THE DEVELOPMENT OF NASAL FIELD DETECTION IN YOUNG INFANTS

By

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Abstract

This thesis investigated the monocular detection of temporal and nasal stimuli in infants who were newborn, 1 month old and 2 months old. They were shown three stimuli: a blank field, a single line $3^{\circ}18'$ wide located in the temporal visual field and the same line located in the nasal visual field. Their eye movements were recorded with corneal photography. To assess peripheral detection, I compared the probability that an infant moved his eyes from the centre of the visual field toward a line with the probability that he moved his eyes first in the same direction when the field was blank.

When the lines were located at 10° in the periphery, newborns detected both the temporal line and the nasal line with their left eye (Experiment 1, n = 32). These results showed that newborns can demonstrate both temporal and nasal detection monocularly. When the lines were located further in the periphery, newborns detected the temporal line at 30°, but they showed no evidence of detecting the nasal line at 20°. This was true both when I tested the left eye (Experiment 2, n = 33) and when I tested the right eye (Experiment 3, n = 30).

The results show clearly that in newborns detection in the temporal visual field is better than detection in the nasal visual field. In cats the direct projection from retina through superior colliculus can mediate good detection in the temporal visual field but the Y-pathway through the cortex is necessary for good detection in the nasal visual field. Thus, in the human newborn, the Y-pathway through

the cortex might be too immature to mediate good detection in the nasal visual field.

There appear to be major electrophysiological changes in the human's geniculo-cortical pathway at about 2 months of age. Moreover, only at that age do human infants begin to show smooth pursuit and symmetrical optokinetic nystagmus, behaviours which in cats depend on the Y-pathway through the cortex. Those data suggest that in human infants, the Y-pathway through the cortex might begin to influence visual behaviour at about 2 months of age. Thus, if poor nasal field detection in human newborns were to reflect an immature Y-pathway through the cortex, infants should show an improvement in nasal field detection at 2 months of age, but not before. Experiments 4 and 5 confirmed that prediction. One-month-olds, like newborns, detected the temporal line at 30° but appeared not to detect the nasal line at 20° (Experiment 4, n = 30). In contrast, 2-month-olds detected both the temporal and the nasal lines (Experiment 5, n = 32).

The data reported in this thesis suggest that, in human infants, good nasal field detection depends at least on the Y-pathway through the cortex. That pathway appears to be too immature to mediate good nasal field detection prior to 2 months of age.

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To Milton, Steven, and Jay

Table of Contents

List of Figures

List of Figures (cont'd)

Several investigators have examined the visual behaviour of the human infant and on the basis of the behaviour observed, they have made inferences about the maturity of the nervous system (e.g., Bronson, 1974; Salapatek, 1975; Atkinson, Note 1). Typically they note some limitation in the infant's visual behaviour and find out at what age that limitation is no longer present. They then attribute the change in behaviour to the development of some part of the visual system. In order to do so, they have to know what structures mediate the behaviour in question. Knowledge of the relevant structures comes from studies of anatomy, electrophysiology and neurophysiology. That knowledge is based mainly on animal data. While it is inappropriate to generalize uncritically, the animal data do provide a framework for understanding the development of the visual pathways in human infants.

In this thesis, I will use a similar approach in the investigation of peripheral detection. Studies in animals have provided a great deal of information about the brain structures necessary for peripheral vision. In the cat, for example, two projections appear to mediate peripheral detection: one from retina to superior colliculus and one from retina to lateral geniculate to visual cortex to superior colliculus. Recent behavioural evidence from cats suggests that the projection from retina to superior colliculus mediates detection mainly in the temporal visual field (the left visual field for the left eye), and that the projection through the cortex is necessary for good detection in the nasal visual field (the right visual field for the left eye) (Sherman, 1974b, 1977b). That appears to be the case since cats with extensive lesions of the visual cortex show no evidence of detection in the nasal visual field even though their detection in the temporal visual field is normal. Human adults with cortical lesions also have better detection in the temporal visual field than in the nasal visual field (Koerner & Teuber, 1973); and this difference between temporal and nasal detection is considerably larger than in normal adults (Frisen & Glansholm, 1975). Since human newborns have an immature visual cortex (Conel, 1939), they also might have better detection in the temporal than in the nasal visual field.

There have been no studies of temporal and nasal detection in human newborns. Studies of peripheral vision have all tested infants binocularly rather than monocularly (Harris & MacFarlane, 1974; Lewis, Maurer, & Kay, 1978; MacFarlane, Harris, & Barnes, 1976); and under binocular conditions a stimulus in the left visual field would be both a temporal stimulus for the left eye and a nasal stimulus for the right eye. However, in one study (Lewis et al., 1978) the investigators recorded only the left eye and found better detection to the left than to the right. In fact, there was no evidence for the detection of any stimulus 20° or 30° to the right. Since nonconjugate eye movements are common in newborns (Blanton, 1917; Fonarev, 1959; Guernsey, 1929; Wickelgren, 1969), only the right eye might have detected the lines at 20° and 30° in the right visual field and only the left eye might have detected the lines at 20° and 30° in the left visual field. If that were so, human newborns, like cats and human adults with cortical lesions, would have better detection in the temporal visual field than in the nasal visual field. However, to investigate temporal and nasal vision, it would be necessary to measure detection monocularly, rather than binocularly.

The purpose of the research reported in this thesis was to measure monocular detection in young infants. Specifically, the purpose was to: (a) determine if there are large differences in temporal and nasal detection at birth (Experiments 1, 2, and 3) and (b) to see if those differences are still present in 1- and 2-month-old infants (Experiments 4 and 5). Chapter 1 provides a general background by considering the brain structures necessary for peripheral vision in the cat, monkey and human.

Chapter 1

The Role of the Superior Colliculus and Visual Cortex in Peripheral Vision

Many brain structures are thought to play a role in peripheral vision. Included in the list of possibilities are the superior colliculus (Goldberg & Wurtz, 1972a,b; Schiller & Koerner, 1971; Sprague, 1972), visual cortex (Schiller, 1972, 1977; Spiegel & Scala, 1937), parietal lobes (Lynch, Mountcastle, Talbot, & Yin, 1977; Robinson, Goldberg, & Stanton, 1978; Yin & Mountcastle, 1977) and the frontal eye fields (Bizzi, 1968; Latto & Cowey, 1971; Marrocco, 1978; Mohler, Goldberg, & Wurtz, 1973; Robinson & Fuchs, 1969; Schiller, 1977; Spiegel & Scala, 1937). The pathways through the superior colliculus and visual cortex project on to the parietal lobes and frontal eye fields (Chalupa, 1977; Pearson, Brodal, & Powell, 1978; Trojanowski & Jacobson, 1976, 1977). Following dual lesions in comparable regions of the visual cortex and superior colliculus, animals appear to have no peripheral vision whatsoever in the affected portion of the visual field (Anderson & Symmes, 1969; Mohler & Wurtz, 1977; Sprague, 1966). Thus the projections to or through the superior colliculus and/or visual cortex appear to be necessary for peripheral vision. Studies of electrical stimulation and electrophysiology in the superior colliculus and visual cortex of intact animals suggest how both these structures may be involved.

1.1 Evidence from Intact Animals

Studies in intact cats and monkeys suggest that both the superior colliculus and visual cortex might be involved in peripheral vision. The results for both organisms are virtually identical where comparable investigations have been carried out and unless otherwise noted, all results refer to both the cat and monkey.

1.1.1 The superior colliculus

Cells in the superficial layers of the superior colliculus appear to be involved in detection, while cells in the deeper layers appear to be closely associated with eye movements. Specifically, all cells in the superficial layers (superficial gray and optical layers) respond to visual stimuli located at particular points in the visual field (Goldberg & Wurtz, 1972a; Schiller & Stryker, 1972; Stein, Magalhaes-Castro, & Kruger, 1976). These cells are topographically organized so that adjacent points on the surface of the superior colliculus represent adjacent points in the visual field (Apter, 1945; Berman & Cynader, 1972; Feldon, Feldon, & Kruger, 1970; Humphrey, 1968; Schiller & Stryker, 1972; Sterling & Wickelgren, 1969). Anterior cells respond to stimuli in the near periphery and posterior cells respond to stimuli the far periphery, both for the contralateral visual field; medial cells respond to stimuli in the upper visual field, while lateral cells respond to stimuli in the lower visual field. So, for example, in a dorsal view of the left superior colliculus, the upper (anterior) portion would represent the near periphery of the right visual field, while the lower (posterior) portion would represent the far periphery of the right visual field. The right (medial) side would represent the upper visual field and the left (lateral) side, the lower visual field. Thus, the superficial cells appear to be well suited for detecting the location of stimuli in the visual field. In contrast, they appear to be poorly suited for analyzing patterns since they respond to stimuli independent of their shape, size or orientation (Berman & Cynader, 1972; Cynader & Berman, 1972; Goldberg & Wurtz, 1972a; Sterling & Wickelgren, 1969). Finally, in the monkey, about half the superficial cells show an enhanced response if a stimulus in the receptive field[1] will be the target for a saccade (Goldberg & Wurtz, 1972b; Robinson & Wurtz, 1976; Wurtz & Goldberg, 1972; Wurtz & Mohler, 1974, 1976b). These cells may facilitate a shift in attention toward a peripheral stimulus since they show this enhanced response even when an eye movement is intended but not made (Wurtz & Mohler, 1976b).

In the intermediate layers of the superior colliculus, most cells respond before eye movements, rather than to visual stimuli. These eye movement cells fire prior to all saccades, even those that occur spontaneously or in the dark (Mohler & Wurtz, 1976; Wurtz & Goldberg, 1972).[2] Each cell has a movement field (comparable to a receptive field in a sensory unit) which represents the direction and size of all eye movements that alter the discharge frequency of the cell. The parameters of the discharge prior to eye movements vary

[1] The receptive field of a visual cell represents all of the locations in the visual field where a small stationary stimulus can alter the discharge frequency of that cell.

[2] The eye movement cells have been identified only in the monkey, although similar studies have not yet been carried out in the cat.

systematically as a function of the position of the saccade within the movement field (Sparks & Mays, 1978). This suggests that the eye movement cells might be capable of initiating very precise eye movements. Anterior cells discharge prior to small saccades and posterior cells discharge prior to large saccades; medial cells fire before upward eye movements and lateral cells fire before downward eye movements (Sparks, Holland, & Guthrie, 1976). Thus, there appears to be a "movement" map in the intermediate layers of the superior colliculus and this map appears to be in close correspondence to the sensory map in the superficial layers. In addition, some eye movement cells show a special high frequency discharge only when the eye movement is directed toward a visual stimulus in their receptive fields (Sparks, 1978). These "saccade-related burst neurons" may be involved in peripheral vision. Specifically, they may be involved in initiating the eye movements necessary to bring the fovea to a visual stimulus (Sparks, 1978).

Between the visual cells in the superficial layers and the eye movement cells in the intermediate layers are a special class of cells which have both visual receptive fields and movement fields (Mohler & Wurtz, 1976; Sparks, 1978). These cells seem to integrate the sensory map from above with the movement map from below and may provide the major source of output from the superior colliculus to the brainstem motor areas (Mohler & Wurtz, 1976) where the commands for a specific eye movement are carried out (Edwards & Henkel, 1978; Harting, 1977).

In summary, the electrophysiological data suggest that the superior colliculus plays an important role in peripheral vision. The visual cells, located primarily in the superficial layers, appear to be well suited for coding the location of a stimulus and shifting attention to it. The eye movement cells, located in the intermediate layers, appear well suited for initiating eye movements which will bring the fovea to the peripheral stimulus.

1.1.2 The visual cortex

There are two pieces of evidence from intact animals which suggest that the visual cortex may be involved in peripheral vision. First, electrical stimulation applied to the surface of the visual cortex elicits conjugate eye movements; and the size and direction of those eye movements depend on the location of the stimulation (Schiller, 1972, 1977; Spiegel & Scala, 1937). The visual cortex then, may play a role in programming eye movements. Second, electrophysiological studies have shown that there is a topographic map in area 17 of the visual cortex such that adjacent points in the visual field are represented by adjacent points on the surface of the cortex (Daniel & Whitteridge, 1961; Tusa, Palmer, & Rosenquist, 1978). In both the monkey and the cat, the centre of gaze is represented on the lateral surface of area 17 and the far periphery, on the medial surface. The lower visual field is represented in the anterior portion and the upper visual field, in the posterior portion. This suggests that the visual cortex may register the location of visual stimuli. However, the centre of the visual field is magnified on the cortical surface and relatively small amounts of surface are devoted to peripheral stimuli. Only 50% of the visual cortex in the cat and only 10% in the monkey are devoted to stimuli beyond 10° in the periphery (Tusa et al., 1978).

Briefly, studies of electrical stimulation and electrophysiology suggest that both the superior colliculus and the visual cortex may be involved in peripheral vision. However, a clearer understanding of the role of each structure can be obtained by examining peripheral detection in organisms with either collicular or cortical lesions.

1.2 Evidence from Organisms with Lesions of the Superior Colliculus

Following bilateral destruction of the superior colliculus, cats, monkeys and humans viewing stimuli monocularly show evidence of detection both in the temporal visual field (the left visual field for the left eye) and in the nasal visual field (the right visual field for the left eye) (Heywood & Ratcliff, 1975; Loop, Note 2; Pasik, Note 3). The size of the monocular visual field following collicular lesions has not been reported. However, under binocular viewing conditions, lesioned monkeys can detect stimuli out to 40° (Butter, Weistein, Bender, & Gross, 1978) and lesioned cats, out to 60° (Sprague & Meikle, 1965). This represents a deficit since intact cats and monkeys can detect objects out to 90° in the periphery (Sherman, 1974b, 1977b; Sprague & Meikle, 1965; Weiskrantz, 1972). Moreover, in lesioned animals, the latency of eye movements is longer than those in unoperated controls (Latto, 1978; Mohler & Wurtz, 1977; Sprague, 1966; Sprague & Meikle, 1965) and when eye movements do occur, they tend to undershoot the target (Mohler & Wurtz, 1977; Sprague, 1972; but see Anderson & Symmes, 1969). Similar oculomotor deficits appear to occur in humans with lesions in the superior colliculus (Heywood & Radcliffe, 1975).

In short, the projections through the superior colliculus are not necessary for detection in the temporal and nasal visual fields, at least when the stimuli are no more than 40° to 60° off to the side. However, the projections through the colliculus appear to be necessary for facilitating normal eye movements to peripheral stimuli and for any vision in the far periphery.

1.3 Evidence from Organisms with Lesions of the Visual Cortex

Following lesions of the visual cortex which result in total retrograde degeneration of the lateral geniculate, cats and monkeys viewing stimuli binocularly have normal visual fields; they can detect stimuli out to 90° in the periphery (Humphrey, 1972, 1974; Sherman, 1974b, 1977b).[3] After partial lesions of the visual cortex, monkeys will move their eyes toward stimuli in the affected portion of the visual field (Mohler & Wurtz, 1977). The eye movements to peripheral stimuli are normal both in latency and velocity (Humphrey, 1972, 1974; Mohler & Wurtz, 1977), although they tend to be slightly less accurate than those of intact monkeys (Mohler & Wurtz, 1977). In addition, the threshold for detection is higher postoperatively than preoperatively (Cowey, [illegible]; Cowey & Weiskrantz, 1963; Mohler & Wurtz, 1977). Humans viewing stimuli binocularly after cortical lesions also can localize stimuli accurately in the affected portion of the visual field, providing the stimuli are sufficiently large or sufficiently bright

[3] Note that in the cat, the lateral geniculate projects directly to areas 17, 18 and 19 of the visual cortex, whereas in the monkey, the lateral geniculate projects mainly to area 17. Consequently, in order to obtain total retrograde degeneration of the lateral geniculate, larger cortical lesions are required in the cat than in the monkey.

(Perenin & Jeannerod, 1975; Poppel, Held, & Frost, 1973; Torjussen, 1976; Weiskrantz, Warrington, Sanders, & Marshall, 1974; Williams & Gassel, 1962). Under binocular viewing conditions then, animals and humans with cortical lesions seem to display only minor deficits in peripheral detection.

In contrast, extensive deficits become apparent under monocular viewing conditions. Sherman (1974b, 1977b) used a perimetry test to measure the size of the monocular visual field in cats, both before and after bilateral ablation of the visual cortex (which resulted in total retrograde degeneration of the lateral geniculate nucleus). He found that preoperatively, cats could detect a piece of food or a small circle monocularly out to 90° in the temporal visual field and out to 45° in the nasal visual field. Postoperatively, they could still detect the stimuli out to 90° in the temporal visual field. But they showed no evidence for detection when the stimuli were at least 15° in the nasal visual field. Thus, in cats, the visual cortex appears to be necessary for detection beyond 15° in the nasal visual field, but not for detection in the temporal visual field. Note however, that Sherman did not test stimuli between 0° and 15° in the nasal visual field. Moreover, had he also used larger stimuli, he might have found evidence for some detection beyond 15° in the nasal field. Nonetheless, this would still at least imply that cats with cortical lesions have poorer detection in the nasal than in the temporal field.

There are no comparable studies in the monkey which have tested monocular perimetry after cortical lesions. However, human adults with cortical lesions appear to have poorer detection in the nasal visual field than in the temporal visual field (Koerner & Teuber, 1973; Teuber, Battersby, & Bender, 1960); and this difference between temporal and nasal detection is considerably larger than in normal adults (Aulhorn & Harms, 1972; Frisen & Glansholm, 1975; Harvey & Poppel, 1972; Stanek, 1973). Therefore, impairment to the visual cortex appears to result in poorer detection in the nasal visual field than in the temporal visual field, both in the cat and in the human adult.

The results of studies on organisms with cortical lesions suggest that the direct projection from retina through superior colliculus is insufficient to mediate good detection in the nasal visual field. Moreover, an intact cortex appears to be necessary for good detection in the nasal field, but not for good detection in the temporal field. The next section attempts to explain these results by examining the differences between the projections from retina to superior colliculus and from retina to visual cortex.

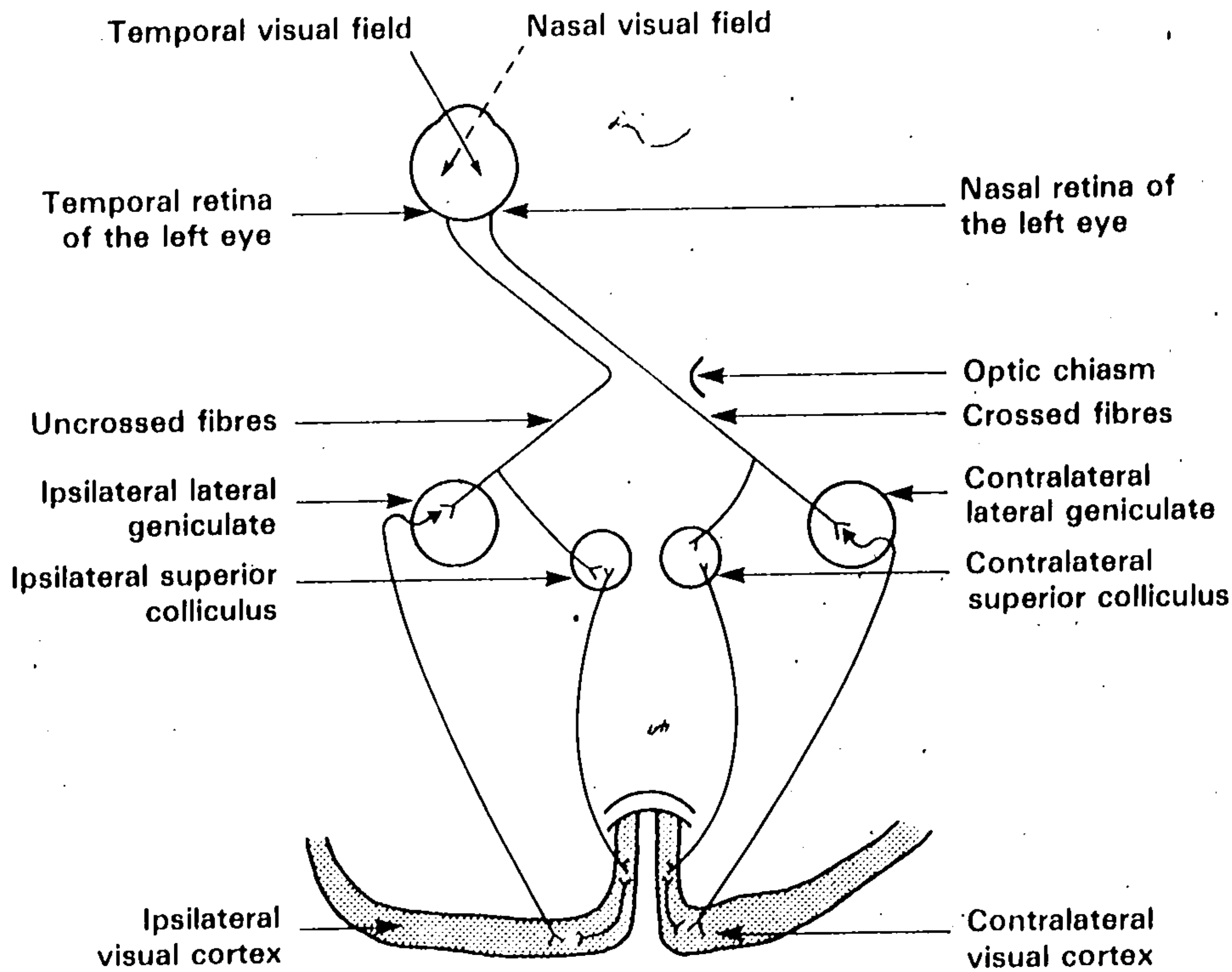
1.4 Temporal-nasal Asymmetry in the Direct Projection to the Superior Colliculus

In the cat, monkey and human, there is a direct projection from retina to superior colliculus and a projection from retina to lateral geniculate to visual cortex to superior colliculus. In all three organisms, fibres from the nasal retina of each eye cross at the optic chiasm and project directly to the contralateral lateral geniculate and superior colliculus. In the monkey and human, fibres from the temporal retina of each eye remain uncrossed and project directly to the ipsilateral lateral geniculate and superior colliculus. The crossed fibres from the nasal retina mediate detection in the temporal visual field and the uncrossed fibres from the temporal retina mediate detection in the nasal visual field (reviewed in Thompson, 1967). Fig. 1 illustrates these relationships for the left eye of the human.

Using anatomical and electrophysiological techniques, investigators have attempted to estimate the proportion of crossed fibres from the nasal retina vs. uncrossed fibres from the temporal retina, in the direct projection to the superior colliculus. For anatomical estimates, investigators typically remove one eye from the animal and note the degenerating axons which project directly to the contralateral or ipsilateral superior colliculus (representing crossed and uncrossed axons respectively). Anatomical studies in the cat all show that there are more crossed than uncrossed axons projecting directly to the superior colliculus (Altman, 1962; Garey & Powell, 1968; Kaneski & Sprague, 1974; Laties & Sprague, 1966; Singleton & Peele, 1965; Sterling, 1973). Quantitative estimates of the percentage of fibres in the direct collicular pathway which are crossed range from 80% to 99% (Kaneski & Sprague, 1974; Laties & Sprague, 1966; Sterling, 1973).

However, in the cat all the crossed fibres do not originate in the nasal retina. In fact, 33% of the cat's crossed fibres come from the <u>temporal</u> retina (Kirk, Levick, & Cleland, 1976a,b; Stone, 1966; Stone & Fukuda, 1974). The method of eye enucleation does not differentiate between crossed fibres which originate in the temporal retina and crossed fibres which originate in the nasal retina (Laties & Sprague, 1966). Since some of the crossed fibres from the temporal

Fig. 1. The projections of the left eye to the superior colliculus, lateral geniculate, and visual cortex in the human (adapted from Thompson, 1967).



Temporal visual field
Nasal visual field
Temporal retina of the left eye
Nasal retina of the left eye
Optic chiasm
Crossed fibres
Uncrossed fibres
Ipsilateral lateral geniculate
Contralateral lateral geniculate
Ipsilateral superior colliculus
Contralateral superior colliculus
Ipsilateral visual cortex
Contralateral visual cortex

retina project directly to the superior colliculus (Berman & Cynader, 1972; Feldon et al., 1970; Harting & Guillery, 1976), the reported percentages overestimate the proportion of crossed fibres in this projection which originate in the nasal retina. Consequently electrophysiological estimates may be more accurate, at least for the cat.

Electrophysiological techniques involve recording from single units in one superior colliculus while a stimulus is presented in the visual field contralateral to that superior colliculus. So, for example, if cells in the left superior colliculus were being recorded, the stimulus is presented in the right visual field. Then the investigators note the percentage of cells that are driven by the right eye (representing crossed axons from the nasal retina) and the percentage of cells driven by the left eye (representing uncrossed axons from the temporal retina). Since axons project both directly to the superior colliculus and indirectly to the superior colliculus via the visual cortex (Altman, 1962; Hoffmann, 1973; Sprage, 1975), recordings from the superior colliculus of the intact animal would reflect the input from both pathways. Estimates for the direct projections alone can be calculated by recording in the superior colliculus after total ablation of the visual cortex.

The results of studies in cats with extensive lesions in the visual cortex show that, in the direct projection to the superior colliculus, about 75% to 80% of the axons are crossed fibres from the nasal retina (Rosenquist & Palmer, 1971; Wickelgren & Sterling, 1969). Since the crossed fibres from the nasal retina of each eye mediate detection in the temporal visual field, the observed asymmetry suggests that the direct projection to the superior colliculus favors temporal detection. This asymmetry could explain why cats with cortical lesions appear to detect stimuli only in the temporal visual field (see Section 1.3).

In contrast, electrophysiological studies have shown that the cat has an equal number of crossed fibres from the nasal retina and uncrossed fibres from the temporal retina which project to the lateral geniculate (Ikeda, Plant, & Tremain, 1977).[4] There is no reason to assume that these proportions differ from those in the projection from geniculate to visual cortex since all fibres projecting from retina to cortex relay in the lateral geniculate and fibres cross only at the optic chiasm (reviewed in Thompson, 1967). Thus, the pathway from retina to lateral geniculate to visual cortex may contain an equal number of crossed fibres from the nasal retina and uncrossed fibres from the temporal retina. This equal proportion could explain why cats with collicular lesions can detect stimuli in both visual fields (see Section 1.2).

In the monkey, only one electrophysiological study investigated the proportion of crossed axons from the nasal retina vs. uncrossed axons from the temporal retina, which project directly to the superior colliculus. Schiller, Stryker, Cynader, & Berman (1974) reported that

[4]One anatomical study reported that about 65% of the axons in the projection from retina to lateral geniculate are crossed (Laties & Sprague, 1966). However, this estimate would include crossed fibres originating both in the nasal retina and in the temporal retina (Laties & Sprague, 1966) since some crossed axons from the temporal retina project to the lateral geniculate (Sanderson & Sherman, 1971).

the monkey, unlike the cat, has an equal number of crossed and uncrossed fibres in this projection, even after the visual cortex is ablated. But this estimate may be inaccurate because of sampling bias. In fact, most of the cells that Schiller et al. recorded had input from receptors within 10° of the fovea (Stryker, Note 4) and anatomical results show that the proportion of crossed fibres from the nasal retina is greater for more peripheral points (Hubel, LeVay, & Wiesel, 1975).

The results of anatomical studies show that the monkey does have an asymmetry in the direct projection from retina to superior colliculus. By staining degenerating axons after the removal of one eye (Hendrickson, Wilson, & Toyne, 1970; Wilson & Toyne, 1970) or by using audioradiographic tracing methods after the injection of radiographic label into one eye (Hubel et al., 1975; Pollack & Hickey, 1979), investigators found that more crossed fibres from the nasal retina than uncrossed fibres from the temporal retina project directly to the colliculus. Although this asymmetry is not as pronounced in the monkey as in the cat (Graybiel, 1975; Hubel et al., 1975), about 73% of the monkey's axons in this pathway are crossed (Pollack & Hickey, 1979).[5] In contrast, the proportion of crossed and uncrossed fibres is equal in the projection from retina to lateral geniculate and striate cortex (Hubel et al., 1975).

[5]Note that in both monkey and man, all fibres from the nasal retina are crossed and all fibres from the temporal retina are uncrossed (Hubel et al., 1975; Kupfer, 1963; Stone, Leicester, & Sherman, 1973), at least beyond 1/2° in the periphery (Stone et al., 1973). Consequently, the reported proportions of crossed fibres originate almost entirely in the nasal retina.

In humans there are no data on the proportion of crossed vs uncrossed fibres projecting directly to the superior colliculus or to the visual cortex. However, the anatomy of the visual system is remarkably similar in man and monkey (Cooper, 1945; Kupfer, 1962, 1963; Rakic, 1976) and there is no reason to believe that any major differences exist between the two organisms in these projections. More crossed than uncrossed fibres in the direct projection to the superior colliculus, but not in the projection from retina to cortex, could explain why human adults appear to need the pathway from retina to visual cortex for good detection in the nasal visual field (see Section 1.3).

1.5 Conclusions about the Pathways which Mediate Temporal and Nasal Detection

The superior colliculus and/or visual cortex are necessary for peripheral vision in the cat and monkey (Anderson & Symmes, 1969; Mohler & Wurtz, 1977; Sprague, 1966) and probably in the human (Cowey, 1979; Rakic, 1976). Studies in organisms with collicular or cortical lesions show that cats, monkeys and humans still have some peripheral vision in the absence of either the superior colliculus or the visual cortex (Sections 1.2 and 1.3). However, there appear to be important differences in the projections to these two structures. The direct projection from retina to superior colliculus contains many more crossed fibers from the nasal retina (which mediate detection in the temporal visual field) than uncrossed fibres from the temporal retina (which mediate detection in the nasal visual field). In contrast, the geniculo-cortical projection contains about an equal number of crossed fibres from the nasal retina and uncrossed fibres from the temporal retina (Section 1.4). These differences could explain why the direct pathway from retina through superior colliculus seems to be insufficient for good detection in the nasal visual field and the geniculo-cortical pathway seems to be necessary for that detection (Sections 1.2 and 1.3).

Note however, that evidence for the necessity of the geniculo-cortical pathway for good detection in the nasal visual field comes from organisms with cortical lesions. Once the cortex is lesioned, there is retrograde degeneration in the lateral geniculate nucleus. Perhaps the projection from retina to lateral geniculate, but not the projection from geniculate to cortex, is necessary for good detection in the nasal visual field. This is possible since the geniculate projects to structures other than the visual cortex (Altman, 1962; Chalupa, 1977; Sprague, 1975). Nonetheless, at least part of the projection from retina through visual cortex appears to be necessary for good detection in the nasal visual field.

1.6 The Pathway which Mediates Peripheral Vision in the Human Newborn

There is ample evidence that the human newborn can detect peripheral stimuli binocularly (Brown, 1961; Dayton & Jones, 1964; Harris & MacFarlane, 1974; Lewis et al., 1978; MacFarlane et al., 1976; White, Castle, & Held, 1964). This suggests that the direct projection from retina through superior colliculus and/or at least part of the geniculo-cortical projection are functional at birth (Section 1.5). However, anatomical evidence shows that the lateral geniculate and visual cortex are very immature in the human newborn. For example, in the lateral geniculate, cells are very small in area, nuclei are larger than in the adult and Nissl bodies are poorly granulated (Dekaban, 1954; Hickey, 1977). In the visual cortex, many cells are in inappropriate layers, fibres are poorly myelinated, and there is little evidence of dendritic or axonal processes (Conel, 1939).

Electrophysiological evidence suggests that the geniculo-cortical pathway may be too immature to mediate at least some behaviours until after 1 month of age. Hoffmann (1978) showed checkerboards with large checks to 1- and 3-month-old infants and recorded the visually evoked response at several locations on the scalp. In all infants, he identified both a short latency positive-negative complex which could be recorded only over area 17 and a long latency negative component which could be recorded over a wide scalp area. In 1-month-olds, the amplitude of only the long- latency component varied as a function of check size, whereas in older infants, the amplitude of both components varied as the stimulus varied.

In cats, the long latency component of the visually evoked response is mediated by the direct projection from retina through superior colliculus and the short latency positive-negative complex, by the projection from retina through lateral geniculate through visual cortex (Rose & Lindsley, 1968). Hoffmann (1978) claimed that the presence of the early component in all his subjects suggests that the geniculo-cortical pathway is present at least by 1 month of age. But, he argued that since the amplitude of the early component was not related to the characteristics of the stimulus in his younger infants, the geniculo-cortical pathway is too immature to differentiate stimuli until after 1 month of age. Although Hoffmann's data do not warrant such a general conclusion (see General Discussion), they do suggest that, in young infants, the geniculo-cortical pathway may be too immature to differentiate the characteristics of large checks. Similarly, this pathway might be too immature to mediate peripheral detection at birth.

This is also suggested by the behavioural data. Although the newborn scans a stationary stimulus, shows optokinetic nystagmus and tracks a moving object, he shows limitations in each of these behaviours, limitations which might reflect an immature projection through the cortex.

(a) Scanning. During the first month of life, infants tend to scan only a very limited region of the external contour (Hainline, 1978; Haith, Bergman, & Moore, 1977; Leahy, 1976; Maurer & Salapatek, 1976; Salapatek, 1968, 1975; Salapatek & Kessen, 1966, 1973; Maurer, Note 5). They rarely look at the internal elements of a geometric figure or of a face, even though they scan those elements once the border is removed (Maurer & Salapatek, 1976; Salapatek, 1975; Maurer, Note 5). This limited scanning probably accounts, in part, for the apparent inability of 1-month-olds to discriminate stimuli which differ only internally, especially since they can discriminate those stimuli once the borders are removed (Fantz, Fagan, & Miranda, 1975; Milewski, 1976; Maurer & Barrera, Note 6, Note 7). Finally, when shown two stimuli simultaneously, young infants rarely shift their gaze between them (White, 1971; Ames & Silfen, Note 8).

Indirect evidence suggests that monkeys with cortical lesions also do not scan extensively. For example, they can detect black currants on a white floor, but appear not to see them once the currants are surrounded by a border (Humprhey, 1974). They can discriminate geometric shapes, but not if they are enclosed in identical circles (Butter, 1972). Unlike normal monkeys, their discrimination of shapes is not affected by misleading internal stimuli (Schilder, Pasik, & Pasik, 1972). Moreover, they rarely shift their gaze between alternative stimuli (Oscar-Berman, Heywood, & Gross, 1974). These data suggest that, in monkeys, extensive scanning might depend on an intact geniculo-cortical pathway. Human newborns may not scan extensively because the geniculo-cortical pathway is very immature.

(b) Optokinetic Nystagmus. Typically, when the visual field consists of moving stripes, the eye repeatedly follows one stripe for a brief period of time, saccades back to centre and then follows another stripe. This phenomenon, called optokinetic nystagmus, occurs readily in newborns (Gorman, Cogan, & Gellis, 1957, 1959; Brazelton, Scholl, & Robey, 1966). However, an interesting limitation becomes apparent when young infants are tested monocularly. Atkinson (Note 1) tested a group of 1-month-olds monocularly and found that the optokinetic nystagmus was asymmetrical. Although it was normal when stripes moved from the temporal visual field toward the nasal visual field, it was either absent or very irregular when stripes moved in the opposite direction. A similar asymmetry occurs when optokinetic nystagmus is tested monocularly in cats which are missing part of the geniculo-cortical pathway, either because it has been lesioned (Wood, Spear, & Braun,

1973) or because it is very immature (Van Hof-van Duin, 1978). Thus, in the young human infant, asymmetrical optokinetic nystagmus might reflect an immature geniculo-cortical pathway.

(c) Tracking. The newborn can track a slowly moving object, but he does so with jerky, rather than smooth eye movements. His eyes repeatedly lag behind the target, then overshoot it and then saccade back to it (Barten, Birns, & Ronch, 1971; Dayton & Jones, 1964; Dayton, Jones, Steele, & Rose, 1964; White et al., 1964). The development of smooth pursuit seems to depend on an intact visual cortex in humans since an infant missing most of his visual cortex shows jerky tracking when he is 4 months old (Aylward, Lazzara, & Meyer, 1978) and so do adults with cortical lesions (Sharpe, Lo, & Rabinovitch, 1979). In contrast, normal infants track smoothly when they are only 2 months old (White, 1971; White et al., 1964). Moreover, kittens have an immature geniculo-cortical pathway and they also track with jerky eye movements (Norton, 1974). Thus, an absence of smooth pursuit in the human newborn again suggests that the geniculo-cortical pathway may be immature.

In summary, the anatomical data show that the lateral geniculate and visual cortex are immature at birth. Electrophysiological data suggest that at least part of the projection from retina through lateral geniculate through visual cortex might be too immature to differentiate some stimuli. The behavioural data suggest that at least part of that pathway might be too immature to mediate extensive scanning, normal optokinetic nystagmus and smooth pursuit. Similarly, it may be too immature to mediate peripheral detection at birth.

In contrast, the direct projection from retina through superior colliculus appears to be functional at a very young age. When Hoffmann (1978) showed checkerboards to young infants, he found that the amplitude of the late component of the visually evoked response varied as check size varied, even in 1-month-olds (the youngest age tested). Since the late negative component is mediated by the direct projection from retina through superior colliculus in cats (Rose & Lindsley, 1968), Hoffmann's results suggest that, in humans, the direct collicular pathway is functional at least by 1 month of age.

In addition, behavioural data are often cited to support the notion that the direct projection through the colliculus is functional in human newborns. Monkeys with lesions of the visual cortex can discriminate differences in brightness (Humphrey, 1974; Kluver, 1941), in amount of contour (Humphrey, 1974; Weiskrantz, 1963), and between moving and stationary targets (Anderson & Symmes, 1969; Humphrey, 1974; Weiskrantz, 1963). Human adults with cortical lesions can make similar discriminations even when the stimuli are presented in the affected portion of the visual field (Bender & Krieger, 1951; Teuber et al., 1960; Weiskrantz, et al., 1974). Thus, the direct collicular pathway might be able to mediate these discriminations both in monkeys and in human adults. The human newborn also can discriminate differences in brightness (Hershenson, Kessen, & Munsinger, 1967), in amount of contour (Fantz, Fagan, & Miranda, 1975; Fantz, Ordy, & Udelf, 1962; Hershenson, 1964; Hershenson et al., 1967), and between moving and stationary targets (Fantz, 1967; Haith, 1966). Since the geniculo-cortical pathway appears to be very immature at birth, several investigators have postulated that these discriminations are mediated by the direct projection from retina through superior colliculus in the human newborn (Bronson, 1974; Salapatek, 1975; Volkmann & Dobson, 1976). However, those investigators assumed that the geniculo-cortical pathway is too immature at birth to mediate <u>any</u> visual behaviour. That assumption is not firmly established (see General Discussion).

In cats and human adults, the direct projection from retina through superior colliculus appears to be insufficient to mediate good detection in the nasal visual field (Section 1.3). Consequently, if human newborns were to depend on that pathway for peripheral detection, they should have poorer detection in the nasal visual field than in the temporal visual field. Moreover, in cats and human adults, the geniculo-cortical pathway appears to be necessary for good detection in the nasal visual field (Section 1.3). Therefore, as that pathway develops, human infants might show a corresponding improvement in detecting stimuli in the nasal visual field.

The purpose of the research reported in this thesis was to investigate the monocular detection of temporal and nasal stimuli in newborns, 1-month-olds and 2-month-olds. Infants were shown either a blank field or a single line $3^{\circ}18'$ wide, located either in the temporal or nasal visual field. If infants could see the line, they should move their eyes toward it significantly more often than expected by chance (Harris & MacFarlane, 1974; Lewis et al., 1978; MacFarlane et al., 1976). If young infants were to detect the temporal, but not the nasal line, this might mean that some part of the geniculo-cortical pathway is too immature to mediate peripheral detection. Chapter 2 presents the experiments which test temporal and nasal detection in newborns. If they are found to have better temporal than nasal vision, I will consider alternative explanations which might account for the phenomenon.

Chapter 2

Detection in the Temporal and Nasal Visual Fields by the Newborn Infant

Experiment 1

When young infants look binocularly, they often have biases to look to the left or to the right (Cohen, 1972; Haaf & Diehl, 1976; Adams, Note 9). Despite these biases, newborns looking binocularly move their eyes toward stimuli that they detect in the periphery (Brown, 1961; Dayton & Jones, 1964; Haith, in press; Harris & MacFarlane, 1974; Lewis et al., 1978; MacFarlane et al., 1976).

When young infants look monocularly, they also appear to have biases. For example, when checkerboards are placed at 15° or 30° in the periphery, they often fixate the most peripheral part of the stimulus on the temporal side (the left side when infants look with the left eye) (Maurer, 1974). Moreover, although they spend a great deal of time scanning stimuli placed 10° to 30° in the temporal visual field (the left visual field for the left eye), they rarely scan those stimuli when they are placed at the same locations in the nasal visual field (the right visual field for the left eye) (Maurer, 1974; Mendelson & Haith, 1976; Slater & Findlay, 1972). The temporal biases in these behaviours could indicate that newborns looking monocularly have difficulty moving their eyes toward any stimulus they detect in the periphery, particularly any stimulus in the nasal visual field. Consequently, the first experiment was designed to find out if, under monocular viewing conditions, the direction of the first eye movement were still a feasible measure of newborns' peripheral detection.

Newborns viewed single lines monocularly with the left eye. The lines were $3^{\circ}18'$ wide and were located at 10° in the left (temporal) or right (nasal) visual field. The infants' eye movements were recorded with corneal photography (Haith, 1969; Maurer, 1975). To assess peripheral detection, I compared the probability that an infant moved his eyes from the centre of the visual field toward a line with the probability that he moved his eyes first in the same direction when the field was blank. The blank field was included for comparison because infants seem to have response biases under monocular conditions (Maurer, 1974; Mendelson & Haith, 1976; Slater & Findlay, 1972). The blank field should be an appropriate control for response biases since most investigators assume that any biases are independent of the stimulus (Green & Swets, 1966). I assumed that infants could see a line if they moved their eyes toward it significantly more often than they moved their eyes in the same direction on the blank field (Lewis et al., 1978).

If the direction of eye movements were a feasible measure of peripheral detection monocularly, newborns should detect at least the line in the temporal field. Under binocular conditions the left eye appears to detect even narrower lines at 10° in the left visual field (Lewis et al., 1978); and cats with cortical lesions can detect small stimuli monocularly out to 90° in the temporal field (Sherman, 1974b, 1977b).

There is no way of predicting whether newborns will also detect the line at 10° in the nasal field. In a previous study which tested newborns binocularly, the left eye moved toward lines only 1° wide at 10° in the right visual field (Lewis et al., 1978). But this could have occurred either because the left eye detected the line or because the right eye moved toward it and the left eye followed the right eye. If newborns were to detect the line at 10° in the temporal visual field and at 10° in the nasal visual field, this result would not speak to the issue of cortical maturity. Studies of cats with cortical lesions showed that these cats could not detect small stimuli at 15° in the nasal visual field but they did not test less peripheral stimuli (Sherman, 1974b, 1977b). Moreover, human adults with cortical lesions can detect some stimuli at 10° in the nasal visual field (Koerner & Teuber, 1973). However, the detection of both lines would show that the method is feasible for demonstrating monocular detection at 10° in both the temporal and nasal fields. If it were, the method might also be feasible for measuring the detection of stimuli further off to the side.

If newborns were to detect the line at 10° in the temporal visual field, but show no evidence of detecting it at 10° in the nasal visual field, this might demonstrate very poor detection in the nasal visual field of the left eye. This result might suggest that the geniculo-cortical pathway is too immature to mediate peripheral detection at birth.

Detection of only the nasal line would be very surprising for three reasons. First, it is unlikely that vision in the nasal field is better than vision in the temporal field of the left eye. Binocularly, the left eye appears to detect stimuli out to 30° in the left visual field but only out to 10° in the right visual field (Lewis et al., 1978). Moreover, in both normal (Frisen & Glansholm, 1975) and lesioned (Koerner & Teuber, 1973) human adults, detection in the nasal field is poorer than detection in the temporal field. Second, this outcome would imply that only the uncrossed temporal fibres (which mediate detection in the nasal visual field) are sufficiently mature to mediate peripheral detection at birth. This is unlikely since there is no evidence in animals that the uncrossed fibres from the temporal retina develop before the crossed fibres from the nasal retina (Diamond & Hall, 1969; LeVay, Stryker, & Shatz, 1978; Rakic, 1976). Finally, there is no reason to assume that response biases prevent the newborn from demonstrating detection in the temporal visual field, but not in the nasal visual field.

The detection of neither line would suggest either that newborns have no peripheral vision or that the measuring technique was invalid. Since newborns have previously demonstrated peripheral vision binocularly (see for example, Lewis et al., 1978), the most reasonable conclusion would be that monocularly, newborns' biases are too strong to demonstrate any peripheral detection. If that were so, a new method would have to be devised to test newborns' peripheral detection monocularly, since all previous investigators have used the direction of eye movements to determine newborns' ability to detect peripheral stimuli binocularly.

Method

Subjects

The subjects were 32 healthy full-term newborns (at least 38 weeks gestation and at least 2500 gms at birth) born in Hamilton, Ontario ($\bar{X}$ age = 3.4 days, range 1 to 7 days). An additional 81 babies were tested but not included because they provided insufficient data (see section on data reduction).

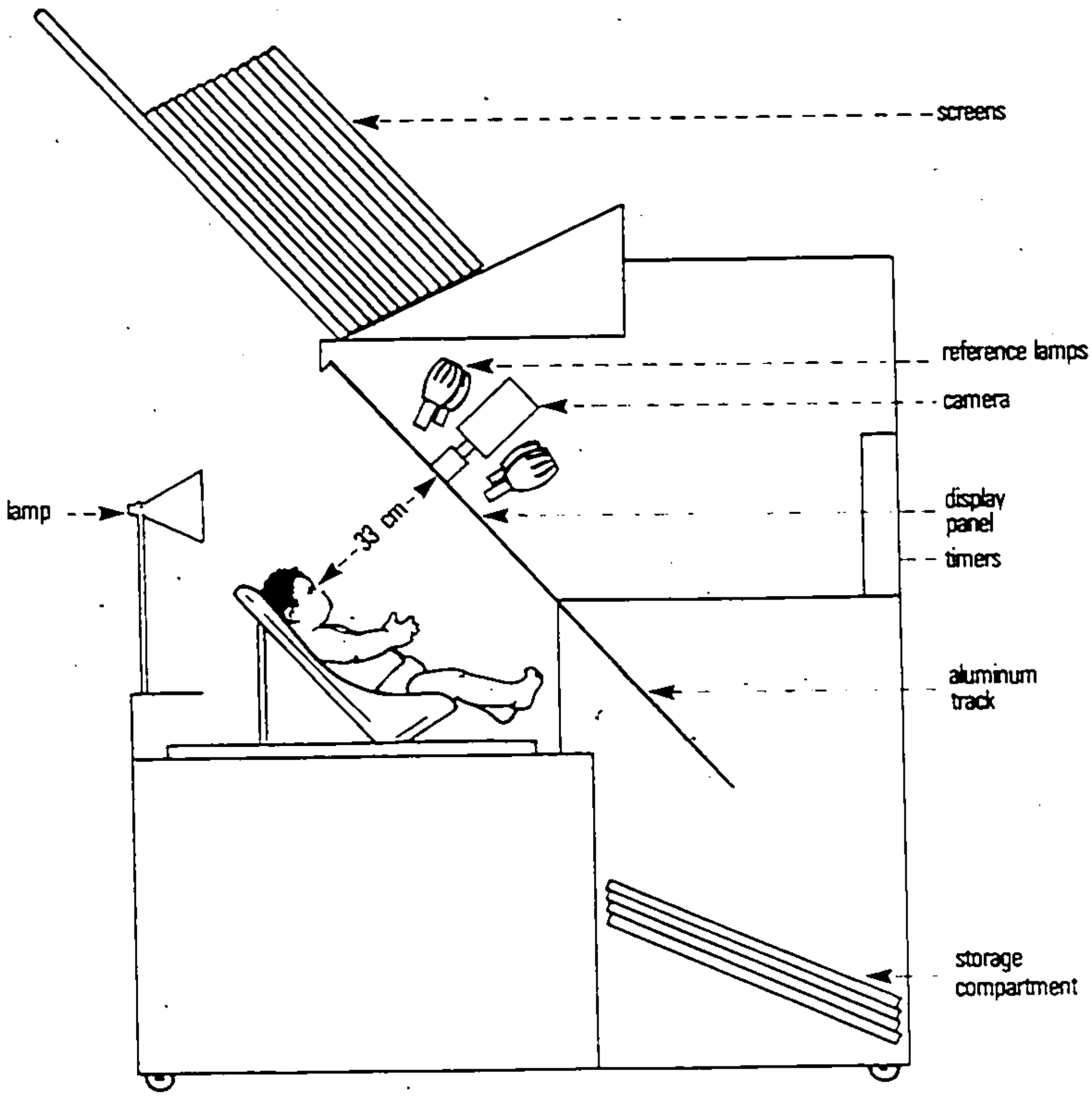
Stimuli

The stimuli were a plain black mesh screen (91.4 cm or 70°6' wide x 61.0 cm or 61°34' high) and two similar black screens, each with one vertical white line (1.9 cm or 3°18' wide x 15.0 cm or 24°27' long) attached to it, either to the left or right of centre. The left line was attached with the right edge 10° out horizontally to the left of centre (temporal visual field for the left eye) and the right line was attached with the left edge 10° to the right of centre (nasal visual field for the left eye). The luminance of the lines was 9.25 cd/m^2 and that of the blank field was .52 cd/m^2 (Spectra Brightness Spot Meter, Model UB, Photo Research Corporation, Hollywood, California). The contrast of the lines relative to the background was 89%.

Apparatus

The apparatus is shown in Fig. 2. The baby sat in an infant seat inclined at 45° and faced a display panel inclined parallel to him. The stimuli appeared directly in front of this display panel and were illuminated by a 15-watt lamp located slightly behind and above the infant. In the middle of the display panel was a 15°51' x 31' vertical strip of red neon lights which was turned on between trials.

Fig. 2. The apparatus.



Directly behind the display panel were a 16 mm movie camera and eight reference lamps, all aimed at the infant's left eye. The reference lamps were Bausch and Lomb Nicholas microscope illuminators, each fitted with a Corning Filter type 7-69 and a Kodak Wratten filter type 87C to cut out hot wavelengths and most of the visible spectrum. Most of the light transmitted was between 860 and 960 nm, so infrared film could detect it even though it was nearly invisible (at least to an adult). The camera was loaded with Kodak High Speed Infrared Film, and photographed the eye four times each second with an exposure time of .1 sec.[6] Timers controlled the lengths of trials and intertrial intervals.

Procedure

An experimenter placed a sterile patch over the baby's right eye, set him in the infant seat, and secured his head in place with foam cubes. The seat was adjusted so the baby's left eye was in the field of the camera and 33 cm from the stimuli. One experimenter sat to the left of the baby and usually held a pacifier in his mouth to restrict head movement. A second experimenter, on the baby's right, managed the controls and slid the screens into place. For 7 sec before each trial, the room was dark except for the column of red lights, which was designed to attract the infant's gaze to the centre of the visual field. When the trial began, the red lights went out and the lamp behind the infant came on, illuminating the stimulus. Each trial

[6] Four frames per sec is sufficient to record all fixations. Should the eye be photographed during a saccade, an exposure time of .1 sec leaves it identifiably blurred (Maurer, 1975).

lasted 5 sec. A sequence consisted of six trials: two trials with a blank field, two trials with the left line and two trials with the right line, all presented in a random order. The same sequence was repeated until the baby was no longer alert.

Data Reduction

The data consisted of films of each infant's left eye with the reflections of the reference lamps superimposed on it. The location of those reflections relative to the centre of the pupil changed systematically as the infant changed his fixation (see Maurer, 1975 for a detailed explanation). For each trial, two of four scorers independently decided whether the infant began by looking centrally, and if he did, whether the direction of his first eye movement was to the left or to the right. I was always one of the two scorers.

Before the scoring began, I established the criteria for looking centrally. Central fixations included all fixations which were no more than 4^{o} horizontally from the exact centre of the visual field (since that was the limit of precision of the measuring technique) and no more than 15^{o} vertically from the exact centre of the visual field (since the lines extended nearly that far above and below centre) (see Fig. 3). Fixations outside this central region were either left (to the left of the central region), right (to the right of the central region), up (above the central region) or down (below the central region).

To score the data, first I filmed the left eye of an adult in the apparatus as she fixated specific points in the visual field. This film showed the relation between the lamps' reflections and the centre

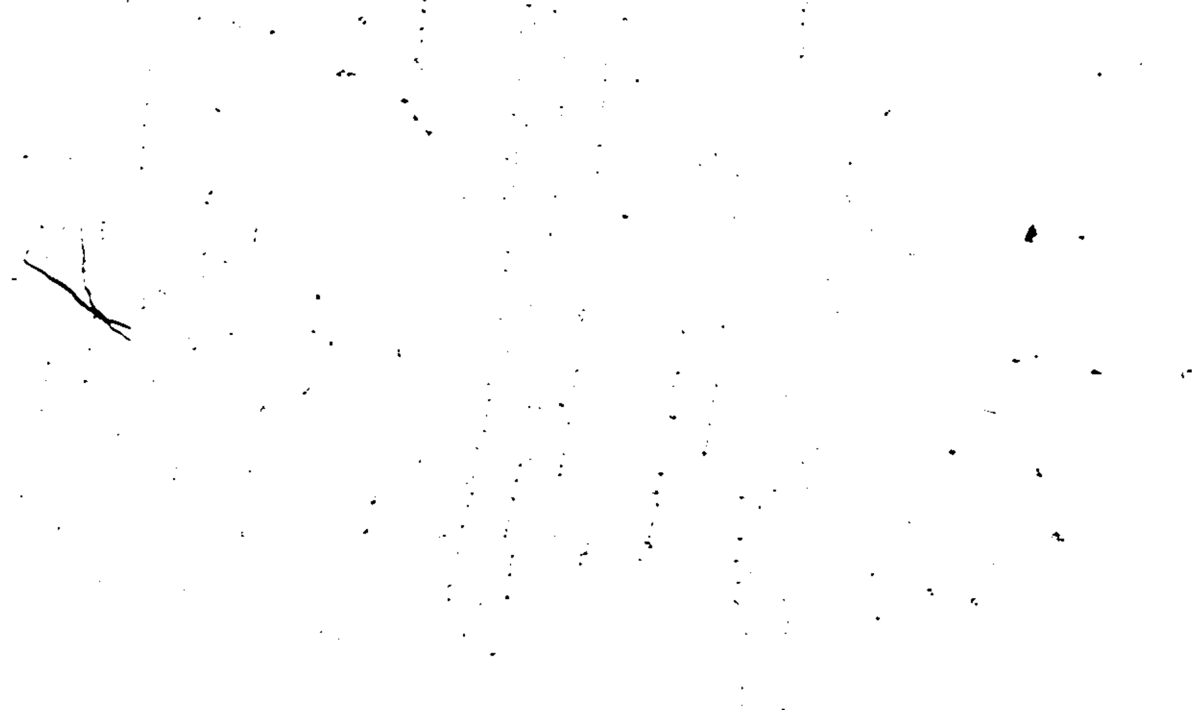
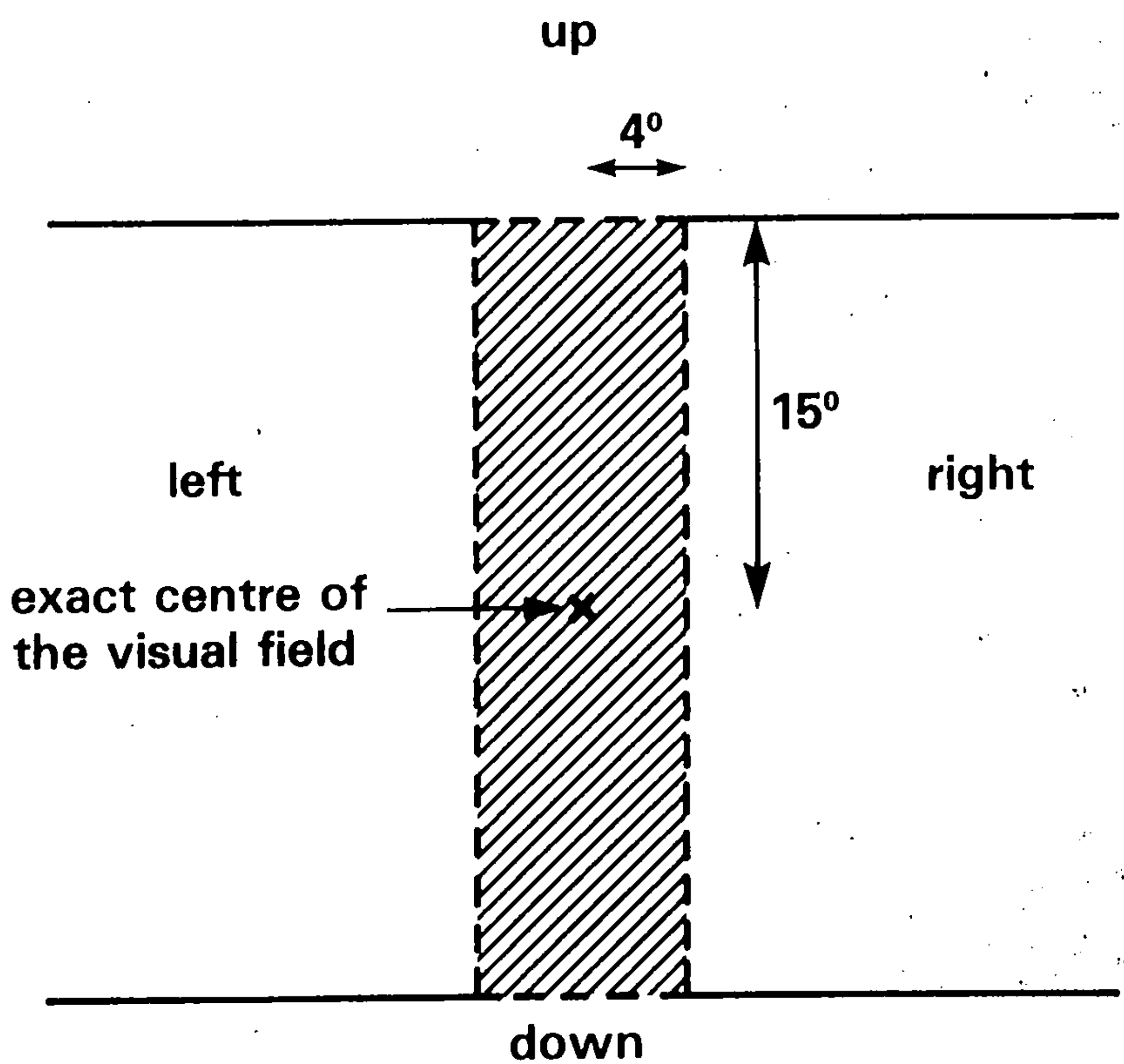


Fig. 3. Criteria for looking centrally. Central fixations included all fixations within the hatched region. Fixations outside that region were either left, right, up or down.


up
4°
15°
left
right
exact centre of
the visual field
down

of the pupil for each fixation point. However, this relation may vary slightly between individuals and between infants and adults (Maurer, 1975; Slater & Findlay, 1972, 1975b). The variation is caused by individual differences in the relation of the line of sight to the centre of the pupil, although that relation is constant in any one individual. Therefore, the scorers established a separate criterion for central fixation for each baby. They assumed that at the beginning of a trial, the baby usually would be fixating the red lights, or within 16' of the horizontal centre of the field. They noted the location of the lamps' reflections on the baby's eye at the beginning of each trial. Subsequently, they calculated the most frequent horizontal deviation of the reflections from the centre of the pupil. This deviation was the horizontal criterion for fixating the centre of the field for that baby so long as the deviation fell within an expected range (equivalent to a 2° to 8° temporal displacement of the centre of the pupil from the line of sight). The scorers used this individual horizontal criterion to decide if an infant began each trial by looking centrally. Any fixations that were no more than 4° horizontally from the infant's criterion for centre were scored as centred providing they were also within the vertical criterion for centre (see Fig. 3). Fixations to the left of this region were scored as left and fixations to the right of this region were scored as right.

The scorers decided where an infant was fixating vertically by comparing his film to the film of the adult. Vertically, they required the infants to fixate within 15° of the exact centre of the visual field. They used both this vertical criterion and the horizontal criterion to decide if the infant began each trial by looking centrally. Fixations above this region were scored as up and fixations below this region were scored as down. The vertical criterion was also used to decide if the first eye movements away from centre were up or down, rather than left or right.

The scorers were always unaware of the stimulus shown on a particular trial. The scorers agreed with each other 85% of the time on whether the infant began the trial by fixating centrally. On trials which they agreed began centrally, they agreed 83% of the time on the direction of the first eye movement. Anytime they disagreed, they rescored the trial together and attempted to reach an agreement.

Many of the data were excluded from the analysis. A trial was used only if the infant began the trial by fixating centrally and then made a scorable eye movement either to the left or to the right. An infant was included only if he provided data on at least two trials for each of the three stimuli (the left line, the right line and the blank field). In the present study, for example, 68% of the data were excluded from the final sample of 32 babies. All of the data were excluded from an additional 81 babies.

Results

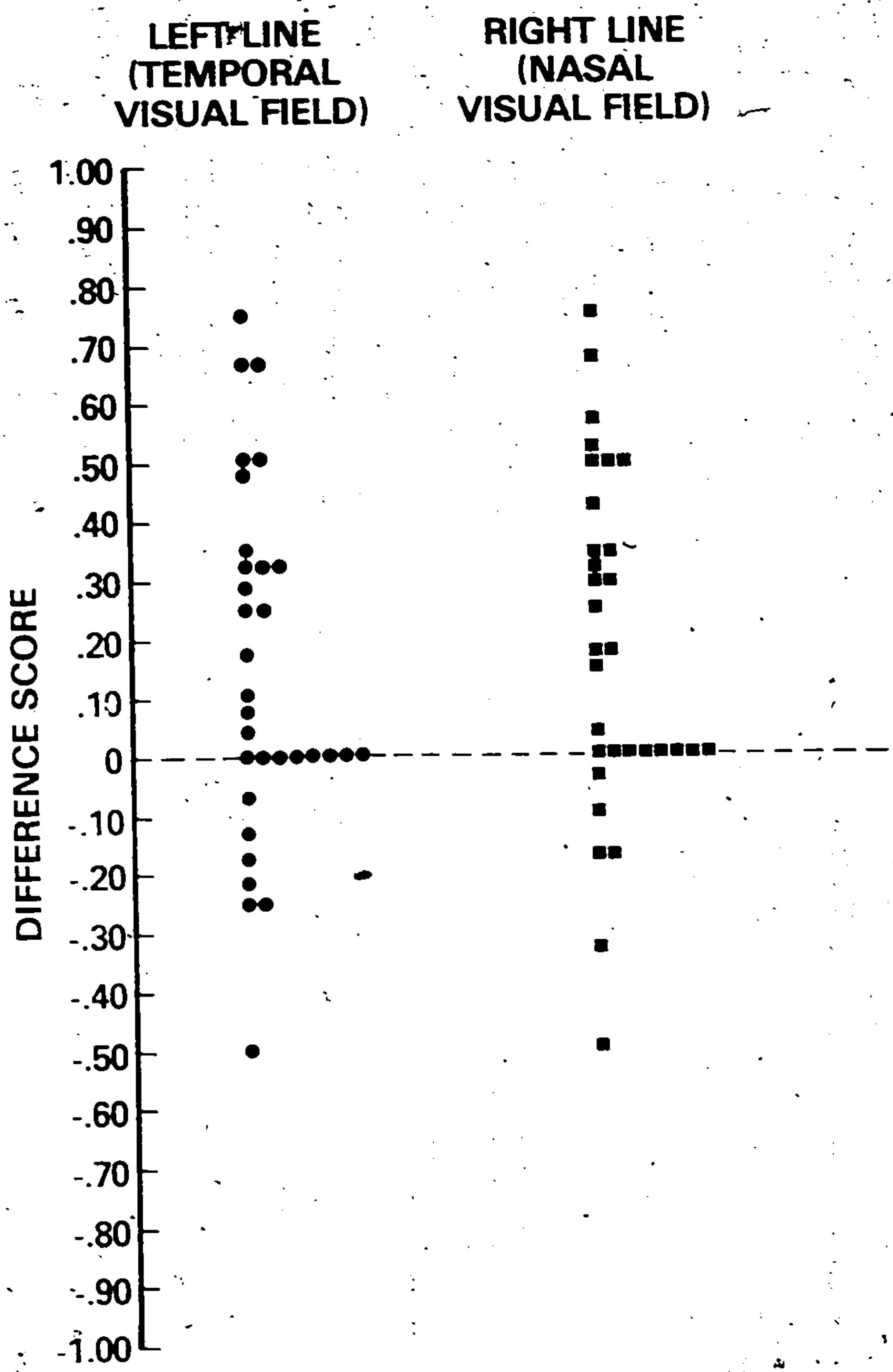
When the field was blank, 49% of the infants' first eye movements away from centre were toward the left visual field. For each subject, the probability that the first eye movement was toward the left visual field was compared for trials with the left line, trials with the right line and trials with the blank field. To compare these three probabilities, I used a Friedman Analysis of Variance (Siegel, 1956).[7] The results showed a significant difference between stimuli ($\chi^2 = 17.06$, df = 2, $p < .001$). Then, I compared the difference between these probabilities, first comparing the left line to the blank field and then comparing the right line to the blank field. For each comparison, I used a two-tailed Wilcoxon test of matched pairs (Siegel, 1956), with α adjusted according to Ryan's (1960) procedure.[8] The Wilcoxon tests showed that infants detected both the left line, T(24) = 62, $p < .02$, $\alpha' = .033$, and the right line, T(24) = 48.5, $p < .01$, $\alpha' = .033$.

Fig. 4 shows the difference between the probability that a baby moved his eyes first away from centre toward a line and the probability that he moved his eyes first in the same direction when the field was blank. When the line was at 10° in the left visual field, many scores were positive - i.e., in many cases, the probability that a baby moved his eyes first toward a line was <u>greater</u> than the probability that he moved his eyes first in the same direction when the field was blank.

[7] The Friedman test is a nonparametric within-subject analysis of variance. I used a nonparametric statistic because probabilities are not normally distributed.

[8] The Wilcoxon test is a nonparametric within-subject test for comparing two stimuli. Since the study included three stimuli, there were three possible comparisons (the left line vs. the blank field, the right line vs. the blank field and the left line vs. the right line). Ryan's (1960) procedure adjusts α for each of these three comparisons so the overall level of significance does not exceed .05. α' represents the adjusted α level for each comparison. When there are three possible comparisons, the two stimuli with the highest and lowest total ranks on the Friedman test are compared with α' set at .0167. That comparison must be significant before other comparisons can be made. If it is, α' is set at .033 for the remaining two comparisons. Only two of the three possible comparisons are reported in the text (the left line vs. the blank field and the right line vs. the blank field).

Fig. 4. The difference between the probability that a newborn moved his left eye toward a line and the probability that he moved his left eye in the same direction when the field was blank. The data are for lines located at 10° in the left visual field and at 10° in the right visual field (Experiment 1).


LEFT LINE
(TEMPORAL
VISUAL FIELD)
RIGHT LINE
(NASAL
VISUAL FIELD)
DIFFERENCE SCORE
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
-.10
-.20
-.30
-.40
-.50
-.60
-.70
-.80
-.90
-1.00

Very few scores were negative. By negative scores, I mean that the probability that a baby moved his eyes first toward a line was <u>less</u> than the probability that he moved his eyes first in the same direction when the field was blank. Similarly, when the line was at 10° in the right visual field, there still were many more positive than negative scores.

Discussion

The results showed that a newborn looking only with his left eye can detect a line 3°18' wide when it is located at 10° in the temporal (left) or nasal (right) visual field. Thus, although newborns have biases when they scan stimuli monocularly (Maurer, 1974; Mendelson & Haith, 1976; Salapatek, 1968; Slater & Findlay, 1972), they can overcome those biases sufficiently well to demonstrate both temporal and nasal vision.

Detection of the temporal line might have been mediated by the direct projection from retina through superior colliculus since that projection appears to be functional at birth while the geniculo-cortical pathway appears to be too immature to mediate a variety of other visual behaviours (Section 1.6). Moreover, cats and human adults with cortical lesions have good detection in the temporal visual field (Section 1.3), detection which might be mediated by the direct collicular pathway (Sherman, 1974b, 1977b).

Currently, there is no way of determining which pathways mediated the detection of the nasal line. Studies in animals with cortical lesions have not tested detection at 10° in the nasal visual field. Even the cat has some uncrossed fibres from the temporal retina (which mediate nasal detection) in the direct projection to the superior colliculus (Kaneski & Sprague, 1974; Laties & Sprague, 1966; Sterling, 1973); and on the basis of this projection, the cat might be able to detect stimuli at 10° in the nasal visual field (Sherman, Note 10). Moreover, compared to the cat, the monkey has more uncrossed fibres from the temporal retina which project directly to the colliculus (Graybiel, 1975; Hubel et al., 1975). Thus, perhaps in the human newborn, the direct projection to the superior colliculus has a sufficient number of uncrossed fibres from the temporal retina to mediate the detection of some stimuli at least out to 10° in the nasal visual field. Or, perhaps the geniculo-cortical pathway is sufficiently mature at birth to mediate this behaviour.

Human adults with lesions in the visual cortex still can detect some stimuli at 10° in the nasal visual field (Koerner & Teuber, 1973). However, their threshold for detection in the nasal visual field is higher than their threshold for detection in the temporal visual field and this difference is considerably larger than in normal adults (reviewed in Section 1.3). Although the infants in the present study detected the line in both the temporal and nasal visual fields, the presence or absence of detection for a line 3°18' wide is a gross measure of peripheral vision. Consequently, one way to find out if nasal vision is poorer than temporal vision would be to determine newborns' threshold for detection at 10° in the temporal and nasal visual fields. If the threshold for detection were higher in the nasal field than in the temporal field at birth, older infants could be tested to find out if they have a similar asymmetry. If the differences between younger and older infants were to resemble those between lesioned and normal adults, this might suggest that the geniculo-cortical pathway is too immature to mediate peripheral detection at birth. An alternative way of examining temporal-nasal differences in detection is described in Experiment 2.

Experiment 2

In cats, the detection of stimuli at least 15° in the nasal visual field appears to depend on the geniculo-cortical pathway (Sherman, 1974b, 1977b). Electrophysiological and behavioural evidence suggests that the geniculo-cortical pathway might be too immature to control at least some behaviours in the human newborn (reviewed in Section 1.6). At birth, that pathway might also be too immature to mediate peripheral detection beyond 15°. Thus, the purpose of Experiment 2 was to find out if newborns can detect stimuli monocularly which are beyond 15° in the periphery. Based on the results of Experiment 1, I assumed that the direction of the first eye movement away from centre might be a valid measure of both temporal and nasal vision. Despite the possibility of biases to look to one side, the infants in Experiment 1 initiated eye movements toward temporal and nasal lines at 10° more than they initiated eye movements in the same direction when the field was blank. In that study, infants were required only to initiate eye movements in the appropriate direction; the size of those eye movements was not measured. Thus, if the lines were further in the periphery, infants might still initiate eye movements toward them more than they initiate eye movements in the same direction when the field is blank - providing they can see the lines.

Newborns viewed single lines monocularly with the left eye. The lines were 3°18' wide and were located at 30° in the left (temporal) visual field and at 20° in the right (nasal) visual field. Except for the location of the lines, this study was identical to Experiment 1. I expected that infants would detect the line in the temporal visual field since newborns viewing stimuli binocularly can detect a line only 1° wide when it is 30° off to the side (Lewis et al., 1978). If newborns have good nasal vision at birth, they should also detect the line at 20° in the nasal visual field, since in normal human adults, detection at 20° in the nasal visual field is <u>better</u> than detection at 30° in the temporal visual field (Frisen & Glansholm, 1975).

Method

Subjects

The subjects were a new group of 33 healthy full-term newborns (at least 38 weeks gestation and at least 2500 gms at birth) born in Hamilton, Ontario ($\bar{X}$ age = 3.8 days, range 1 to 7 days). An additional 75 babies were tested but not included because they provided insufficient data.

Stimuli

The stimuli were identical to those described in Experiment 1 except for the location of the lines. The left line was attached to the screen with the right edge 30° out horizontally to the left of centre (temporal visual field for the left eye) and the right line was attached with the left edge 20° out horizontally to the right of centre (nasal visual field for the left eye).

Apparatus, Procedure, and Data Reduction

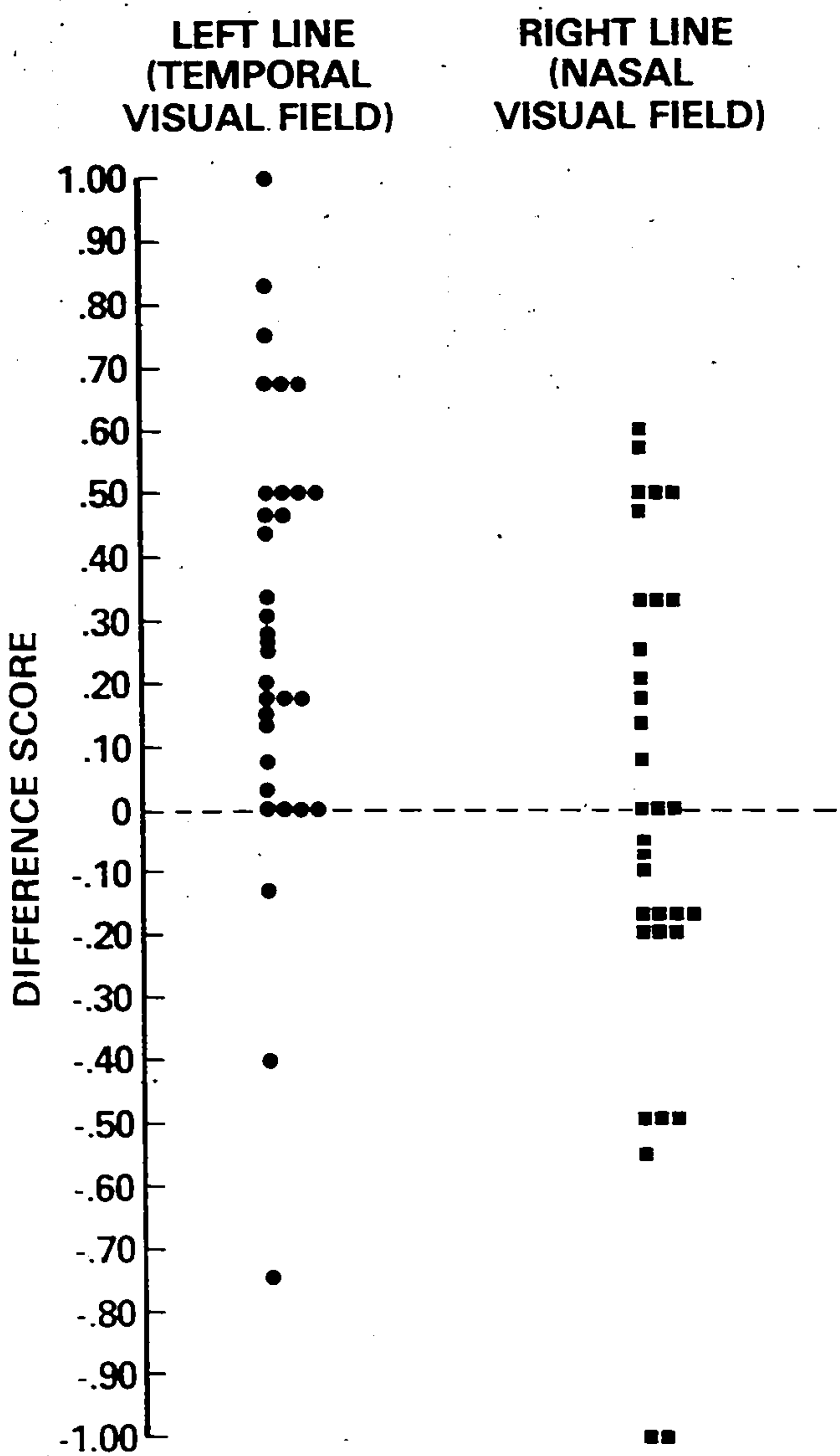
The apparatus, procedure and scoring were identical to Experiment 1. The scorers agreed with each other 87% of the time on whether the infant began the trial by fixating centrally. On trials which the scorers agreed began centrally, they agreed 77% of the time on the direction of the first eye movement.

Results

The analyses were identical to those described in Experiment 1. When the field was blank, 48% of the infants' first eye movements away from centre were toward the left visual field. A Friedman Analysis of Variance showed that the probability that the first eye movement was toward the left visual field differed for the left line, the right line and the blank field ($X^2 = 22.01$, $df = 2$, $p < .001$). I compared the differences between these probabilities for the left line vs. the blank field and for the right line vs. the blank field using Wilcoxon tests of matched pairs with α adjusted according to Ryan's (1960) procedure. Wilcoxon tests showed that the babies detected the left line, $T(29) = 45$, $p < .001$, $\alpha' = .0167$, but that the babies showed no evidence of detecting the right line, $T(30) = 230.5$, $p > .90$, $\alpha' = .033$.

Fig. 5 shows, for each baby, the difference between the probability that he moved his eyes first away from centre toward a line and the probability that he moved his eyes first away from centre in the same direction when the field was blank. When the line was at 30° in the left visual field, most scores were positive, i.e., the probability that a baby moved his eyes first toward a line was greater

Fig. 5. The difference between the probability that a newborn moved his left eye toward a line and the probability that he moved his left eye in the same direction when the field was blank. The data are for lines located at 30° in the left visual field and at 20° in the right visual field (Experiment 2).


LEFT LINE
(TEMPORAL
VISUAL FIELD)
RIGHT LINE
(NASAL
VISUAL FIELD)
DIFFERENCE SCORE
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
-.10
-.20
-.30
-.40
-.50
-.60
-.70
-.80
-.90
-1.00

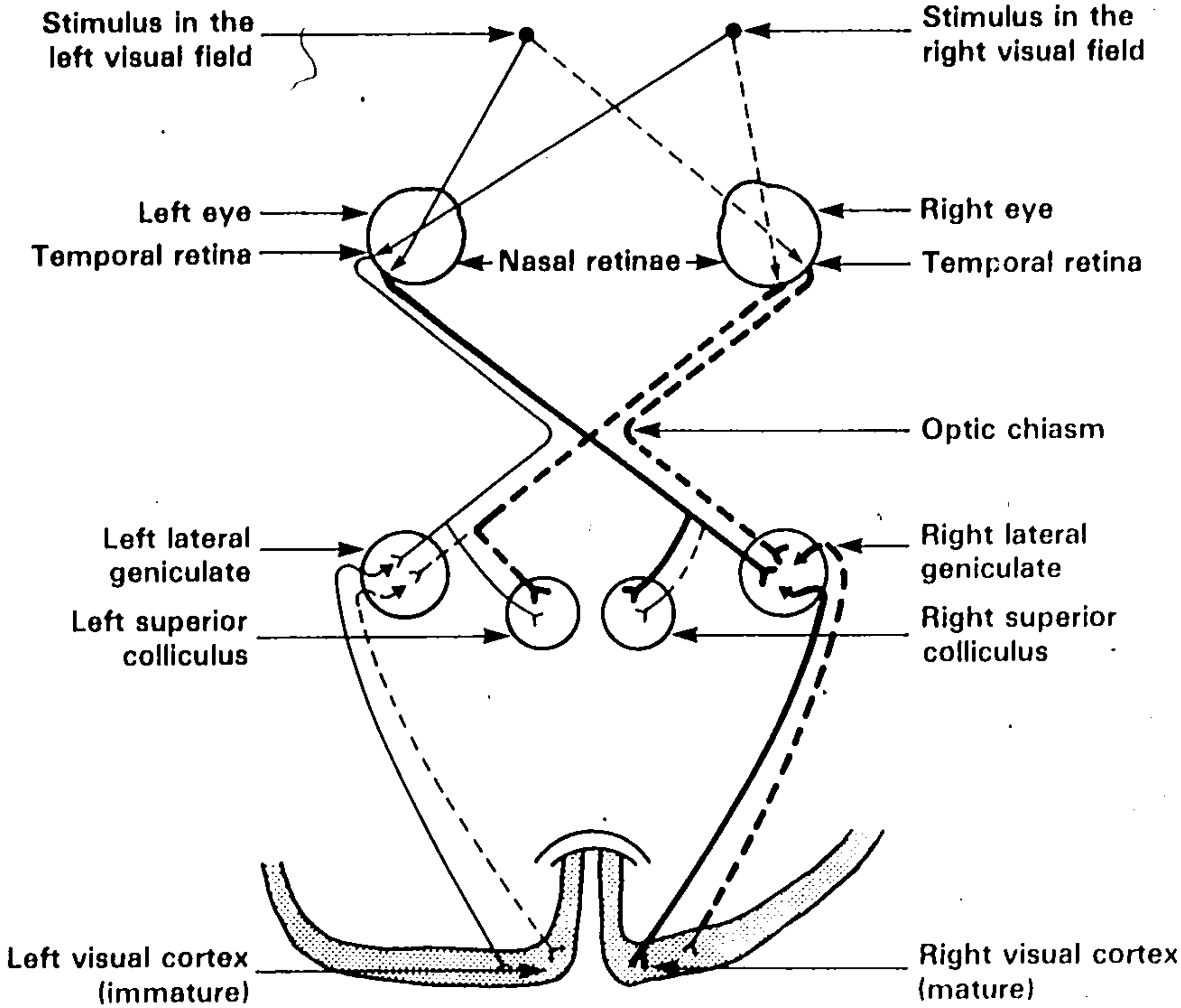
than the probability that he moved his eyes first in the same direction when the field was blank. In contrast, when the line was at 20° in the right visual field, there were about an equal number of positive and negative scores.

Discussion

When newborns viewed stimuli monocularly with the left eye, they detected a line 3°18' wide at 30° in the temporal (left) visual field. But they showed no evidence of detecting the same line when it was at 20° in the nasal (right) visual field. These results suggest that with the left eye, newborns have better detection in the temporal visual field than in the nasal visual field. This might mean that at birth, the projection from retina through visual cortex is too immature to mediate any peripheral detection at 20°.

However, it is possible that the projection through the cortex is sufficiently mature to mediate detection in the left visual field, but not in the right visual field. In humans, stimuli in the left visual field stimulate cells in the right visual cortex and stimuli in the right visual field stimulate cells in the left visual cortex (reviewed in Thompson, 1967). If the projections from the retina to the right hemisphere were to develop earlier than the projections to the left hemisphere, at birth, only the superior colliculus and right hemisphere of the visual cortex might be mature enough to mediate peripheral detection (see Fig. 6). Under these circumstances, the left eye would have poor detection in the nasal (right) visual field. A stimulus in the right visual field would activate receptors in the temporal retina of the left eye which would project mainly to an

Fig. 6. The projections which might mediate peripheral detection if the pathways from the retina to the right cortex were to develop earlier than those to the left cortex. Solid lines represent the projections of the left eye and broken lines represent the projections of the right eye. Heavy lines represent the pathways which might mediate detection. Light lines represent pathways which would not, either because they would be too sparse or too immature.


Stimulus in the left visual field
Stimulus in the right visual field
Left eye
Temporal retina
Nasal retinae
Right eye
Temporal retina
Optic chiasm
Left lateral geniculate
Right lateral geniculate
Left superior colliculus
Right superior colliculus
Left visual cortex (immature)
Right visual cortex (mature)

immature left visual cortex. But the left eye would have good detection in the temporal (left) visual field because the crossed axons from the nasal retina of the left eye would project both to the right superior colliculus and to a mature right visual cortex.

If only the projections to the colliculi and to the right hemisphere of the visual cortex were sufficiently mature to mediate peripheral detection, the right eye should have good detection in both visual fields. Detection in the temporal (right) visual field could be mediated by crossed axons from the nasal retina of the right eye which project directly to the left superior colliculus and detection in the nasal (left) visual field could be mediated by the uncrossed axons from the temporal retina of the right eye which project mainly to a mature right visual cortex (see Sherman, 1977b, for a similar explanation in cats with unilateral lesions of the visual cortex).

To control for this possibility, Experiment 3 tested the right eye of a new group of newborns using the same procedure described in Experiment 2. If, with their right eye, newborns again were to appear to detect only the line at 30° in the temporal visual field, this would suggest that newborns have poorer detection in the nasal, than in the temporal visual field, both for the left eye and for the right eye. This outcome might imply that the projections through both the left and right hemispheres of the visual cortex are too immature to mediate peripheral detection.

Experiment 3

Method

Subjects

The subjects were a new group of 30 newborns ($\bar{X}$ age = 3.7 days, range 1 to 7 days) similar to those described in Experiment 2. An additional 38 babies were tested but not included because they provided insufficient data.

Stimuli

The stimuli were identical to those described in Experiment 2 except for the location of the lines. The right line was attached to the screen with the left edge 30° out horizontally to the right of centre (temporal visual field for the right eye) and the left line was attached with the right edge 20° out horizontally to the left of centre (nasal visual field for the right eye).

Apparatus, Procedure, and Data Reduction

The apparatus and procedure were identical to Experiment 2 except a sterile patch was placed over the baby's left eye and the baby's right eye was filmed. The scoring was identical to Experiment 2 except that I filmed the right eye of an adult in the apparatus for calibration. The scorers agreed with each other 92% of the time on whether the infant began the trial by fixating centrally. On trials which they agreed began centrally, they agreed 88% of the time on the direction of the first eye movement.

Results

The analyses were identical to those described in Experiment 1. When the field was blank, 59% of the infants' first eye movements away from centre were toward the left visual field. A Friedman Analysis of Variance showed that the probability that the first eye movement was toward the left visual field differed for the right line, the left line and the blank field ($X^2 = 15.65$, df = 2, $p < .001$). I compared the differences between these probabilities for the right line vs. the blank field and the left line vs. the blank field, using Wilcoxon test of matched pairs. Wilcoxon tests showed that babies detected the right line, $T(27) = 37$, $p < .001$, $\alpha' = .0167$, but they appeared not to detect the left line, $T(27) = 179$, $p > .80$, $\alpha' = .033$.

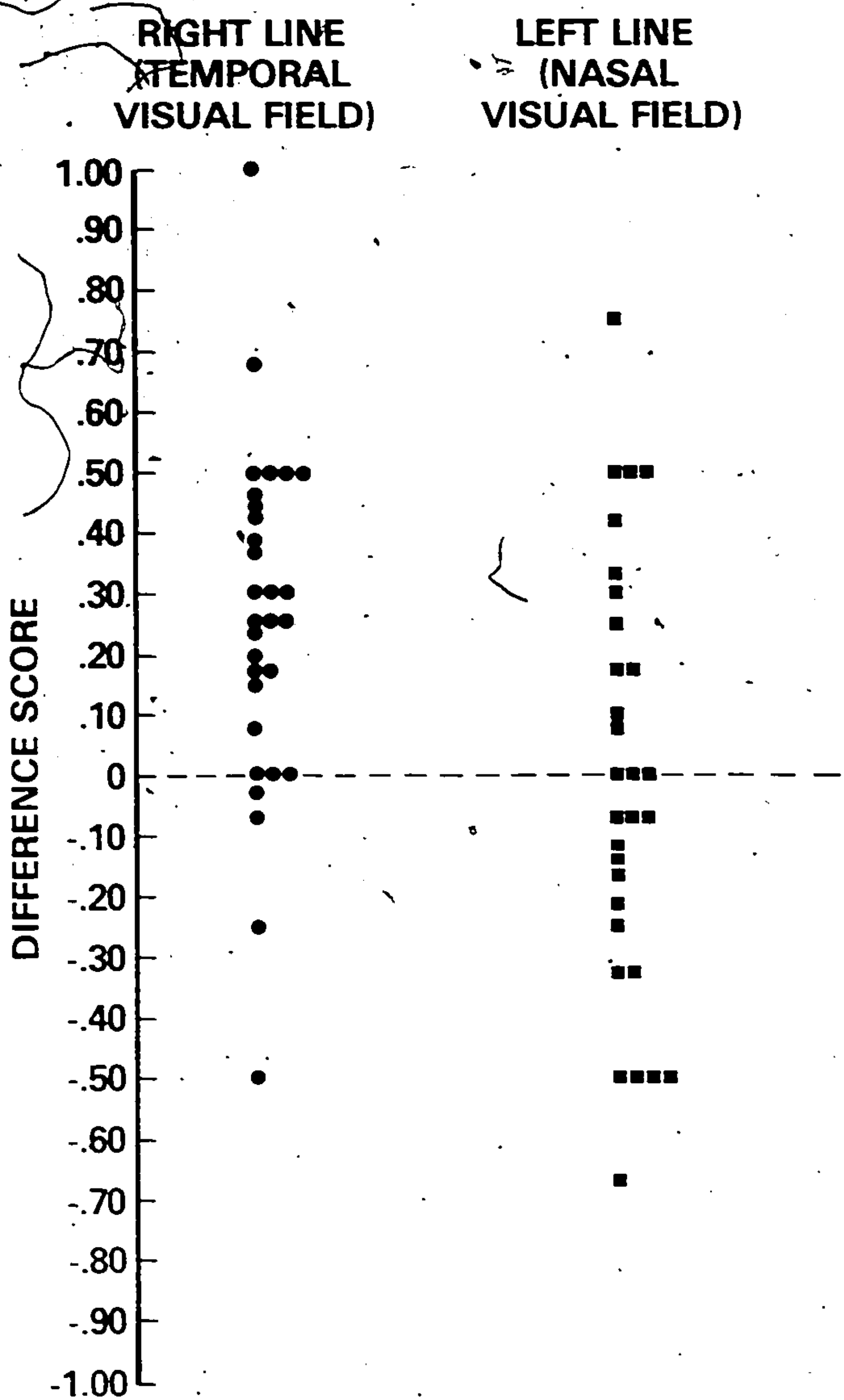
Fig. 7 shows, for each baby, the difference between the probability that he moved his eyes first toward a line and the probability that he moved his eyes first in the same direction when the field was blank. When the line was at 30° in the right visual field, most scores were positive. But when the line was at 20° in the left visual field, about an equal number of scores were positive and negative.

Discussion

Newborns detected a line 3°18' wide at 30° in the temporal (right) visual field but they appeared not to detect the same line when it was at 20° in the nasal (left) visual field. Thus, both with their left eye alone (Experiment 2) and with their right eye alone (the present study) newborns appeared to detect the temporal line but not the nasal line. These results cannot be explained by postulating that one hemisphere of the visual cortex develops before the other. For if it did, one eye should have good detection in both visual fields (Sherman, 1977b). Rather, it is more likely that at least some of the

Fig. 7. The difference between the probability that a newborn moved his right eye toward a line and the probability that he moved his right eye in the same direction when the field was blank. The data are for lines located at 30° in the right visual field and at 20° in the left visual field (Experiment 3).

57


RIGHT LINE
(TEMPORAL
VISUAL FIELD)
LEFT LINE
(NASAL
VISUAL FIELD)
DIFFERENCE SCORE
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
-.10
-.20
-.30
-.40
-.50
-.60
-.70
-.80
-.90
-1.00

projections through both the left and right visual cortices are too immature to mediate peripheral detection at birth.

Detection in the nasal visual field

Studies on lesioned cats and human adults have shown that the direct projection through the superior colliculus is insufficient to mediate good detection in the nasal visual field (Section 1.3). Moreover, at least part of the geniculo-cortical pathway appears to be necessary for that detection (Section 1.3). Since the newborns in Experiments 2 and 3 appeared to show poor detection in the nasal visual field, this might mean that the uncrossed fibres from the temporal retina through the visual cortex (which mediate nasal field detection) are too immature to mediate detection at 20° in the nasal visual field. However, there are explanations other than immaturity of part of the geniculo-cortical pathway which might account for this phenomenon. These are listed below.

1. Differences in the ease of eye movements toward the temporal and nasal visual fields

The results of most monocular studies suggest that, because of temporal response biases, it may be difficult for a newborn to scan stimuli in the nasal visual field (Haith, in press; Maurer, 1974; Mendelson & Haith, 1976; Slater & Findlay, 1972). Those biases might also prevent him from moving his eyes first away from centre toward a stimulus in the nasal field, even though he can see it. If that were so, newborns might appear to have better detection in the temporal than in the nasal visual field. However, the newborns in Experiments 1, 2 and 3 moved their eyes both temporally and nasally when the field was blank. Moreover, in Experiment 1, eye movements toward the nasal field occurred more often when a line was there than when it was not. Thus, at least for stimuli at 10°, newborns seem to be able to overcome any response biases sufficiently well to demonstrate nasal field detection.

Although the stimuli were further off to the side in Experiments 2 and 3 than in Experiment 1, the requirements were the same in all three studies. All eye movements away from centre which were to the left or to the right were included in the analyses, regardless of their size (providing the infant had a sufficient number of usable trials). Moreover, under binocular conditions, newborns are capable of moving the left eye at least 20°, both to the left and to the right (Lewis et al., 1978, unpublished observations). Consequently, it seems reasonable to assume that if newborns could see stimuli at 20° in the nasal visual field under monocular conditions, they might at least start to move their eyes toward those stimuli. Thus, even if there were differences in the ease of eye movements toward the temporal and nasal visual fields, it is unlikely that those differences could account for detection in the nasal visual field at 10° (Experiment 1), but not at 20° (Experiments 2 and 3).

2. <u>Differences in receptor density on the nasal and temporal hemiretinae</u>

It is possible that poor detection in the nasal visual field could be due to a lower density of rods and cones in the temporal retina (which receives input from the nasal visual field) than in the nasal retina. In the human adult, there are fewer receptors per unit area in the temporal retina than in the nasal retina (Osterberg, 1935).

Yet, despite these differences in receptor density, acuity in the normal human adult is only slightly poorer in the nasal visual field than in the temporal visual field (Aulhorn & Harms, 1972; Frisen & Glansholm, 1975; Harvey & Poppel, 1972; Stanek, 1973). In contrast, there appear to be large temporal-nasal differences in detection at birth. Binocularly, the left eye of the newborn detects a line only 33' wide at 20° in the left visual field (Lewis et al., 1978) even though monocularly, he shows no evidence for the detection of a line 3°18' wide at 20° in the nasal visual field (Experiments 2 and 3). It is unlikely that such gross differences in detection could be accounted for by differences in receptor density, especially since Mann (1964) does not note any striking differences between the two hemiretinae at birth.

3. Optical factors in temporal and nasal vision

Since the eye acts as a refracting medium, optical factors cause peripheral stimuli to appear blurred (Davson, 1963; Duke-Elder & Abrams, 1970) and peripheral blur increases with increasing distance from the optic axis (Davson, 1963; Duke-Elder & Abrams, 1970). However, the line of sight is displaced about 5° temporal from the optic axis in the retina of adults (Alpern, 1962). Consequently, a stimulus at 20° in the nasal visual field would be further from the optic axis than a stimulus at 20° in the temporal visual field, causing the nasal stimulus to be slightly more blurred than the temporal stimulus. This effect might be exaggerated slightly in the newborn because his line of sight may be displaced about 8° temporal from the optic axis (Slater & Findlay, 1972, 1975b).

Thus, temporal-nasal differences in detection could occur both as a result of optical factors and as a result of differential receptor density on the two hemiretinae. In adults, each of these factors contributes to poorer detection in the nasal visual field than in the temporal visual field. Their effects might be exaggerated slightly in the newborn. Yet, even with these two effects combined, adults' detection at 20° in the nasal visual field is still better than their detection at 30° in the temporal visual field (Frisen & Glansholm, 1975). For infants, optical factors and differential receptor density might reduce the detection of a target in the nasal visual field relative to a target in the temporal visual field. But these factors should cause gradual, rather than sudden, transitions in behaviour. Thus, it is unlikely that optical factors and differential receptor density could account for an absence of detection at 20° in the nasal visual field of a stimulus that was above threshold at 30° in the temporal visual field (Experiments 2 and 3).

Therefore it seems unlikely that differences in the ease of eye movements, differences in receptor density, or optical factors could account adequately for poor detection at 20° in the nasal field. Note that some cortical areas other than the geniculo-cortical pathway also might be necessary for nasal field detection (see for example Elberger, 1979). If that were so, newborns might have poor nasal field detection even if the geniculo-cortical pathway were mature. However, anatomical, electrophysiological and other behavioural data suggest that the geniculo-cortical pathway is very immature at birth (reviewed in Section 1.6). Whether or not other cortical areas are also immature, it seems likely that at least part of the geniculo-cortical pathway is too immature to mediate detection at 20° in the nasal field.

Detection in the temporal visual field

At birth, detection in the temporal visual field is most likely to be mediated by the direct projection from retina through superior colliculus (see the Discussion of Experiment 1). The projection through the visual cortex also might mediate that detection. Perhaps the crossed fibres from the nasal retina are sufficiently mature to mediate temporal field detection, while the uncrossed fibres from the temporal retina are too immature to mediate nasal field detection. It is possible that the crossed projections are functional earlier than the uncrossed projections in the human since the crossed projections are phylogenetically older (Diamond & Hall, 1969). However, anatomical data in both the cat (LeVay et al., 1978) and monkey (Rakic, 1976) show that the crossed and uncrossed axons develop simultaneously and reach the visual cortex well before birth. Initially, they overlap within the cortex and later begin to segregate into separate alternating columns. Thus, the crossed and uncrossed axons do not appear to develop at different rates, at least in the cat and monkey. The marked similarities in the anatomical development of the visual system for monkey and man (Rakic, 1976) suggest that the same may be true for the human infant.

In conclusion, some part of the pathway from retina through visual cortex appears to be too immature to mediate peripheral detection. It is possible that the pathway from the nasal retina through the visual cortex is sufficiently mature to mediate temporal field detection. It is also possible that the pathway from the temporal retina through the visual cortex is sufficiently mature to mediate some nasal field detection. Nonetheless, at least part of the pathway from the temporal retina through the visual cortex appears to be too immature to mediate the detection of a line $3^{\circ}18'$ wide at 20° in the nasal visual field.

Implications of Poor Detection in the Nasal Visual Field at Birth

In addition to suggesting that the geniculo-cortical pathway may be too immature to mediate some peripheral detection at birth, poor detection in the nasal field has other implications for understanding and studying vision in newborns.

1. The region of binocular overlap

The region of binocular overlap refers to the portion of the visual field which is represented on the retinae of both eyes. In human adults, the nasal visual field of each eye extends out to 60° (Moses, 1970) and consequently, the central 120° of the visual field is represented on the retinae of both eyes. Thus, in human adults, the binocular region of overlap includes the central 120° of the visual field. In phylogenetically older species, the binocular region is considerably smaller than in the human adult (Moses, 1970). The results of the experiments reported in this chapter suggest that the binocular region also might be considerably smaller in the human newborn than in the human adult. It appears to include at least the central 20°, but less than the central 40° of the visual field (since newborns detect stimuli at 10° in the nasal field but appear not to detect stimuli at 20° in the nasal field).

2. Conjugate eye movements

Since the entire visual field is at least 60° when newborns view stimuli binocularly, i.e., they can detect stimuli at least out to 30° in the left and right visual fields (Harris & MacFarlane, 1974; MacFarlane et al., 1976), a considerable amount of information might have access only to one eye. Beyond the binocular region, the left eye would see stimuli only on the left, and the right eye would see stimuli only on the right. Thus, it is not surprising that the newborn often has problems with binocular coordination (Blanton, 1917; Fonarev, 1959; Guernsey, 1929; Maurer, 1974; Wickelgren, 1969). In fact, when newborns view stimuli monocularly, the left eye moves reliably toward lines at 30° in the left visual field, but not toward lines at 20° in the right visual field (Experiment 2). In contrast, the right eye moves reliably toward stimuli at 30° in the right visual field, but not toward stimuli at 20° in the left visual field (Experiment 3). Thus, when stimuli are at least 20° off to the side under binocular conditions, the two eyes might move independently. However, each eye moves reliably toward lines at 10° in the left and right visual fields (Experiment 1). Therefore, conjugate eye movements might occur mainly when the eyes are moving toward stimuli which are less than 20° in the periphery - i.e. toward stimuli which are in the binocular region.

Estimates of the percentage of eye movements which are conjugate at birth range from 20% to 94% (Fonarev, 1959; Guernsey, 1929; Slater & Findlay, 1975a; Wickelgren, 1969). Although some of the variance is due to individual differences, some of it might also be due to the location of the stimuli in the visual field. However, none of the studies has investigated this possibility systematically. One way to do so, would be to present stimuli at various locations in the visual field and record both eyes to find out how often the two eyes move together toward each stimulus. If eye movements toward stimuli were conjugate mainly when the stimuli fall in the binocular region, the two eyes should move together frequently when the stimuli are 10° off to the side, but infrequently when the stimuli are 20° off to the side.

3. Stereoscopic depth perception

Stereopsis occurs when two slightly different images on each retina are fused to form the perception of a single three dimensional object. However, if the images on each retina are too disparate, either one is suppressed or a double image is perceived (Moses, 1970). Even when each eye of the newborn fixates the same point in the visual field (for evidence this does not always occur, see Aslin, 1977; Ling, 1942; Maurer, 1974; Slater & Findlay, 1975a), stereopsis could occur only within the region of binocular overlap (since only in this region does each eye receive similar input). Consequently, if stereopsis were present at birth, it might occur over a much narrower part of the visual field than in adults.

Unfortunately, very little is known about stereopsis in the human newborn, mainly because there are no reliable response measures suitable for young infants (reviewed in Salapatek & Banks, in press). Measuring stereopsis in the periphery would be even more difficult since infants would be required to fixate centrally while a stimulus was present in the periphery (see Harris & MacFarlane, 1974, for evidence that newborns move their eyes reliably toward detectable peripheral stimuli even when a stimulus is present centrally).

4. Temporal bias in monocular scanning

When newborns scan stimuli monocularly they tend to look longer at the temporal side of a figure than at the nasal side and they tend to ignore stimuli in the nasal visual field (Haith, in press; Maurer, 1974; Mendelson & Haith, 1976; Salapatek, 1968; Slater & Findlay, 1972). Although some of this effect might be due to measurement error (Maurer, 1974; Slater & Findlay, 1975b), some of it is not (Maurer, 1974). One reason for this bias might be that newborns have very little vision in the nasal field. Consequently, temporal field input might pull the eye in a temporal direction.

5. Implications for studying newborn's perception

(a) Tests for hemispheric dominance

When adults are presented with identical stimuli in the left and right visual fields, the direction and latency of the first eye movement away from centre appears to depend on the nature of the stimulus (Kinsbourne, 1974). For unfamiliar stimuli, subjects tend to look first and/or faster toward stimuli in the right visual field. For familiar stimuli, subjects tend to look first and/or faster toward stimuli in the left visual field. Kinsbourne (1974) argued that the left hemisphere (which responds to stimuli in the right visual field) is specialized for initial feature analysis and when an unfamiliar object is presented to both hemispheres, the left hemisphere is activated more than the right. This imbalance causes subject to look first (and/or faster) toward the right visual field. Similarly, the right hemisphere is specialized for the simple detection of familiar objects, so when those are presented, the right hemisphere is activated more than the left, causing subjects to look to the left.

Recently, investigators have attempted to find behavioural evidence for hemispheric specialization in young infants (Barrera, Dalrymple, & Witelson, Note 11) and anatomical evidence for cortical dominance, even in newborns (Witelson & Pallie, 1973). However, there would be a difficulty in using Kinsbourne's (1974) behavioural techniques to test for hemispheric specialization in newborns. Specifically, the experiments reported in this chapter suggest that the geniculo-cortical pathway is too immature to mediate detection at 20° in the nasal visual field. Even if crossed fibres in this pathway were sufficiently mature to mediate detection in the temporal visual field, the left hemisphere would have input mainly from the right eye and the right hemisphere, mainly from the left eye. Consequently, any observed differences in reaction time or in the direction of eye movements might reflect eye dominance rather than cerebral specialization. Moreover, the entire geniculo-cortical pathway might be too immature to mediate peripheral detection at birth. If this were so, peripheral stimuli might have no representation in the visual cortex. Under these circumstances, any observed differences in behaviour certainly would not reflect hemispheric specialization.

(b) <u>Tests for visual preference</u>

A common method of determining whether newborns can discriminate between stimuli involves presenting those stimuli in pairs and recording how long infants look at each member of the pair. When infants spend more time looking at one stimulus than the other, this provides evidence for discrimination (e.g., Fantz, 1965; Fantz et al., 1975). However, since the left eye sees mainly stimuli on the left, and the right eye, mainly stimuli on the right, the wrong inferences could be drawn by observing only one eye. Moreover, even if both eyes were observed, it is unclear whether newborns process the disparate information from both eyes or whether they suppress the information from one eye. Thus, investigators might be wise to present single stimuli which fall within the binocular region (within the central 20° of the visual field). In addition, it would be interesting to find out if the conclusions would differ for monocular and binocular viewing.

(c) Tests for peripheral acuity

It is well known that peripheral acuity in adults decreases as stimuli are placed further off toward the side. This is true both when adults are tested binocularly (reviewed in Alpern, 1962; Aulhorn & Harms, 1972) and when they are tested monocularly (e.g. Frisen & Glansholm, 1975). In contrast, very little is known about newborns' peripheral detection.

Recently, Lewis et al. (1978) measured peripheral detection binocularly in newborns by presenting single lines at various locations in the visual field. To assess peripheral detection, they determined the narrowest line that would elicit eye movements toward it significantly more often than chance. However, they were recording only from the left eye and found no evidence for the detection of any stimulus 20° or 30° to the right. This is not surprising since the results of Experiments 2 and 3 showed that monocularly, each eye has poor detection at 20° in the nasal visual field. Thus, in the study of Lewis et al., the right eye probably detected the stimuli at 20° and 30° in the right visual field (Experiment 3). Despite this, eye movements toward peripheral stimuli still would be a suitable measure of peripheral detection binocularly if both eyes were recorded. Moreover, the results of the experiments in this chapter suggest that thresholds for monocular detection could be tested peripherally using a method similar to that described by Lewis et al.

In adults, peripheral detection is better for single lines than for striped stimuli (Low, 1951). It would be interesting to determine if the same were true in newborns. To measure peripheral acuity for stripes, it might seem logical to show infants a striped stimulus and a plain stimulus, one in the left visual field and the other in the right visual field. If infants could detect the stripes, they should move their eyes toward them significantly more often than toward the plain stimulus (Fantz et al., 1975); and the narrowest stripes that elicited eye movements toward them would be a measure of acuity. Several investigators have used a similar method to measure acuity in newborns (Fantz et al., 1975; Miranda, 1970; Doris, Felzen, & Poresky, Note 12), although those investigators measured how long infants looked at each stimulus rather than the direction of the infants' first eye movements away from centre.

However, there is a problem in using eye movements as a measure of newborns' peripheral acuity for stripes. If they were to view the stimuli binocularly, it would be difficult to interpret the results (see the discussion of tests for visual preferences). If they were to view the stimuli monocularly, the results of Experiments 2 and 3 suggest that they might not even see the stimulus in the nasal visual field if it were more than 10° off to the side. Thus, if infants were to move their eyes toward the striped stimulus, it would not necessarily be because they detected the stripes. Rather, it might be because that was the only stimulus they could see. Consequently, the direction of eye movements appears to be an inappropriate measure of newborns' peripheral acuity for stripes, particularly their monocular acuity. Unlike the tests for visual preferences, presenting the stimuli in pairs is necessary since newborns move their eyes toward a single peripheral stimulus whether it is patterned (Harris & MacFarlane, 1974) or plain (Lewis et al., 1978). Thus, some other measure, such as the visually evoked response, might be more suitable.

In conclusion, the first three experiments show that although newborns can detect a line $3^{\circ}18'$ wide at 10° in the nasal visual field, they show no evidence of detecting the same stimulus at 20° in the nasal visual field. This sudden transition in behaviour suggests that some part of the geniculo-cortical pathway may be too immature to mediate peripheral detection at birth. If detection in the nasal visual field were to depend on the geniculo-cortical pathway, then as that pathway develops, infants might show a corresponding improvement in nasal field detection. The following chapter considers evidence for the development of the geniculo-cortical pathway and presents the data on peripheral detection in older infants (Experiments 4 and 5).

Chapter 3

Detection in the Temporal and Nasal Visual Fields by 1- and 2-month-old Infants

There appears to be considerable development in the geniculo-cortical pathway during the first few months of life. In the visual cortex, dendrites and axons increase in length, size and number of branches; the cellular organization comes to more closely resemble that of an adult; and fibres become myelinated, especially those in the projection from lateral geniculate to visual cortex (Conel, 1939, 1941, 1947). Physiological studies measuring visually evoked responses suggest that important changes in the geniculo-cortical pathway take place between 1 and 2 months of age. Hoffmann (1978) found that when 1-month-olds view checkerboards with large checks, the amplitude of the early component of the visually evoked response (which supposedly reflects activity in the geniculo-cortical pathway) is unrelated to check size. This suggests that the geniculo-cortical pathway might be too immature to differentiate at least some stimuli during the first month of life (see Section 1.6). In contrast, when 2-month-olds view the same checkerboards, the amplitude of the early component varies as check size is varied (Karmel, Hoffmann, & Fegy, 1974).

Behavioural data also imply that there are important changes in the geniculo-cortical pathway at about 2 months of age. Only when the infant is at least 2 months old does he scan extensively (Salapatek, 1975) and only then does he look frequently at the internal elements of a figure (Maurer & Salapatek, 1976; Salapatek, 1975). This extensive scanning probably accounts, in part, for the ability of 2-month-olds to discriminate, for the first time, stimuli which differ only in the shape or arrangement of their internal elements (Fantz et al., 1975; Maurer & Barrera, Note 6). Moreover, only at that age, does tracking become smooth (White, 1971; White et al., 1964), and only then does symmetrical optokinetic nystagmus begin to occur monocularly (i.e., it begins to occur reliably both for stripes moving temporally to nasally and for stripes moving nasally to temporally) (Atkinson, Note 1). Extensive scanning, the discrimination of stimuli which differ only internally in shape or arrangement, smooth pursuit and symmetrical optokinetic nystagmus probably depend on the geniculo-cortical pathway (reviewed in Section 1.5). Thus, in the human infant, the geniculo-cortical pathway might be capable of influencing those behaviours at 2 months of age, but not before.

The human newborn appears not to detect stimuli at 20° in the nasal visual field (Experiments 2 and 3). In cats, this behaviour depends on the geniculo-cortical pathway (Sherman, 1974b, 1977b). If the same were true in the human infant, he might show a marked improvement in nasal field detection at 2 months of age, but not at 1 month of age. The following two studies tested peripheral detection in the left eyes of 1-month-olds and 2-month-olds. In each experiment, the method was identical to that described in Experiment 2, except for the age of the subjects. Experiment 4 presents the data for 1-month-olds.

Experiment 4

Method

Subjects

The subjects were 30 healthy full-term 1-month-olds (at least 38 weeks gestation and at least 2500 gms at birth) residing in or near Hamilton, Ontario ($\bar{X}$ age = 35.4 days, range 28 to 41 days). An additional 76 babies were tested but not included because they provided insufficient data. Babies who had participated in Experiments 1, 2 or 3 were not tested.

Stimuli, Apparatus, Procedure and Data Reduction

The stimuli, apparatus, procedure and scoring were identical to Experiment 2. The scorers agreed with each other 95% of the time on whether the infant began the trial by fixating centrally. On trials which the scorers agreed began centrally, they agreed 91% of the time on the direction of the first eye movement.

Results

The analyses were identical to those described in Experiment 1. A Friedman Analysis of Variance showed that the probability that the first eye movement was toward the left visual field differed for the left line, the right line and the blank field (χ^2 = 10.52, df = 2, p < .01). I compared the differences between these probabilities for the left line vs. the blank field and for the right line vs. the blank field using Wilcoxon tests of matched pairs with α adjusted according to Ryan's (1960) procedure. Wilcoxon tests showed that the babies detected the left line, T(23) = 49, p < .01, α' = .033, but that the babies showed no evidence of detecting the right line, $T(21) = 82.5$, $p = .25$, $d' = .033$.

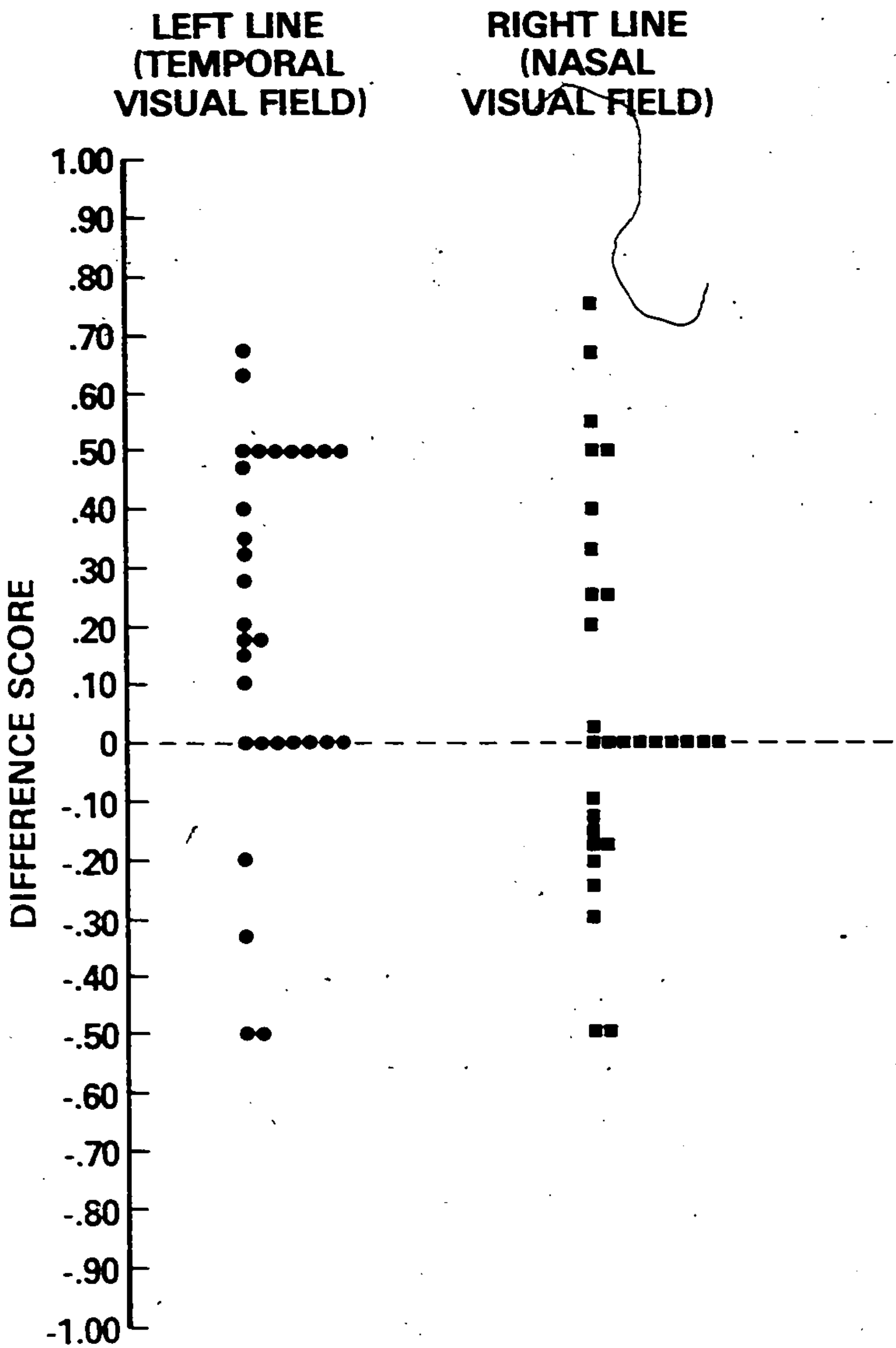
Fig. 8 shows, for each baby, the difference between the probability that he moved his eyes first away from centre toward a line and the probability that he moved his eyes first away from centre in the same direction when the field was blank. When the line was at 30° in the left visual field, most scores were positive, i.e. the probability that a baby moved his eyes first toward a line was greater than the probability that he moved his eyes first in the same direction when the field was blank. In contrast, when the line was at 20° in the right visual field, there were about an equal number of positive and negative scores.

Discussion

When 1-month-olds viewed stimuli monocularly with the left eye, they detected a line $3^{\circ}18'$ wide at 30° in the temporal visual field. But they showed no evidence of detecting the same line when it was at 20° in the nasal visual field. Thus, 1-month-olds seem to have poorer detection in the nasal than in the temporal visual field of the left eye. These results are similar to those reported for the left eye of newborns (Experiment 2) and for the right eye of newborns (Experiment 3).

During the first month of life there appear to be no obvious changes in the visually evoked response, or in the infant's ability to scan extensively, to track smoothly or to show symmetrical optokinetic nystagmus. Those results suggest that the geniculo-cortical pathway still might be too immature to influence many visual behaviours at 1

Fig. 8. The difference between the probability that a 1-month-old moved his left eye toward a line and the probability that he moved his left eye in the same direction when the field was blank. The data are for lines located at 30° in the left visual field and at 20° in the right visual field (Experiment 4).


LEFT LINE (TEMPORAL VISUAL FIELD)
RIGHT LINE (NASAL VISUAL FIELD)
DIFFERENCE SCORE
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
-.10
-.20
-.30
-.40
-.50
-.60
-.70
-.80
-.90
-1.00

month of age. The results of Experiment 4 suggest that there are no marked improvements in nasal field detection during the first month of life. Consequently, they strengthen the conclusion that, in the human infant, good detection in the nasal field depends on some part of the pathway through the visual cortex.

In addition, the results have other implications similar to those discussed for newborns (see the Discussion of Experiment 3). They suggest that there is little, if any, change in the binocular region of overlap during the first month of life; that conjugate eye movements might occur mainly within a limited region of the visual field; and that stereoscopic depth perception might be poor, particularly beyond the region of binocular overlap. Moreover, since 1-month-olds appear to have poor detection in the nasal field, precaution is necessary in studying their vision (see the Discussion of Experiment 3 for a detailed explanation). Tests for hemispheric specialization and tests for visual preferences that use paired stimuli might result in misleading data; and the direction of eye movements toward peripheral stimuli would not be a feasible measure of their peripheral acuity for striped stimuli.

Experiment 5

Studies of visually evoked responses and visual behaviour suggest that the geniculo-cortical pathway is sufficiently mature to begin to influence several behaviours at about 2 months of age. If the poor nasal field detection observed in newborns (Experiments 2 and 3) and in 1-month-olds (Experiment 4) were to reflect an immature geniculo-cortical pathway, then 2-month-olds should have good detection in both visual fields. Moreover, their detection in the nasal visual field should be considerably better than in newborns or in 1-month-olds. Experiment 5 tested this possibility by examining peripheral detection in the left eyes of 2-month-olds. The method was the same as that described in Experiment 2.

Method

Subjects

The subjects were 32 2-month-olds ($\bar{X}$ age = 64.5 days, range 56 to 70 days) similar to those described in Experiment 4. An additional 43 babies were tested but not included because they provided insufficient data. Babies who had participated in any previous experiment were not tested.

Stimuli, Apparatus, Procedure and Data Reduction

The stimuli, apparatus, procedure and scoring were identical to Experiment 2. The scorers agreed with each other 89% of the time on whether the infant began the trial by fixating centrally. On trials which the scorers agreed began centrally, they agreed 83% of the time on the direction of the first eye movement.

Results

The analyses were identical to those described in Experiment 1. A Friedman Analysis of Variance showed that the probability that the first eye movement was toward the left visual field differed for the left line, the right line and the blank field (X^2 = 22.26, df = 2, p < .001). Wilcoxon tests showed that babies detected both the left line, T(24) = 64, p = .01, α' = .033, and the right line, T(29) = 74.5, p < .01, α' = .033.

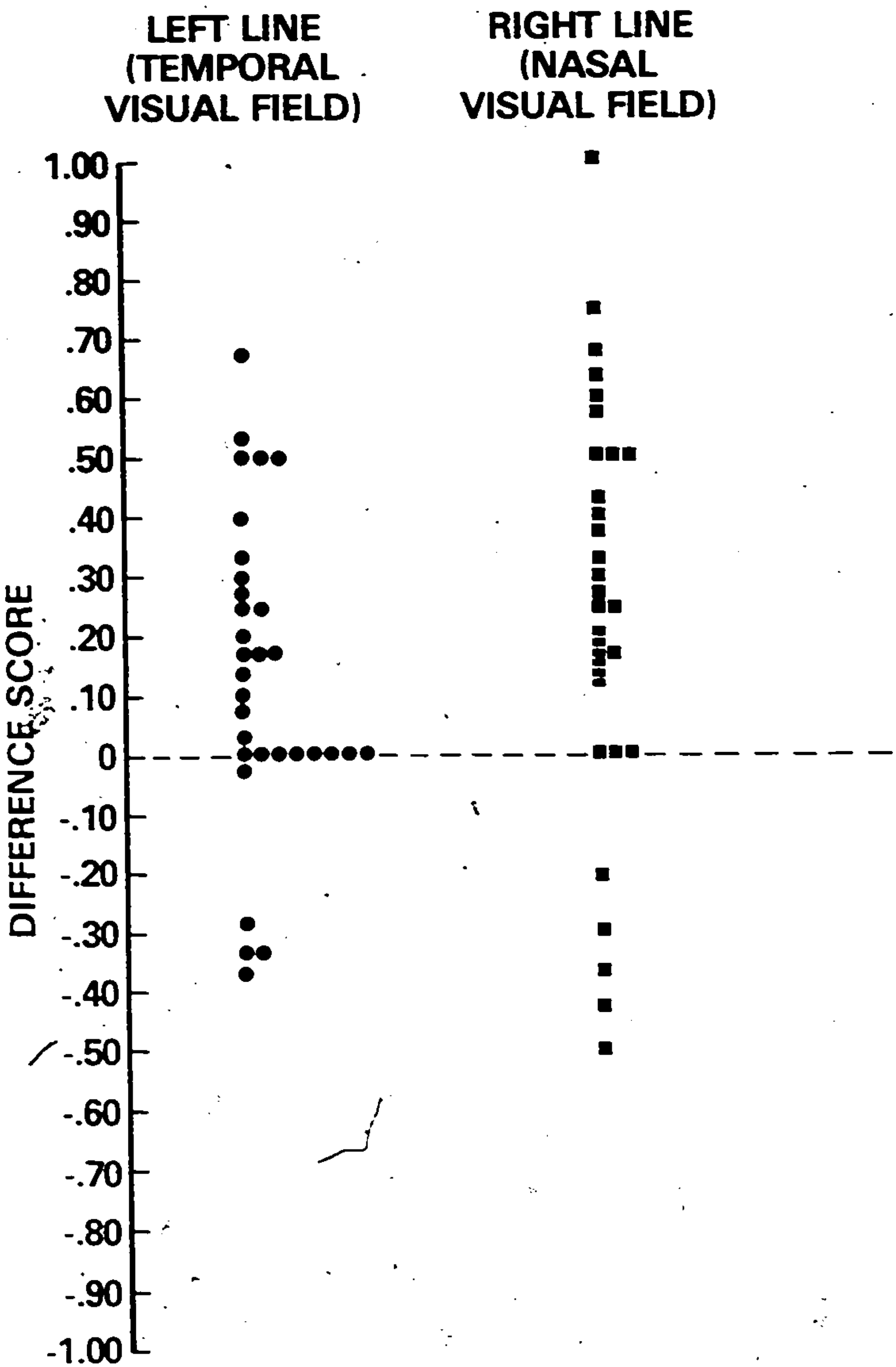
Fig. 9 shows, for each baby, the difference between the probability that he moved his eyes first toward a line and the probability that he moved his eyes first in the same direction when the field was blank. When the line was at 30° in the left visual field or at 20° in the right visual field, most scores were positive - i.e. the probability that a baby moved his eyes first toward each line was greater than the probability that he moved his eyes first in the same direction when the field was blank.

Discussion

When 2-month-olds viewed stimuli monocularly with the left eye, they detected a line 3°18' wide at 30° in the temporal (left) visual field. This behaviour is similar to that observed for the left eye of newborns (Experiment 2) and 1-month-olds (Experiment 4). However, 2-month-olds also detected the line when it was at 20° in the nasal (right) visual field. Neither newborns (Experiment 2) nor 1-month-olds (Experiment 4) showed evidence for this detection. Consequently, there appears to be a marked improvement in nasal field detection for the left eye between 1 and 2 months of age.

Anatomical and electrophysiological changes in the geniculo-cortical pathway (Conel, 1941, 1947; Hoffmann, 1978; Karmel et al., 1974) might underly the marked improvement in nasal field detection at about 2 months of age. However, there are explanations other than geniculo-cortical development which might account for this improvement.

Fig. 9. The difference between the probability that a 2-month-old moved his left eye toward a line and the probability that he moved his left eye in the same direction when the field was blank. The data are for lines located at 30° in the left visual field and at 20° in the right visual field (Experiment 5).


LEFT LINE
(TEMPORAL
VISUAL FIELD)
RIGHT LINE
(NASAL
VISUAL FIELD)
DIFFERENCE SCORE
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
-.10
-.20
-.30
-.40
-.50
-.60
-.70
-.80
-.90
-1.00

1. An improvement in the ease of eye movements toward the nasal visual field

During the first month of life, infants seem to have temporal biases when they scan peripheral stimuli monocularly (Haith, in press; Maurer, 1974; Mendelson & Haith, 1976; Slater & Findlay, 1972). If those biases were no longer present in 2-month-olds, infants might appear to detect the nasal line for the first time at that age. However, there is evidence that temporal biases are not mitigated during the first two months of life (Maurer, 1974). Moreover, even newborns can overcome any response biases sufficiently well monocularly to demonstrate detection at 10° in the nasal visual field (Experiment 1); and it is unlikely that response biases prevented them from demonstrating detection at 20° in the nasal field (see the Discussion of Experiment 3). Thus, it is unlikely that an improvement in the ease of eye movements toward the nasal visual field could account for the observed improvement in nasal field detection between 1 and 2 months of age.

2. Changes in the anatomy and optics of the eye

There are many anatomical and optical changes in the eye which might cause an improvement in peripheral vision between birth and adulthood. Some of these changes probably occur during the second month of life. First, there are changes in the shape of the eyeball (Mann, 1964; Sorsby, Benjamin, Sheridan, Stone, & Leary, 1961), cornea and lens (Brown, 1961; Mann, 1964; Parks, 1966). But, since these changes appear to be symmetrical around the optic axis, it is unlikely that they underlie the observed improvement in nasal field detection.

Second, the line of sight probably shifts nasally on the retina and approaches the adult location of 5° temporal to the optic axis (Alpern, 1962; Mann, 1964; Maurer, 1974). If this were so, a target at 20° in the nasal visual field would be optically less blurred for the 2-month-old than for the newborn (see the Discussion of Experiment 3 for a detailed explanation). However, it is unlikely that this would be sufficient to account for the observed improvement in nasal field detection, especially since optics are relatively unimportant in determining the adult's ability to detect peripheral stimuli (Clarke & Belcher, 1962; Frisen & Glansholm, 1975). Finally, since the peripheral retina is practically mature at birth (Mann, 1964), differential changes in receptor density in the two hemiretinae are also an unlikely explanation.

In summary, electrophysiological and behavioural data suggest that there are important changes in the functioning of the geniculo-cortical pathway between 1 and 2 months of age. There appears to be a corresponding improvement in nasal field detection during that time. Since factors such as changes in the control of eye movements and anatomical changes in the eye appear to be insufficient to account for the results, it seems likely that maturation of the geniculo-cortical pathway underlies the observed improvement in nasal field detection. It also seems likely that poor nasal field detection at birth reflects at least in part, an immature projection through the visual cortex. However, it is possible that some part of the visual system, other than the geniculo-cortical pathway, is also necessary for good detection in the nasal field. Certainly, many other parts of the cortex are maturing anatomically between 1 and 2 months of age (Conel, 1941, 1947).

Other Implications of Improved Nasal Field Detection Between 1 and 2 Months of Age

1. The region of binocular overlap

Two-month-olds can detect stimuli at least out to 20° in the nasal visual field of the left eye. If the same were true for the right eye, at least the central 40° of the visual field would be represented on the retinae of both eyes. Thus, the binocular region would be at least 40° in the 2-month-old. Since newborns (Experiments 2 and 3) and 1-month-olds (Experiment 4) appear not to detect stimuli at 20° in the nasal visual field, the binocular region appears to expand beyond 40° only at about 2 months of age.

2. Conjugate eye movements

Newborns' eye movements are frequently nonconjugate (Blanton, 1917; Fonarev, 1959; Guernsey, 1929; Maurer, 1974; Wickelgren, 1969). Perhaps at birth, conjugate eye movements occur mainly in the binocular region, although this possibility has not been tested adequately (see the Discussion of Experiment 3). The frequency of coordinated eye movements increases with age (Brown, 1961; Fonarev, 1959; Guernsey, 1929), but even 2-month-olds still show some eye movements which are nonconjugate (Fonarev, 1959). Since the binocular region also appears to expand between 1 and 2 months of age, it would be interesting to determine if there were any relationship developmentally between conjugate eye movements and the location of stimuli in the visual field. Perhaps during the first few months of life, conjugate eye movements occur mainly toward stimuli which are in the binocular region. Obviously, this is not the case in normal adults, because they appear to show conjugate eye movements 100% of the time, even when they move their eyes toward stimuli beyond the binocular region.

3. Implications for studying perception in the 2-month-old infant

At 2 months of age, eye movements are frequently conjugate (Fonarev, 1959), the binocular region seems to include at least the central 40° of the visual field and the geniculo-cortical pathway appears to be sufficiently mature to mediate peripheral detection (Experiment 5). Consequently, most of the problems outlined in studying the perception of newborns (see the Discussion of Experiment 3) and of 1-month-olds (see the Discussion of Experiment 4), no longer seem to apply to the study of 2-month-olds. For 2-month-olds, the direction of eye movements would be an appropriate test for hemispheric dominance. It also would be appropriate to present paired stimuli in tests for visual preferences or for peripheral acuity. However, it is unknown whether 2-month-olds can detect stimuli beyond 20° in the nasal visual field. Thus, for paired presentations, investigators would be wise to present stimuli which are no more than 20° off to the side.

Chapter 4

General Discussion

The first three experiments reported in this thesis were designed to find out if human newborns, like cats and human adults with cortical lesions, have poorer detection in the nasal than in the temporal visual field. The results of Experiment 1 showed that newborns viewing stimuli monocularly move their eyes reliably toward single lines $3^{\circ}18'$ wide located at 10° in the temporal or nasal visual field. Thus, even under monocular conditions, newborns can overcome any response biases sufficiently well to demonstrate both temporal and nasal vision. When the stimuli were placed further in the periphery, newborns still moved their eyes reliably toward single lines $3^{\circ}18'$ wide located at 30° in the temporal visual field. But they showed no evidence of detecting the same line at 20° in the nasal visual field (Experiments 2 and 3). These results suggest that human newborns have poorer detection in the nasal than in the temporal visual field.

It is unlikely that the results were due to differences in the ease of temporal and nasal eye movements. It is also unlikely that they were due to differences in the density of receptors on the two hemiretinae or to optical factors (see the Discussion of Experiment 3). Rather, the similarities in peripheral detection among lesioned cats, lesioned human adults, and normal human newborns suggest that in human newborns at least part of the geniculo-cortical pathway is immature. Moreover, at least part of the projection through <u>both</u> hemispheres of the visual cortex might be very immature since newborns seem to have poor nasal field detection both for the left eye and for the right eye (Experiments 2 and 3).

Other data also suggest that at least some part of the geniculo-cortical pathway is very immature at birth. Anatomically, the lateral geniculate, the visual cortex and the projections between them are poorly developed in the human newborn (Conel, 1939; Dekaban, 1954; Hickey, 1977). Studies of visually evoked responses suggest that the geniculo-cortical pathway might be too immature to influence at least some visual behaviours, even in 1-month-olds (Hoffmann, 1978). Moreover, in many respects, the behaviour of the young infant resembles that of cats, monkeys and humans with lesions of the visual cortex (reviewed in Section 1.6).

There appears to be considerable development in the geniculo-cortical pathway between 1 and 2 months of age. During that time, the visual cortex continues to develop anatomically (Conel, 1941, 1947). Electrophysiological data suggest that the geniculo-cortical pathway influences some visual behaviours for the first time at about 2 months of age (Hoffmann, 1978; Karmel et al., 1974). Behavioural data lead to a similar conclusion. Not until 2 months of age do human infants show that they can discriminate shapes or arrangements enclosed in identical frames. Nor until that age do they scan extensively, track smoothly and display symmetrical optokinetic nystagmus when tested monocularly. Evidence from lesioned and immature organisms suggests that these behaviours depend on the geniculo-cortical pathway (reviewed in Section 1.6 and Chapter 3). Thus, in human infants, that pathway might be sufficiently mature to influence at least some visual behaviours at 2 months of age, but not before.

The human newborn appears not to detect stimuli at 20° in the nasal visual field (Experiments 2 and 3). If that apparent limitation also were to reflect an immature projection through the visual cortex, infants might show a marked improvement in nasal field detection for the first time at about 2 months of age. Experiments 4 and 5 confirmed that prediction. One-month-olds, like newborns, detected a line $3^{\circ}18'$ wide at 30° in the temporal visual field but appeared not to detect the same line at 20° in the nasal visual field (Experiment 4). Two-month-olds, unlike newborns and 1-month-olds, detected both the temporal and nasal lines (Experiment 5). These results suggest that there is an improvement in nasal field detection between 1 and 2 months of age, but not between birth and 1 month of age.

It is unlikely that the observed improvement in nasal field detection was due to an improvement in the ease of eye movements toward the nasal field. Nor is it likely that it was due to the anatomical development of the eye or to changes in the optics of the eye (reviewed in Chapter 3). Rather, it is more likely that the observed improvement was due, at least in part, to maturation of the geniculo-cortical pathway. Poor nasal field detection perhaps can be added to the list of limitations which reflect an immature geniculo-cortical pathway at birth.

Several authors have postulated that, prior to 2 months of age, the geniculo-cortical pathway is too immature to influence <u>any</u> visual behaviour (Bronson, 1974; Karmel & Maisel, 1975; Salapatek, 1975; Volkmann & Dobson, 1976). They argue that during that time, visual behaviour is mediated entirely by other parts of the visual system and in particular, by the direct projection from the retina to the superior colliculus. Until recently, there was no evidence which contradicted that view.

However, new behavioural evidence requires a reconsideration of the traditional view that the entire geniculo-cortical pathway is nonfunctional during the first 2 months. It is now known that human infants less than 2 months old differ from monkeys and cats with cortical lesions in two important respects. Human infants can easily discriminate orientation and shape (providing the stimuli are not enclosed in identical frames) but lesioned animals have great difficulty in making similar discriminations. Specifically, human newborns can discriminate horizontal from vertical stripes (Slater & Sykes, 1977) and straight bars from curved bars which are equated in intensity, area and amount of contour (Fantz & Miranda, 1975). Moreover, they can make these discrimination in only one or two trials. At least by 1 month of age, infants can learn easily to discriminate a circle from a triangle (Milewski, 1976) and oblique stripes oriented to the left from oblique stripes oriented to the right (Martello, 1978; Maurer & Martello, in press).

In contrast, monkeys and cats with cortical lesions (which result in virtually complete retrograde degeneration of the lateral geniculate) discriminate orientation and shape with great difficulty. For example, lesioned monkeys appear not to discriminate horizontal from vertical stripes, even after 1200 training trials (Weiskrantz, 1963). Although normal monkeys can learn to discriminate a circle from a triangle in 200 trials, lesioned monkeys need at least 2050 trials to relearn that discrimination and sometimes they appear not to relearn it even after 6700 trials (Schilder, Pasik, & Pasik, 1972). Lesioned cats seem to have similar difficulties (Bauman & Spear, 1977; Chow, 1968; Cornwell, Warren & Nonneman, 1976; Loop & Sherman, 1977b; Spear & Braun, 1969; Wood, Spear & Braun, 1974). For example, they show no evidence of relearning a horizontal-vertical discrimination in six times the trials taken to learn that discrimination prior to surgery (Loop & Sherman, 1977b); and they make about [illegible] times more errors when relearning a circle-triangle discrimination than do sham-operated controls (Cornwell et al., 1976). Moreover, humans with lesions of the geniculo-cortical pathway appear to have difficulty discriminating orientation and shape when the stimuli are placed in the affected portion of the visual field. Most patients show no evidence whatsoever for the discrimination of stimuli which are equated in intensity, area and amount of contour (Perenin & Jeannerod, 1975, 1978); and the others show evidence of discrimination only if the stimuli are very large (Weiskrantz, et al., 1974).

Briefly, in the absence of the geniculo-cortical pathway, monkeys, cats and human adults appear to learn orientation and shape discriminations only with great difficulty. The ease with which newborns learn similar problems suggests that at least some part of the geniculo-cortical pathway is functional at birth.

Electrophysiological data support that contention. Hoffmann (1978) concluded that the geniculo-cortical pathway was too immature to influence visual behaviour in 1-month-olds because the amplitude of the early component of the visually evoked response (which supposedly reflects geniculo-cortical activity) was unrelated to the size of check. However, when Sokol and Jones (1979) measured the latency of the evoked response, rather than its amplitude, they found that the latency of the early complex varied systematically with check size in 4-week-olds (the youngest age tested). When Harter, Deaton, and Odom (1977) tested small checks in addition to large ones, they found that the amplitude of the early component reflected the size of small checks, even in a 6-day-old infant (but see Sokol & Jones, 1979). Therefore, when appropriate stimuli are tested, changes in both the amplitude and the latency of the visually evoked repsonse suggest that the geniculo-cortical pathway is sufficiently mature to differentiate at least some stimuli during the first month of life. The anatomical data are consistent with that possibility. Although the visual cortex is anatomically very immature in full-term newborns, many synapses are present well before that time (Purpura, Note 13).

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This points out an interesting problem in the interpretation of the experiments reported in this thesis. If the entire geniculo-cortical pathway were too immature to influence visual behaviour during the first month of life, it seemed reasonable to conclude that poor nasal field detection at birth results at least in part from an immature geniculo-cortical pathway. But the behavioural data suggest that the geniculo-cortical pathway is sufficiently mature to mediate the discrimination of orientation and shape. Moreover, the electrophysiological data suggest that that pathway is sufficiently mature to differentiate at least some stimuli. The particular part of the geniculo-cortical pathway which is sufficiently mature to mediate those behaviours also might be capable of mediating good nasal field detection. If that were so, poor nasal field detection at birth might result from the immaturity, not of the geniculo-cortical pathway, but rather of some other part of the visual system.

Recent physiological and anatomical evidence suggests that the projection from retina to lateral geniculate to visual cortex contains separate pathways, some which are involved in peripheral detection and others which are involved in the discrimination of orientation and shape. Since most of the relevant data have been collected from the cat, I will begin by reviewing the evidence that the cat has three separate but parallel pathways in that projection: an X-pathway, a Y-pathway and a W-pathway. I will then attempt to show that monkeys and humans appear to have similar pathways with similar projections. Next, I will consider the function of each pathway and I will attempt to show that, at least in cats, the Y-pathway through the cortex appears to be necessary for good detection in the nasal field. The X- and/or W-pathways appear to be sufficient for the discrimination of shape and orientation and insufficient for good nasal field detection. Finally, I will attempt to show that in cats, the X-pathway is functional at, or shortly after birth, but the Y-pathway through the cortex does not appear to be functional until several months later. I will argue that the behaviour of the human newborn resembles that of a cat missing a functional Y-pathway through the cortex and that poor nasal field detection by the human newborn might reflect specifically an immature Y-pathway through the cortex.

4.1 Parallel Pathways to the Visual Cortex in the Cat

4.1.1 Electrophysiological evidence for separate classes of cells in the cat's retina

For many years, physiologists have attempted to classify the ganglion cells of the retina into distinct categories. Traditionally, these cells were classified as either ON-cells (those with excitatory receptive field centres) or as OFF-cells (those with inhibitory receptive field centres) (Kuffler, 1953). But in 1966 Enroth-Cugell and Robson introduced a new classification which was independent of the traditional ON-OFF distinction. They recorded the responses of single ganglion cells in the cat's retina to stationary stripes placed at various positions in the receptive field and to moving stripes which drifted across the receptive field. Two types of cells, which they arbitrarily called X-cells and Y-cells, could be distinguished on the basis of their summation properties. X-cells showed linear summation. They responded to broad stationary stripes only if the stripes were placed at certain positions within their receptive fields; and they fired at a constant mean rate to moving stripes, regardless of the width of the stripe. Y-cells, on the other hand, showed nonlinear summation. They responded to broad stationary stripes placed at any position within their receptive fields; and they changed their mean rate of discharge as the width of moving stripes changed. Recently several authors have verified these distinctions (Cleland, Dubin, &

Levick, 1971; Hickey, Winters, & Pollack, 1973; Ikeda & Wright, 1972b; Linsenmeier & Jakiela, 1979).

Aside from their differences in summation properties, retinal ganglion cells in the cat have been classified into separate groups on the basis of two other defining criteria. First, one group of cells, "sustained cells," fires continuously during the presentation of a stimulus, while the other group, "transient cells," fires only when a stimulus is turned on or off (Cleland et al., 1971). Second, one group has slowly conducting axons while the other group has fast conducting axons (Bishop, Clare, & Landlaw, 1969; Bishop, Jeremy, & Lance, 1953; Fukada, 1971; Hoffmann, 1973).

Fortunately, for the most part, the separate criteria based on summation properties, firing patterns and conduction velocities merge into two distinct classes. One class shows linear summation, sustained firing and slow conduction along its axons in the optic nerve; the other class shows nonlinear summation, transient firing and fast conduction (Chino, Shansky, & Hamaski, 1978; Cleland et al., 1971; Hickey et al., 1973; Ikeda & Wright, 1972b). Thus, there appear to be at least two distinct classes of cells in the cat's retina. Since the terminology varies from author to author, I will adopt Enroth-Cugell and Robson's (1966) labels and refer to these classes as X-cells and Y-cells, respectively.

Investigators have discovered many more characteristics which tend to differentiate X- and Y-cells in the cat's retina. Compared to X-cells, Y-cells tend to respond with shorter latencies (Cleland et al., 1971; Cleland & Levick, 1974b; Hoffmann, 1973; Lee & Willshaw, 1979; Wilson, Rowe, & Stone, 1976), and to have larger receptive field centres (Cleland, Harding, & Tulunay-Keesey, 1979; Cleland, Levick, & Sanderson, 1973; Enroth-Cugell & Robson, 1966; Fukada, 1971; Ikeda & Wright, 1972c; Stone & Fukuda, 1974), and weaker and more extended inhibitory surrounds (Cleland et al., 1973; Hickey et al., 1973; Ikeda & Wright, 1972b; Lee & Willshaw, 1979). They tend to respond better than X-cells to fast moving or flickering stimuli (Cleland et al., 1971, 1973; Frishman & Schweitzer-Tong, 1978; Fukada & Saito, 1971; Hamasaki & Cohen, 1977; Lee & Willshaw, 1979), to broad stripes (Enroth-Cugell & Robson, 1966), to large stimuli (Ikeda & Wright, 1972a; Lee & Willshaw, 1979), to diffuse light (Fukada, 1971; Hickey et al., 1973), to defocused images (Ikeda & Wright, 1972a) and to large moving stimuli outside their receptive fields (Cleland et al., 1971, 1973; Derrington, Lennie, & Wright, 1979; Ikeda & Wright, 1972d). Finally, compared to X-cells, Y-cells are relatively numerous in the periphery and relatively scarce in the area centralis (Cleland & Levick, 1974a; Cleland et al., 1973; Enroth-Cugell & Robson, 1966; Fukada, 1971; Ikeda & Wright, 1972a).

In contrast, X-cells tend to respond with longer latencies than Y-cells (Cleland et al., 1971; Cleland & Levick, 1974b; Hoffmann, 1973; Lee & Willshaw, 1979; Wilson et al., 1976), to have smaller receptive field centres (Cleland et al., 1973, 1979; Enroth-Cugell & Robson, 1966; Fukada, 1971; Ikeda & Wright, 1972c; Stone & Fukuda, 1974), and stronger and narrower inhibitory surrounds (Cleland et al., 1973; Hickey et al., 1973; Ikeda & Wright, 1972b; Lee & Willshaw, 1979). Thus, they tend to respond better than Y-cells to narrow stripes

(Cleland et al., 1979; Enroth-Cugell & Robson, 1966) and to small stimuli (Ikeda & Wright, 1972a; Lee & Willshaw, 1979). Finally, compared to Y-cells, X-cells are relatively numerous in the area centralis and relativley scarce in the periphery (Cleland & Levick, 1974a; Cleland et al., 1973; Enroth-Cugell & Robson, 1966; Fukada, 1971; Fukuda & Stone, 1974; Ikeda & Wright, 1972a).

Recently, investigators have identified a third class of cells in the cat's retina, usually called W-cells (Cleland & Levick, 1974a, b; Levick & Cleland, 1974; Stone & Fukuda, 1974; Stone & Hoffmann, 1972). These cells appear to comprise a distinct class because their axons conduct at the slowest rate in the optic tract. Unlike other cells, W-cells tend to respond with very long latencies and they tend to have very small receptive field centres with large surrounds (Cleland & Levick, 1974a; Stone & Fukuda, 1974). However, some fire in a sustained fashion, while others fire transiently (Cleland & Levick, 1974a; Lee & Willshaw, 1979; Stone & Fukuda, 1974). Some, like X- and Y-cells, have a circular receptive field centre which is surrounded by an inhibitory zone, while others do not. Among those which do not, some respond best to uniform fields, some to edges, some to colour and some to a specific direction of movement (Cleland & Levick, 1974b). Thus, W-cells comprise a heterogeneous population of cells.

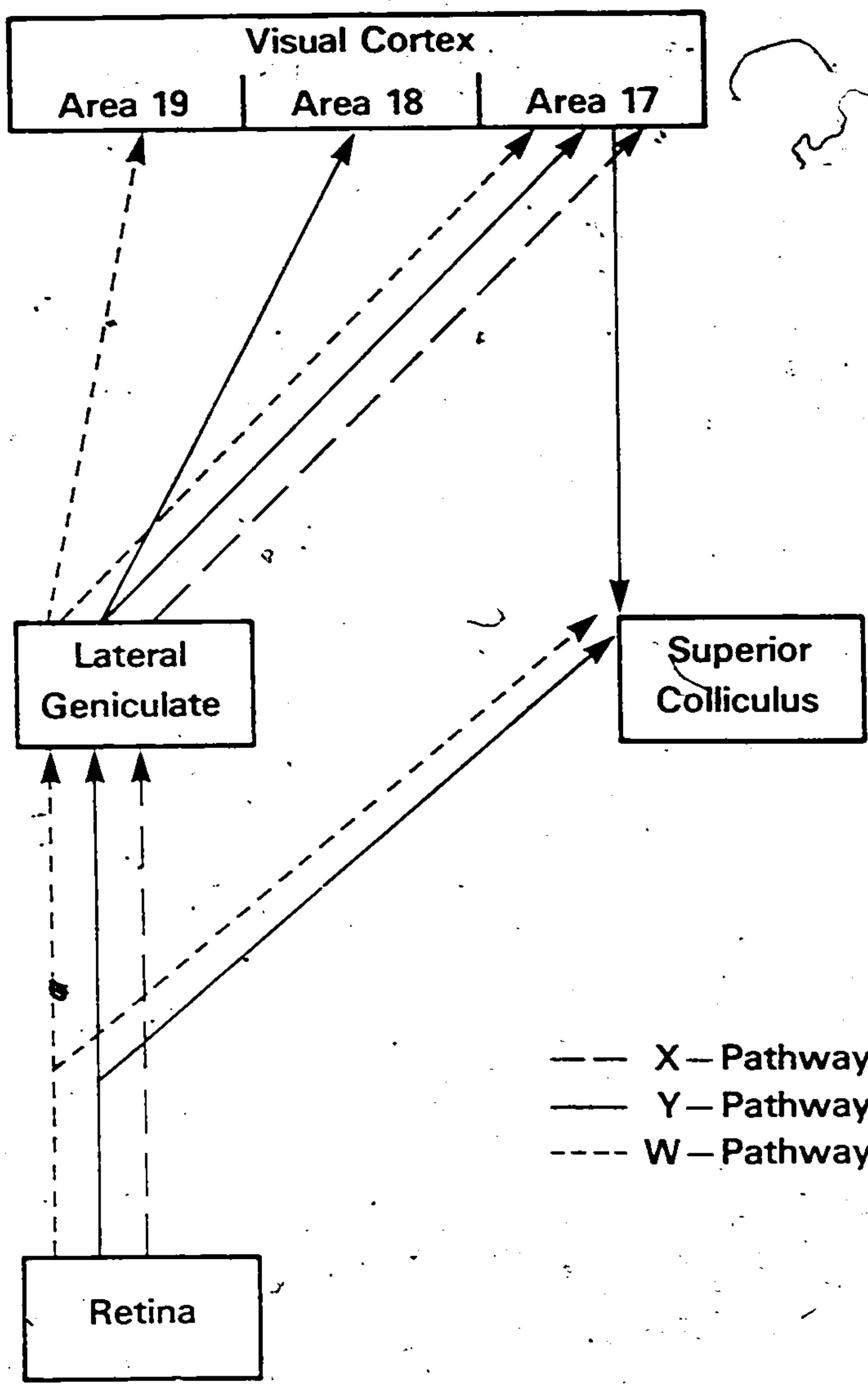
4.1.2 Anatomical confirmation of separate classes of cells in the cat's retina

Anatomical studies have verified the existence of three separate morphological types in the cat's retina: alpha cells, beta cells and gamma cells. Alpha cells have thick axons, large cells bodies, wide dendritic fields, and are found mainly in the peripheral retina. Beta cells have medium-sized axons, small cell bodies, small dendritic fields, and are found mainly in the area centralis. Gamma cells have very thin axons, very small cell bodies and wide dendritic fields (Boycott & Wassle, 1974; Cleland, Levick, & Wassle, 1975; Fukuda & Stone, 1974; Wassle, Levick, & Cleland, 1975). Studies combining anatomical and physiological techniques have shown that alpha, beta and gamma cells correspond to the physiologically defined Y-, X- and W-cells, respectively (Cleland et al., 1975; Fukuda & Stone, 1974, 1975).

4.1.3 Projections through the visual cortex

Each class of cell in the cat's retina appears to project along a separate pathway to the visual cortex via the lateral geniculate nucleus (see Fig. 10). Specifically, Y-cells in the retina send fast conducting axons through the optic tract (Cleland et al., 1971; Hoffmann et al., 1972) which relay on Y-cells in the lateral geniculate (Bullier & Norton, 1979a,b; Cleland, Levick, Morstyn, & Wagner, 1976; Cleland, Morstyn, Wagner, & Levick, 1975; Stone & Dreher, 1973; Wilson et al., 1976). These, in turn, project along fast conducting axons directly to areas 17 and 18 of the visual cortex (Dreher, Leventhal, & Hale, 1979; Hollander & Vanegas, 1977; LeVay & Ferster, 1977; Stone & Dreher, 1973). Within area 17, they project mainly to the upper part of layer IV, although some collaterals also project to layer VI (Ferster & LeVay, 1978; Gilbert & Wiesel, 1979; Leventhal, 1979; Mitzdorf, & Singer, 1978).

Fig. 10. Schematic diagram of the major X-, Y-, and W-pathways in the cat's visual system.


Visual Cortex
Area 19
Area 18
Area 17
Lateral Geniculate
Superior Colliculus
Retina
X—Pathway
Y—Pathway
W—Pathway

There is evidence which suggests that at least part of this Y-pathway projects through area 17 to the superior colliculus. Cells in the upper part of layer IV (which receive input from Y-cells in the geniculate) appear to send fast conducting axons to a special class of Y-like cells in layer V of the visual cortex (Gilbert, 1977; Gilbert & Wiesel, 1979; LeVay & Gilbert, 1976; Mitzdorf & Singer, 1978; Singer, Tretter, & Cynader, 1975). These, in turn, appear to project to the superior colliculus (Gilbert, 1977; Gilbert & Wiesel, 1979; Kawamura & Konno, 1979; Leventhal & Hirsch, 1978) along a fast conducting pathway (Hoffmann, 1973; Schoppmann & Hoffmann, 1979). Within the superior colliculus, this pathway terminates mainly in the superficial layers (McIlwain, 1977; McIlwain & Fields, 1971; Sprague, 1975; Updyke, 1977).

In contrast, X-cells in the retina send slowly conducting axons through the optic tract (Cleland et al. 1971; Hoffmann et al., 1972). These relay on X-cells in the lateral geniculate (Bullier & Norton, 1979a,b; Cleland et al., 1975, 1976; Stone & Dreher, 1973; Wilson et al., 1976) which are spatially distinct from the Y-cells located there (Mitzdorf & Singer, 1977). The geniculate X-cells send slowly conducting axons to area 17 (Dreher et al., 1979; Hollander & Vanegas, 1977; LeVay & Ferster, 1977; Stone & Dreher, 1973). Here, they project mainly to the lower part of layer IV and also send some collaterals to layer VI (Ferster & LeVay, 1978; Gilbert & Wiesel, 1979; Leventhal, 1979; Mitzdorf & Singer, 1978).

Finally, W-cells project along a third pathway from retina to visual cortex. They send very slowly conducting axons through the optic tract, relay on W-cells in the lateral geniculate, and project along very slowly conducting axons to the visual cortex (Cleland et al., 1975, 1976; Wilson et al., 1976). They project mainly to areas 17 and 19 (Dreher et al., 1979) and within area 17 they project mainly to layers I and III (Ferster & LeVay, 1978; Leventhal, 1979). Neither W- nor X-cells appear to project through the cortex to the superior colliculus (Hoffmann, 1973).

Both the Y- and W-axons bifurcate in the optic tract, sending one branch to the visual cortex via the lateral geniculate and the other directly to the superior colliculus (see Fig. 10) (Fukuda & Stone, 1974; Hayashi, Sumitomo, & Iwama, 1967; Hoffmann, 1973; McIlwain & Lufkin, 1967; Schoppmann & Hoffmann, 1979). Within the superior colliculus, the Y- and W-axons terminate mainly in the superficial layers (McIlwain & Fields, 1971; McIlwain & Lufkin, 1976) where they overlap with the projection from cortex to superior colliculus (Hoffmann, 1973; McIlwain & Fields, 1971).

In summary, physiological and anatomical evidence has shown that the cat's retina is composed of three distinct classes of ganglion cells: X-, Y- and W-cells. Each of these appears to project along separate but parallel pathways from retina, to lateral geniculate, to area 17 of the visual cortex. Areas 18 and 19 also receive direct input from the geniculate: area 18, mainly from Y-cells; and Area 19, mainly from W-cells. In addition, at least part of the Y-pathway through the cortex appears to project down to the superior colliculus, where it overlaps with the direct projection to the colliculus from Y- and W-cells in the retina.

4.2 Evidence for Similar Pathways through the Cortex in the Monkey.

X-, Y- and W-cells have also been identified in the retina of the monkey. Y-cells show nonlinear summation to stationary and moving stripes, tend to fire transiently to stationary stimuli, respond well to fast movement, have shorter latencies than X-cells, and send information along the fastest conducting axons in the optic tract (De Monasterio, 1978a,b; De Monasterio & Gouras, 1975; De Monasterio, Gouras, & Tolhurst, 1976; Gouras, 1969; Scoby & Horowitz, 1976). Moreover compared to X-cells, Y-cells tend to be relatively common in the periphery and relatively scarce in the fovea (De Monasterio, 1978b; Gouras, 1969). All of these characteristics resemble those of Y-cells in the cat's retina.

X-cells in the monkey's retina show linear summation to stationary and moving stripes, tend to fire in a sustained fashion to stationary stimuli, have longer latencies than Y-cells, and send information along slowly conducting axons. In addition compared to Y-cells, they tend to be relatively more numerous in the fovea and relatively scarce in the periphery (De Monasterio, 1978a,b; De Monasterio & Gouras, 1975; De Monasterio et al., 1976; Gouras, 1969). All of these characteristics resemble those of X-cells in the cat's retina.

Like W-cells in the cat's retina, W-cells in the monkey's retina appear to comprise a heterogeneous population. They appear to comprise a distinct class because they have an atypical receptive field organization; i.e., unlike X- and Y-cells, they do not have a circular receptive field centre which is surrounded by an inhibitory zone

(De Monasterio, 1978c). However, one subgroup is inhibited by motion. Another subgroup responds only to coloured stimuli, shows linear summation, and responds in a sustained manner with latencies that are shorter than those of X-cells but longer than those of Y-cells. A third subgroup prefers edges, shows nonlinear summation, and responds transiently with the longest latencies in the optic tract (De Monasterio, 1978c; Schiller & Malpeli, 1977).

Studies of X- and Y-cells in the monkey's lateral geniculate reveal more properties which are characteristic of X- and Y-cells in the cat. The Y-cells have larger receptive field centres (Sherman, Wilson, Kaas, & Webb, 1976), and they respond well to broad stripes but tend to respond poorly to narrow stripes (Dreher, Fuakada, & Roderick, 1976; Sherman et al., 1976). In contrast, the X-cells have smaller receptive field centres and they respond poorly to broad stripes but well to narrow stripes. Unfortunately, these properties have not been tested in the monkey's retina, but they are virtually the same as those reported for X- and Y-cells in the cat's retina and lateral geniculate (Cleland et al., 1971; Derrington & Fuchs, 1979; Maffei & Fiorenti, 1973; Sherman, 1979). Thus, the monkey appears to have X- and Y-cells which are remarkably similar to those in the cat.

The projections of X- and Y-cells in the monkey also appear to be similar to those in the cat except that, in the monkey, Y-cells from the geniculate appear to project directly only to area 17, rather than to both areas 17 and 18 (Yukie, Umitsu, Kido, Niihara, & Iwai, 1979). Specifically, the Y-cells in the monkey's retina send fast conducting axons through the optic tract which relay on Y-cells in the lateral geniculate (De Monasterio, 1978b; Schiller & Malpeli, 1977, 1978; Sherman et al., 1976). These, in turn, send fast conducting axons to area 17 of the visual cortex (Doty, Wilson, Bartlett, & Pecci-Saavedra, 1973; Mitzdorf & Singer, 1979; Schiller & Malpeli, 1978; Sherman et al., 1976). Y-cells appear to be spatially distinct from other classes of cells both in the geniculate (Dreher et al., 1976; Schiller & Malpeli, 1978; Sherman et al., 1976; but see Bunt, Hendrickson, Lund, Lund, & Fuchs, 1975) and in the visual cortex (Hendrickson, Wilson, & Ogren, 1978; Hubel & Wiesel, 1972; LeVay, Hubel, & Wiesel, 1975; Lund, 1973; Lund & Boothe, 1975; Mitzdorf & Singer, 1979). From the visual cortex the Y-pathway then projects down to the superior colliculus (Schiller, Malpeli, & Schein, 1979) where it terminates in the superficial layers (Hubel et al., 1975; Kuypers & Lawrence, 1967; Lund, 1972; Schiller et al., 1974; Wilson & Toyne, 1970).

X-cells in the monkey's retina project along slowly conducting axons to X-cells in the lateral geniculate (De Monasterio, 1978b; Schiller & Malpeli, 1977, 1978; Sherman et al., 1976). These then send slowly conducting axons to area 17 (Doty et al., 1973; Mitzdorf & Singer, 1979; Schiller & Malpeli, 1978; Sherman et al., 1976). There appears to be no X-pathway from the cortex to the superior colliculus (Schiller et al., 1979).

As in the cat then, X- and Y-cells in the monkey appear to project along parallel pathways from retina to lateral geniculate to visual cortex. It is uncertain whether the W-cells in the monkey's retina also project to the visual cortex, although some evidence suggests that they might project along a separate pathway from the retina to the lateral geniculate to area 18 of the visual cortex (De Monasterio, 1978c; Yukie et al., 1979).

Y- and W-cells also appear to project along parallel pathways directly from the retina to the superior colliculus (De Monasterio, 1978b,c; Marrocco, 1978; Schiller & Malpeli, 1977). Within the superior colliculus, the Y- and W-axons partially overlap with the projection from the visual cortex (Lund, 1972; Schiller et al., 1974; Wilson & Toyne, 1970).

4.3 Evidence for Similar Pathways in the Human

The retinae of both the cat and the monkey appear to contain at least three distinct classes of cells: X-, Y- and W-cells. The electrophysiological properties of these cells and their projections within the visual system are remarkably similar in the two species. The important question is whether similar cells with similar projections exist in the human visual system. Electrophysiological, anatomical and psychophysical data strongly suggest that the human has X- and Y-cells much like those in the cat and monkey. Although W-cells have not been identified as yet in humans, it is likely that they exist since the human's visual system resembles that of the monkey in so many other respects (Cowey, 1979; Rakic, 1976).

4.3.1 Electrophysiological evidence for X- and Y-cells in the human

The electrophysiological studies which identified X- and Y-cells in animals were based mainly on recordings from single cells in the visual system. There is only one similar study in humans. Weistein, Hobson, and Baker (1971) recorded from two ganglion cells in the human's peripheral retina. They presented chromatic stimuli and, for each unit, plotted the rate of discharge as a function of the wavelength of the stimulus. The resulting spectral sensitivity function was remarkably similar to that of Y-cells in the monkey's retina (Gouras, 1968); both the human's and the monkey's curves showed a peak sensitivity at about 555 nm. However, these data are too sparse to justify the conclusion that the human retina does, in fact, contain Y-cells.

Most of the electrophysiological evidence for X- and Y-cells in humans comes from studies which measured occipital potentials with surface electrodes placed on the scalp. These potentials reflect postsynaptic activity induced in the visual cortex by a visual stimulus. Two types of occipital potentials have been measured: steady-state and transient. Steady-state occipital potentials are obtained by presenting repetitive stimuli at a rate sufficient to cause overlap of the individual evoked responses. The responses are then averaged and the amplitude and phase of the resulting wave form constitutes the steady-state occipital potential. In contrast, a transient occipital potential is the response to a physiologically distinct stimulus because the interval between stimulus presentations is sufficiently long to prevent overlap of the individual responses. Response averaging is still necessary, however, in order to separate the waveform from background activity.

Campbell and Maffei (1970) measured steady-state occipital potentials induced by striped stimuli varying in contrast and spatial frequency.[9] They derived a regression line by plotting the amplitude of the evoked potential as a function of contrast at each spatial frequency. A straight regression line fit the data when the spatial frequency of the inducing stimulus was more than 3 cycles/degree. However, for lower spatial frequencies two straight lines were needed. This suggests the existence of two independent components of the occipital potential at low spatial frequencies, but only one component at higher spatial frequencies.

Jones and Keck (1978) reached a similar conclusion but because they measured transient instead of steady-state occipital potentials, they were able to identify the separate components in the waveform itself. At high spatial frequencies (at least 3 cycles/degree), the amplitude and latency of the one component observed varied with the contrast and the spatial frequency. At lower spatial frequencies, an additional short latency component was also present. The authors suggested that the short latency component may provide electrophysiological evidence for the existence of Y-cells in human vision, and that the other component may provide evidence for X-cells.

Recently, Kaufman, Brenner, and Williamson (1978) provided evidence which further supports this notion. They varied both the spatial frequency and the temporal frequency[10] of striped stimuli and

[9] Spatial frequency is a measure which reflects the width of stripe. The unit of measurement is the number of cycles per degree of visual angle (cycles/degree) where a cycle consists of one white stripe and one black stripe. Narrow stripes have many cycles/degree and a high spatial frequency. Conversely, broad stripes have few cycles/degree and a low spatial frequency.

[10] Temporal frequency is a measure of the rate of movement or flicker. The most common unit of measurement is the hertz (Hz) which indicates the amount of movement or flicker per second. Fast moving or flickering stimuli have many Hz and a high temporal frequency. Slowly moving (or flickering) stimuli have few Hz and a low temporal frequency. Stationary stimuli are at one extreme end of this dimension and can be expressed as zero temporal frequency or zero Hz.

noted the effects on the steady-state occipital potentials. By examining the phase of the response relative to the stimulus, they could deduce the latency of the evoked potential. The results showed that latency increased monotonically as spatial frequency increased above 1 cycle/degree. At lower spatial frequencies, latency was independent of stripe width. But this was true only for low temporal frequencies. For temporal frequencies greater than 30 Hz, the latency was always independent of spatial frequency. These results suggest the presence of two distinct components in the occipital potential: one component which varies with pattern and another component which does not. The authors concluded that the component which varies with pattern may be related to the activity of X-cells since it dominates at a high spatial frequencies and at low temporal frequencies. The other component may be related to the activity of Y-cells since it dominates at low spatial frequencies and at high temporal frequencies.

In short, the electrophysiological studies demonstrate the existence of two distinct mechanisms in human vision. One of these mechanisms, like X-cells, responds with a longer latency, and is more prevalent both at high spatial frequencies and at low temporal frequencies. The other mechanism, like Y-cells, responds with a shorter latency, and is more prevalent both at low spatial frequencies and at high temporal frequencies. These data suggest that the human has X- and Y-cells much like those in the cat and monkey.

4.3.2 Anatomical evidence for X- and Y-cells in the human

There are two pieces of anatomical evidence which suggest that the human lateral geniculate nucleus may contain cells which resemble

X- and Y-cells in animals. First, in the human, cells in the two most ventral layers (magnocellular layers) of the geniculate are relatively large while cells in the four dorsal layers (parvocellular layers) are relatively small (Cooper, 1945; Dekaben, 1954; Hickey, 1977). In the monkey, the ventral layers also contain mainly larger cells while the dorsal layers contain mainly smaller cells (Bunt et al., 1975; Cooper, 1945). Electrophysiological tests in monkeys suggest that the larger cells in the ventral layers are Y-cells and that the smaller cells in the dorsal layers are X-cells (De Monasterio, 1978b; Dreher et al., 1975; Marrocco, 1976; Schiller & Malpeli, 1978; Sherman et al., 1975). Thus, the larger cells in the ventral layers of the human's lateral geniculate may also be Y-cells and the smaller cells in the dorsal layers, X-cells.

Second, in the cat's geniculate Y-cells (larger cells) are retarded in development relative to X-cells (smaller cells) (Daniels, Pettigrew, & Norman, 1978; LeVay & Ferster, 1977; Norman, Pettigrew, & Daniels, 1977). The larger cells in the human's lateral geniculate also develop at a much slower rate than the smaller cells (Hickey, 1977). This similarity in the relative rates of development suggests again that the larger cells in the human's lateral geniculate might be Y-cells, while the smaller cells might be X-cells.

4.3.3 Psychophysical evidence for X- and Y-cells in the human

Numerous psychophysical studies have shown that the human visual system has separate channels, one for the detection of movement, and one for the detection of pattern. Keesey (1972) was one of the first investigators to suggest this possibility. She showed subjects a flickering vertical line and had them adjust the contrast of that line until they could just detect either the flicker (flicker threshold) or the edges (pattern threshold). She found that when the contrast was very low, subjects saw only the flicker; and only at higher contrast levels did the edges of the line become apparent. Since the results were similar for normal and stabilized images, the separate flicker and pattern thresholds were not an artifact of eye movements. Rather, they appeared to reflect distinct mechanisms in human vision.

Other investigators have confirmed the existence of separate flicker and pattern thresholds both for single lines (King-Smith & Kulikowski, 1975) and for striped stimuli (Hilz, Rentschler, & Brettel, 1977; Kulikowski & Tolhurst, 1973; Levi & Harwerth, 1977; Tolhurst, 1973). For striped stimuli, the threshold for flicker detection and the threshold for pattern detection vary independently as a function of spatial frequency. At spatial frequencies below 2 to 3 cycles/degree (broad stripes) the threshold for flicker detection is lower than the threshold for pattern detection, whereas at higher spatial frequencies (narrower stripes) the inverse is true. Above 30 cycles/degree, only a threshold for pattern detection can be obtained since movement is not perceived even when the contrast is very high (Kulikowski & Tolhurst, 1973).

The threshold for flicker detection and the threshold for pattern detection also vary independently as a function of temporal frequency. At low temporal frequencies, including stationary stimuli, the threshold for pattern detection is lower than the threshold for movement detection, while at higher temporal frequencies (at least 3

Hz) the threshold for movement detection is lower than the threshold for pattern detection (King-Smith & Kulikowski, 1975; Kulikowski & Tolhurst, 1973; Tolhurst, 1973). These results confirm and extend Keesey's (1972) findings. They suggest the existence of two separate mechanisms in human detection which Kulikowski and Tolhurst (1973) labelled "form-analyzers" and "movement-analyzers." Form-analyzers respond well to narrow stripes and stationary stimuli while movement-analyzers respond well to broad stripes and fast rates of movement or flicker. In the cat and monkey, X-cells prefer narrow stripes and stationary stimuli, whereas Y-cells prefer broad stripes and fast rates of movement or flicker (Cleland et al., 1971, 1973; Dreher et al., 1976; Enroth-Cugell & Robson, 1966; Fukada & Saito, 1973; Sherman et al., 1976). This suggests that form-analyzers in the human may be analagous to X-cells in the cat and monkey. Similarly, movement-analyzers in the human may be analagous to Y-cells in the cat and monkey.

Subsequent work has shown that form-analyzers and movement-analyzers interact differently with different types of movement (Kulikowski & Tolhurst, 1973; Stromeyer, Madsen, Klein, & Zeevi, 1978; Tolhurst, 1973), with the duration of the test stimulus (Legge, 1978), and with the duration, contrast, and location of masking stimuli (King-Smith & Kulikowski, 1975; Tolhurst, 1975; Wilson, 1978). Thus, form-analyzers appear to exhibit linear summation (King-Smith & Kulikowski, 1975) and to fire in a sustained fashion to continued stimulation (Legge, 1978; Tolhurst, 1975). They also appear to have small receptive field centres with strong and narrow inhibitory surrounds (King-Smith & Kulikowski, 1975; Wilson, 1978). X-cells in the cat and monkey have all of these characteristics. Movement-analyzers, on the other hand, appear to exhibit non-linear summation (King-Smith & Kulikowski, 1975) and to fire transiently to continued stimulation (Legge, 1978; Tolhurst, 1975). They appear to have large receptive field centres with weak and extended inhibitory surrounds (King-Smith & Kulikowski, 1975; Wilson, 1978). All of these characteristics resemble those of Y-cells in the cat and monkey. These data strengthen the conclusion that form-analyzers and movement-analyzers are the psychophysical equivalent of X- and Y-cells, respectively.

Recently King-Smith and his associates (King-Smith, Rosten, & Bhargava, 1979) reported a clinical case in which the patient's vision appeared to be mediated only by the Y-channel. This patient displayed normal thresholds for the detection of flickering stimuli and normal contrast sensitivity for broad stripes. However, his acuity was greatly reduced, as was his contrast sensitivity for narrow stripes. In addition, he showed little or no colour discrimination and was most sensitive to wavelengths near 555 nm (normally indivdiuals are equally sensitive to wavelengths of 440, 520 and 600 nm). Finally, afterimages lasted only briefly instead of the usual 20 seconds, suggesting that they were mediated by transient, rather than by sustained mechanisms.

In monkeys, Y-cells fire transiently (De Monasterio, 1978b) and they appear to predominate in the detection of flicker and of broad stripes (Dreher et al., 1976). Moreover, they are most sensitive to wavelengths near 555 nm (De Monasterio & Gouras, 1975; Gouras, 1968).

X-cells, on the other hand, fire in a sustained fashion (De Monasterio, 1978b), and they appear to predominate in the detection of small stimuli, narrow stripes and colour (De Monasterio & Gouras, 1975; Dreher et al., 1976; Schiller & Malpeli, 1977). In addition, each X-cell shows a peak sensitivity to one of three wavelengths: 440, 520 or 600 nm (De Monasterio & Gouras, 1975; Gouras, 1968). Thus, the vision in the patient of King-Smith et al. resembles the vision that might be present in a monkey with normal Y-pathways but a nonfunctional X-pathway. This again suggests that the human has a separate Y-mechanism much like that in the monkey.

The psychophysical evidence then, supports the assertion that X- and Y-cells exist in the human visual system. However, some caution is required in drawing this conclusion since it depends on the validity of correlating psychophysical data in humans with electrophysiological data in animals. This correlation assumes that (a) comparable psychophysical studies across species would yield similar results; (b) the underlying physiology of single cells is similar across species; and (c) within a species, the psychophysical results accurately reflect the underlying physiology of single cells.

There is some evidence to support each of these assumptions. First, the results are remarkably similar for comparable psychophysical studies relevant to the identification of X- and Y-channels in the cat, monkey and human. When pattern thresholds were plotted as a function of spatial and temporal frequency both in the cat (Blake & Camisa, 1977) and in the human (Kulikowski & Tolhurst, 1973; Tolhurst, 1973), the shape of the resulting curves was virtually identical in both species. The same was true when pattern thresholds were plotted as a function of stimulus duration in the monkey (Harwerth, Boltz, & Smith, 1979) and in the human (Legge, 1978). This suggests a similarity in cat, monkey and human psychophysics, at least for the relationships which have been tested.

Second, there is some evidence which suggests that single-cell recordings yield similar results in the human and in the monkey. When Weistein et al. (1971) recorded from ganglion cells in the human's peripheral retina, the resulting spectral sensitivity function was remarkably similar to that of Y-cells in the monkey's retina (Gouras, 1968); both the human's and the monkey's curves showed a peak sensitivity at about 550 nm.

Finally, there appears to be a close correspondence between psychophysics and single-cell recordings within a species. For the cat, pattern thresholds plotted as a function of spatial and temporal frequency yield the same results whether the curves are derived from psychophysical methods (Blake & Camisa, 1977) or from single-cell recordings (Enroth-Cugell & Robson, 1966). The same seems to be true in the human as well. The spectral sensitivity function derived psychophysically by King-Smith et al. (1979) is very similar to the spectral sensitivity function derived from single-cell recordings by Weinstein et al. (1971). Therefore, although the evidence is sparse, it lends support to the interpretations of psychophysical data in terms of electrophysiological findings.

4.3.4 Probable projections of X- and Y-cells in humans

The electrophysiological, anatomical and psychophysical evidence strongly suggests that the human has two distinct classes of cells which are remarkably similar to X- and Y-cells in the cat and monkey. There is, unfortunately, no evidence on the projections of these cells within the human visual system. However, it seems reasonable to hypothesize that their projections might be similar to those of X- and Y-cells in the cat and monkey. If that were so, the human would have separate X- and Y-pathways from retina to lateral geniculate to visual cortex.

4.4 The Function of the Pathways through the Cortex

4.4.1 Evidence from the electrophysiological properties of cells in the cat's retina

The electrophysiological properties of cells in the cat's retina (reviewed in Section 4.1.1) suggest that X- and Y-cells may be specialized to perform different functions. Compared to X-cells, Y-cells have larger receptive field centres, and relatively weak and extended inhibitory surrounds. Consequently, they respond better than X-cells to large stimuli and low spatial frequencies. Moreover, they tend to respond better than X-cells to motion, diffuse light, defocused images, and to large, moving stimuli outside their receptive fields. X-cells, on the other hand, tend to respond better than Y-cells to small stimuli and high spatial frequencies. Finally Y-cells are relatively more numerous in the peripheral retina, while X-cells are relatively more numerous in the area centralis. Because of these characteristics, several authors have postulated that Y-cells in the cat's retina are primarily involved in peripheral vision, in the analysis of low spatial frequencies and/or in the analysis of movement, while X-cells are involved in the detailed analysis of pattern (Cleland et al., 1971; Ikeda & Wright, 1972b,c, 1974; Sherman, 1979; Stone & Fukuda, 1974). Because X- and Y-cells appear to share so many characteristics in cats, monkeys and humans, the function of X- and Y-cells is also likely to be similar in all three organisms.

The function of W-cells is unknown. Since they comprise a heterogeneous group (see Section 4.1.1), they are probably involved in a wide variety of visual functions (Stone & Fukuda, 1974), perhaps even in both peripheral detection (Hoffmann & Sherman, 1974, 1975) and pattern analysis.

4.4.2 Evidence from visually deprived cats

Cats which have been visually deprived during a critical period provide an excellent model for determining the function of the Y-pathway through the cortex. This is because only that pathway appears to be seriously affected following binocular deprivation. Specifically, in all layers of the lateral geniculate, large cells (Y-cells) shrink considerably more than smaller cells (X-cells) (LeVay & Ferster, 1977; Sherman et al., 1972; but see Hickey, Spear, & Kratz, 1977), and changes in the size of genicualte W-cells are minimal or nonexistent (Hickey, 1978). In addition, the frequency of recordable Y-cells relative to X-cells in the lateral geniculate drops from 55% in normal cats to 29% in binocularly deprived cats (Sherman et al., 1972). These data suggest that in the lateral geniculate there is a selective loss of Y-cells following binocular deprivation.

In the visual cortex of binocularly deprived cats, only half the cells respond normally to visual stimulation; the other half respond either weakly or not at all (Sherman, 1972; Watkins, Wilson, & Sherman, 1978). Those cells which respond poorly probably would normally have received input from geniculate Y-cells (Sherman, 1972).

The response properties of cells in the cat's superior colliculus following binocular deprivation resemble those following ablation of the visual cortex; very few of the cells are directionally selective and most of the input is from the contralateral eye (Dec, Sarna, Tarnecki, & Zernicki, 1976; Flandrin & Jeannerod, 1977; Hoffmann & Sherman, 1975; Sherman, 1972; Sterling & Wickelgren, 1970). These properties are very different from those of collicular cells in the normal cat, most of which are directionally selective and receive input from both eyes (Berman & Cynader, 1972; Rosenquist & Palmer, 1971; Wickelgren & Sterling, 1969). The input to the superior colliculus from the cortex normally comes from Y-cells (Hoffmann, 1973). Thus, binocularly deprived cats appear to be missing functional input from Y-cells in the geniculate to visual cortex to superior colliculus.

Hoffmann & Sherman (1975) provided additional evidence that the Y-pathway through the cortex is functionally missing in binocularly deprived cats. They recorded from cells in the superior collliculus of both normal and deprived animals while they electrically stimulated the optic chiasm and the optic tract. A comparison of the conduction velocities in the two groups of animals revealed that the superior colliculus of deprived animals had no input whatsoever from the Y-pathway through the cortex. In contrast, the direct input to the superior colliculus was essentially normal. Moreover, Sherman and Stone (1973) reported that all cells in the retina of binocularly deprived cats are normal, both in terms of their morphology and electrophysyiological responses.

In summary, binocularly deprived cats appear to show a selective loss in the function of the Y-pathway through the cortex. The retina, the X- and W-pathways to the cortex, and the direct projections to the superior colliculus all show little or no loss.

The effects of monocular deprivation in cats are even more severe than those of binocular deprivation. This is probably because the deprived eye is at a competitive disadvantage relative to the normal eye.[11] Yet, only the Y-pathway through the cortex seems to be seriously affected by monocular deprivation. In the deprived layers of the lateral geniculate, large cells (Y-cells) shrink more than smaller cells (X-cells) (Hickey et al., 1977; Hoffmann & Hollander, 1978; LeVay & Ferster, 1977; Sherman et al., 1972); and this shrinkage is more pronounced after monocular deprivation than after binocular deprivation (Hickey et al., 1977). Nonetheless, monocular deprivation has little or no effect on the size of geniculate W-cells (Hickey, 1978). Second, cells projecting from lateral geniculate to area 18 of the visual cortex (Y-cells) shrink much more than cells projecting to

[11] This competitive disadvantage for the deprived eye occurs only in regions where input from the two eyes overlaps (the binocular segment). In the monocular segment (representing the far periphery of the temporal visual field), there is input from only one eye and consequently there is no competitive imbalance. Correspondingly, the effects of monocular deprivation are far more severe in the binocular segment than in the monocular segment of the lateral geniculate (Hickey et al., 1977; Sherman et al., 1972), the visual cortex (Wilson & Sherman, 1977), and the superior colliculus (Heitlander & Hoffmann, 1978; Hoffmann & Sherman, 1974). The anatomical and physiological consequences reported for monocular deprivation will include only the binocular segment since the visual behaviour of deprived cats which I will describe below involved stimuli located within that segment.

area 17 (X- and Y-cells) (Garey & Blakemore, 1977). In fact, the projection from geniculate to area 18 virtually disappears following monocular deprivation (Lin & Sherman, 1978). Thus, anatomical evidence suggests that Y-cells in the lateral geniculate are affected considerably more than W- or X-cells; and the consequences of monocular deprivation are more severe than the consequences of binocular deprivation.

Electrophysiological studies lead to the same conclusions. Following monocular deprivation, only 10% to 20% of the cells in the deprived layers of the lateral geniculate are Y-cells (Hoffmann & Hollander, 1978; Sherman et al., 1972). This is considerably less than the percentage of Y-cells in normal or binocularly deprived cats (Sherman et al., 1972). In contrast, X-cells in the same layers show only minor losses. They respond normally to broad stripes and to movement or flicker (Lehmkuhle, Kratz, Mangel, & Sherman, 1978). Only their response to narrow stripes is affected (Lehmkuhle et al., 1978; Maffei & Fiorentini, 1976).

In the visual cortex, very few cells are visually driven by the deprived eye, probably because of the competitive disadvantage of the deprived eye relative to the normal eye (Shatz & Stryker, 1978; Sherman, 1972; Tsumoto & Suda, 1978; Wilson & Sherman, 1977). Consequently, it is not surprising that the Y-pathway through the cortex to the superior colliculus is missing from the deprived eye (Hoffmann & Sherman, 1974) and that there are no normal cells representing the nasal visual field of the deprived eye in the superior colliculus (Heitlander & Hoffmann, 1978). However, the X-, Y- and W-cells in the retina are normal (Mangel, Kratz, Lehmkuhle, & Sherman, 1979; Sherman & Stone, 1973), as is the pathway which projects directly to the superior colliculus (Hoffmann & Sherman, 1974). Thus, following monocular deprivation, the Y-pathway from the deprived eye through the cortex is functionally missing, while the other pathways remain virtually unchanged.

One way to determine the function of the Y-pathway through the cortex would be to examine the behaviour of visually deprived cats. If they were to show limitations in a particular behaviour, this would suggest that the Y-pathway through the cortex is necessary, and the remaining pathways are insufficient, to mediate the normal occurrence of that behaviour. In contrast, if a particular behaviour were normal in visually deprived cats, this would suggest that the Y-pathway through the cortex is not necessary for that behaviour and that the other pathways are sufficient to mediate it. Thus, if good detection in the nasal visual field were to depend on the Y-pathway through the cortex, visually deprived cats should show deficits in this detection. Similarly, if smooth pursuit and symmetrical optokinetic nystagmus were to depend on that pathway, visually deprived cats also should show deficits in those behaviours. Finally, if the discrimination of shape and orientation could be mediated by some other pathway(s), visually deprived cats should be able to discriminate shape and orientation.

Behavioural tests in visually deprived cats bear out these predictions. Following binocular deprivation, cats show no evidence for detection beyond 15° in the nasal visual field, while detection in the temporal visual field is normal out to 90° (Sherman, 1972, 1977a).

Following monocular deprivation, cats also appear not to detect stimuli beyond 15° in the nasal visual field of the deprived eye (Heitlander & Hoffmann, 1978; Sherman, 1974a; Van Hof-van Duin, 1977).[12] Moreover, visually deprived cats track moving objects with jerky eye movements (Van Hof-van Duin, 1976) and show asymmetrical optokinetic nystagmus (Van Hof-van Duin, 1976, 1978).

Briefly, studies on visually deprived cats suggest that the Y-pathway through the cortex is necessary for good detection in the nasal visual field, for smooth pursuit and for symmetrical optokinetic nystagmus. Although some of the remaining pathways also might be necessary to mediate those behaviours, they appear to be insufficient to do so. In particular, the X-pathway through the cortex might be insufficient to mediate nasal field detection because it appears to be specialized to analyze pattern and not to detect peripheral stimuli (Section 4.4.1). The direct projection to the superior colliculus might be insufficient for good nasal field detection because that projection appears to contain relatively few uncrossed fibres from the temporal retina (which mediate detection in the nasal visual field) (see Section 1.4).

[12] Monocularly deprived cats show poor detection even in the temporal visual field of the deprived eye. This may be because the direct input to the superior colliculus from the deprived eye is suppressed by the Y-pathway from the normal eye through the cortex to the superior colliculus (Berman & Sterling, 1976; Heitlander & Hoffmann, 1978; Hoffmann & Sherman, 1974; Sterling & Wickelgren, 1970). Once the visual cortex is lesioned, full detection is restored in the temporal visual field and as expected, there is still no evidence for detection in the nasal visual field of the deprived eye (Sherman, 1974a).

However, visually deprived cats still can detect stimuli in the temporal visual field. This suggests that the Y-pathway through the cortex is not necessary for that behaviour. Nor does the X- or W-pathway through the cortex appear to be necessary since binocularly deprived cats show good detection in the temporal visual field even after the visual cortex is ablated (Sherman, 1977a). Thus, in visually deprived cats, temporal field detection appears to depend on some other pathway, likely on the direct projection from retina through superior colliculus (Sherman, 1977a). Certainly, the direct collicular pathway has a large number of crossed fibres from the nasal retina, fibres which could mediate detection in the temporal visual field (see Section 1.4). Moreover, visually deprived cats can discriminate changes in brightness, amount of contour and movement (Ganz & Fitch, 1968; Ganz, Hirsch, & Tieman, 1972; Loop & Sherman, 1977a). Thus the Y-pathway through the cortex also appears not to be necessary for those behaviours.

Visually deprived cats also can discriminate orientation and shape. For example, they can discriminate horizontal from vertical stripes, oblique stripes oriented to left from oblique stripes oriented to right, and a circle from a triangle equated in mean luminance (Loop & Sherman, 1977a; Van Hof-van Duin, 1976; Zernicki, 1979). This suggests that the Y-pathway through the cortex is not necessary for these discriminations. Moreover, the X and/or W-pathways through the cortex appear to be sufficient for the discrimination of orientation and shape since binocularly deprived cats no longer can make those discriminations following lesions of the visual cortex (Loop & Sherman, 1977a; but see Zernicki, 1979).

In summary, visually deprived cats appear to be missing a functional Y-pathway through the cortex, while the other pathways appear to be virtually normal. Without the Y-pathway through the cortex, cats appear to have poor detection in the nasal visual field. Moreover, they appear not to be able to track smoothly or to show optokinetic nystagmus when stripes move from the nasal to the temporal visual field. In contrast, cats missing the Y-pathway through the cortex have good detection in the temporal visual field and they can discriminate brightness, contour, movement, orientation and shape.

There are no studies in the monkey or human which have tested the necessity of the Y-pathway through the cortex for nasal field detection, smooth pursuit or symmetrical optokinetic nystagmus. However, some pathway through the cortex may be necessary for these behaviours since humans with cortical lesions have poor nasal vision (Section 1.3) and track with jerky eye movements (Section 1.6). The Y-pathway through the cortex is the most likely candidate for two reasons. First, the X-pathway seems to be involved mainly in the detailed analysis of pattern (Tolhurst, 1973). Second, because the Y-pathway in humans shares so many characteristics with that pathway in the cat, it may perform similar functions in both organisms.

4.5 Differences in Maturation of the Visual Pathways

In cats, the direct projection to the superior colliculus appears to develop before the Y-pathway through the cortex. During the first month of life, cells in the superior colliculus of the kitten respond better to stationary than to moving stimuli, show little or no directional selectivity, and receive input mainly from the contralateral eye (Norton, 1974; Stein, Labos, & Kruger, 1973). These properties are identical to those observed in the superior colliculus of decorticate cats (Berman & Cynader, 1972; Flandrin & Jeannerod, 1977; Rosenquist & Palmer, 1971; Wickelgren & Sterling, 1969) and of visually deprived cats (Dec et al., 1976; Flandrin & Jeannerod, 1977; Hoffmann & Sherman, 1974, 1975; Sterling & Wickelgren, 1970). In decorticate and visually deprived cats the direct projection to the superior colliculus is virtually normal, but the Y-pathway through the cortex is nonfunctional (Hoffmann & Sherman, 1974, 1975). The similarity in the response properties of collicular cells in immature, decorticate and deprived cats suggests that, in young kittens, the direct projection to the superior colliculus is functional, while the Y-pathway through the cortex is not.

During the second month of life, cells in the cat's superior colliculus acquire adult properties. Specifically, they respond better to moving than to stationary stimuli, most are directionally selective and most receive binocular input (Norton, 1974; Stein et al., 1973). These changes probably are due to the development of the Y-pathway through the cortex (Flandrin & Jeannerod, 1977; Norton, 1974; Stein & Edwards, 1979; Stein et al., 1973; reviewed in Daniels & Pettigrew, 1976). Thus, in kittens, the direct projection to the superior colliculus appears to be functional at birth whereas the Y-pathway through the cortex does not appear to be functional until several months later.

Studies of cells in the lateral geniculate of the cat suggest that the X-pathway develops earlier than the Y-pathway through the cortex. At least some X-cells in the lateral geniculate display mature receptive field properties between 14 and 21 days of age, while the Y-cells located there develop mature receptive field properties later than 34 days of age and later than all the X-cells (Daniels et al., 1978; Norman et al., 1977). Very little is known about the maturation of the W-pathway through the cortex although there is some evidence that W-cells in the cat's lateral geniculate mature at least as early as X-cells (Daniels et al., 1978).

The electrophysiological properties of cells in the visual cortex of young kittens resemble those in binocularly deprived cats (reviewed in Daniels and Pettigrew, 1976). In binocularly deprived cats, the X- and W-pathways through the cortex appear to be virtually normal while the Y-pathway through the cortex seems to be nonfunctional (Section 4.4.2). This suggests that the X- and W-pathways might be functional at, or shortly after, birth but the Y-pathway through the cortex might not be. Since, at about 5 weeks of age, cells in the kitten's visual cortex resemble those in normal adult cats (reviewed in Daniels & Pettigrew, 1976), this again suggests that the Y-pathway through the cortex begins to function during the second month of life.

There is some evidence which implies that a similar sequence of development might occur in the human infant. Evoked responses suggest that the direct collicular pathway is functional during the first month (Hoffmann, 1978) and that the geniculo-cortical pathway is functional in some respects but not in others (Harter et al., 1977; Hoffmann, 1978; Sokol & Jones, 1979; reviewed in Section 1.6). Specifically, during the first month the amplitude of the early component of the evoked response (which supposedly reflects geniculo-cortical activity) varies with the size of small elements, elements to which the X-pathway would be most sensitive; but it does not vary with the size of large elements, elements to which the Y-pathway would be most sensitive (Harter et al., 1977; but see Sokol & Jones, 1979). Moreover, the cells in the lateral geniculate which near their adult size first are in the parvocellular layers (Hickey, 1977), layers which in the monkey contain mainly X-cells (Dreher et al., 1976; Sherman et al., 1976; but see also Bunt et al., 1975). The cells which attain their adult size later are in the magnocellular layers, layers which in the monkey contain mainly Y-cells (Bunt et al., 1975; Dreher et al., 1976; Sherman et al., 1976).

If the visual pathways in the human infant were to show the same sequence of development as those in the kitten, the behaviour of human newborns should resemble that of immature and visually deprived cats, both of which appear to be missing a functional Y-pathway through the cortex. That appears to be the case. Prior to 2 months of age, human infants appear to have poor detection in the nasal visual field (Experiments 2, 3 and 4). They also track a moving object with jerky eye movements (Barton et al., 1971; Dayton & Jones, 1964; Dayton et al., 1964; White et al., 1964) and show asymmetrical optokinetic nystagmus when tested monocularly (Atkinson, Note 1). However, even newborns have good detection in the temporal visual field (Experiments 1, 2 and 3). In addition, even newborns can easily discriminate moving from stationary stimuli (Fantz, 1967; Haith, 1966), changes in intensity (Hershenson, 1964), in amount of contour (reviewed in Fantz et al., 1975), in orientation (Slater & Sykes, 1977) and in shape (Fantz & Miranda, 1975). All of these behaviours resemble those in visually deprived cats (Section 4.4.2). Unfortunately, the ability of young kittens to detect peripheral stimuli and to discriminate shape or orientation has not been tested during the first month of life. However kittens, like young human infants, have jerky tracking (Norton, 1974) and show asymmetrical optokinetic nystagmus when tested monocularly (Van Hof-van Duin, 1978).

For the first time at about 2 months of age, human infants show a marked improvement in nasal field detection (Experiment 5), track smoothly (White, 1971; White et al., 1964) and begin to show symmetrical optokinetic nystagmus when tested monocularly (Atkinson, Note 1). These behaviours resemble those of cats which have a functional Y-pathway through the cortex (Norton, 1974; Sherman, 1972, 1977b; Van Hof-van Duin, 1978). Thus, perhaps in the human infant, the Y-pathway through the cortex begins to influence visual behaviour at about 2 months of age.

4.6 Summary and Conclusions

Human newborns have good detection in the temporal visual field (Experiments 1, 2 and 3). In cats and human adults, the direct projection from retina through superior colliculus appears to be sufficient for good temporal field detection and the geniculo-cortical pathway appears not to be necessary for that behaviour (Section 1.3). Since the direct collicular projection appears to be functional in human newborns while the geniculo-cortical pathway seems to be too immature to influence a variety of visual behaviours (Section 1.6), temporal field detection might be mediated by the direct collicular pathway at birth.

Human newborns appear to have poor detection in the nasal visual field (Experiments 2 and 3). The geniculo-cortical pathway appears to be necessary for good nasal field detection in human adults and cats (Section 1.3). This may be because the direct projection from retina to superior colliculus seems to contain many more crossed fibres from the nasal retina (which mediate detection in the temporal visual field) than uncrossed fibres from the temporal retina (which mediate detection in the nasal visual field). In contrast, the projection from retina to lateral geniculate to visual cortex contains about an equal number of crossed fibres from the nasal retina and uncrossed fibres from the temporal retina (Section 1.4). Thus, poor nasal field detection at birth might reflect an immature geniculo-cortical pathway.

However, the entire projection through the visual cortex might not be involved in peripheral detection. Evidence from visually deprived cats suggests that the Y-pathway through the cortex is necessary for good nasal field detection, whereas the X- and W-pathways through the cortex appear to be insufficient for that behaviour (Section 4.4.2). Both monkeys and humans appear to have pathways similar to those in the cat, with similar functions (Sections 4.2 and 4.3). Thus, poor nasal field detection in the human newborn might reflect specifically an immature Y-pathway through the visual cortex.

Converging evidence supports that hypothesis. First, electrophysiological and anatomical data in cats suggest that the direct collicular pathway and the X- and W-pathways are functional at birth, whereas the Y-pathway through the cortex appears to be nonfunctional (Section 4.5). Anatomical and electrophysiological data suggest that the same might be true in human newborns (Section 4.5). Second, in cats, smooth pursuit and symmetrical optokinetic nystagmus appear to depend on the Y-pathway through the cortex (Section 4.4.2). Those behaviours are absent both in young kittens and in human newborns (Section 1.6). Third, although the human newborn shows a variety of visual behaviours (e.g., he can discriminate intensity, contour, movement, shape and orientation), evidence from lesioned and visually deprived animals suggests that none of these behaviours depends on the Y-pathway through the cortex (Sections 1.6 and 4.4.2). Fourth, electrophysiological data from human infants suggest that important changes occur in the geniculo-cortical pathway at about 2 months of age (Chapter 3). At that age, human infants begin to show smooth pursuit and symmetrical optokinetic nystagmus (Chapter 3). Moreover, only at that age do they appear to show an improvement in nasal field detection (Experiments 4 and 5). Together, these data suggest that poor nasal field detection reflects an immature Y-pathway through the cortex and that in humans, that pathway begins to influence visual behaviour at about 2 months of age.

It is interesting to note that in cats missing the Y-pathway through the cortex, the discrimination of orientation and shape appears to depend on the X- and/or W-pathways through the cortex (Section

4.4.2). Since human newborns can easily make those discriminations, the X-pathway (and the W-pathway through the cortex, if it exists in humans) might be functional at birth.

Some investigators (Bronson, 1974; Harter et al., 1977; Karmel & Maisel, 1975; Salapatek, 1975; Volkmann & Dobson, 1978) have examined the anatomical, physiological, and/or behavioural evidence and have concluded that the visual cortex probably plays no role in visual behaviour at birth. Others (Fantz et al., 1975; Haith, in press; Purpura, Note 13) have examined similar evidence and have concluded that all aspects of the visual cortex are functional at birth, at least to some degree. This is not surprising since the evidence is conflicting when one takes an "all or none" approach to cortical involvement.

In contrast, the "X-Y" theory can account for all the data in a logical way. By assuming a sequence of development for the various pathways, the geniculo-cortical projection can be immature in some respects and mature in others. Specifically, the evidence presented in the first three chapters of this thesis suggests that, prior to 2 months of age, part of the geniculo-cortical projection (the Y-pathway) is too immature to mediate smooth pursuit, symmetrical optokinetic nystagmus and good nasal field detection. Yet, other parts (the X- and/or W-pathways) seem to be sufficiently mature to mediate the discrimination of shape and orientation. Because each pathway is relatively specialized, this theory can be a valuable tool for predicting visual behaviour in situations which have not been tested (see Maurer & Lewis, in press). Thus, poor nasal field detection at birth is not only of empirical interest, but also of theoretical interest in that it provides support for an "X-Y" theory of perceptual development in the human infant.

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