I : Two-choice discrimination training procedures.

### (A) Pretraining:

All animals were pretrained in the manual apparatus to acquire the essential behavioural skills of operating the two choice discrimination box. This was done in the same manner as described in detail in experiment 1.

### A.1. Brightness Training:

When the pretraining phase was ended, all animals were binocularly trained in brightness discrimination using the standard procedure (described in experiment 1). After reaching the training criterion of two consecutive days of 90% correct responses the animals were then tested for monocular retention of this task. Using the face mask, animals were tested for 50 trials with the right eye uncovered and the left eye patched. After this the face mask was reversed such that a further 50 training trials were given with the left eye uncovered and the right eye patched. This was continued on an alternating daily basis until the performance with each eye met the criterion of two days consecutive 90% correct responses.

A.2. Pattern Training:

Following the completion of the previous phase all animals were binocularly trained in the same manner on a horizontal versus a vertical striation discrimination task. After reaching the 90% criterion, they were tested for retention under monocular conditions. Again, the first 50 trials were with the right eye uncovered and the second 50 trials with the left eye open, as described for the brightness task.

The purpose of this pretraining phase was to ensure that all animals were adequately test-sophisticated before any interocular transfer training was undertaken. Not only were they trained on two different problems binocularly, but these were subsequently retention tested monocularly. This was intended to ensure that all animals would be equally experienced and adapted to the requirement of monocular learning. Furthermore each eye was trained equally to access the same information. Thus the binocular training was intended to maximize the likelihood that animals would be able to transfer information from binocular conditioning to monocular and also to access the same information between the two eyes i.e. interocular transfer. This procedure was designed to prevent the possibility that the rabbits would develop any "state-dependent"oculomotor habits during monocular training (Russell et al., 1979).

## (B) Interocular Transfer (IOT)

### B.1. Oblique Striation Task:

After the completion of the pretraining or facilitation phase, all animals were exposed to a third and novel problem, de novo monocularly. This was an oblique striation task, where one set of stripes was oriented at 45° and the other at 135°.

All animals were given 50 daily trials using the same eye until the criterion of 90% correct choices for two consecutive days was reached. Following this the second eye was then trained to criterion in the same way with the same oblique striation task.

B.2. Inverted Triangle Task:

Four animals were trained on a second visual task using a triangle discrimination. As in previous experiments they were trained over consecutive days monocularly using the right eye first. On reaching criterion reversed eye patching enabled the left eye to be used for retention of the same problem.

Group II : Pavlovian conditioning of NM response procedures.

(A) Pretraining:

All animals were first exposed to an adaptation procedure which enabled them by successive approximations to adjust to the restraining apparatus. On the first day the animals were placed in the restraining stock where their head was secured by the neck yoke and the body by the back plate (see Fig.III,2). They were then placed in the sound-proof enclosure for 15 minute. On the second day the same routine was followed and the animal's time in the stock and sound-proof enclosure was extended by 15m daily

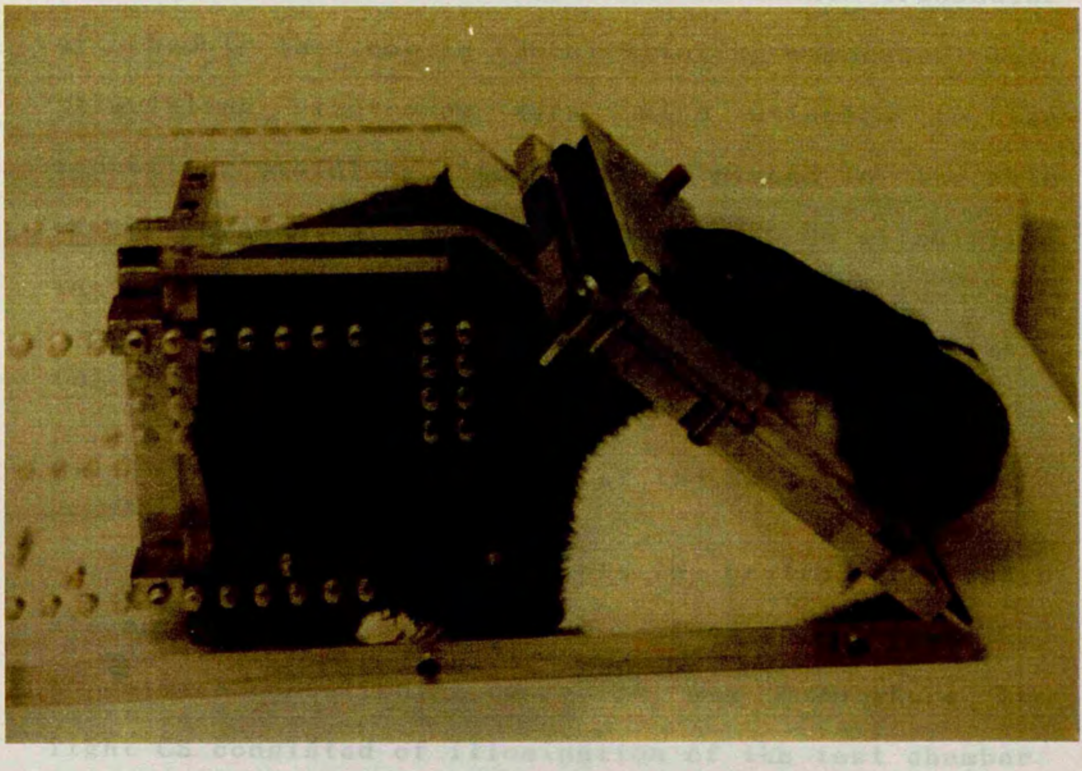


Figure (III,2). The rabbit is placed in the restraining stock where its head is secured by the neck yoke and the body by the back plate.

until they were accommodated to restraint for one hour. On the 5th day all animals were placed in this apparatus with the recording transducer on their head for one hour daily session. The following day this procedure was repeated with the movement transducer attached to the loop in the nictitating membrane. The stimulating electrodes were also attached to the indwelling stainless steel sutures placed in the skin of the paraorbital region of the cheek. No stimulation was given during this final adaptation day.

(B) Interocular Transfer (IOT)

Visual Pavlovian Conditioning of the NM Response.

After completion of the pretraining phase all animals were monocularly trained to a visual CS. A delayed conditioning paradigm was used where the light CS consisted of illumination of the test chamber by two incandescent lamp located behind milk glass screen to produce a light intensity of 1.3 lux. Additionally the animals wore a monocular face mask which occluded either the right or the left eye. This was the same technique that was used for all animals in previous Group I.

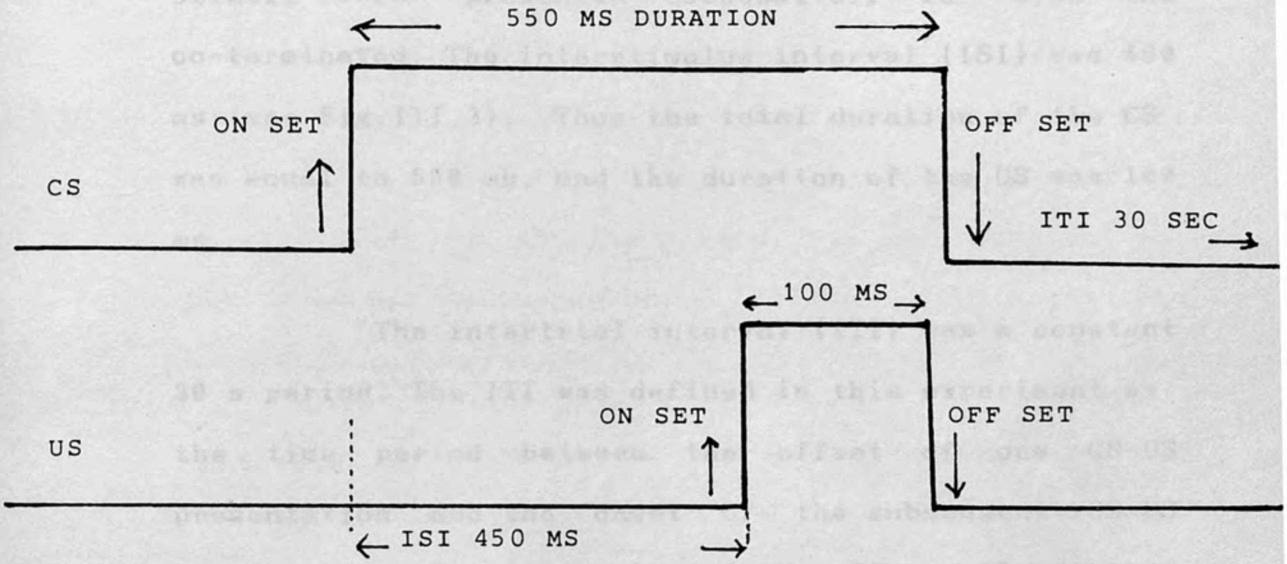


**Figure (III,3). Pavlovian conditioning of the NM . The duration between conditioned stimulus (CS) on set and unconditioned stimulus (US) off set is 550 ms, by using delayed training paradigm. The duration of the US on set-off set is 100 ms. ISI, the interstimulus interval is 450 ms. ITI, intertrial interval is 30 s.**

The duration of the CS-US complex was 550 ms. This used a delayed training paradigm where both stimuli were presented successively in time and co-terminated. The interstimulus interval (ISI) was 450 ms (see Fig.III,3). Thus the total duration of the CS was equal to 550 ms, and the duration of the US was 100 ms.

The intertrial interval (ITI) was a constant 30 s period. The ITI was defined in this experiment as the time period between the offset of one CS-US presentation and the onset of the subsequent CS-US presentation. The intensity of the CS was 85 dB, and the intensity of the US stimulation was adjusted until a threshold value was reached for each animal, where a 4 mm movement of the nictitating membrane was consistently obtained.

The movement of nictitating membrane was measured by the low-torque rotary potentiometer (Penny and Giles Ltd, Model RP08/1/FD 12767, coil resistance 20 K $\Omega$). This was possible by attaching a radial armature to the rotary spindle of the potentiometer, which in turn was mechanically linked to the nictitating membrane. This was achieved by a silk thread attached to the tip of the armature, which was then hooked to the loop in the nictitating membrane (see chapter II Fig.II.7). The signal from the movement of the nictitating membrane was recorded on one channel of a Washington 400 Md4 four channel rectilinear recorder with model FC 100 coupler units. Paper speed in all trials was 25 mm/s. Conditioned responses were defined as a deflection of the recording pen of at least 1 mm during the ISI period, i.e. any movement of the membrane which occurred following CS onset but before US presentation.

A second measure of conditioning responses was obtained on probe trials, where only the CS alone was presented without any delayed presentation of US. On these occasions a conditioned response (CR) was a minimal deflection of the recording pen of 1 mm during the CS presentation. Any response occurring in the ITI period was considered to be an alpha response and not evidence of a CR. All daily sessions consisted of 50 training trials (i.e. 50 CS-US presentations) as well as six probe trials. At the beginning of the session, three probe trials were given where the animals were tested with the CS alone, US alone, and no stimuli. This triad was repeated at the end of the training session. These separate probe trials provided measures where: (a) CS alone trials gave a pure measure of conditioning, (b) US alone trials gave a monitor of reflex sensitivity, and (c) zero stimulation gave a measure of either temporal conditioning or of sensitisation in terms of alpha responding.

All animals were given 50 daily trials using the same eye until a criterion of 90% conditioned responses were made for two consecutive days. Following this, the second eye was trained to the same criterion in the same way using the same visual CS. For half of the animals (NA1,NA2,NA4 and NA5) both the light and shock electrode were changed from the left eye to the right eye. For the remaining animals (NA3, NA6,NA7, and NA8) only the light was switched from the left eye to the right eye, and electrode placement remained adjacent to the left eye. Using this design it was thereby hoped to evaluate whether: (a) IOT would occur when both the CS and US was transferred, or (b) whether IOT would occur with only the CS alone being switched. This design would then enable us to determine the transfer of either conditioned or unconditioned responses to either the CS or US.

## III.4. THE RESULTS

### (A) Pretraining:

The results of the binocular training for group I on the brightness discrimination are given in terms of daily error scores for individual animals in Table III.1. As can be seen all animals reach the criterion of two consecutive days at 90% correct with slightly different times, varying between 5-8 days of training. Following this binocular training all animals were tested for monocular retention of the brightness task with each eye. Table III.2 gives the individual results of this test, where performance with each eye was examined for five consecutive days. It can be seen that all animals show comparable and equal retention with either eye.

Similar results are seen in individual error scores of binocular learning of the pattern (H/V+ discrimination), which are given in Table III.3. After all animals reached criterion they were tested for monocular retention with each eye. Results for all animals are shown in Table III.4 where as before every animal shows equal performance on the pattern task with either left or right eye.

The purpose of this pretraining was to ensure that all rabbits were equally test sophisticated for visual learning either binocularly or monocularly before they were tested for IOT. It was important to ensure therefore that : (a) no animals were used in the

Table III,1

Brightness Test.
B/W+ (Binoc.)

| | Daily Errors | | | | | | |
|---|---|---|---|---|---|---|---|
| Animal | 1 | 2 | 3 | 4 | 5 | Errors | Trials |
| N1 | 25 | 20 | 10 | 13 | 10 | 78 | 250 |
| N2 | 20 | 15 | 20 | 13 | 10 | 78 | 250 |
| N3 | 25 | 22 | 20 | 15 | 10 | 98 | 300 |
| N4 | 20 | 25 | 15 | 10 | 5 | 70 | 200 |
| N5 | 20 | 20 | 10 | 5 | 2 | 50 | 150 |
| N6 | 20 | 15 | 20 | 10 | 5 | 65 | 200 |
| N7 | 25 | 12 | 15 | 10 | 5 | 62 | 200 |
| N8 | 20 | 25 | 20 | 15 | 10 | 90 | 250 |
| Mdn | 20 | 20 | 18 | 12 | 8 | 78 | 225 |
| Mean | 22 | 19 | 16 | 11 | 7 | 74 | 225 |
| SEM | 1 | 2 | 2 | 1 | 1 | 16 | 2 |

Table (III,1). Binocular training performance of normal rabbits on brightness discrimination. The table gives the median,mean and standard errors of the daily errors and trials to the final criterion during binocular training. 50 daily training trials were given. B/W+, black vs. white discriminations the white was rewarded.

Opposite:

Table (III,2). Monocular training performance of normal rabbits on brightness discrimination. The table gives the median,mean and standard errors of the daily errors and trials to the final criterion during monocular training. 100 daily training trials were given. B/W+, black vs. white discriminations the white was rewarded. RE, the right eye which trained first. LE, the left eye which trained second.

Table III,2 See opposite for legend.

Brightness Test.
B/W+ (Monoc.)

| Animal | | Daily Errors | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Animal | | 1 | 2 | 3 | 4 | 5 | Errors | Trials |
| N1 | RE | 20 | 12 | 10 | 5 | 2 | 42 | 150 |
| | LE | 15 | 15 | 9 | 3 | 0 | 34 | 150 |
| N2 | RE | 15 | 15 | 9 | 7 | 5 | 46 | 200 |
| | LE | 12 | 13 | 7 | 5 | 4 | 32 | 150 |
| N3 | RE | 15 | 10 | 10 | 5 | 3 | 35 | 150 |
| | LE | 10 | 9 | 5 | 4 | 2 | 19 | 100 |
| N4 | RE | 17 | 15 | 10 | 7 | 2 | 49 | 200 |
| | LE | 15 | 10 | 9 | 5 | 2 | 34 | 150 |
| N5 | RE | 15 | 10 | 9 | 5 | 2 | 34 | 150 |
| | LE | 12 | 9 | 5 | 3 | 0 | 21 | 100 |
| N6 | RE | 18 | 14 | 15 | 10 | 5 | 57 | 200 |
| | LE | 15 | 12 | 10 | 5 | 5 | 37 | 150 |
| N7 | RE | 15 | 12 | 10 | 4 | 2 | 37 | 150 |
| | LE | 10 | 10 | 9 | 5 | 0 | 29 | 150 |
| N8 | RE | 20 | 18 | 19 | 5 | 0 | 49 | 150 |
| | LE | 15 | 10 | 10 | 4 | 2 | 35 | 150 |
| Mdn | RE | 16 | 13 | 10 | 5 | 2 | 44 | 150 |
| | LE | 14 | 10 | 9 | 5 | 2 | 33 | 150 |
| Mean | RE | 17 | 13 | 10 | 6 | 3 | 44 | 169 |
| | LE | 13 | 10 | 8 | 4 | 2 | 30 | 139 |
| SEM | RE | 1 | 3 | 1 | 1 | 1 | 3 | 9 |
| | LE | 1 | 1 | 1 | 0 | 1 | 3 | 8 |

Table III,3

Pattern Test.
H/V+ (Binoc.)

| | Daily Errors | | | | | | |
|---|---|---|---|---|---|---|---|
| Animal | 1 | 2 | 3 | 4 | 5 | Errors | Trials |
| N1 | 20 | 15 | 5 | 0 | - | 35 | 100 |
| N2 | 15 | 7 | 5 | 5 | - | 22 | 100 |
| N3 | 18 | 7 | 7 | 10 | 5 | 42 | 200 |
| N4 | 20 | 17 | 10 | 5 | 0 | 47 | 150 |
| N5 | 25 | 18 | 5 | 0 | - | 43 | 100 |
| N6 | 15 | 10 | 5 | 0 | - | 25 | 100 |
| N7 | 18 | 15 | 10 | 5 | 5 | 42 | 150 |
| N8 | 20 | 10 | 5 | 2 | - | 30 | 100 |
| Mdn | 19 | 13 | 5 | 4 | - | 39 | 100 |
| Mean | 19 | 12 | 7 | 3 | - | 36 | 125 |
| SEM | 1 | 2 | 1 | 1 | - | 4 | 13 |

Table (III,3). Binocular training performance of normal rabbits on pattern discrimination. The table gives the median, mean and standard errors of the daily errors and trials to the final criterion during binocular training. 50 daily training trials were given. H/V+, horizontal vs. vertical discriminations the vertical was rewarded.

Opposite:

Table (III,4). Monocular training performance of normal rabbits on brightness discrimination. The table gives the median,mean and standard errors of the daily errors and trials to the final criterion during monocular training. 100 daily training trials were given. H/V+, horizontal vs. vertical striations; the vertical was rewarded. RE, the right eye which trained first. LE, the left eye which trained second.

Table III,4 See opposite for legend.

Pattern Test.
H/V+(Monoc.)

| | Daily Errors | | | | | | |
|---|---|---|---|---|---|---|---|
| Animal | 1 | 2 | 3 | 4 | 5 | Errors | Trials |
| N1 RE | 10 | 7 | 7 | 5 | 2 | 24 | 150 |
| LE | 7 | 5 | 5 | 4 | 0 | 7 | 50 |
| N2 RE | 10 | 15 | 8 | 5 | 3 | 33 | 150 |
| LE | 7 | 10 | 7 | 5 | 2 | 24 | 150 |
| N3 RE | 10 | 5 | 7 | 5 | 2 | 22 | 150 |
| LE | 7 | 4 | 5 | 3 | 0 | 11 | 100 |
| N4 RE | 5 | 8 | 7 | 5 | 2 | 20 | 150 |
| LE | 4 | 5 | 5 | 3 | 0 | 4 | 50 |
| N5 RE | 7 | 8 | 5 | 3 | - | 15 | 100 |
| LE | 5 | 5 | 2 | 0 | - | 0 | 0 |
| N6 RE | 20 | 15 | 10 | 5 | 2 | 45 | 150 |
| LE | 17 | 10 | 5 | 5 | 0 | 27 | 100 |
| N7 RE | 10 | 10 | 5 | 3 | - | 20 | 100 |
| LE | 7 | 5 | 0 | 0 | - | 7 | 50 |
| N8 RE | 7 | 2 | 0 | 0 | 0 | 7 | 50 |
| LE | 15 | 10 | 7 | 2 | 2 | 32 | 150 |
| Mdn RE | 10 | 8 | 7 | 5 | - | 21 | 150 |
| LE | 7 | 5 | 5 | 3 | - | 9 | 75 |
| Mean RE | 10 | 9 | 6 | 4 | - | 23 | 125 |
| LE | 9 | 7 | 5 | 3 | - | 14 | 81 |
| SEM RE | 2 | 2 | 1 | 0 | - | 4 | 13 |
| LE | 2 | 1 | 1 | 1 | - | 4 | 15 |

experiment that had a pronounced ocular dominance. Such rabbits by definition would have IOT. (b) that each animal had equal learning ability under binocular as well as monocular conditions. The present results clearly established that no animals had any ocular dominance.

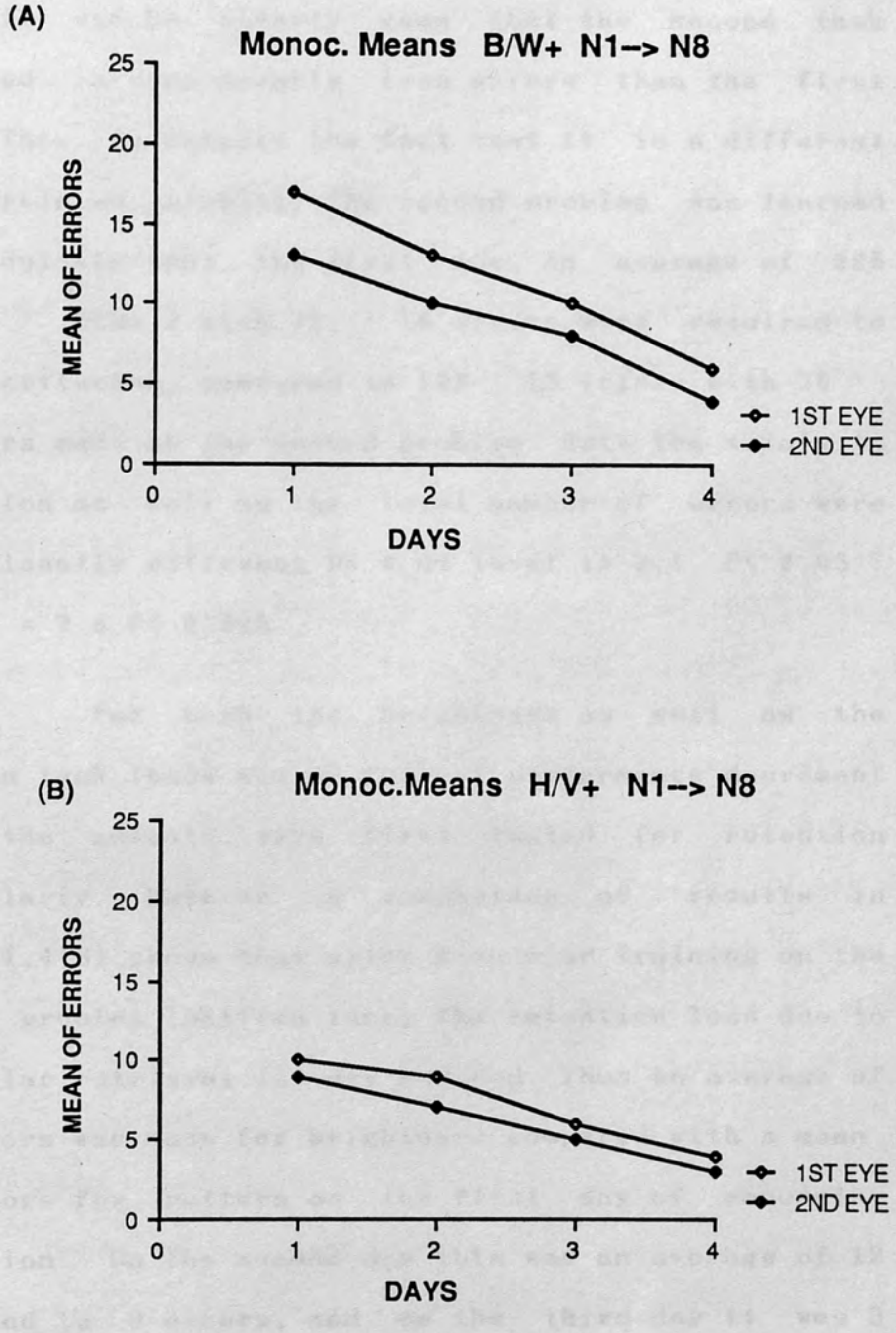
(B) Monocular Retention:

Figs.III,4(A) gives the results for group I on the monocular testing for the brightness task and Fig.III,4(B) on the monocular testing for the pattern task. There it can be seen that the daily average number of errors for each eye is the same, both for brightness and for pattern tasks. Furthermore, if we look at individual daily error scores in Tables III,2 and III,4 there is no case of any animal showing any significant asymmetry in the performance of the brightness or the pattern task between eyes. These results clearly establish that binocular training resulted in the information being stored in a form within the brain that was equally accessible monocularly to either eye. Further, it also shows that all animals at the end of this training phase were equally experienced and competent at discrimination learning with either eye.

Opposite:

Figure (III,4). Training performance of normal rabbits on the two visual discriminations. The graphs show the average errors of four days of monocular training needed to reach successive criterion levels on the two tasks during training of the first eye and the second eye. 4(A), This graph shows the mean of monocular training errors of the brightness discrimination for all 8 rabbits (N1 --> N8). 4(B), this graph shows the average of monocular training errors of pattern discrimination for all 8 rabbits (N1 --> N8).
B/W+, black vs. white discriminations, the white was rewarded. H/V+, horizontal vs. vertical striations, the vertical was rewarded. -o- 1ST EYE, the first eye which trained first (right eye). -●- 2ND EYE, the second eye which trained second (left eye).

Figure (III,4). See opposite for legend.



Comparing the second task with the first task it can be clearly seen that the second task resulted in considerably less errors than the first one. This is despite the fact that it is a different and unrelated problem. The second problem was learned more quickly that the first one. An average of 225 trials ± SEM= 2 with 72 ± 16 errors were required to reach criterion, compared to 125 ± 13 trials with 36 ± 4 errors made on the second problem. Both the trials to criterion as well as the total number of errors were significantly different $P < 0.05$ level $t = 2.1$, $P < 0.05$ : errors = 2.5 $P < 0.025$.

For both the brightness as well as the pattern task there was an initial performance decrement when the animals were first tested for retention monocularly. However a comparison of results in Fig.III.4(B) shows that after binocular training on the second problem (pattern task) the retention loss due to monocular retrieval is very reduced. Thus an average of 15 errors was made for brightness compared with a mean 9 errors for pattern on the first day of monocular retention. On the second day this was an average of 12 compared to 8 errors, and on the third day it was 9 versus 5 errors for brightness and pattern retention respectively. Thus, the monocular retention on the second problem was improved.

(C) Interocular Transfer (IOT) Test :

C.1. Oblique Discrimination:

Looking at the results in Table III,5 giving individual scores during IOT training we can see that there is no animal showing any evidence of IOT. Here we define IOT in terms of the second eye having access to the information learned by the first eye. This means we would expect a typical learning curve from the first eye on the discrimination problem. When the second eye is exposed to the same material we would then expect to see no learning required if there was direct access to the learned information with the new eye.

Looking at the individual learning curves for each eye in Figs. III,5; III,6; III,7 and III,8 in no single case is there any evidence of the second eye having direct access to the information acquired with the first eye. In six out of eight animals the learning of the second eye is both: (a) starting from the same point close to chance as did the first eye, and (b) gradually improving over many days of training. In two cases N7 and N5 the second eye shows high initial level of performance at 70 or 80% on the first day. However, in both of those animals, this initial

Table III,5

Interocular Transfer (10T) Test
Oblique 45+/135°

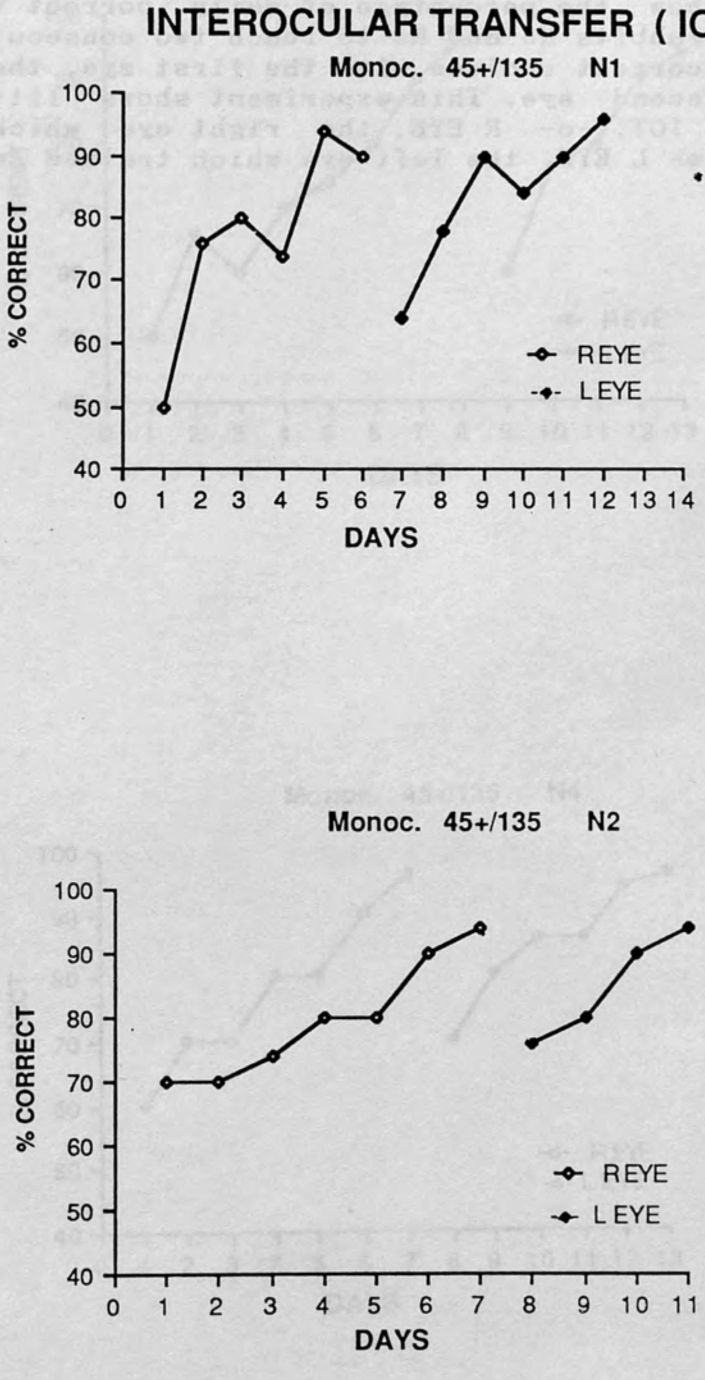
| Animal | Trials |  | Errors |  |
|---|---|---|---|---|
|  | RE | LE | RE | LE |
| N1 | 300 | 300 | 68 | 49 |
| N2 | 350 | 200 | 71 | 30 |
| N3 | 400 | 250 | 107 | 50 |
| N4 | 350 | 300 | 77 | 44 |
| N5 | 300 | 200 | 71 | 23 |
| N6 | 300 | 300 | 68 | 58 |
| N7 | 350 | 300 | 83 | 53 |
| N8 | 400 | 250 | 102 | 55 |
| Mdn | 350 | 275 | 74 | 50 |
| Mean | 344 | 263 | 81 | 54 |
| SEM | 15 | 16 | 6 | 4 |

Table (III,5). Acquisition performance of normal rabbits on the IOT test. The table gives the median,mean and standard errors of the trials and errors for both eyes to final criterion during oblique striation training test. 50 daily training trials were given. RE, the right eye which trained first. LE, the left eye which trained second.

Opposite:

Figure (III,5). Monocular performance of normal rabbits on the IOT test, oblique striation 45°+/135°. The graphs show the percentage of daily correct trials of the two rabbits N1 and N2 to reach two consecutive days of 90% correct choices with the first eye, then shift to the second eye. This experiment shows little or no sign of IOT. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second.

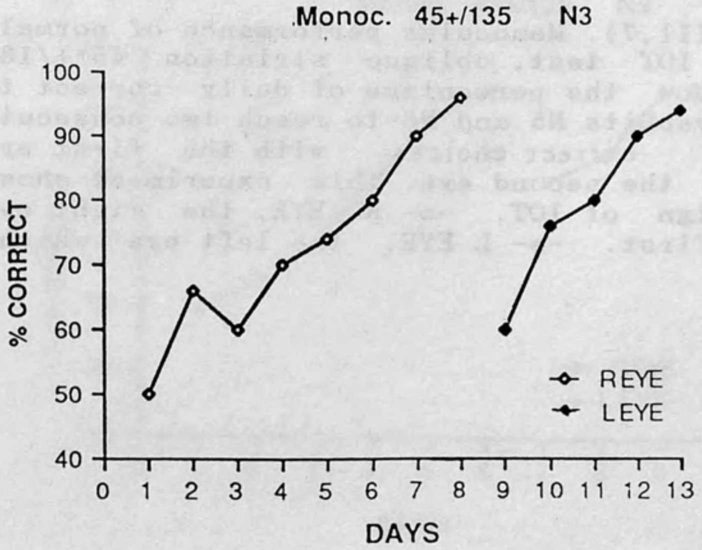
Figure (III,5). See opposite for legend.

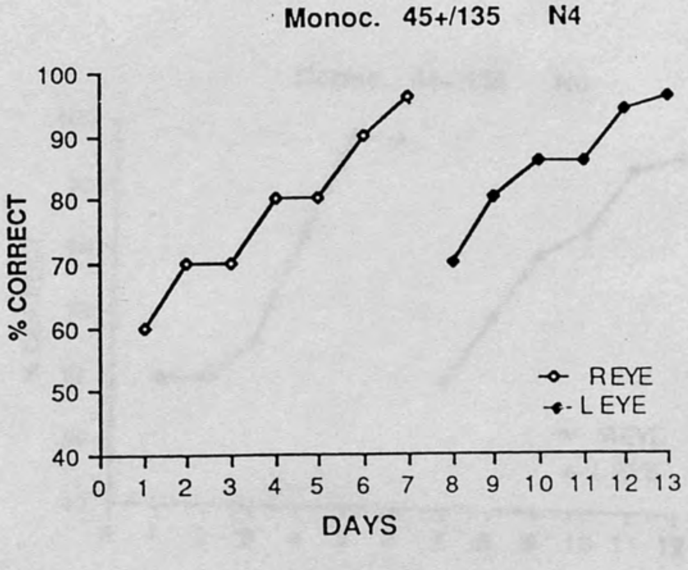


Opposite:

Figure (III,6). Monocular performance of normal rabbits on the IOT test, oblique striation 45°+/135°. The graphs show the percentage of daily correct trials of the two rabbits N3 and N4 to reach two consecutive days of 90% correct choices with the first eye, then shift to the second eye. This experiment shows little or no sign of IOT. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second.

Figure (III,6). See opposite for legend.

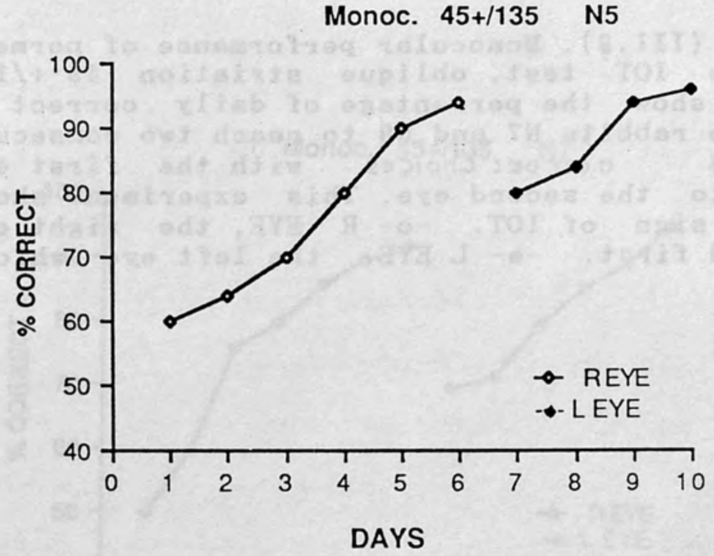


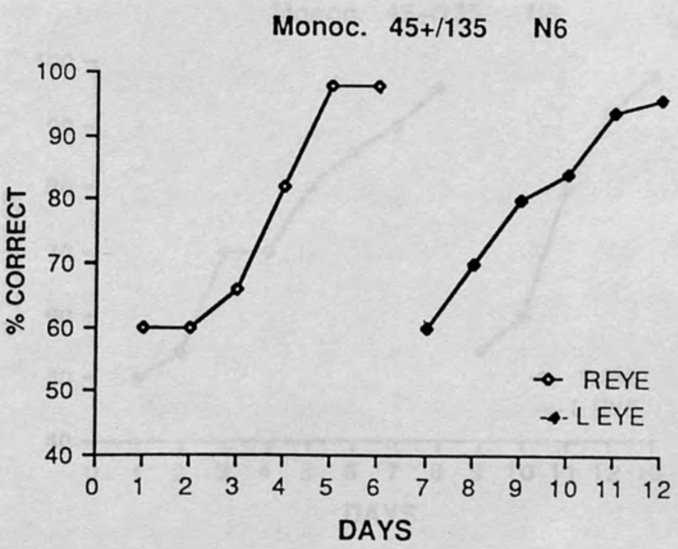


Opposite:

Figure (III,7). Monocular performance of normal rabbits on the IOT test, oblique striation 45°+/135°. The graphs show the percentage of daily correct trials of the two rabbits N5 and N6 to reach two consecutive days of 90% correct choices with the first eye, then shift to the second eye. This experiment shows little or no sign of IOT. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second.

Figure (III,7). See opposite for legend.

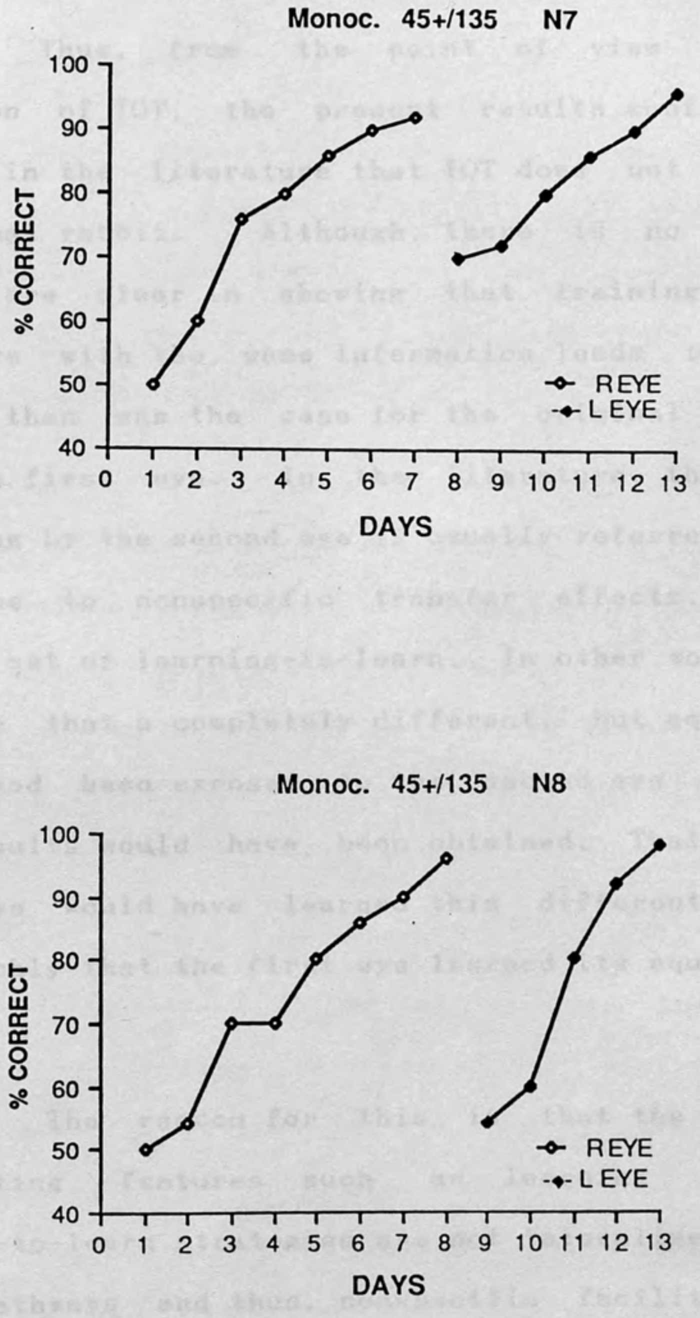




Opposite:

Figure (III,8). Monocular performance of normal rabbits on the IOT test, oblique striation 45°+/135°. The graphs show the percentage of daily correct trials of the two rabbits N7 and N8 to reach two consecutive days of 90% correct choices with the first eye, then shift to the second eye. This experiment shows little or no sign of IOT. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second.

Figure (III,8). See opposite for legend.



success does not automatically trigger subsequent criterion performance. Several more days of training are required before that is obtained.

Thus, from the point of view of any definition of IOT, the present results confirm the findings in the literature that IOT does not exist in the normal rabbit. Although, there is no IOT the results are clear in showing that training in the second eye with the same information leads to faster learning than was the case for the original training with the first eye. In the literature, the rapid relearning by the second eye is usually referred to as being due to nonspecific transfer effects.such as learning set or learning-to-learn. In other words, if we assume that a completely different, but equivalent problem had been exposed to the second eye then the same results would have been obtained. That is the second eye would have learned this different problem more quickly that the first eye learned its equivalent problem.

The reason for this is that the general facilitating features such as learning set and learning-to-learn strategies are not lateralised to the visual pathways and thus, nonspecific facilitation is possible.

One of the features of this argument is that as each animal becomes experienced over a range of problems the amount of nonspecific facilitation gradually reduces or gets less and less.

Some support for this notion can be seen from the results given in Fig.III,9(A) where the average daily errors are plotted for the first four days of training on the first two problems of brightness and pattern tasks.

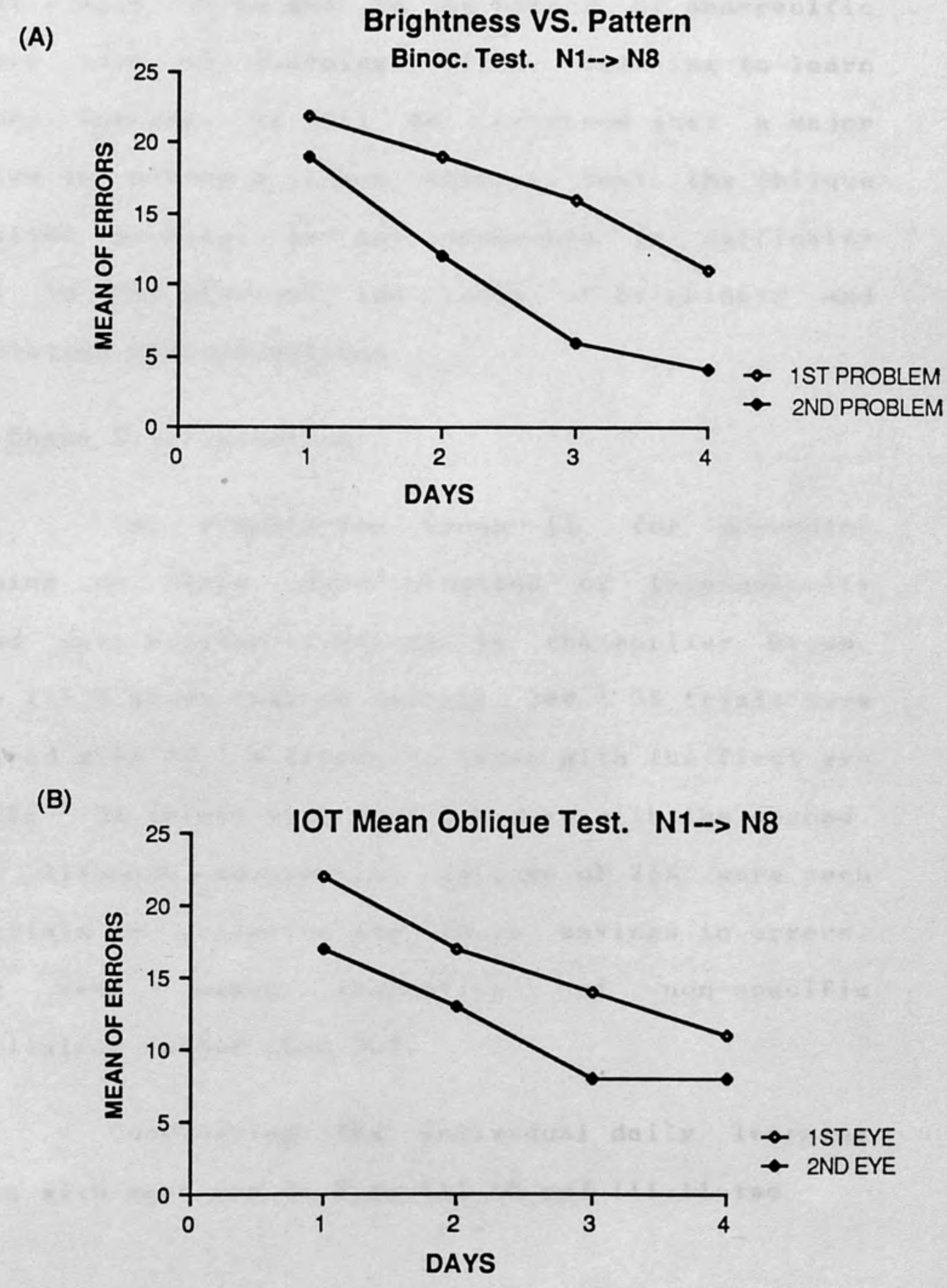
In III,9(B) the daily error scores for the first four days of training are plotted for the third problem (oblique striation) with the first and second eye. Binocular learning with the second problem shows saving scores on the first day, where there are 14% savings (Fig.III,9(A)). On the second day there are 37% savings, on the third day 62% and on the fourth day 73% savings.

In Fig.III,9(B) we can see that the second eye also shows savings in learning the same problem. The amount of these savings are similar compared to those seen in the Fig. 9(A). With the oblique striations the first day of training on the second eye shows 23% saving, on the second day 23% saving, on the

Opposite:

Figure (III,9). Learning performance of normal rabbits on the brightness versus pattern and on the IOT test (oblique striation). The graph 9(A) gives the average daily errors of the first four days of training on the first two problems of brightness and pattern tasks. The graph 9(B) gives the agerage daily error scores for the first four days of training on the oblique striation with the first and second eye.

Figure (III,9). See opposite for legend.



third day 43% and on the fourth day 27% saving.

These results are not evidence for IOT and appear likely to be due to the effect of nonspecific factors such as learning set or learning-to-learn factors. However, it must be stressed that a major problem in making a strong case, is that the oblique striation problem, is not comparable in difficulty level to the previous two tasks of brightness and orientation discriminations.

C.2. Shape Discrimination:

The results for Group II for monocular training on shape discrimination of triangularity showed very similar findings to the earlier Group. Table III,6 shows that on average 300 ± 35 trials were required with 49 ± 8 errors to learn with the first eye and 225 ± 32 trials with 33 ± 8 errors with the second eye. Although, substantial savings of 25% were seen for trials to criterion and 33% in savings in errors, these were again indicative of non-specific facilitation rather than IOT.

Considering the individual daily learning curves with each eye in Figs.III,10 and III,11 two

Table III,6

### Interocular Transfer (10T) Test
### Inverted Triangle Shape

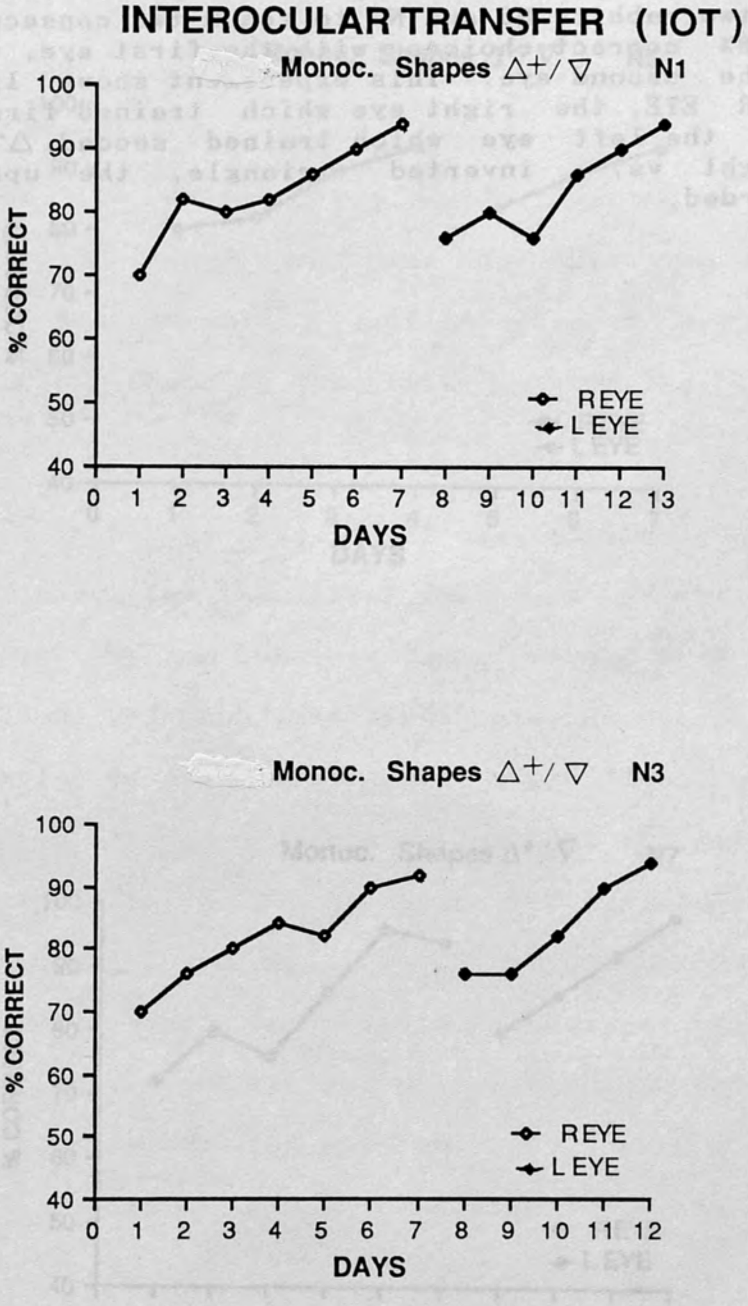
| Animal | Trials |  | Errors |  |
|---|---|---|---|---|
|  | RE | LE | RE | LE |
| N1 | 350 | 300 | 58 | 49 |
| N3 | 350 | 250 | 63 | 45 |
| N5 | 200 | 150 | 27 | 16 |
| N7 | 300 | 200 | 48 | 22 |
| Mdn | 325 | 225 | 53 | 34 |
| Mean | 300 | 225 | 49 | 33 |
| SEM | 35 | 32 | 8 | 8 |

Table (III,6). Acquisition performance of normal rabbits on the IOT test. The table gives the median,mean and standard errors of the trials and errors for both eyes to final criterion during shape striation training test. 50 daily training trials were given. RE, the right eye which trained first. LE, the left eye which trained second.

**Opposite:**

Figure (III,10). Monocular performance of normal rabbits on the IOT test, inverted triangle shape. The graphs show the percentage of daily correct trials of the two rabbits N1 and N3 to reach two consecutive days of 90% correct choices with the first eye, then shift to the second eye. This experiment shows little IOT. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second. $\triangle^{+}/\bigtriangledown$ , the upright vs. inverted triangle, the upright was rewarded.

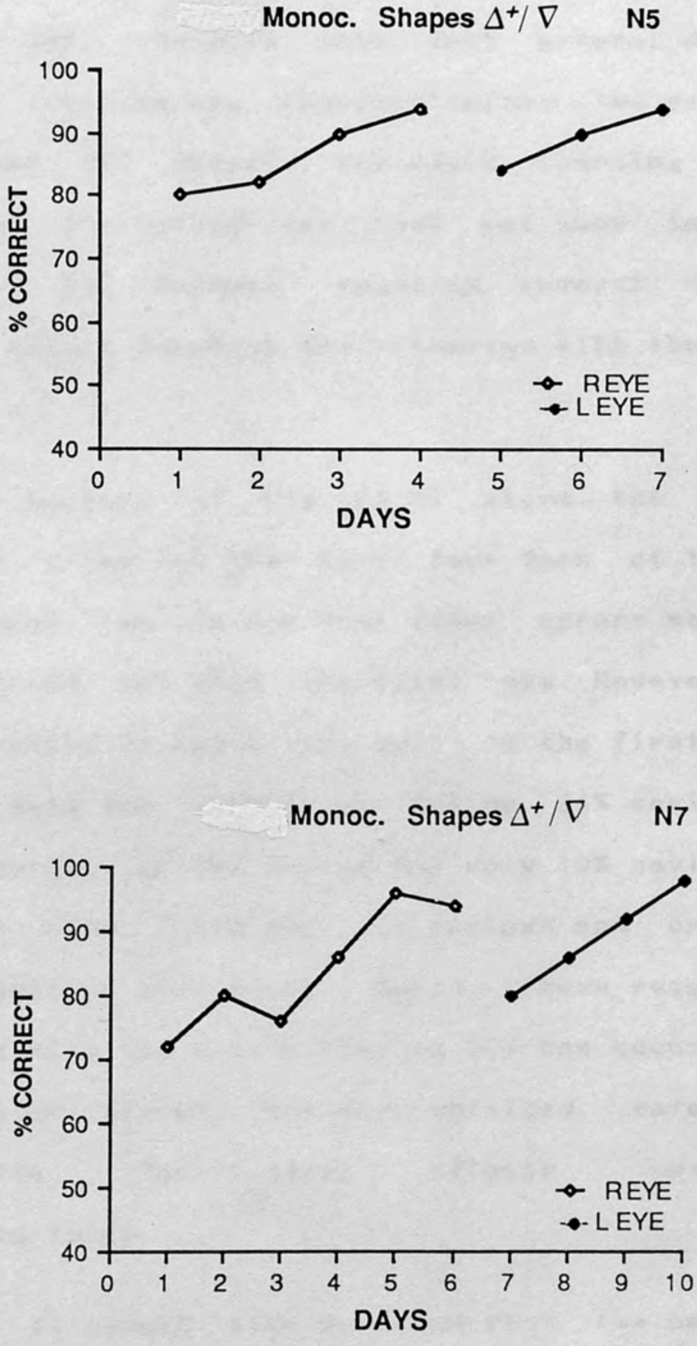
Figure (III,10). See opposite for legend.



Opposite:

Figure (III,11). Monocular performance of normal rabbits on the IOT test, inverted triangle shape. The graphs show the percentage of daily correct trials of the two rabbits N5 and N7 to reach two consecutive days of 90% correct choices with the first eye, then shift to the second eye. This experiment shows little IOT. -o- R EYE, the right eye which trained first. -●- L EYE, the left eye which trained second. $\triangle^{+}/\nabla$, the upright vs. inverted triangle, the upright was rewarded.

Figure (III,11). See opposite for legend.



points can be made : (1) evidence of learning set influence can be seen in the facilitated performance with the first eye on the first day of training at around 70-80%. Despite this fact several days of continued training are required before the criterion was reached, (2) despite the rapid learning by the first eye, the second eye does not show immediate transfer. All animals required several days of training before reaching the criterion with the second eye.

Looking at Fig.III,12 where the average errors are given for the first four days of training for both eyes, we can see that fewer errors were made by the second eye than the first eye. However, the level of saving is again very small on the first day of training with the second eye making 21% savings on errors, whereas, on the second day only 10% savings on errors are made. Third day 22% savings and on fourth day 50% savings were found. Again, these results are consistent with the notion that no IOT has occurred and the amount of savings that were obtained, were due to non-specific facilitation effects such as learning-to-learn.

It should also be noted that the amount of savings on the first and second eye on this last set of

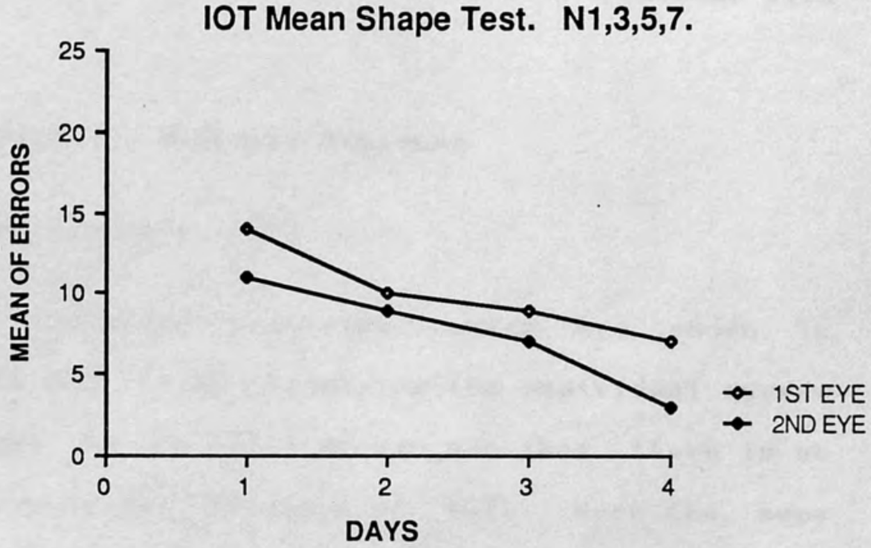


Figure (III,12). Training performance of normal rabbits on the interocular transfer (IOT) test of inverted triangle task for all subgroup of four rabbits (N1,N3,N5 and N7). The graph shows the average of errors of four days of monocular trials needed to reach successive criterion levels during training of the first eye and the second eye.

-o- 1ST EYE, the first eye which is the right eye.

-●- 2ND EYE, the second eye which is the left eye.

problems is smaller than it was on the first set. This again is consistent with the predictions of the fact that monocular training with each eye is equivalent to training with different but equivalent problems with each eye.

### C.3. Nictitating Membrane Response

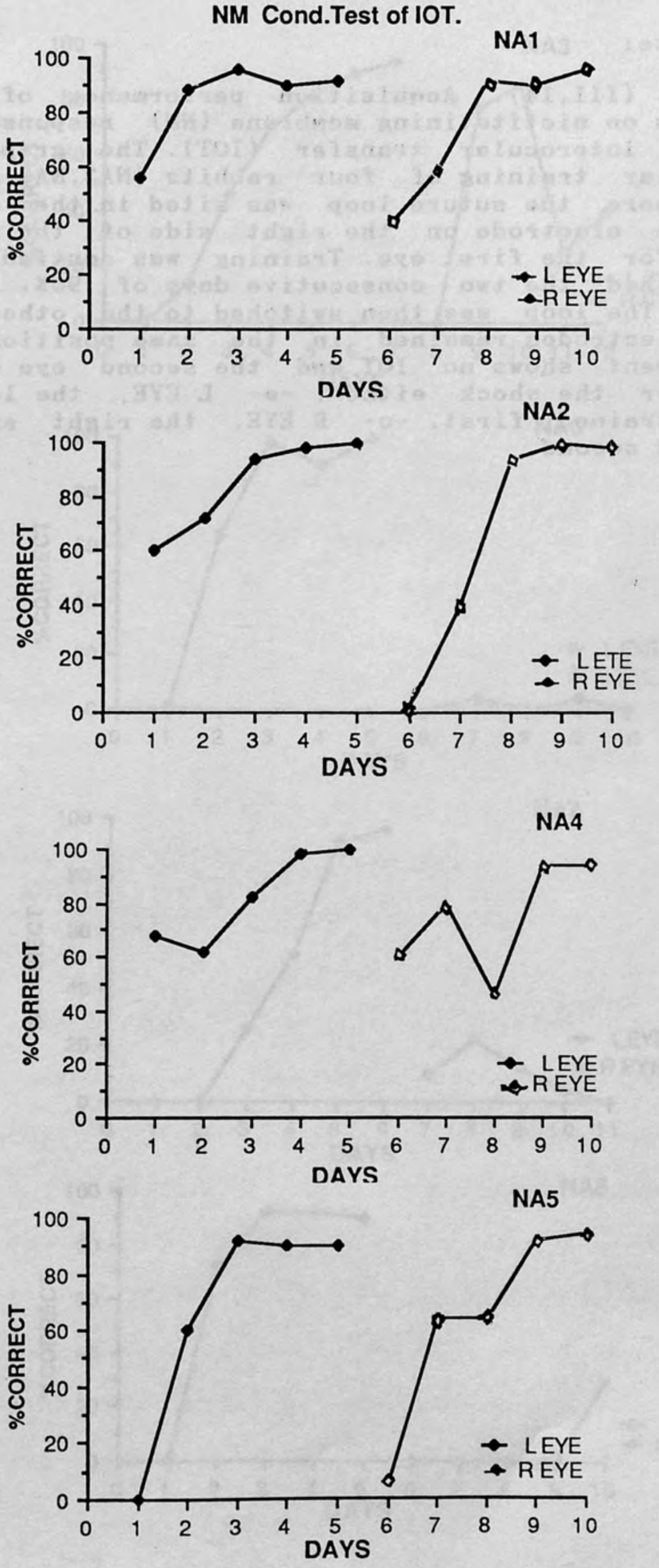
### Interocular Transfer (IOT)

Individual learning curves are shown in Figs.III,13 and III,14. Examining the individual curves for each eye in Fig.III,4 we can see that there is no animal showing any evidence of IOT. Here the same definition of IOT is used as in the previous experiment. That is, IOT is present, when after training information with the first eye the second eye would have immediate access to that learning. Thus with NM conditioning one would expect typical acquisition curves, with the first eye. On the first day there would be a low frequency of conditioning responses and over subsequent days this would systematically increase to greater than 90% performance level. When the second eye is exposed to the same CS-US input, then it would be expected to give immediate criterion performance.

Opposite:

Figure (III,13). Acquisition performance of normal rabbits on the nictitating membrane (NM) response during interocular transfer (IOT). The graphs show monocular training of four rabbits (NA1,NA2,NA4 and NA5) where the suture loop was sited in the right NM and the right side of the rabbit's cheek for the first eye. Training was continued until it reached the two consecutive days of 90%. Then the loop and the electrode were switched to the other NM and the left rabbit's cheek. -●- L EYE, the left eye which trained first. -o- R EYE, the right eye which trained second.

Figure (III,13). See opposite for legend.

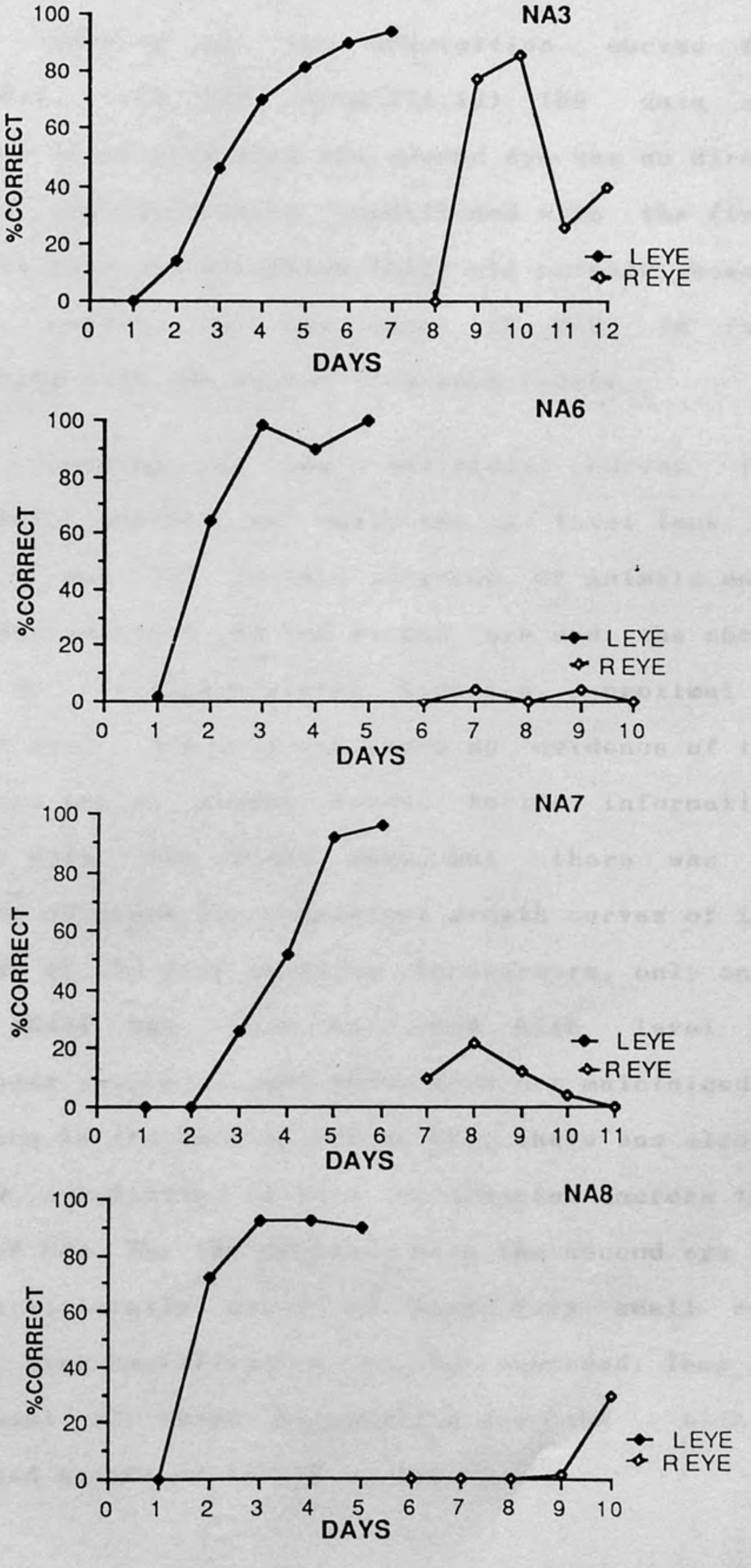


Opposite:

Figure (III,14). Acquisition performance of normal rabbits on nictitatining membrane (NM) response during interocular transfer (IOT). The graphs show monocular training of four rabbits (NA3,NA6,NA7 and NA8) where the suture loop was sited in the right NM and the electrode on the right side of the rabbit's cheek for the first eye. Training was continued until it reached the two consecutive days of 90%.

The loop was then switched to the other NM but the electrodes remained in the same position. This experiment shows no IOT and the second eye did not transfer the shock either. -●- L EYE, the left eye which trained first. -o- R EYE, the right eye which trained second.

Figure (III,14). See opposite for legend.



Looking at the acquisition curves for NA1,NA2,NA4, and NA5 (Fig.III,13) the data are consistent in showing that the second eye has no direct access to the information conditioned with the first eye. With only one exception (NA2) all animals showed parallel curves. In the case of NA2 in fact conditioning with the second took much longer.

Looking at the individual curves for NA3,NA6,NA7, and NA8 we again see a total lack of evidence of any IOT. In this subgroup of animals only the CS was switched to the second eye and the shock remained on the contralateral side i.e. proximal to the first eye). Not only was there no evidence of the second eye having direct access to the information acquired with the first eye, but there was no convincing evidence for consistent growth curves of the percentage of CRs over training. Furthermore, only one animal (NA3) was able to show high level of conditioning responses, but these were not maintained. In addition to the lack of IOT of CRs, there was also a large and substantial failure of transfer across the midline of URs. The URs obtained with the second eye to the contralaterally sited US were very small and required high amplification to be recorded. Thus a major point of these observation was the highly lateralised nature of the UR to the US.

Although the contralateral UR was small (reduced by a factor of 3) it did not show any conditioning to the CS. This was only examined for five days of training, and it is possible that with extended training visual conditioning could have occurred.

## III.5. DISCUSSION AND CONCLUSION

The present experiments have examined the question of whether or not IOT of visual information exists in the normal rabbit. The method used to measure IOT was that of the monocular training paradigm where first one eye is exposed to visual learning and then the second eye is subsequently and independently exposed to the same visual learning.

In normal cats and monkeys access by the second eye to the information acquired by the first eye would be immediate and automatic. In the rabbit, and to lesser extent in the rat, this has not been found to be the case. When the same visual information is presented to the second eye, the rabbit shows no ability to access the previous learning acquired with the first eye. It is as if what is visually learned with either eye goes to separate and entirely inaccessible storage sites. From this point of view the rabbit would appear to be nature's natural split brain animal.

The present experiments were designed to test the question that monocular visual learning, in the rabbit, creates special problems. This is due to the massive change in the visual field when the learning becomes state-dependent upon the animals monocular scanning and oculomotor guidance strategies. Thus when the animal is placed in the same situation with the opposite eye opened,it has to " decouple" its choice behaviour from its previously acquired state-dependent conditioning.

For this reason the animals in Group I were exposed to a pretraining procedure which was designed to break any state-dependent tendencies. For the first two problems of brightness and pattern tasks the animals were first trained binocularly on each task, and then each eye was subsequently retrained monocularly.

The results showed that when animals were retraining monocularly on the same problem that had been learned binocularly, there was still a substantial performance loss. The animals did not however lose all information, because they required only one to two days monocularly pretraining to reach criterion. This clearly suggests that the animal had a performance deficit when it was tested on familiar material for the first time with monocular vision.

After two problems have been trained first binocularly and then monocularly, the performance deficit produced by monocular testing on the second problem was considerably reduced. This finding was strong evidence that the animals retention was state-dependent on such visual field conditions as binocularity versus monocularity. It would suggest that the repeated regime from binocular to monocular training was a successful "decoupling" procedure analogous to that developed by Russell et al (1979) in the rat.

The results of the two subsequent IOT tests are therefore contrary to any state-dependent explanation of IOT failure in the rabbit. On both the oblique striation and the inverted triangle problems all animals showed equal lack of IOT. In no case was there any evidence of access by the second eye to the information learned by the first eye.

Although some facilitation was seen, there was in no case of evidence of specific information transfer between eyes. This facilitation was indicative of nonspecific effects such as learning set or learning-to-learn. These results cast considerable doubt on the theory that IOT is blocked in the rabbit due to monocular training leading to state-dependent information retrieval cues.

Monocular training using visual Pavlovian conditioning of the NM also failed to produce any evidence of IOT. Considering the results of the first Group of animals where both the CS and US were transferred "across-midline", then similar findings were found to those obtained using the visual two choice apparatus. Despite the simple nature of the assertive learning task no evidence was found to indicate access by the second eye to the learning of the first eye. This combined with the findings that the second Group of animals suggest remarkable lateralisation of NM learning in the normal rabbit. This second Group of animals had only the CS transferred across the midline, with the US remaining at the original input location adjacent to the first eye. Under these conditions there was almost no transfer of the UR across the midline. It is not therefore surprising that no signs of learning with the second eye were found on this subgroup. It could be that given the very small size of the UR (obtained from contralateral stimulation) that associative learning would take much longer than the animals were tested for in this experiment.

The importance of the failure to obtain IOT to simple visual NM conditioning cannot be over-estimated. In this type of simple associative learning no visual scanning or oculomotor control strategies are possible or relevant. The failure to get IOT to such a simple form of visual learning cannot therefore be in any way attributed to any oculomotor state-dependency induced by monocular training.

These findings strongly suggest that some other explanation must be considered to explain the present finding of a total lack of visual IOT in the rabbit. Several possibilities can be considered.

(a) Firstly it may be possible that the rabbit is indeed incapable of integrating information binocularly. If this is the case then it would suggest that the rabbit does not use its uniquely small binocular overlap of 24°. This position is a reasonable summary of a long series of experimental failures to demonstrate IOT in the rabbit. Such a position however cannot be sustained on scientific grounds in any serious manner. There is a small but important body of evidence that indicates that the rabbit does use its binocular segment during proximal vision (van Hof & Lagers Haselen, 1970). Furthermore, there is also evidence that a normal rabbit can be trained to use binocular vision to integrate separate and different inputs from each eye (van Hof & Russell, 1976).

Finally, the presence of binocular visual units on the borders of visual areas 17 and 18 conforms to exactly the same "ground plan" as that seen in such higher mammals as cats and monkeys. For these reasons it seems unlikely that IOT does not exist in the rabbit.

(b) It may will be that the present findings of a lack of IOT for a visual NM response should be considered cautiously. It is true that no scanning or oculomotor control strategies are required for such learning, however this is then only evidence that oculomotor state-dependency theory cannot be the explanation for every failure of IOT. It does not say more than that. It may be furthermore that a separate explanation must be found to explain the failure of IOT, first for NM conditioning and second for two choice discrimination learning. It could well be that very different explanations apply for the two types of visual learning. For example, in the case of NM conditioning it should be noted that the animal solely responds to ambient illumination without any specific retinal cues of position or orientation. In other words in this type of visual learning the animal merely has to detect light onset, and nothing else. The location or orientation of the light is irrelevant, hence no specific retinal cues are important. Under these conditions, the response of the retina would be quantitive to indicate the intensity of the CS signal. It could be that the information that is processed is entirely in terms of the number of ganglion cells involved. In which case the major signal would be via the crossed fibre projection, and the main information could go to monocular cortical units , and thus be inaccessible by the other eye. If this is the case under conditions where the CS of ambient illumination forces the eye to act as a light meter it would not then be surprising that no IOT occurs. Such speculation if true, would suggest that IOT for Pavlovian conditioning could occur in the chiasma sectioned rabbits where only retinal projections to binocular cortical cells remain. To test this notion adequately a different response than the NM must be found. It is hoped this will be the subject for future research.

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# APPENDIX

## Histological Procedure

## Fixing, Embedding, Sectioning and Staining Techniques:

### (1) Perfusing and Fixing solutions:-

(A) Physiological saline: Sodium Chloride "Mammals, 0.9%" 18 g in 2000 ml Distilled water.

(B) Neutral buffered 10% formalin: Sodium phosphate, monobasic 8g Sodium phosphate, dibasic 12.8g Formaldehyde 200 ml Distilled water 1800 ml.

(C) Sucrose-Formalin: Sucrose 300 g dissolve first in 725 ml of Distilled water then add Formaldehyde 100 ml.

### (2) Embedding technique:

Gelatin preparation:-

1. 50 g gelatin . 2.50 g sucrose.

3. 250 ml of buffer solution (mixture of $KH_2\ PO_4$=1.7 g in 125 ml of $H_2O$ and $Na_2\ HPO_4$=4.5 g in 125 ml $H_2O$). The buffer mixture was warmed to 50 °C and added 250 ml of $H_2O$, stirred with the gelatin added very slowly, then the sucrose in the same way. When the embedding

solution had been prepared, the stored fixed brains were washed for 24 hrs. They were then put in 10% gelatin, 10% sucrose for one hour at 37 °C. The brains were then put in 10% of formalin, 30% sucrose and left until the brains sank (3 days minimum). The brains were blocked in the gelatin preparation, each in a small container and kept in the refrigerator until they hardened. The brains were removed from the containers and the unwanted gelatin was cut until it became near to the brain section tissue. Blocks were stored in the 10% formalin, 30% sucrose for sectioning procedure.

(3) Sectioning technique:

Frozen sections:- Blade-Wedge type at about 10°C on a base sledge microtome, for frozen sections "Kryomat 1700".

Liquid carbon dioxide $CO_2$ was used for the freezing of the tissue block. For freezing the brain, a special freezing medium such as Tissue-Tek O.C.T compound onto the base sledge was used. The tissue was placed on O.C.T and held until it pointed in a desired direction and kept the O.C.T around the brain. That made the tissue freeze gradually and solidly. A hole was made on one side with a needle in the white matter, to indicate the correct orientation when mounting sections on slides. Wetting tissue and knife with 70% alcohol using camel hair brush and the brains were cut at 30 µm. Collect sections in distilled water and mount them onto subbed slides coated with a drop of Glycerin albumen, and allow to dry on warming plate at 45°C for 1-2 hours, then in oven overnight, same temperature.

Subbing solution:-

1 gm phenol crystals, 2.5 g gelatin powder, 100 ml distilled water. The phenol was first dissolved in water, gelatin then added and warm until the gelatin dissolved. Slides were cleaned with 70% alcohol and placed in the subbing solution for 20 min. at 37°C

(4) Staining technique:

Cresyl Fast Violet Stain Method

Cresyl fast violet 1 g, Distilled water 1000 ml, 10% Acetic acid 10 mlwas used. Filter, and kept in the oven at 45°C. The frozen sections were mounted on the subbed slides and kept to dry over night. Slides were put in the slide holder through staining programme.

1. Xylene--- 3 min.
2. Xylene--- 3 min.

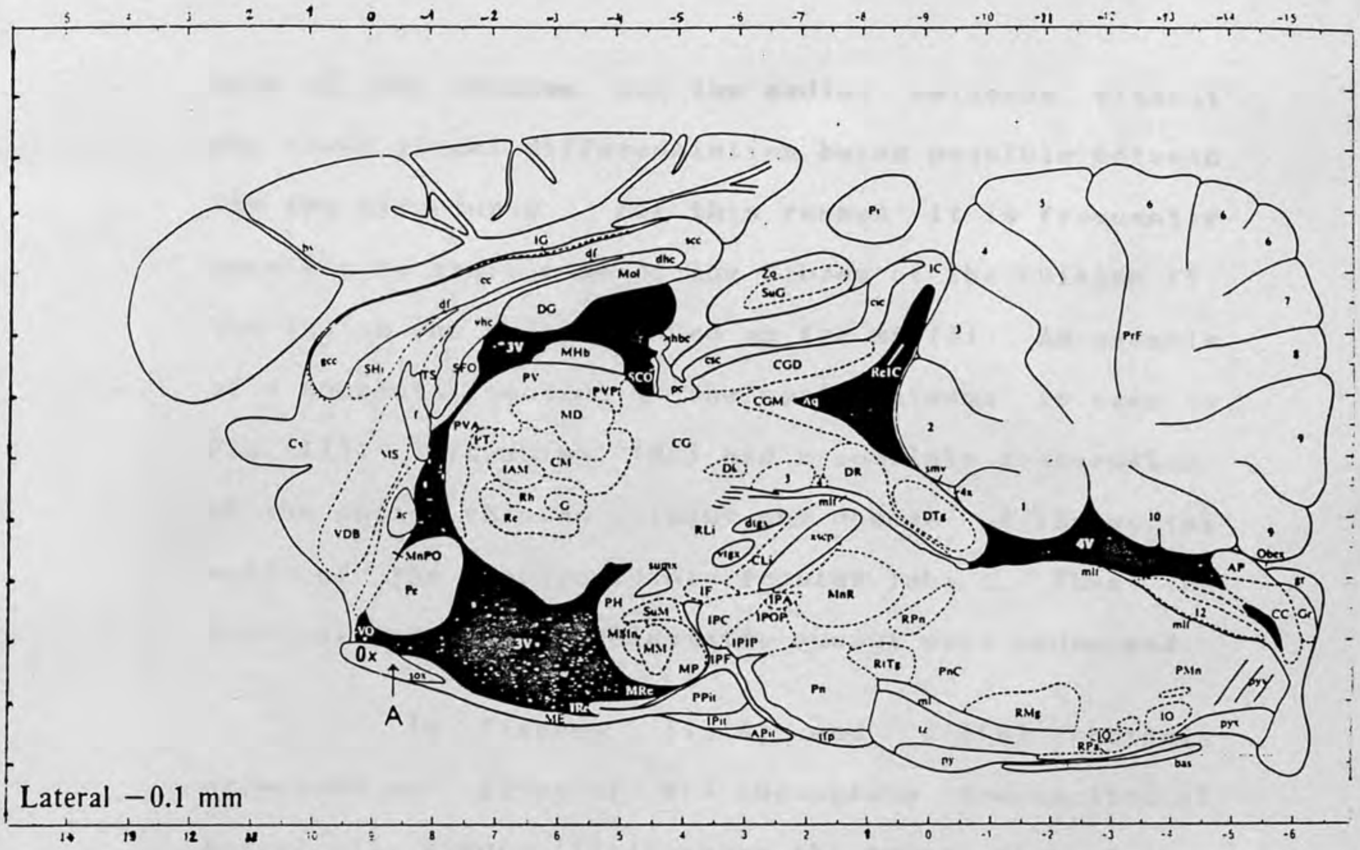
3. 100%, 95%, 70% Propanol --- 3 min each.
4. Distilled water --- 3 min.
5. Cresyl stain --- 2 min (warm at 45°C).
6. Distilled water --- rinse.
7. 70%, 95%, 100% Propanol --- 3 min each.
8. Choloroform --- 5 min.
9. 95% alcohol & two drops Acetic acid --- 5 min.
10.95%, 100% Propanol --- 3 min each (differentiation stage, if sections are not differentiated completely, then returned back to stage 9).
11. Xylene (two changes) 3 min each.
12. Apply resin (DPX) and cover glass.

After that, the slides left to dry for 2-3 days then analysed under the microscope.

### (5) Lesions:

Figure (I) gives a schematic of the lateral view of the rat brain where the midline structures are shown 0.1 mm from the sagittal plane. The longitudinal view of the optic chiasma can be seen, where it merges into the supra optic decussation laterally and posteriorally into the medial eminence.

When the chiasma is approached from the dorso-frontal aspect direct visual access is gained



| | |
|---|---|
| 3 | principal oculomotor nu |
| 3V | third ventricle |
| 4 | trochlear nu |
| 4V | fourth ventricle |
| 4x | trochlear decussation |
| 12 | hypoglossal nu |
| ac | ant commissure |
| AP | area postrema |
| APit | ant lobe pituitary |
| Aq | cerebral aqueduct |
| bas | basilar artery |
| bv | blood vessel |
| CC | central canal |
| cc | corpus callosum |
| CG | central grey |
| CGD | central grey, dors |
| CGM | central grey, med |
| cic | commissure inf colliculus |
| CLi | caudal linear nu raphe |
| CM | central med th nu |
| csc | commissure sup colliculus |
| Cx | cerebral cortex |
| df | dors fornix |
| DG | dentate gyrus |
| dhc | dors hip commissure |
| Dk | nu of Darkschewitsch |
| DR | dors raphe nu |
| DTg | dors tegmental nu |
| dtgx | dors tegmental decussation |
| f | fornix |
| G | gelatinosus nu thalamus |
| gcc | genu corpus callosum |
| Gr | gracile nu |
| gr | gracile fasciculus |
| hbc | habenular commissure |
| IAM | interanteromedial th nu |
| IC | inf colliculus |
| IF | interfascicular nu |
| IG | induseum griseum |
| IO | inf olive |
| IPA | interpeduncular nu, apical |
| IPC | interpeduncular nu, central |
| IPF | interpeduncular fossa |
| IPIP | interpeduncular nu, inner post subnu |
| IPit | intermediate lobe pituitary |
| IPOP | interpeduncular nu, outer post subnu |
| IRe | infundibular recess third ventricle |
| MD | mediodorsal th nu |
| ME | median eminence |
| MHb | med habenular nu |
| ml | med lemniscus |
| mlf | med longitudinal fasciculus |
| MM | med mammillary nu, med |
| MMn | med mammillary nu, median |
| MnPO | median preoptic nu |
| MnR | median raphe nu |
| Mol | molecular layer dentate gyrus |
| MP | med mammillary nu, post |
| MRe | mammillary recess third ventricle |
| MS | med septal nu |
| Obex | obex |
| ox | optic chiasm ← |
| pc | post commissure |
| Pe | periventricular hy nu |
| PH | post hy nu |
| Pi | pineal gland |
| PMn | paramedian reticular nu |
| Pn | pontine nuclei |
| PnC | pontine reticular nu, caudal |
| PPit | post lobe pituitary |
| PrF | primary fissure |
| PT | paratenial th nu |
| PV | paraventricular th nu |
| PVA | paraventricular th nu, ant |
| PVP | paraventricular th nu, post |
| py | pyramidal tr |
| pyx | pyramidal decussation |
| Re | reuniens th nu |
| ReIC | recess inf colliculus |
| Rh | rhomboid th nu |
| RLi | rostral linear nu raphe |
| RMg | raphe magnus nu |
| RPa | raphe pallidus nu |
| RPn | raphe pontis nu |
| RtTg | reticulotegmental nu pons |
| scc | splenium corpus callosum |
| SCO | subcommissural organ |
| SFO | subfornical organ |
| SHi | septohippocampal nu |
| smv | sup medullary velum |
| sox | supraoptic decussation ← |
| SuG | superficial grey layer sup colliculus |
| SuM | supramammillary nu |
| sumx | supramammillary decussation |
| tfp | transverse fibers pons |
| TS | triangular septal nu |
| tz | trapezoid body |
| VDB | nu vertical limb diagonal band |
| vhc | vent hip commissure |
| VO | vascular organ lamina terminalis |
| vtgx | vent tegmental decussation |
| xscp | decussation sup cerebellar peduncle |
| Zo | zonal layer sup colliculus |

The ten lobules of the cerebellum are indicated by the numerals 1-10

Figure (I). Schematic view of the rabbit's brain showing the optic chiasma and all midline structures. A lest of abreviations is given above (Paxions & Watson, 1982).

both of the chiasma and the medial eminence, without any clear visual differentiation being possible between the two structures. For this reason it is frequently possible to spare some of the fibres of the chiasma if the lesion was only extended as far as (A). An example of a complete section of the optic chiasma is seen in Fig.(II). This animal (R2) had a complete transection of the optic chiasma without any damage of the medial wall of the ventromedial frontal lobe . Thus the critical supra-optic chiasmatic nuclei were undamaged.

In Figures III(A) and III(B) photomicrographs are given of the incomplete transection of animal V71. Figure III(A) shows the transection of the anterior part of the chiasma where it is clear the chiasma fibres are completely cut from dorsal to ventral in a vertical section. Some damage to the right ventromedial wall of the frontal hemisphere is seen. Figure III(B) shows the posterior part of the chiasma to be intact and also shows the ventro-medial walls of both hemispheres to be undamaged. In this animal approximately 15% of the posterior part of the chiasma was intact. It is interesting to note that this animal showed normal oculomotor reflexes postoperatively. There was a normal OKN of 12 responses per minute at stimulus velocity of 12° per second. Also the acquisition of the NM response to light was normal.

Figure (II). This animal(R2) has a complete transection of the optic chiasma without any damage of the medial wall in the frontal lobe.

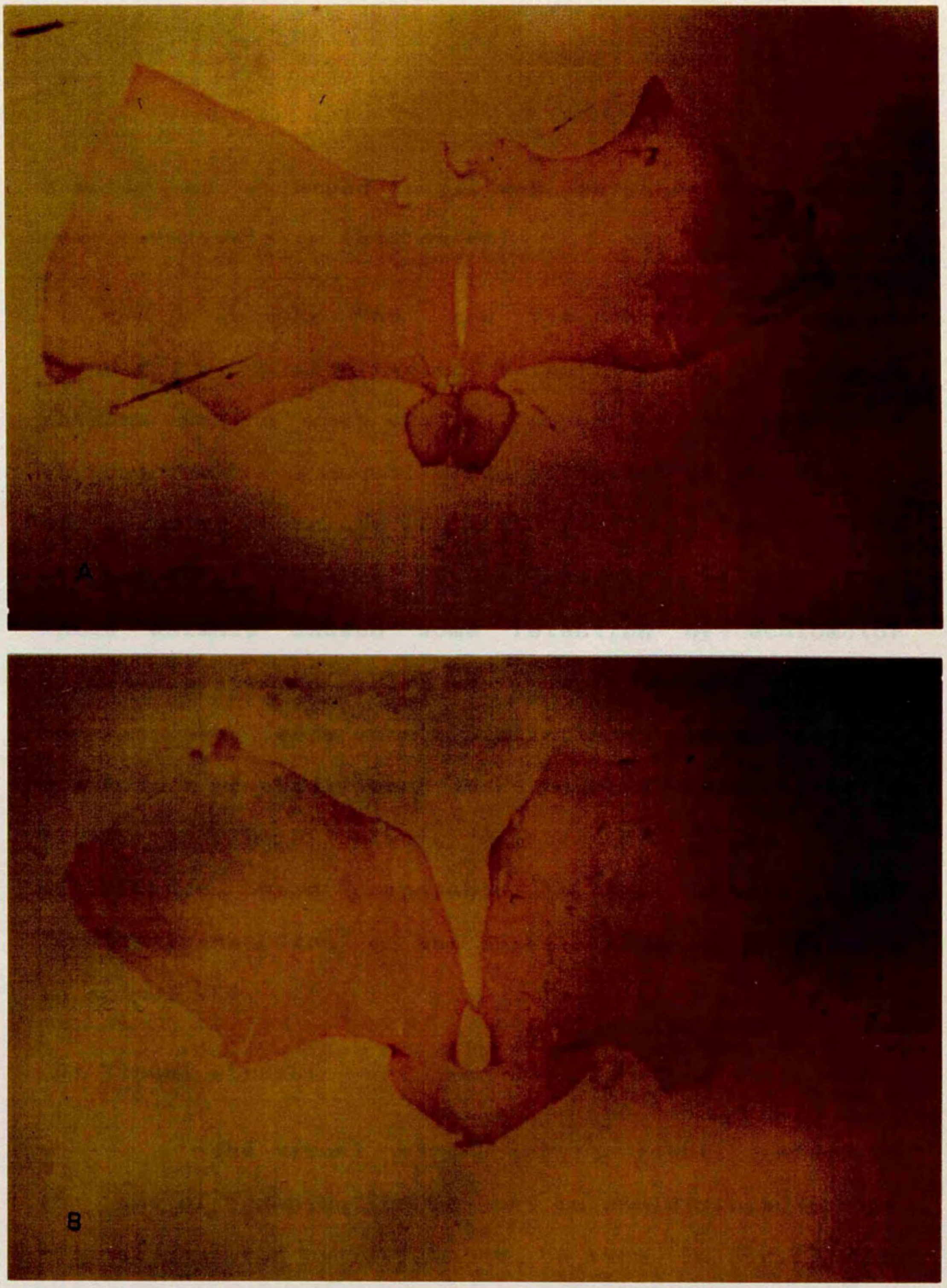


Figure (III). Transection of the optic chiasma in V71. A: shows a section of the anterior part of the chiasma. There if can be seen that the cut is vertical and that there is also some damage to the medial wall. B: shows a section of the anterior part of the chiasma where the section failed to reach the outer limits of the chiasma.

However an enlarged pupil was permanently observed postoperatively in this animal.

Animals V69 and V70 showed a similar transection of the anterior portion of the optic chiasma with a much smaller amount of the posterior chiasma remaining uncut. Crude estimates of the amount of spared tissue place it in the region of less than 5% of the total chiasma. It is important to note that these animals showed some retention of oculomotor reflexes postoperatively. Small amplitude and sluggish OKN responses were seen. Similarly a significant but low number of conditioned NM responding was possible to light. In both animals neither of these reflex performances were comparable to the normal level. Finally transection of the optic chiasma was complete in animal V66.

(6) Visual streak:

The visual streak in the rabbit refers to the type of organisation present in the distribution of retinal ganglion cells. As can be seen in Fig.IV when ganglion cell isodensity curves are plotted, there is a conspicuous organisation along the horizontal meridian. Unlike the cat, with its dart-board concentric organisation, the rabbit does not resolve detail toward

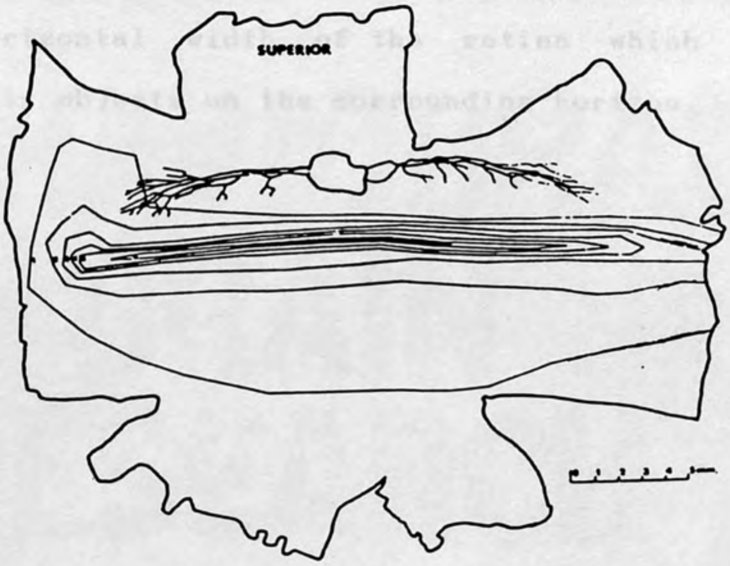


Figure (IV). A flat mount of the retina of the right eye of a rabbit. The blood vessels which overlay the myelinated band spread out from the optic nerve head. Ganglion cell isocount density lines are drawn in indicating the position of the visual streak. Numbers represent the ganglion cell count in thousands per mm². Note the area of high count under the optic nerve head and the upward bulge of the 3,2 and 1 x $10^3$ isocount lines in the region of nasal retina which deals with the ground under the animal nose (Hughes, 1971).

the centre of its retina. It has a broad band across the horizontal width of the retina which resolves uniformly objects on the surrounding horizon.

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complete contrast sensitivity function (CSF) of the rat's visual system. The current study was undertaken to establish the CSF of the rat by investigating the relationship between the VECP amplitude and the spatial and contrast features of patterned stimuli. The findings can then be compared with those in animals that have a reduced number of retinal ganglion cells as a result of neonatal tectal ablation or in an increase in their number in one eye as a result of neonatal removal of the other eye.

In adult animals, anaesthetized by fentanyl/fluanisone (Hypnorm, JANSSEN) and diazepam (Valium, ROCHE), pattern reversal VECPs were recorded in Area 17 in the region of representation of the central binocular visual field. Stimuli consisted of horizontal sinusoidally modulated gratings generated by a microcomputer displayed on a black/white video monitor subtending 40° x 26°. Mean screen luminance was 14.4 cd/m². The number of averaged responses varied between 256 and 2048, depending on the contrast and spatial frequency of the display. Transient responses (band-passed from 0.5-100 Hz, attenuated 49 dB/decade) were obtained with a 1 Hz contrast reversal. Various measures of VECP amplitude were used, namely: P1-N1, peal-to-peak value, second harmonic amplitude and peak amplitude of P1 in an even harmonics synthesized wave form.

The mean monocular CSF peaked around 0.1 c/deg, with a threshold sensitivity of 20-25 (1/ contrast threshold), showing a low frequency attenuation and a high frequency cut-off of 1.06 c/deg. The mean binocular CSF showed a cut-off of 1.20 c/deg, which matches several behavioural measurements of visual acuity. The greater bincoular sensitivity in the low frequency range (0.04 cycles/ degree) could be tentatively interpreted to the greater influence of the population of large ganglion cells that reaches its maximal density in the ipsilateral projection.

## THE ROLE OF THE UNCROSSED FIBRE SYSTEM IN INTEROCULAR TRANSFER IN THE RABBIT AND RAT

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At least 90% of the optic nerve fibres decussate in the optic chiasma in both rabbit and rat. Contralaterally projecting ganglion cells are found throughout the rabbit retina, whereas ipsilateral projecting cells are restricted to a very narrow strip on the margin of the temporal retina. Relevant to this is the fact that the binocular field of the rabbit is small at 24° and that the retinal origin of binocular cortical cells derives in the main from the temporal part of the retina. The rat has a wider binocular field of 80°. It also has a much greater distribution of the ipsilateral projecting ganglion cells over the temporal retina. Otherwise the two animals are strikingly similar.

In order to directly examine the role of the uncrossed optic fibre projection to vision, a technique of midsagitally cutting the optic chiasma was developed. Both normal and chiasma-sectioned rabbits and rats were tested on a variety of visual discrimination tasks.

Following transection of all contralateral retinal projections, naive rabbits had great difficulty in learning such simple visual discriminations as intensity and orientation differences. In contrast rabbits previously trained on these tasks showed perfect retention following chiasma-section. In addition these animals had a complete loss of the optokinetic reflex and a profound disruption of the vestibulo-ocular reflex[1]. In rats chiasma-section had no effect on either de novo acquisition or retention of brightness and pattern discrimination learning. Additionally interocular transfer of visual information was dramatically improved following the removal of the monocular crossed fibre system in rat. The significance of these findings was discussed in terms of the role of the ipsilateral fibre system in interhemispheric integration.

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## THE EFFECT OF PASSIVE AVOIDANCE TRAINING ON SYNAPTIC CONTACT CURVATURE IN THE CHICK PALEOSTRIATUM AUGMENTATUM (PA) AND LOBUS PAROLFACTORIUS (LPO)

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One-trial passive avoidance training, in which day-old chicks are trained to avoid pecking at a bead coated with an aversive tasting substance such as methylanthranilate, has been used for some time in our laboratory as a model for studying the cellular correlates of memory formation. Recent studies[1] have demonstrated that after training enhanced metabolic activity (as measured by the $^{14}$C-2-deoxyglucose technique) occurs in the forebrain in the medial hyperstriatum ventrale and two regions of the paleostriatal complex, the paleostriatum augmentatum (PA) and lobus parolfactorius (LPO).

Within the paleostriatal complex, following training, alterations in a number of synaptic parameters have also been observed in the LPO but not in the PA[2,3]. These changes occur largely in the left hemisphere and include alterations in the length of the synaptic contact zone, in the volume density of the pre-synaptic bouton and, most significantly, an increase in the number of synaptic vesicles per pre-synaptic bouton.

Because of recent suggestions that changes in the curvature of the synaptic contact zone might be indicative of alterations in synaptic efficacy[4], this parameter was measured in the LPO and PA of both left and right hemispheres of chicks following either methylanthranilate training (M-chicks) or in water control birds (C-chicks). Synaptic contact curvature was estimated from the ratio of the post-synaptic thickening length - chord length (measured on a Kontron Videoplan) and expressed on a scale from A (zero curvature) to J (highly curved). Synapses were also classified as either pre-synaptically concave or pre-synaptically convex.

No significant differences were found in the synaptic contact curvature of either pre-synaptically concave or pre-synaptically convex synapses, in either left or right LPO or PA of M- or W-Chicks, nor did the percentage distribution of these two classes of contact curvature differ. These results, which are in marked contrast to those observed in synapses from mammalian brains following behavioural studies, may reflect differences due to the species involved or the very different nature of the experimental paradigms.