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Binocular Interactions In Individuals With Anomalous Early Visual History

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**BINOCULAR INTERACTIONS
IN INDIVIDUALS WITH ANOMALOUS
EARLY VISUAL HISTORY**

by

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**Submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy**

**Faculty of Graduate Studies
The University of Western Ontario
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ABSTRACT

The present set of experiments used adaptation procedures to explore binocularity in individuals with abnormal binocular vision. The first series of experiments examined interocular transfer because this measure has been used previously to test for the presence of binocular neurons (Movshon, Chambers and Blakemore, 1972). Experiment I examined the test-retest reliability of this measure. Interocular transfer was found to be reliable. The results of Experiments II-IV clearly show that individuals with anomalous early visual history (A.E.H.) are capable of interocular transfer of a magnitude associated with normals.

Experiments III and IV also addressed the organization of binocular channels in individuals with varying levels of stereopsis. The results from Experiment III supported the presence of two binocular channels in Normal subjects whereas the A.E.H. group showed evidence for only one binocular channel. This pattern of results for the A.E.H. group was not as clear in Experiment IV, but the Normal group displayed data consistent with two binocular channels.

A different paradigm, alternating monocular adaptation, was used in Experiments V and VI in a further attempt to evaluate the number of binocular channels present. The results from Experiment V were quite clear. Individuals without stereopsis showed evidence of only one binocular channel and the Normal group portrayed the pattern of results indicative of two binocular channels. The results from Experiment VI were equivocal regarding both the Normal and A.E.H. group.

Experiment VII revealed that all subjects of the A.E.H. group were capable of obtaining a level of binocular summation associated with probability summation. The Normals showed summation levels indicative of neural summation. In Experiment VIII, the data show that if the stimuli presented to each eye are not spatially matched, then summation decreases. However, this was true only for the Normal group. The Stereoblind group maintained a level of probability summation throughout the stimulus phase shifts. The final experiment used subthreshold summation and adaptation procedures to affect the purely binocular channel in order to reduce summation. Summation decreases after adaptation of this channel, but remains unchanged if this channel is not adapted. The results for the Stereoblind group were the same as the Normal group, suggesting that Stereoblinds maintain a binocular channel affected by simultaneous stimulation.

These results clearly show that individuals with anomalous early visual histories show evidence for binocular channels previously thought to be absent.

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I am finishing my PhD at a time when my son, Adam, is turning five and Nicole is already one and a half. I feel that they, more than anyone else, have allowed me to enjoy my PhD. They have forced me, albeit willingly, to slow down and appreciate what is important for that moment. Without them I would have finished much quicker but with far less fulfilment. I appreciate that my advisor, Dr. Brian Timney, has recognized this and never given me concern. He has always supported me and for this I am truly thankful.

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Chapter 1 -- Introduction

The way in which the two eyes coordinate the slightly different images of the world with which they are presented, has been an enduring topic in Psychology. In some fashion, the visual system is able to combine the slightly disparate views into a single fused image, and to use that disparity to generate a three-dimensional percept of the world. Over the past 30 years or so, a great deal has been learned about the neural mechanisms that serve stereopsis. To a first approximation, many binocular capacities can be attributed to the action of sub-populations of neurons that have excitatory connections to both eyes. However, if one considers the operation of these neural mechanisms in detail, it is clear that much needs to be learned. The present paper sets out to determine the nature of binocular neurons in individuals where the two eyes are not, or previously have not been, working together.

In order to approach this issue, several aspects of binocularity will be discussed. The first section contains relevant background material from animal research on the physiological response of binocular neurons and their association with stereopsis (depth perception). Since the primary interest of this paper is with human subjects, the next section looks at aftereffect studies with humans as a means of tapping into the binocularity of the human visual system. Several models of human binocularity have been proposed to account for the findings in aftereffect studies and these will be discussed in the following section.

Investigations of individuals with binocular abnormalities have also shed light on the organization of the visual system. Since most of the work with human visual disorders is based on the physiological findings from animal research, the last section deals with the development of binocular neurons in animals that experience abnormal visual conditions. This is explored from a physiological and behavioral view-point. In turn, the goal of the following chapters will be to investigate the binocularity in individuals lacking, or thought to be lacking, binocular neurons.

Physiological Descriptions of Binocularity

Hubel and Wiesel (1962) led the physiological investigation into the binocularity of the cat's visual cortex. They used microelectrodes to record from a large number of cells and then rated each cell's ability to respond to visual stimulation of the left eye or the right eye. Some cells responded from stimulation to just one eye. The majority of cells responded either when the left eye or the right eye was stimulated, and it is these cells that represent one type of binocular neuron. Hubel and Wiesel (1962) put forth a classification of 7 different categories of neurons based upon the responses. For example, those cells responding only to contralateral eye stimulation would be in the first category, those responding equally to the ipsilateral or contralateral eye would belong to the fourth category and those cells responding exclusively to ipsilateral eye stimulation would be in the seventh category.

Most of the early experiments on binocularity looked at the stimulus requirements and response characteristics from stimulating one eye at a time. However, Barlow,

Blakemore and Pettigrew (1967) reported that many cells respond to binocular stimulation. They described a type of binocular neuron that responded to simultaneous stimulation of both eyes. Barlow et al. (1967) reported that these binocular cells were sensitive to small differences in horizontal disparity.

If the eyes are fixated at a certain distance, then any object that falls in front of, or behind this fixation plane, will be projected to slightly different positions on the retina. This horizontal retinal disparity is the cue that provides information about stereoscopic depth. The type of binocular neuron described by Barlow et al. (1967) that responds to simultaneous stimulation of both eyes is thought to be responsible for information regarding the perception of objects in depth, known as stereopsis. Since this report, many other researchers (Fischer and Kruger, 1979; Poggio and Talbot, 1981; Ferster, 1981; Poggio, Gonzalez and Krause, 1988) have also posited that binocular neurons serve as the neural substrate of stereoscopic depth perception.

There is evidence to suggest that there is more than one type of depth-sensitive binocular neuron present in the visual system. Poggio and Talbot (1981) found cells responding to a range of disparities in front of the horopter as well as behind it. They also report neurons that display binocular facilitation to stimuli present at zero disparity and a small range surrounding the horopter. Other researchers have corroborated these findings, although they may be described under a different classification scheme. Ferster (1981) also found distinct groups of binocular neurons responding to disparities surrounding the horopter as well as near and far disparities. He found that these different groups of disparity cells were located in different areas

of the visual cortex. He suggests that because these two groups are responsive to different types of disparities and are located in different areas of the cortex, they play different roles in depth vision. LeVay and Voigt (1988), however, did not find a neat representation of binocular neurons in separate categories. Instead, they suggest that the response of binocular neurons forms a continuum across the range of disparities. For the present discussion, it is important to note that more than one type of binocular neuron exists.

The nature of the microelectrode recording techniques used with animals means that one cannot obtain the same direct evidence for the existence of these binocular neurons in human subjects. Consequently, more indirect methods of assessment are required to explore the relationship between binocularity and depth perception. One way this can be accomplished is to relate what we know about neurophysiology to some form of behavioral, or perceptual evidence. Since psychophysics explores the relationship between the physical attributes of stimuli and the perception of them, this field has helped to integrate the knowledge from neurophysiology and apply it to the study of sensation and perception. In particular, visual aftereffects have been studied extensively and their results have been interpreted to reflect the neurophysiological organization of the human visual cortex. The next section will briefly discuss aftereffects before examining their role in the study of the binocularity of the human visual system.

Aftereffects and their Neuronal Response Characteristics

When the presentation of a stimulus affects the appearance of subsequently presented stimuli, this visual phenomenon is referred to as an aftereffect. For the spatial aftereffects in the present study, these aftereffects are usually reflected by changes in detectability or perceived position. The typical procedure for aftereffect studies is to allow an observer to view a test stimulus, say a vertical grating, and to respond to a certain aspect of its appearance, say its orientation or its visibility. After this, the observer is adapted to a specific stimulus that is assumed to affect a particular group of neurons. If, for example, the adapting stimulus is a high contrast vertical grating, then the observer's threshold for a subsequently presented vertical grating will be higher than in the initial viewing. In comparison, if a horizontal grating is presented after the adaptation period, the observer's threshold for this stimulus will not be raised. For this reason, it is assumed that aftereffect studies selectively affect one class of neurons and not another. In the above example, neurons responsive to vertical gratings were affected but those responsive to horizontal gratings were not. Thus, aftereffects can be used as a means of examining distinct channels, or groups of neurons, in the visual system.

Visual aftereffects have been studied extensively, so much so that there are widely accepted explanations for the neural events responsible for their occurrence. The classes and examples of some aftereffects will be discussed briefly before turning to their role in investigating binocularity.

A suprathreshold aftereffect refers to distortions in the perception of

suprathreshold stimuli whereas a threshold aftereffect refers to changes in detectability of near-threshold stimuli. Two suprathreshold aftereffects are pertinent to the present discussion: the motion aftereffect and the tilt aftereffect. During the motion aftereffect (MAE) the viewer is exposed to a moving stimulus. After this adaptation, the viewer is presented with a stationary test stimulus. Typically, when viewing the test stimulus, the viewer experiences apparent movement in the direction opposite to that of the adapting stimulus. In the case of the tilt aftereffect (TAE), following exposure to a tilted pattern of lines, a vertical line pattern appears tilted in the opposite direction. These aftereffects are thought to be the result of a redistribution of neuronal firing. The change in firing patterns can be attributed to fatigue of the adapted neurons from prolonged excitation and/or inhibition from the adapted neurons during the test period (Wolfe and O'Connell, 1986; Dealy and Tolhurst, 1974; Over, 1971; Sutherland, 1961).

In a contrast threshold elevation (CTE) experiment, the subject adapts to a high contrast grating of a particular spatial frequency and orientation. It is assumed that during this period a class of cells tuned to those stimulus characteristics will be driven. After prolonged exposure to the adapting grating, the neurons within this group will become less responsive (i.e. their sensitivity will be reduced). Because the threshold of this group of cells is elevated, more contrast will be required to detect the same stimulus in the subsequent test period and the subject's post-adaptation threshold becomes elevated.

Using Aftereffects to Assess Binocularity

One well documented characteristic of aftereffects, that has been used to study binocularity, is that these visual aftereffects will transfer interocularly (Barlow and Brindley, 1963; Lehmkuhle and Fox, 1976; Moulden, 1980). Monocular adaptation produces measurable aftereffects in the unadapted eye, and the transferred effect is usually fifty to eighty percent of the effect measure in the adapted eye (Blake, Overton, and Lema-Stern, 1981). Transfer of the aftereffect indicates that monocular information is somehow combined and made accessible to a group of cells. Barlow and Brindley (1963) have shown that this effect is not mediated by the retina so, in order for interocular transfer (IOT) to occur, there must exist some central binocular mechanism which receives input from both eyes. Thus, the presence of IOT has been taken as evidence of a binocular mechanism in the human visual system.

A number of investigators have used the relationship between interocular transfer and binocularity as a means of developing and testing models of human binocular vision. By identifying potential channels, and making assumptions about their response characteristics, it is possible to make specific predictions about the outcome of adaptation experiments.

Psychophysical Models of Binocularity

Various models have been proposed to account for aftereffects and the amount of IOT. These models fall into three broad classifications that can be distinguished by the number of proposed binocular channels. For the purpose of the present study, the

term "channel" refers to a population of neural units that share the encoding of a particular stimulus dimension (Moulden, 1980). The independence or interaction between channels is something that must be assumed by each model. These models and the assumptions and predictions that accompany them will be described in order to set the logic for the following studies.

The main defining feature relevant to the present discussion concerns the number of binocular channels proposed for each model. The simplest model which only contains a single binocular channel, in addition to 2 monocular channels, is that of Moulden (1980). His three channel model simplified Hubel and Wiesel's (1962) seven class description of cortical binocularity, by proposing that there are three distinct groups of neurons: right monocular, left monocular, and binocular. He proposed that each monocular channel is activated only by input to one eye, while the binocular channel can be driven by stimulation of either eye alone, or both eyes simultaneously.

Two important assumptions must be mentioned before describing the predictions from adaptation paradigms. Moulden assumed that the three channels operated independently of one another, and that the size of an aftereffect would be a function of the proportion of cells that have been adapted and are then driven during testing. A corollary of the latter assumption is that units adapted during the inspection period, but not activated in the test period do not contribute to the aftereffect. Also, neurons that have not been adapted, but are driven in the test period, serve to reduce the aftereffect (Moulden, 1980). It is also important to note that all channels have equal

weighting when determining the size of the aftereffect.

Moulden's (1980) explanation for IOT is as follows. When one eye is exposed to the inspection stimulus, the ipsilateral monocular channel and the binocular mechanism are adapted. During testing of the adapted eye, only the adapted ipsilateral monocular and binocular channels are driven, and the effect is at a maximum. But, when measuring the aftereffect in the unadapted eye (interocular transfer), the output of the monocular units of the unadapted eye combine with the adapted binocular channel, thereby lowering the net size of the aftereffect (Moulden, 1980). This prediction has been confirmed by a number of adaptation experiments, using several types of aftereffects (Gibson and Radner, 1937; Blake et al., 1981; Wilcox, Timney and St. John, 1990; Mohn and von Hof-van Duin, 1983).

The same logic that has been used to explain IOT may be extended to account also for the relative size of the aftereffect if both eyes are tested following monocular exposure. In fact, a series of predictions of the relative sizes of monocular, transferred, and binocular aftereffects following monocular exposure can be generated. The size of the monocular effect will always be at a maximum since all channels that are tested have been driven by the adapting stimulus. The predicted size of the transferred effect is as stated above; the transferred effect should be lower than the adapted monocular effect because only one-half of the tested channels will have been adapted. However, in the binocular test condition all available channels will contribute to the size of the aftereffect. Of the three available channels, one nonadapted monocular channel will serve to dilute the total binocular aftereffect since

it has not been adapted, while the other adapted monocular channel and the binocular channel will positively affect the outcome (refer to Figure 1A). Therefore, in the binocular condition two-thirds of the tested channels have been adapted (one monocular, and the binocular channel). Because a greater proportion of the tested channels will have been adapted in the binocular test condition (two-thirds) than in the transferred condition (one-half), the binocular aftereffect should be larger than the transferred aftereffect. Moulden's (1980) results supported these predictions.

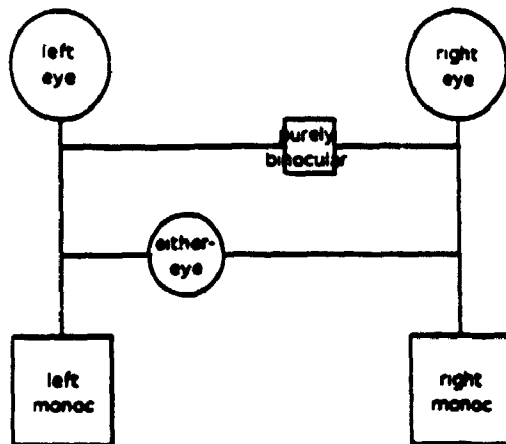
Moulden's model was extended by Wolfe and Held (1981) to include a second binocular channel. This additional binocular channel is thought to be driven only when both eyes are stimulated simultaneously. In the following text, this will be referred to as the "purely" binocular channel and the other binocular channel will be referred to as the "either-eye" channel. If the assumptions outlined for a three channel model are followed, in addition to the assumption of a fourth purely binocular channel, the predicted pattern of results are slightly different (see Figure 1B). Following monocular exposure, a large monocular aftereffect and a lowered transferred aftereffect would be expected; just as the case for the three channel model. The difference, however, concerns the relative size of the binocular aftereffect. During testing of the binocular channel, the ipsilateral monocular and either-eye binocular channels have been adapted whereas the contralateral monocular and purely binocular channels have not been adapted. This scenario, with one-half of the channels contributing positively, should produce an aftereffect equivalent in size to the transferred aftereffect. In both conditions, one-half of the tested channels have been

Figure 1: A schematic drawing showing the pattern of aftereffect sizes following monocular adaptation. The check marks and x's are aligned with the diagram above to indicate the channels affected during adaptation and testing. In this example, the left monocular and either-eye channels are adapted. During testing, the contributing adapted neurons are marked with a check. The diluting influence from the unadapted channels, that are driven during testing, are marked with an "x".

Figure 1A: Pattern of aftereffect sizes based upon a three channel model.

Figure 1B: Pattern of aftereffect sizes based upon a four channel model.

Monocular Adaptation



<u>Adapt</u>	✓	✓		<u>Proportion of Adapted/Total Channels</u>	<u>Predicted Order of Aftereffect Sizes</u>
A. Assume influence of 3 channels (no purely binocular channel)					
<u>Test</u>	✓	✓		=2/2	
Adapted					Adapt > Binoc
Nonadapted		✓		X =1/2	Adapt > NonAdapt
Binocular	✓	✓		X =2/3	Binoc > NonAdapt
B. Assume influence of 4 channels					
<u>Test</u>	✓	✓		=2/2	
Adapted					Adapt > Binoc
Nonadapted		✓		X =1/2	Adapt > NonAdapt
Binocular	✓	✓	X	X =1/2	Binoc = NonAdapt

adapted. This prediction that IOT is equal in size to the binocular aftereffect during monocular adaptation differentiates the three channel model from a four channel model.

Wolfe and Held's (1981) data showed the binocular aftereffect to be *smaller* than the transferred effect, yet they reported that their results were in favour of a four channel model. Although they interpreted these data to reflect a diluting influence of a second binocular channel, their reasoning has been shown to be incorrect (Timney, Wilcox and St. John, 1989). Timney et al. (1989) correctly point out that if all the channels are properly accounted for, Wolfe and Held (1981) should have predicted that the binocular aftereffect would be equivalent to, and not less than, the transferred effect. Thus, Wolfe and Held's (1981) results are not consistent with the presence of a second separate binocular channel. However Wilcox et al. (1990) did find a pattern of results with no significant differences between the size of the binocular and transferred aftereffects, which is indicative of 4 channels.

There is some disagreement concerning the presence of the purely binocular channel. Blake et al. (1981) report data that are not consistent with a four channel model. They based this observation on the comparison between the size of the binocular aftereffect during two different adaptation paradigms. Wilcox, Timney and Girash (1994) have criticized Blake et al.'s (1981) criteria for evaluating the presence of this type of binocular channel. When the criticisms were taken into account, Wilcox et al. (1994) again found data in favour of a four channel model.

Other researchers have suggested the presence of more than one binocular

channel. Anstis and Duncan (1983) have suggested that the binocularity of the visual system involves two binocular channels. Their conclusions are based on the results of a motion aftereffect study. During adaptation, they presented clockwise-rotating motion to each eye separately, and then presented anticlockwise motion to both eyes at the same time. When the subjects were tested monocularly, they saw anticlockwise motion, but during the binocular test condition clockwise movement was apparent. The fact that a binocular aftereffect was observed, and not cancelled by the monocular adaptation, indicates that the binocular aftereffect was not a result of an either-eye channel.

Cogan (1987) has provided evidence for at least two separate binocular channels using detection and discrimination tasks. He has presented a model of binocular interaction using only 2 binocular channels; no independent monocular channels are assumed. In comparison to the three and four channel models, Cogan assumes that the activity of the two binocular channels is combined after monocular information has been processed in one of the channels. The characteristics of the binocular channels in Cogan's model are similar to the binocular channels involved in the four-channel model; one is sensitive to either-eye stimulation where the other is responsive to simultaneous stimulation. Cogan's predictions for aftereffect studies take into account inhibition as well as excitation processes. Similar to the four channel model, the predictions would be that interocular transfer would be expected to be less than the direct effect but approximately equivalent to the binocular effect.

To summarize, the current available information does seem to favour the presence

of 2 binocular channels, although the interactions and response characteristics have not been fully worked out. For the present set of studies we will assume that there are at least two binocular channels.

Abnormal Visual Experience and Binocular Channels

While a large amount of work has focused on the binocular organization of the adult mammal, a considerable amount of research has also been directed to the development of binocularity. In addition, the study of binocular anomalies of the visual system has also aided the search for knowledge regarding the binocular organization of the visual cortex. Depending on the results, research on visual development and disorders can help reinforce or clarify models of binocularity based on visually normal adults. The following section outlines some of the physiological consequences of abnormal visual development in the animal literature.

In adult humans and monkeys, the stereoscopic depth system is finely tuned. One question of interest is the degree to which the development of stereopsis relies on experience. In the physiological literature there are no data that have looked directly at the result of visual deprivation on disparity tuned cells. However, a large number of studies have looked at the effects of deprivation on the proportion of binocularly driven cells. Three types of deprivation studies are pertinent to the present discussion of binocularity because they involve a disruption of normal binocular development: monocular deprivation, dark rearing and artificially induced strabismus. Each will be discussed from a physiological and behavioral view-point. This includes the effect of

the deprivation on the reduction of binocularly driven cells and the development of stereopsis.

Wiesel and Hubel's (1963) monocular deprivation paradigm involved suturing one eye shut shortly after birth. It is well established that this type of deprivation markedly reduces the proportion of binocular cells found in the visual cortex of cats (Wiesel and Hubel, 1963; Olson and Freeman, 1975; Blakemore, 1976) and monkeys (Baker, Grigg, and Von Noorden, 1974; Blakemore, Garey and Vital-Durand, 1978). The explanation for this finding was that the animals did not experience normal, balanced, binocular input and consequently did not develop a full complement of binocular units. In other words, the undeprived eye maintains a competitive advantage over the deprived eye such that it gains control of neurons in the cortex at the expense of the deprived eye. This results in an ocular dominance distribution skewed to the undeprived eye with a very small number of units responsive to binocular stimulation or to stimulation of the deprived eye.

Numerous behavioral studies of stereoscopic depth perception following monocular deprivation have shown that the decline in binocularly driven cells is associated with a decrease in stereoscopic ability. Timney (1981) has used the jumping stand technique (see Mitchell, Kaye and Timney, 1979) to determine a cat's ability to discriminate small differences in depth between two surfaces. The smallest difference that the cats were able to discriminate was their depth threshold. In normal cats, the binocular thresholds were three to six times better than the monocular thresholds. For the monocularly deprived kittens, these differences were not apparent

and the binocular thresholds were approximately equivalent to the monocular thresholds. Therefore, in addition to Wiesel and Hubel's (1965) finding of a reduced number of binocularly driven cells, Timney (1981; 1983) has shown that monocular deprivation can also affect a kitten's binocular advantage for depth perception.

Blake and Hirsch (1975) have used a modified monocular deprivation paradigm, called alternating monocular occlusion, to examine both the physiological and behavioral consequences of deprivation. They temporarily covered one eye for 1 day and then opened this eye and covered the other eye for the same duration and so on until the animals were 6 months old. Physiologically, this type of alternating monocular deprivation reduced the number of binocular neurons found in comparison to that of normal cats. Behaviorally, the deprived animals showed equivalent binocular and monocular depth thresholds. Blake and Hirsch (1975) report that this deficit is probably permanent since a recovery period of 1.5 to 2 years failed to improve the cat's binocular depth threshold. This provided further evidence that binocular neurons are a crucial component of stereoscopic depth perception.

As mentioned previously, there are conditions other than monocular deprivation that can affect the binocularity of the visual cortex. One of these, dark rearing, involves rearing a cat in darkness for a period of time. Kaye, Mitchell and Cynader (1982) have obtained some interesting physiological and behavioral results using this regime. They reared kittens in the dark and then allowed them a 3 month recovery period. Kaye et al. (1982) report that although the number of binocularly driven cortical neurons was definitely reduced, a substantial number of binocular cells were

retained. This is an important finding since these kittens did not possess any binocular advantage. The dark reared animals recovered visual acuity to normal levels but their depth perception remained poor; their binocular performance was only marginally better than their monocular depth judgements. The behavioral results are similar to the effects of monocular deprivation, yet the physiological observations are quite different. The presence of binocular neurons accompanied by an absence of stereopsis leads to the conclusion that the binocular neurons remaining were not those involved in stereopsis.

The final type of deprivation study is the one most applicable to humans. Strabismus, a misalignment of the two eyes, deprives cells in the visual cortex of concordant information from the two eyes. Strabismus can occur as a natural visual disorder but it is also relatively easy to induce in animals. By surgically cutting the muscles of one eye, the coordination between the two eyes is upset due to the muscle imbalance. Hubel and Wiesel (1965) found that binocular neurons of strabismic kittens were decreased in number, in comparison to normal cats. Only 20% of the cells from the cortex of strabismic cats responded to stimulation of either eye whereas approximately 80% of the neurons in a normal cat cortex are responsive to either-eye stimulation. Similarly, Crawford, Smith, Harweth and von Noorden (1984) have induced strabismus in monkeys and found that only 22% of the cells responded to either-eye stimulation.

The results from the animal studies have been applied to human individuals with known binocular visual disorders. Human strabismics fit this description. If they

also have a reduction of binocularly driven cells, then perhaps this reduction would manifest itself in a perceptual manner. This line of thinking has been investigated with aftereffect experiments and the strabismics' performance has been compared to those individuals with normal vision.

While most subjects with normal binocular vision show IOT, many subjects who lack stereopsis have been shown to display little or no transfer of aftereffects (Movshon, Chambers and Blakemore, 1972; Mitchell and Ware, 1974). This has led to the conclusion that there is a relationship between IOT and binocularity. Specifically, it has been proposed that stereoblind subjects do not show interocular transfer because they lack binocular neurons. Furthermore, it has been proposed that the degree of IOT could be used as an index of a subject's binocularity. If an individual showed minimal IOT this would indicate that this individual retained a small complement of binocular neurons, no transfer would indicate a complete absence of binocular neurons and a normal level of IOT would point to a full complement of binocular neurons. The next chapter explores this concept in detail and provides a set of experiments that looks at the relationship between IOT and binocularity.

Chapter 2 -- The relationship between interocular transfer and stereoacuity

Introduction

A person's stereoacuity refers to a minimal value of disparity beyond which no stereoscopic depth effect is produced. Assuming that binocular neurons serve as the basis for stereopsis, individuals may differ in their ability to respond to disparate stimulation based on the proportion of binocular neurons in the visual system. Strabismus occurs naturally in the human population and individuals with these disorders often have poor depth perception. If the findings from the animal work are extended to humans, it is likely that individuals with strabismus have a less than normal complement of binocular neurons. Therefore, these subjects are ideal candidates for participation in aftereffect experiments which explore binocularity.

As mentioned earlier, investigators have looked at the percentage of interocular transfer as an indicator of binocularity. Movshon et al. (1972) were one of the first groups to explore this relationship in detail. Their subjects were classified in the following groups: those subjects with a normal visual history and ability to perceive depth in stereograms, those subjects with a normal visual history but no stereopsis, and those subjects with a history of strabismus and no stereopsis. The normal group exhibited a mean IOT of 70%, the second group showed transfer levels of 49% whereas the strabismics only showed 12% transfer. Movshon et al. (1972) interpreted these results to imply that the decrease in IOT was due to the strabismics' reduced

complement of binocular neurons. Moreover, a person with diminished stereoscopic ability also had smaller than normal levels of IOT. This study led the investigation into the three-way relationship between the presence of binocular neurons (binocularity), stereoscopic ability and IOT.

Mitchell and Ware (1974) reasoned that stereoacuity values may be *directly* related to the extent of IOT. Although their subjects were also divided into three groups (normals, poor stereopsis and stereoblinds) the subjects formed a continuum from low to high values of stereoacuity. (A low stereoacuity value reflects good stereopsis.) Mitchell and Ware (1974) found a significant correlation of .86 between the level of stereoacuity and the amount of IOT in the TAE. In other words, those individuals with good levels of stereopsis showed large, or normal, amounts of transfer, whereas individuals with deficient stereopsis show less than normal levels. Three of the four stereoblind subjects showed a complete absence of IOT and the fourth subject showed less than 13%.

From the animal work mentioned earlier (Hubel and Wiesel, 1965; Crawford et al., 1984; Timney, 1983) one might assume that individuals with normal stereopsis possess a full complement of binocular neurons whereas those with deficient stereopsis possess a reduced number of binocular neurons. A lack of binocular neurons would contribute to the subject's inability to transfer information from one eye to the other. Mitchell and Ware's (1974) results reinforce the notion that both the level of IOT *and* stereoacuity reflect the degree of binocularity. Ware and Mitchell (1974) and Mitchell, Reardon and Muir (1975) extended these findings to the motion

aftereffect and the contrast threshold elevation aftereffect.

Two groups of researchers looked at the relationship between the age of onset of strabismus and the amount of IOT (Banks, Aslin and Letson, 1975; Hohmann and Creutzfeldt, 1975). They reasoned that if strabismus occurred later in life then perhaps some binocular neurons would be spared. This reasoning comes from visual deprivation studies in cats which have shown that a deprivation period sometime before a certain time affects the number of binocular neurons, whereas deprivation inflicted after this time period does not (Hubel and Wiesel, 1970). Banks et al. (1975) and Hohmann and Creutzfeldt (1975) found support for the notion of a sensitive period in humans. Individuals with congenital strabismus showed much less IOT than individuals with late onset strabismus. In addition, higher amounts of IOT were associated with better binocular vision. Both groups of researchers place this critical period before 3 years of age. Again, the inference was made that the decrease in IOT and reduced binocular vision reflected a less than normal complement of binocular neurons.

The initial reports of a lack of interocular transfer in strabismics were soon followed by data to the contrary. Wade (1976) was the first to report a consistent presence of IOT in strabismic individuals. He measured the duration of the motion aftereffect in eighteen individuals with a history of childhood strabismus and no appreciable stereopsis. In contrast to Movshon et al. (1972), Mitchell and Ware (1974) and Ware and Mitchell (1974), Wade (1976) found that eleven out of eighteen strabismic individuals showed some transfer of the aftereffect. The remaining seven

strabismics did not experience any IOT.

Wade (1976) tried to account for his results by dividing the groups of strabismic individuals according to the basis of eye alignment. Of the eleven subjects who exhibited transfer, none of these individuals had any remaining misalignment of the visual axes. Six of the seven that failed to show transfer still exhibited a misalignment of the visual axes. However, others have failed to replicate this division among strabismics (Mohn and van Hof-van Duin, 1983).

Hess (1978) has argued that the relationship between IOT and binocularity has been built on a relatively small number of subjects with abnormal binocular function. Unfortunately, Hess only tested 2 strabismics but did show that one subject was capable of mediating normal levels of IOT for a contrast threshold elevation experiment. Selby and Woodhouse (1981) also report that strabismics show normal levels of IOT of the contrast threshold elevation aftereffect. They looked at the contrast sensitivity function for each eye and the amount of IOT as a function of the spatial frequency. Individuals with differing contrast sensitivity functions for each eye showed a lack of transfer at those spatial frequencies. If the eyes showed similar contrast sensitivities, transfer was evident. Selby and Woodhouse (1981) conclude that IOT is dependent on the similarity of the contrast sensitivity functions for each eye.

Other researchers have sought to differentiate strabismics based on their levels of IOT for different aftereffects. Mann (1978) has found that levels of IOT during the TAE are correlated with levels of stereoacuity, but the correlation is not upheld for

the spiral MAE. She suggested that her results were consistent with the notion that the TAE is mediated at the same level as stereopsis. The MAE would presumably be mediated at a different level and this would account for the lack of correlation between IOT and stereoacuity. Unfortunately, other researchers have not found results consistent with this hypothesis (Mohn and van Hof-van Duin, 1983).

Other reasons have been proposed for the differing levels of IOT found in strabismic subjects. Sireteanu, Fronius and Singer (1981) found that stereoblind strabismics show a reduction, or lack of IOT, of the contrast threshold elevation aftereffect, in the central region of the retina. If the stimulus is projected to the periphery, these same subjects exhibit stereopsis and IOT of this aftereffect. Thus, they suggest the reason some strabismics do not show interocular transfer is due to the lack of stimulation of the peripheral retina. Marzi, Antonucci, Pizzamiglio and Santillo (1986) also argue for this distinction between central versus peripheral retina. They suggest that the IOT found during the tilt aftereffect is induced because it naturally stimulates the extrafoveal retina. This separation of peripheral versus central excitation has not been supported by Mohn and van Hof-van Duin (1983); they report a subject who shows peripheral stereopsis but no IOT of the motion aftereffect.

Anderson, Mitchell and Timney (1980) have also found stereoblind individuals capable of IOT of the contrast threshold aftereffect. In contrast, two of these same individuals, from previously published experiments (Mitchell and Ware, 1974), did not show transfer during the suprathreshold tilt or motion aftereffects.

At first glance this may indicate a difference in binocular functioning of strabismics during threshold (CTE) and suprathreshold (MAE and TAE) tasks. Although it has been suggested that strabismics do not show IOT during suprathreshold tasks, but do exhibit transfer for threshold tasks this result has not been obtained consistently. Buzelli (1981) has reported no difference in levels of IOT between normals and stereoblind subjects for the suprathreshold tilt aftereffect. Mann (1978), Wade (1976) and Keck and Price (1982) have also reported groups of strabismics that do show IOT of the motion aftereffect. Therefore, the clear relationship between IOT and binocularity now appears muddled.

Mohn and von Hof-van Duin (1983) tried to clarify the relationship between IOT, stereopsis and binocularity by examining the tilt and motion aftereffects in forty-three subjects with varying degrees of stereopsis. This was the first large scale study to look at both the motion and tilt aftereffects. Their results show quite clearly that, overall, individuals with deficient levels of stereopsis are no different from normals in the amount of IOT exhibited. Completely stereoblind individuals sometimes showed no transfer of the motion aftereffect but did exhibit a positive but significantly reduced tilt aftereffect in comparison to the control group. Thus, Mohn and von Hof-van Duin (1983) failed to confirm the correlation between stereoacuity values and the amount of IOT found by Mitchell and Ware (1974). They suggest that even when individuals do not have any measurable stereopsis, they may still exhibit IOT through the function of binocular cells not involved in stereopsis but capable of mediating IOT. In other words, stereopsis and IOT may be mediated by cells that are both

binocular in function, but not identical.

To date there has been no general agreement about the appropriateness of using IOT as a index of binocularity. The literature reviewed above presents some reasons for the differing amounts of transfer found in individuals with deficient stereopsis. From this review it appears that two issues are of particular interest and require further investigation.

One of the main obstacles to such an agreement may be the variability in the criterion used to classify subjects as stereoblind. There are no established standards for the type or number of tests that should be used to classify such subjects. For example, Movshon et al. (1972) used two tests of stereoacuity to assess stereopsis: random-dot stereograms and the Gulick-Lawson stereogram (Gulick and Lawson, 1976). Anderson et al. (1980) employed a much stricter criterion. Subjects had to fail four tests of stereoacuity. These included simple line stereograms, Julesz Random-dot stereograms, a test for stereopsis deficiency, and the Bausch and Lomb Orthorater assessment of stereoacuity. Mohn and von Hof-van Duin (1983) used six commercially available tests. In comparison, Mitchell and Ware (1974) used an apparatus specifically designed by Mitchell and O'Hagan (1972) to determine stereoacuity values. This allowed them to generate exact values that were not restricted by the floor or ceiling effects of the commercially available stereoacuity tests mentioned above.

The methods of assessment and selection of stereoblind subjects are crucial to the conclusions drawn from the preceding experiments. If strict assessments are not

employed then there is the possibility that subjects with rudimentary stereopsis could be mistakenly categorized as stereoblind, and produce misleading results. More importantly, if the relationship between IOT and stereoacuity forms a continuum, then it is imperative to have a population of individuals with varying degrees of stereopsis, rather than just the presence or absence of stereopsis. Therefore, in addition to normal and stereoblind subjects, it is desirable to have subjects that have rudimentary stereopsis as well as individuals with stereopsis slightly worse than normal.

Another explanation for the variable amounts of IOT concerns the kind of aftereffect used to study binocularity. More than once, the distinction between threshold and suprathreshold aftereffects has been suggested as an answer for the differing levels of IOT. For that matter, this distinction has also been given as a reason for the different sizes of direct, transferred and binocular aftereffects. There has not been any single study that has examined the effect of threshold and suprathreshold aftereffects on the relative sizes of aftereffects, in addition to the amount of interocular transfer by subjects with abnormal binocular function. Mohn and von Hof-van Duin (1983) undertook a large scale study, but they only looked at suprathreshold aftereffects.

The present large scale study sought to accurately determine stereoacuity values in normal and strabismic individuals. Additionally, the amount of IOT found in various aftereffects for both normal and strabismic individuals was evaluated. This design allowed us to comprehensively investigate the three-way relationship between IOT, stereoacuity and binocularity.

Experiment I -- The reliability of interocular transfer

Introduction

Much importance has been placed on the presence or absence of interocular transfer. It is a measure that is commonly used by many researchers, however no one has addressed the question of whether or not it is a reliable measure. One reason for the varying amounts of interocular transfer could be simply that this variable is not particularly reliable. For this reason, Expt I examined the test-retest reliability of this variable for future examination of IOT from just one session.

Most researchers looking at the importance of IOT as an indication of binocularity have typically used only a single testing session for the preferred eye (Mitchell and Ware, 1974; Anderson, Mitchell and Timney, 1980; Wade, 1976; Hess, 1978) or one session for each eye (Movshon, Chambers and Blakemore, 1972; Buzelli, 1981). As an exception, Mohn and von Hof-van Duin (1983) used 4 sessions. If the measure of IOT is not reliable from one session, this could contribute to the lack of a relationship between stereoacuity and IOT. This would also explain the wide ranging IOT values, from 0% to 90%, throughout the literature associated with strabismic subjects. Indeed, Mohn and von Hof-van Duin (1983) report that even the normal subjects exhibit wide ranging values.

The object of the following experiment was simply to determine if IOT could be

considered a reliable measure. If so, then more credence could be placed in the value of IOT from just one session. The tilt aftereffect was used to examine this variable.

Method

Subjects

Seven subjects with normal or corrected to normal vision were tested. None of these subjects participated in any other experiment reported. All subjects exhibited normal levels of stereopsis, and the preferred eye was always used for adaptation.

Apparatus

The same apparatus was used for a number of experiments to follow, so a thorough description will be provided here. Details specific to individual experiments will be reported where appropriate. Sinusoidal gratings were displayed on two Tektronix 608 CRT monitors with green (P31) phosphors. A micro-computer was used to drive a Picasso image generator (Innisfree). Both the psychophysical procedures and the data acquisition were under software control. The space-averaged luminance of each monitor was held constant at 20.0 cd m^{-2} .

The adaptation and test gratings could be varied in orientation, contrast, spatial frequency or relative phase. For the present experiment the spatial frequency of the adaptation and test gratings was 2.5 c deg^{-1} . The contrast for the adapting and test gratings was held constant at .25. All testing took place in a dark room.

The two monitors were viewed simultaneously through an adjustable haploscopic mirror system. The grating could be presented to the right eye, left eye or both eyes.

This was controlled electronically through the computer. A matte black mask with a circular aperture of 5° covered both monitors. The displays contained a 2° central fixation square; one side of each square was constructed to create nonius lines which allowed the subject to maintain fusion.

A combination chin and head rest, placed at a viewing distance of 57 cm, kept the subject's head position stable. A three-button console was used to make responses and to generate the tone that signalled the onset and offset of the stimulus.

Procedure

The experiment was run in 3 phases: baseline, adaptation and post-adaptation testing. A randomly interleaved dual staircase procedure (Cornsweet, 1962) was used to test each of the test conditions. The subject was tested on the adapted and nonadapted eye as well as binocularly. Two starting points for each staircase were used for each condition. In this procedure, a series of response 'crossover' or reversal points defines a staircase. During baseline measurements one staircase began at 1° to the left of vertical and the other began at 1° to the right. The six staircases (2 for each tested eye condition) were run simultaneously, and on a given trial, the staircase was selected randomly. Each session continued until 7 reversals were obtained on each staircase; a staircase was tested only until its quota of reversals was attained.

During the baseline phase, subjects viewed a blank screen for 2 s, followed by a test interval (0.5 s) delimited by two tones. After the second tone, the subject pressed the appropriate button on the response box to indicate if the target appeared to the left

or right of vertical. The data were collected using the aforementioned randomly interleaved staircase procedure. For example, if on one trial the subject perceived the grating as being tilted to the right, then on the next trial of that staircase the orientation was shifted $.7^\circ$ to the left until his response changed to "left" and then the orientation was shifted in $.7^\circ$ steps to the right. The point at which the subject changes his response from "left" to "right" is considered a reversal point.

During the adaptation phase the subject viewed the grating with his preferred eye. The total adaptation time was 120 s and the subject was instructed to keep his eyes moving across the stimulus. The adapting stimulus was a grating tilted 10° to the right of vertical.

After adaptation, a truly vertical grating would appear to be tilted to the left, thus the subject's perceived vertical would be shifted to the right. In order to expedite measurements, the staircase starting points were placed at 3° to the right of vertical and at the true vertical. The testing procedure was similar to baseline but the 2 s blank interval was replaced by 9 s of readaptation to ensure a constant level of adaptation throughout testing. The readaptation and test cycle continued until the required number of reversals were met for each staircase.

To obtain a measure of the subject's perceived vertical before and after adaptation, the average of the last six reversals on each staircase was calculated for the baseline and for the post-adaptation condition. The magnitude of the aftereffect was taken as the difference between the post- and pre-adaptation measures of perceived vertical. In the present experiment each subject completed 10 sessions.

Results and Discussion

Figure 2 shows the individual results of IOT for each subject and each session. From this figure it appears that each subject's level of interocular transfer does vary from one session to another. We used Cronbach's alpha to determine the test-retest reliability of IOT. This measure determines if the amount of IOT found in one session is similar to the amount of IOT in any other session. In other words, the reliability value reflects the correlation between the scores obtained over 10 sessions. The reliability of the task using Cronbach's alpha was .91. This indicates that one session is a good representation. The high reliability value signifies that interocular transfer is not susceptible to random fluctuations from one session to another. We conclude that IOT can be considered a reliable and accurate measure from just one session.

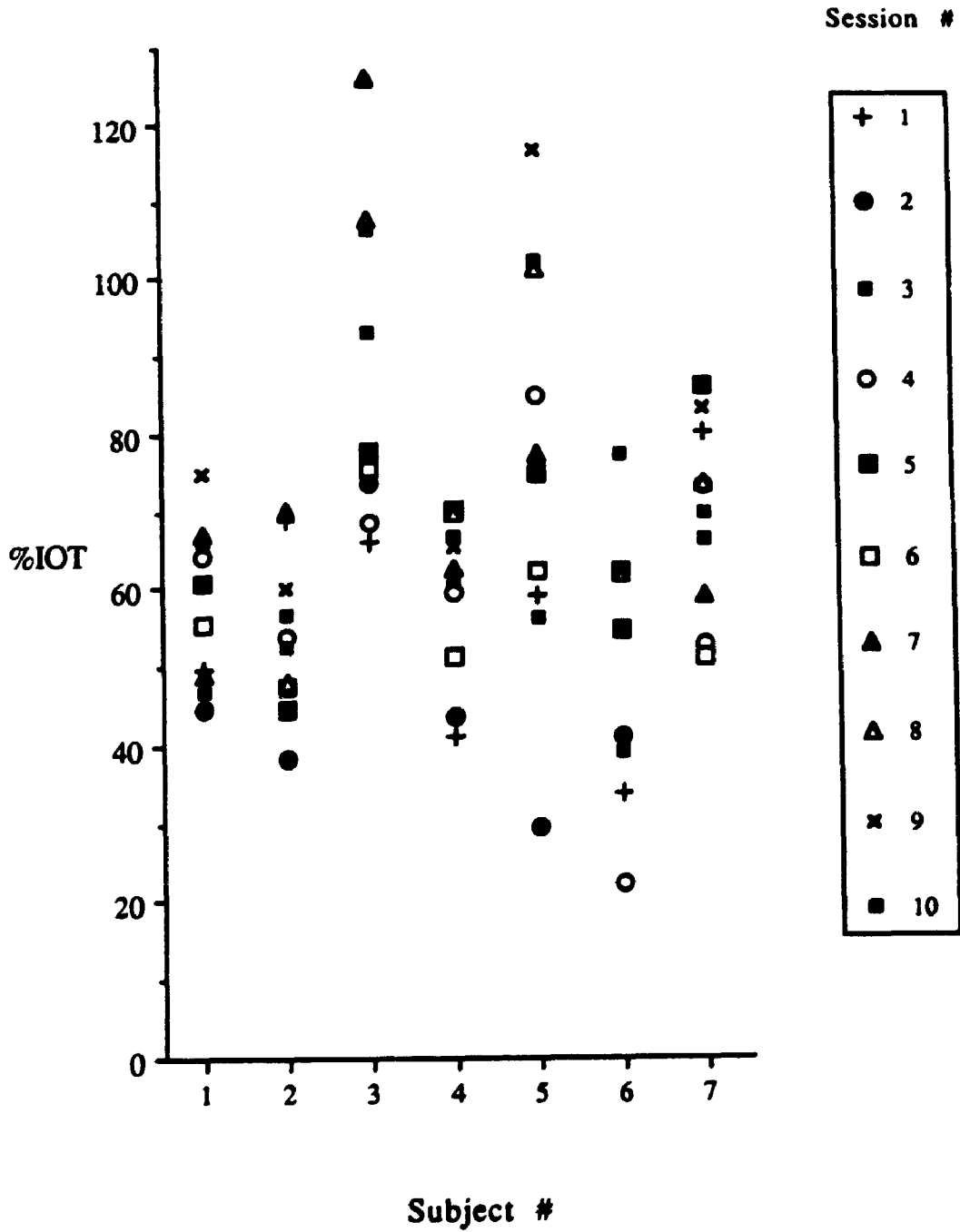
Interocular transfer of different aftereffects

Overview for Experiments II, III, & IV

The present series of experiments was designed to address three issues: 1) Do individuals with reduced stereoacuity demonstrate interocular transfer across a range of different aftereffects? 2) Is there a correlation between stereoscopic depth threshold and IOT? and 3) If stereodeficient individuals do show IOT, is it possible that they lack only a subset of binocular neurons?

Figure 2: The percent of interocular transfer for each subject. Interocular transfer is calculated using the amount of aftereffect in the nonadapted and adapted eyes. Each subject completed 10 sessions of the tilt aftereffect. All subjects had normal vision.

TAE: %IOT for each subject and session



The first two questions will be addressed in all three experiments. The last question will be discussed in Experiments III and IV.

Experiment II -- Motion Aftereffect (MAE)

Method

Subject Selection

A description of the subjects and their performance on stereoacuity tests will be presented in this method section because most of the subjects served in all of the following experiments.

All thirty-nine subjects volunteered to participate in the experiments. They were grouped according to their binocular status. The Normal group was comprised of 20 first year psychology students who were to fulfil a course requirement through participation in a research experiment. They met the specification of normal or corrected to normal vision. A second group of subjects were solicited through posters distributed around campus. They were classified in the Anomalous Early History (A.E.H.) group if they answered "yes" to one or all of the following three statements: i) "You have problems making decisions about objects in depth. eg. difficulties making judgements about the distance of objects." ii) "You had "crossed-eyes" (strabismus) when you were a child. You had surgery on your eyes to correct a "lazy" eye. Or, you presently have strabismus." iii) "You have trouble seeing depth in 3-D movies or a View-Master." Nineteen subjects were recruited in this manner. Subsequent to

this screening procedure the A.E.H. group was broken down into 4 subgroups based on stereoacuity information. A description of their visual history can be found in Table 1.

All of the subjects were naive to the purpose and procedures of the experiment. The subjects ranged in age from 18 to 41 years with a mean of 25 years. Eye preference was determined using a sighting task. Subjects were asked to keep both eyes open and look at a target through a circular aperture in an opaque piece of cardboard held approximately 10 cm from their face. The experimenter determined which eye was used for sighting by recording the eye aligned with, and seen through, the aperture. This task was repeated twice. The preferred eye was always used for adaptation although Wilcox et al. (1990) have shown that the size of the aftereffects are not affected by the eye of adaptation.

Stereoacuity Testing

Three standard clinical tests were used to test stereoacuity: the Titmus Stereotest, Randot Stereotest and Frisby Stereotest. During testing for stereoacuity, subjects were seated at a table fitted with a chin rest to ensure a constant viewing distance of 40cm. During testing for the Randot Stereotest and the Titmus Stereotest the subjects must wear polaroid glasses to separate the images to each eye. The anaglyph is made up of two half-views printed one over the other which results in a perception of depth for a person with normal binocular vision when wearing the polaroid glasses. The depth is created because each half image has an object within it which is shifted in relation to the corresponding area in the other half. One major difference between the

**Table 1: Visual history and stereoacuity results
for the A.E.H. group**

Subject #	Randot/Frisby (sec of arc)	Condition	Age Onset	Treatment Age
1	3000	unequal acuity		
2	40 / 15.4	strabismus		surgery-7 & 28 yrs
3	0	strabismus	birth	surgery-2 & 13 yrs
4	80 / 42.1	unequal acuity		
5	40 / 15.8	monofixation		
6	50 / 16.5	strabismus		surgery-3 yrs
7	200 / 93.4	unequal acuity		
8	0	strabismus		surgery-4 yrs
9	3000	astigmatism		
10	3000	strabismus	birth	surgery- 4 yrs
11	0	strabismus	birth	surgery-2 & 6 yrs
12	0	strabismus	3 yrs	patching
13	40 / 20	strabismus		surgery- 12 yrs
14	40 / 16.1	strabismus	3 yrs	surgery- 7 yrs
15	30 / 29.1	strabismus	birth	patching
16	100 / 60	strabismus	4 yrs	glasses
17	3000	strabismus	3 yrs	patching & surgery 6 yrs
18	0	strabismus	birth	surgery-1 & 7 yrs
19	0	strabismus	2 yrs	patching & glasses

Titmus and Randot is that the objects presented in the Titmus test are recognizable monocularly. The random-dot stereograms of the Randot are not. For this reason, the Titmus Stereotest was used for screening purposes only.

The Titmus Stereotest is made up of several components. One is a large photograph of a housefly with a disparity of 3000 seconds of arc. When viewed with normal binocular vision the wings of the fly appear to be above the plane of the picture. This photograph was used for screening purposes because it allows an examiner to quickly determine if the observer possesses rudimentary stereopsis at 3000 sec of arc. The subject was first asked if the fly appeared to be in depth and then asked to "pinch" the wings of the fly. If subjects could perform this task they were given the Randot Stereotest to determine a stereoacuity value.

The Randot Stereotest is divided into three sections based on disparity values. The first section contains 6 basic shapes, which the subjects must recognize, with a screening disparity of 600 sec of arc. The next section has 3 rows of animal shapes. Within each row, the subjects must identify the animal that appears to be out in front of the picture plane. These disparity values range from 400 to 100 sec of arc. The last section contains 10 patterns ranging from 400 to 20 sec of arc. Within each pattern there are 3 circles and the subject's task is to identify the circle that stands out in depth. If the subject is correct in his identification he progresses to the next and so on until an error is made. At this point, administration of the test is stopped and the stereoacuity value is based on the last correct identification.

A modified version of the Frisby Stereotest was also used. This test consists of a

set of three Plexiglass plates that differ in thickness. Each plate contains four squares of random patterns. In one square, a circle appears to be either behind or in front of the plate, when viewed by a person with normal binocular vision. The third dimension is created by a disparity between the circle and its surround. The circle and its surround are printed on opposite sides of the plate. In the present experiment the Frisby test was modified so that the plates were placed on a motor driven platform that could be activated by the subject. This allowed us to obtain precise measurements of stereoacuity. In the present modification of the Frisby Stereotest, the stereoacuity values ranged from 1000 sec of arc to 7 sec of arc, depending on the plate used and the viewing distance.

The subject's task was to identify the location of the circle that appeared to be out in front or behind the plate. Initially, the thickest plate was moved by the experimenter until the subject detected the circle. If this was accomplished at the farthest viewing point without effort by the subject then the next plate was used. The thinnest plate was used for most subjects. Once the correct plate was chosen it was moved into a range where the subject was just able to detect the circle. From this point on, the movement of the plate was under subject control. The subject was asked to move the plate forward until the circle was apparent. The viewing distance was recorded on 4 trials and 4 separate disparity values were computed. Two of these values were for crossed disparity and 2 for uncrossed disparity. The four values were averaged to yield a final stereoacuity value.

Stereoacuity Results

Normals The average Frisby stereoacuity value for this group was 13.63 sec of arc with a range from 8 to 25 sec of arc. Table 2 shows all the individual values for both the Randot and Frisby Stereotests.

Anomalous Early History Subjects in this group varied widely on their stereoacuity values (refer back to Table 1). Due to the large range, subjects in this group were divided into 4 subgroups based on their Frisby stereoacuity values. The first subgroup was classified as stereoblind since they could not perceive any depth on any of the stereoacuity tests (N=6). The second subgroup possessed rudimentary stereopsis at 3000 sec of arc (N=4). They recognized depth in the Titmus fly but were unable to succeed in any of the other tests. Those individuals whose stereoacuity values were greater than 25 sec of arc but less than 3000 sec of arc (N=4) comprised the third subgroup and those individuals who behaved much like normals with stereoacuity values less than or equal to 25 sec of arc (N=5) comprised the fourth subgroup.

Apparatus

The stimulus used for this experiment was an expanding Archimedes spiral rotating at 110 rpm. It was presented to the subject at a distance of 57 cm. The Michelson contrast of the black lines painted on a white background was over 90%. The spiral subtended an 11° radius with a line width of 1.8°. The room was normally illuminated.

Electronically activated liquid crystal shutters restricted the subject's viewing to

Table 2: Randot and Frisby stereoacuity results for the Normal group.

Subject #	Randot/Frisby (sec of arc)
1	40 / 21.4
2	20 / 8.5
3	30 / 15
4	20 / 10.1
5	50 / 14.1
6	40 / 11.2
7	30 / 9
8	25 / 10.5
9	20 / 6.7
10	50 / 13
11	50 / 15.6
12	20 / 12
13	20 / 15.1
14	20 / 14.9
15	20 / 18.9
16	30 / 12
17	25 / 7.23
18	50 / 24.9
19	20 / 8
20	70 / 20

the left or right eye. The subject viewed the spiral through the shutters while seated at a table fitted with a chin rest.

Procedure

Initially, the subject viewed the spiral with their preferred eye for 60 s. At the end of the adaptation period the spiral stopped and an electronic timer began running. The timer was stopped when the subject reported no more apparent movement.

On alternate trials the adapted and nonadapted eyes were tested. There were 2 trials for each eye. If subjects reported that they could not see any aftereffect in the nonadapted eye, a value of zero was given.

Results

(i) Amount of aftereffect

Figure 3A shows the results of the MAE experiment for the Normal (N=20) group. In this figure, and all of those to follow, the error bars are representative of the standard error. It is clear that the magnitude of the adapted monocular effect was larger than the nonadapted eye. A t-test confirmed this observation. There was a significant difference ($t(19)=4.84$, $p<.001$) in the duration of motion aftereffect between the adapted eye (M=16.18 s) and the nonadapted eye (M=4.79 s).

The results for the entire Anomalous Early History (A.E.H.) group (N=19) are shown in Figure 3B. This group also shows a significant difference ($t(18)=5.64$, $p<.001$) between the adapted (M=19.59 s) and nonadapted eye (M=8.26 s).

Figures 4A, 4B, 4C, and 4D graph the findings for the four subgroups of the A.E.H. group. The group with no stereopsis (Fig. 4A) displays a very small (M=.92

Figure 3: This figure plots the results from monocular adaptation to a moving spiral. The duration of the motion aftereffect is plotted for both the adapted and nonadapted eyes.

Figure 3A: Normal group

Figure 3B: A.E.H. group

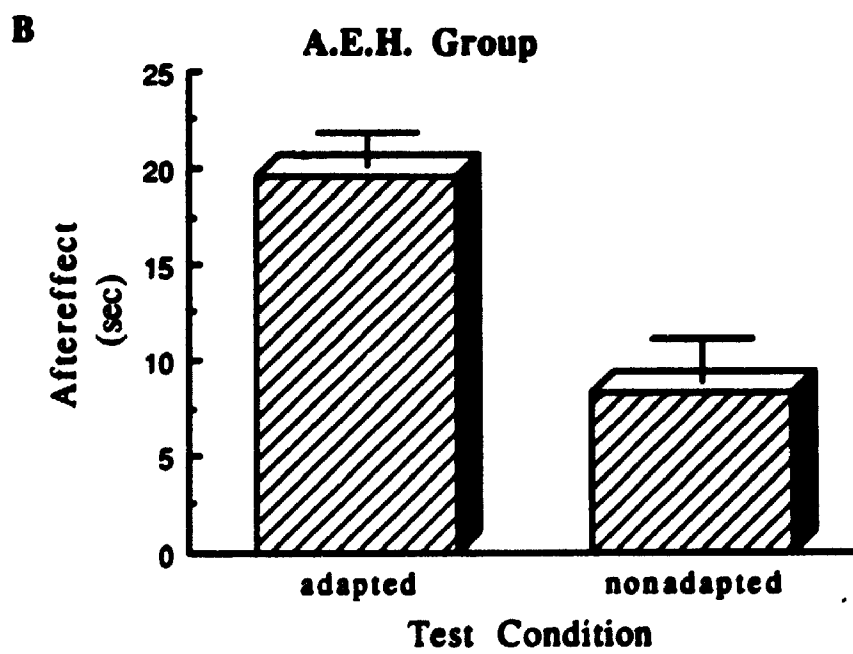
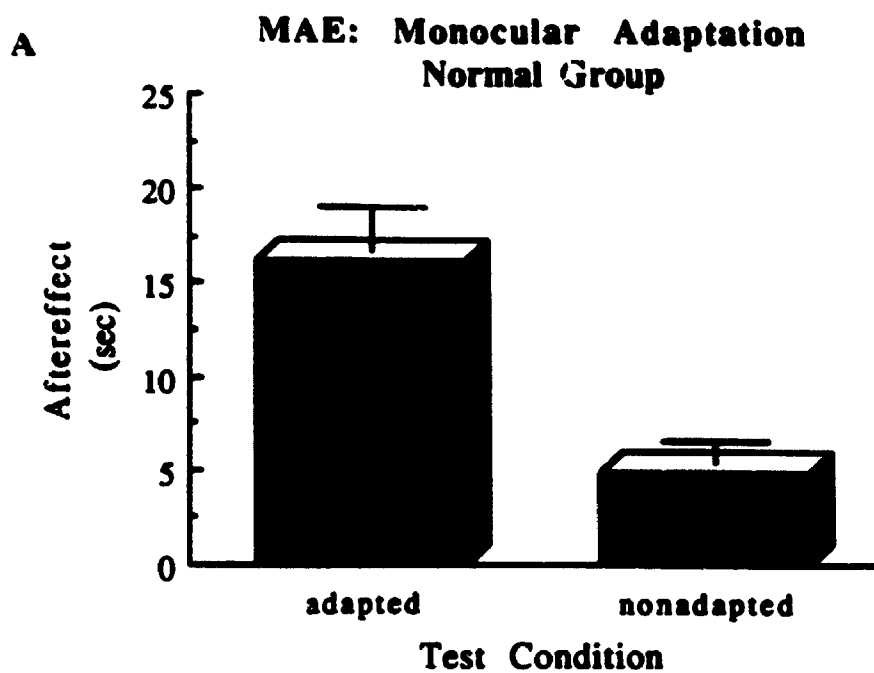


Figure 4: This figure plots the results from monocular adaptation to a moving spiral. The duration of the motion aftereffect is plotted for both the adapted and nonadapted eyes.

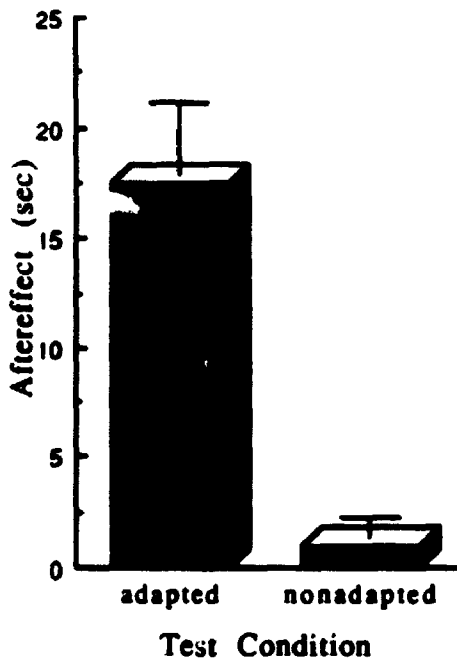
Figure 4A: A.E.H. Stereoblind subgroup

Figure 4B: A.E.H. "3000" subgroup

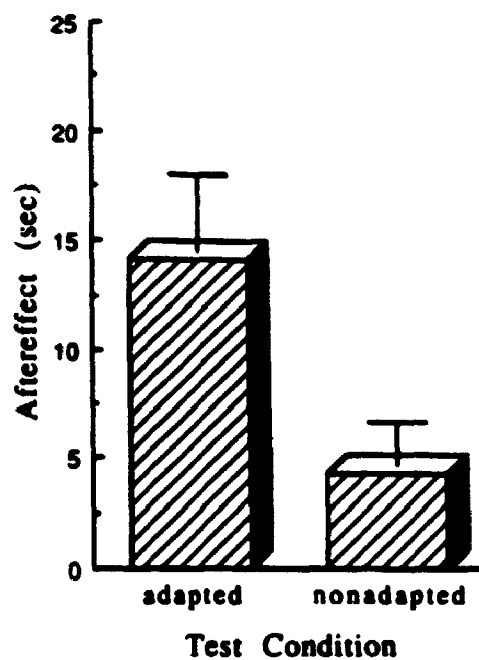
Figure 4C: A.E.H. " >25 " subgroup

Figure 4D: A.E.H. " ≤ 25 " subgroup

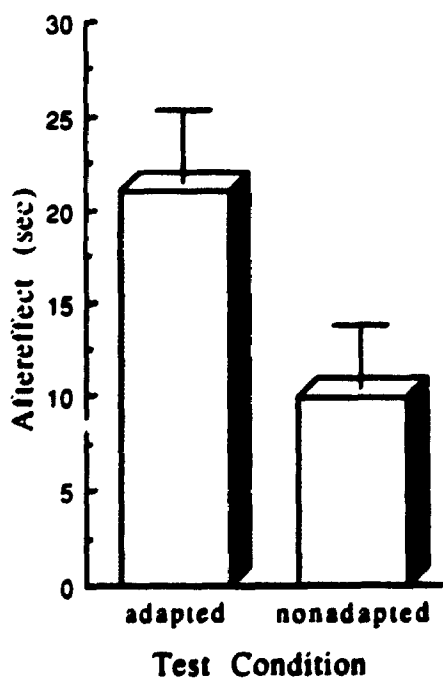
A Stereoblind Subgroup



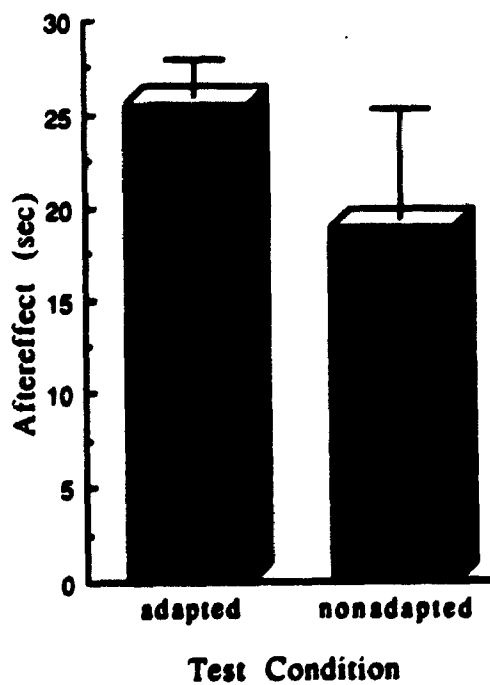
B "3000" Subgroup



C ">25" Subgroup



D "<=25" Subgroup



s) duration of aftereffect in the nonadapted eye which is significantly different from the adapted eye ($M=17.44$ s) ($t(5)=4.35$, $p<.01$). Although some of the other subgroups appear to have a larger adapted aftereffect, there were no significant differences in the duration of aftereffect between the adapted and nonadapted eye in the other 3 subgroups.

(ii) Amount of IOT and its relation to stereoacuity

Figure 5A shows the percent of IOT for both subject groups. A t-test revealed no overall differences in the amount of IOT for the Normal ($M=30.58\%$) versus the A.E.H. ($M=38.37\%$) group ($t(37)=.71$, $p=.68$). However, a one-way ANOVA did reveal a difference among the 4 A.E.H. subgroups ($F(3,15)=4.99$, $p<.05$). Figure 5B plots the percent of IOT for each subgroup. Post-hoc comparisons with Tukey's HSD reveal that the stereoblind subgroup ($M=8.99\%$) showed a significantly lower amount of IOT in comparison to the " ≤ 25 " subgroup ($M=71.3\%$). However, 5 of the 6 in the stereoblind subgroup showed a complete absence of transfer.

Figure 6 plots the percentage of interocular transfer as a function of stereoacuity. No relationship is apparent from these results ($r=-.25$, $p=.18$).

Experiment III -- Tilt Aftereffect (TAE)

As mentioned previously, in addition to the first two questions regarding IOT, the next two experiments also address the additional question about the binocular organization of individuals with an anomalous early visual history. During the testing for these two aftereffects, we were able to introduce a third test condition: a binocular

Figure 5: Percent of interocular transfer for the motion aftereffect. This value is calculated using the amount of aftereffect in the nonadapted and adapted eyes.

Figure 5A: This figure shows the percent of interocular transfer for the Normal and A.E.H. groups.

Figure 5B: This figure shows the percent of interocular transfer for all four subgroups of the A.E.H. group.

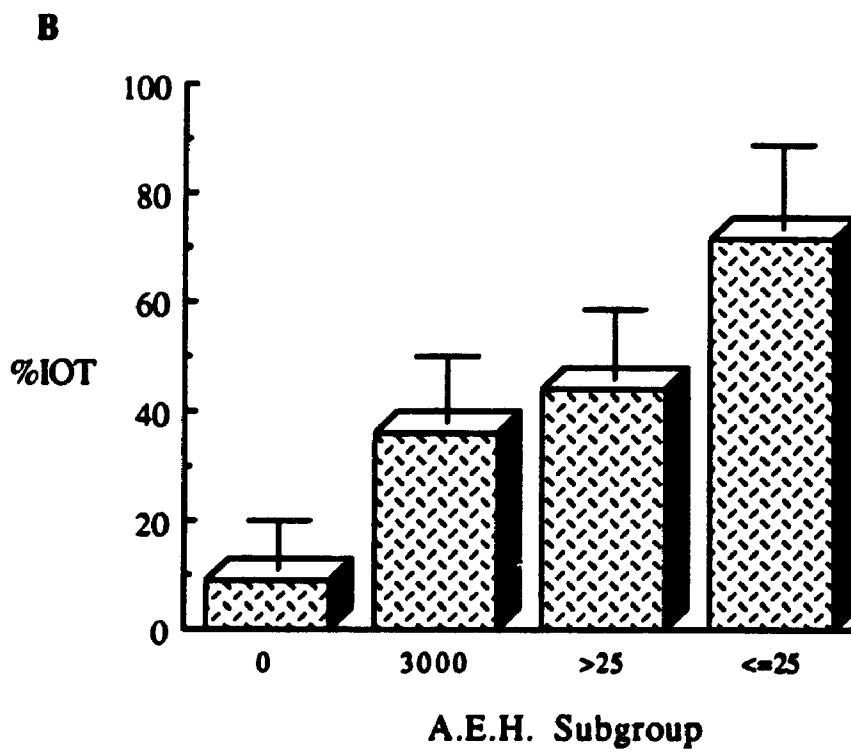
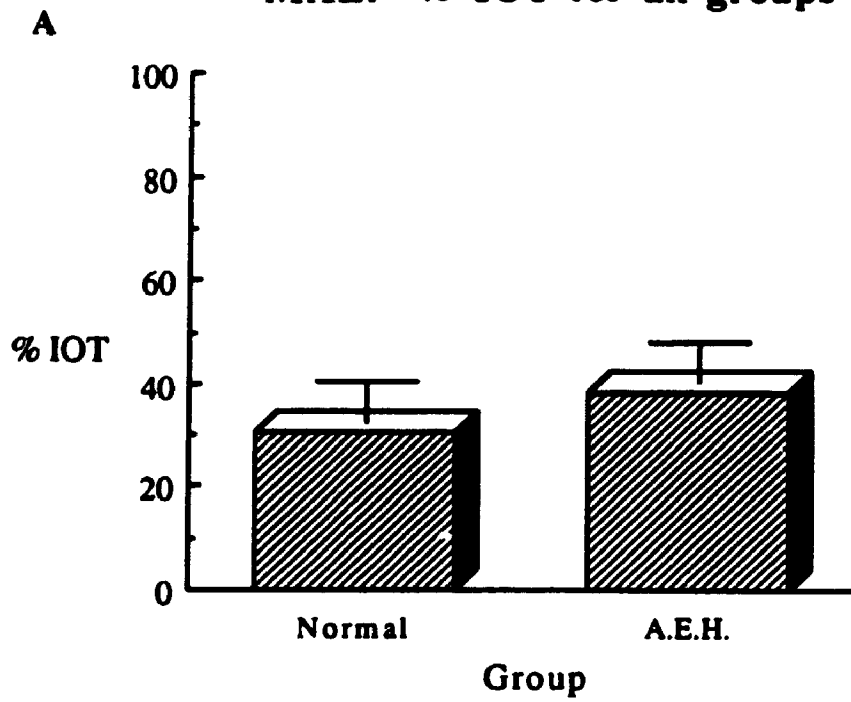
MAE: % IOT for all groups

Figure 6: This figure plots the percent of interocular transfer during the motion aftereffect. The percent of interocular transfer is plotted individually for each subject depending on their level of stereoacuity. However, if more than one subject has the same percent of interocular transfer, these values are represented by only one point.

test. The relative sizes of the adapted, transferred and binocular aftereffects will help to determine the organization of binocular channels in individuals with varying levels of stereopsis. If a four channel model is assumed for individuals with normal binocular functioning, the adapted monocular effect should be larger than the transferred and binocular aftereffect (refer back to Figure 1B and earlier text for logic). The binocular and transferred aftereffects should be equivalent.

However, in the case of those subjects with anomalous early history several possibilities exist. It could be the case that these individuals possess only one binocular channel, and not two, for a total of three channels. In this instance, the adapted monocular effect would still be the largest, but the binocular aftereffect would be expected to be larger than the transferred effect (see Figure 1A). If, on the other hand, these individuals do not possess any functional binocular neurons, the relative size of aftereffects would be a reflection of just two monocular channels. In this case, there would be no transferred (IOT) effect and the adapted monocular effect would be greater than the binocular aftereffect.

Method

The same thirty-nine subjects participated in this experiment. The apparatus and procedure was identical to Expt I. Each subject completed only a single session.

Results

(i) Amount of Aftereffect

Figure 7A shows the results for the Normal group. The aftereffect in the adapted eye appears to be greater than the nonadapted or binocular condition. A repeated measures ANOVA revealed that the amount of aftereffect differed depending on the eye being tested ($F(2,38) = 15.13, p < .01$). Post hoc comparisons, using the Tukey procedure, indicated that the adapted eye condition ($M=3.77^\circ$) was significantly higher ($p < .05$) than both the nonadapted eye ($M=2.50^\circ$) and the binocular condition ($M=2.98^\circ$). The nonadapted and binocular conditions did not differ significantly.

Figure 7B reveals a similar pattern for the A.E.H. group. Again, the amount of aftereffect differed depending on the eye being tested ($F(2,36)=22.32, p < .01$). Tukey's HSD indicated the adapted eye condition ($M=3.28^\circ$) was significantly higher ($p < .05$) than the nonadapted eye condition ($M=1.66^\circ$), but not significantly different from the binocular condition ($M=2.74^\circ$). In this case, the amount of aftereffect in the binocular condition was significantly higher than in the nonadapted condition.

Figures 8A, 8B, 8C & 8D show the pattern of results for the 4 subgroups of A.E.H. group. A repeated measures ANOVA was run for each subgroup. If any significance was found, Tukey's HSD was calculated to determine the differences between conditions. The stereoblind subgroup in Figure 8A show the same pattern as the whole A.E.H. group ($F(2,10)=14.17, p < .01$). The amount of aftereffect in the nonadapted eye was significantly less ($p < .05$) than both the adapted and binocular conditions whereas the latter two did not differ. Figure 8B shows somewhat of a

Figure 7: This figure plots the results of monocular adaptation to a tilted grating. The amount of tilt aftereffect is plotted for the adapted eye, the nonadapted eye and a binocular condition. These values were calculated using the perceived vertical measurements found before and after adaptation.

Figure 7A: Normal group

Figure 7B: A.E.H. group

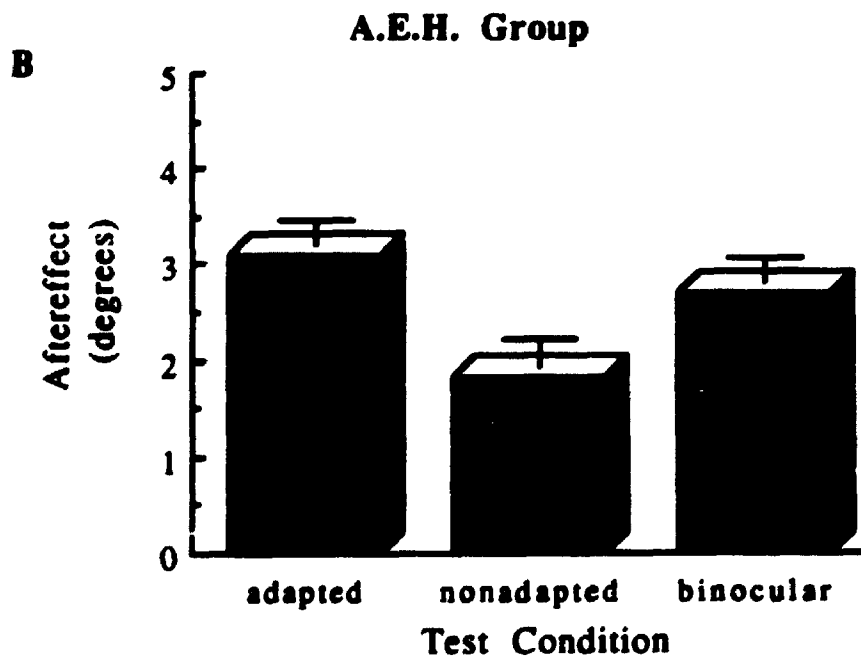
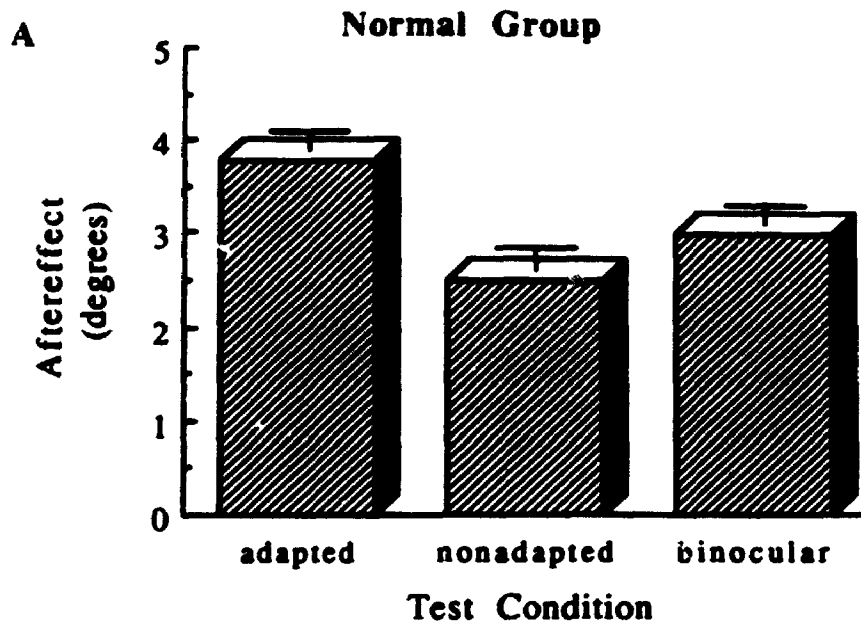
TAE: Monocular Adaptation

Figure 8: This figure plots the results of monocular adaptation to a tilted grating. The amount of tilt aftereffect is plotted for the adapted eye, the nonadapted eye and a binocular condition. These values were calculated using the perceived vertical measurements found before and after adaptation.

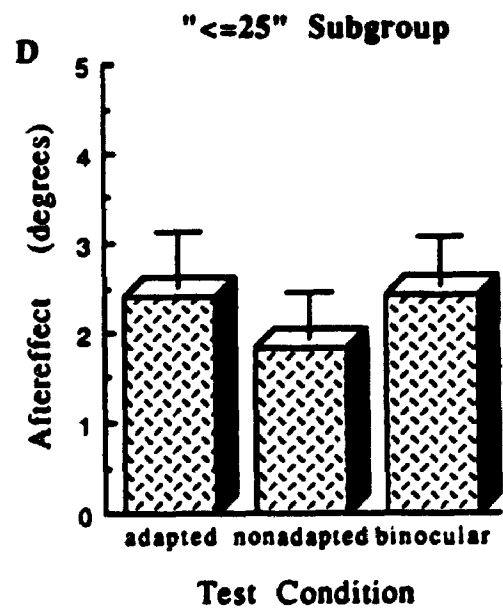
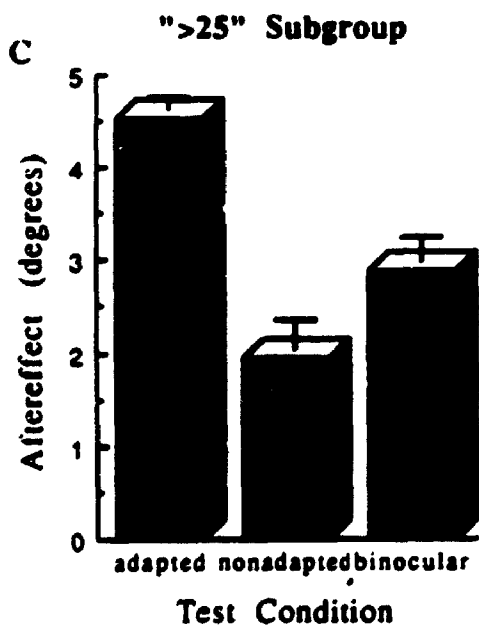
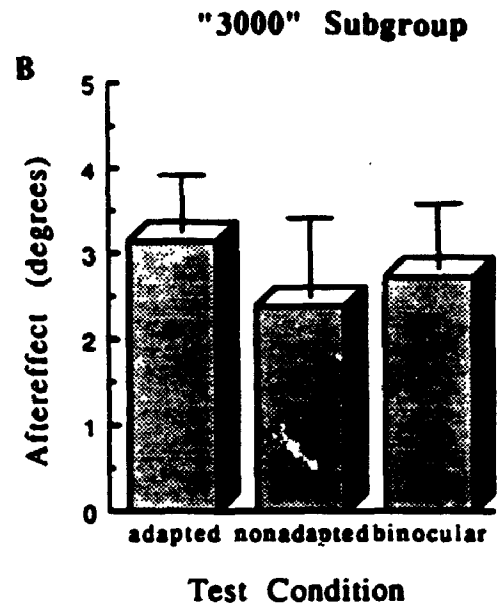
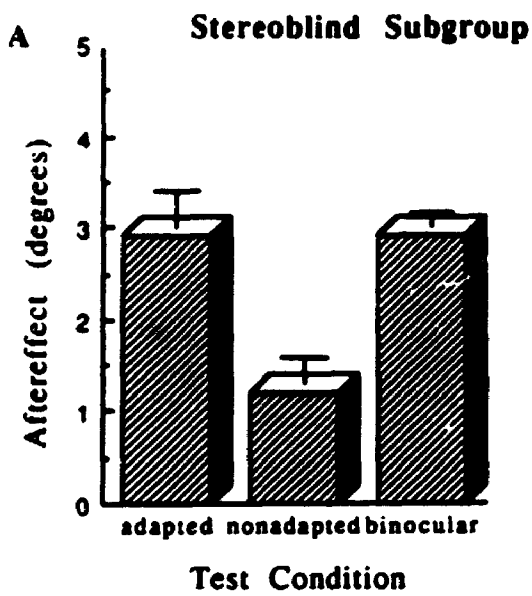
Figure 8A: A.E.H. Stereoblind subgroup

Figure 8B: A.E.H. "3000" subgroup

Figure 8C: A.E.H. " >25 " subgroup

Figure 8D: A.E.H. " ≤ 25 " subgroup

TAE: Monocular Adaptation



similar pattern of results for the "3000" subgroup, but the amount of aftereffect did not differ across the conditions tested ($F(2,6) = .61, p = .576$). The ANOVA for the subgroup of A.E.H. shown in Figure 8C (" >25 ") was significant ($F(2,6) = 14.58, p < .01$). This is the only subgroup that displays a significant difference ($p < .05$) between the amount of aftereffect in the adapted eye and the binocular condition. In addition, the amount of aftereffect in the nonadapted eye was significantly less than that in the adapted and binocular condition. The pattern of results for the last subgroup (" ≤ 25 ") are shown in Figure 8D ($F(2,8) = 6.63, p < .05$). Post-hoc tests revealed that the amount of aftereffect in the nonadapted eye was significantly ($p < .05$) lower than in the adapted eye. The binocular condition fell between the two other conditions but did not differ significantly from either.

(ii) Amount of IOT and its relation to stereoacuity

Figure 9A shows the amount of IOT for both groups. There was no overall difference in the amount of IOT between the Normal ($M = 69.21\%$) and A.E.H. ($M = 52.92\%$) group ($t(37) = 1.63, p = .10$).

Figure 9B shows the four subgroups of the A.E.H. group. Although the "3000" subgroup shows a large amount of transfer, a one-way ANOVA reveals that the amount of IOT does not vary significantly among these 4 subgroups ($F(3,15) = 1.19, ns$).

Figure 10 plots the relation between stereoacuity and the percent of IOT. There does not appear to be any consistent relationship between these two variables and no significant correlation exists ($r = -.34, p = .065$).

Figure 9: The percent of interocular transfer for the tilt aftereffect. This value was calculated using the amount of aftereffect in the nonadapted and adapted eyes.

Figure 9A: This figure shows the percent of interocular transfer for the Normal and A.E.H. groups.

Figure 9B: This figure shows the percent of interocular transfer for all four subgroups of the A.E.H. group.

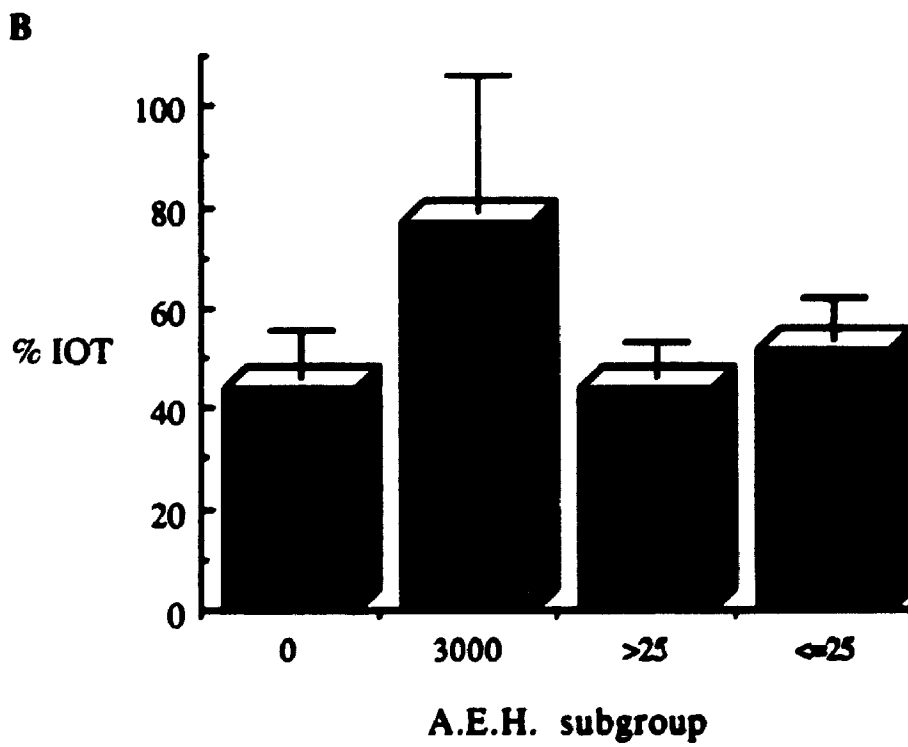
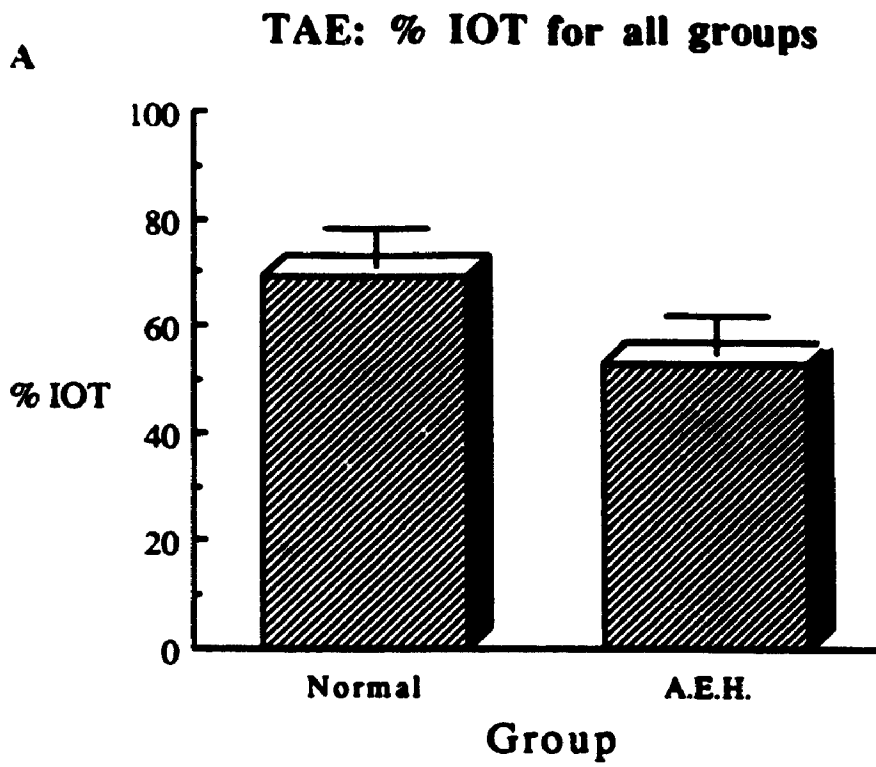
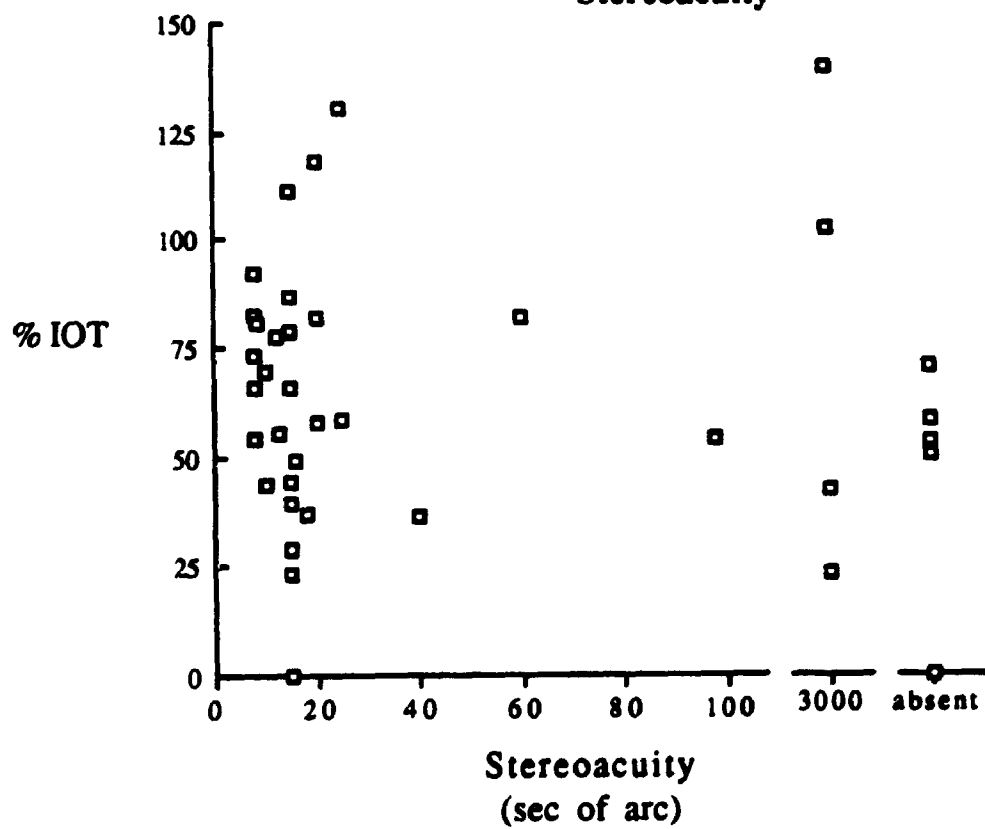


Figure 10: This figure plots the percent of interocular transfer during the tilt aftereffect. The percent of interocular transfer is plotted individually for each subject depending on their level of stereoacuity.

TAE: Percent Transfer as a function of Stereoacuity



Experiment IV -- Contrast Threshold Elevation (CTE)

Method

Subjects and Apparatus

Seventeen subjects from the Normal group and fourteen subjects from the Anomalous Early History (A.E.H.) group participated in this experiment. The others were not available. The apparatus used to generate the stimuli, and to store the data, was the same as that described in the TAE experiment. The grating was kept vertical with a spatial frequency of 2.5 c deg^{-1} .

Procedure

Pre- and post-adaptation thresholds were measured in a similar fashion to those for the TAE with the following exceptions: Instead of starting the staircases at predetermined levels, an approximation of the subject's threshold was obtained prior to running the dual interleaved staircases. Initially, contrast was set clearly above threshold. On subsequent trials the contrast was reduced in 6 dB steps until 2 reversals had occurred. An estimate of the approximate threshold was calculated from the average of these reversals. This value, $\pm 2 \text{ dB}$ was used to start the two staircases for the baseline measurements. In the dual interleaved staircase the step size was set at 2 dB.

Baseline measures of contrast threshold were followed by monocular adaptation with the preferred eye to an identical grating set at a contrast of .25. Adaptation was for 120 s and then a final set of post-adaptation threshold measurements were taken.

The top-up time before each post-adaptation measure was set at 9 s.

The final baseline and adaptation threshold values were calculated separately using the last 6 reversal points. Threshold elevation was taken as the ratio of post-adaptation to baseline contrast thresholds.

Results

(i) Amount of aftereffect

Figure 11A shows the pattern of results for the Normal group. A repeated measures ANOVA revealed that the threshold elevation differed depending on the eye being tested ($F(2,32)=30.04, p < .01$). Using the post-hoc Tukey procedure it was found that the aftereffect for the adapted eye ($M=3.02$) was significantly ($p < .05$) higher than both the nonadapted eye ($M=1.76$) and the binocular condition ($M=1.94$). The nonadapted and binocular conditions did not differ significantly.

Figure 11B shows a similar pattern of results for the A.E.H. group although these differences did not attain statistical significance ($F(2,26)=2.12, p = .14$).

Figures 12A, 12B, 12C & 12D show the results for the four subgroups of the A.E.H. group. In all four subgroups there was no significant difference in the amount of aftereffect between the different eye conditions being tested.

(ii) Amount of IOT and its relation to stereoacuity

Figures 13A & 13B plot the amount of IOT for all subject groups. No significant difference was found in the amount of IOT between the Normal group ($M=61.47\%$)

Figure 11: This figure plots the results of monocular adaptation to a high contrast grating. The contrast threshold elevation ratio is plotted for the adapted eye, the nonadapted eye and the binocular condition. The ratio was calculated using the post-adaption and baseline threshold values.

Figure 11A: Normal group

Figure 11B: A.E.H. group

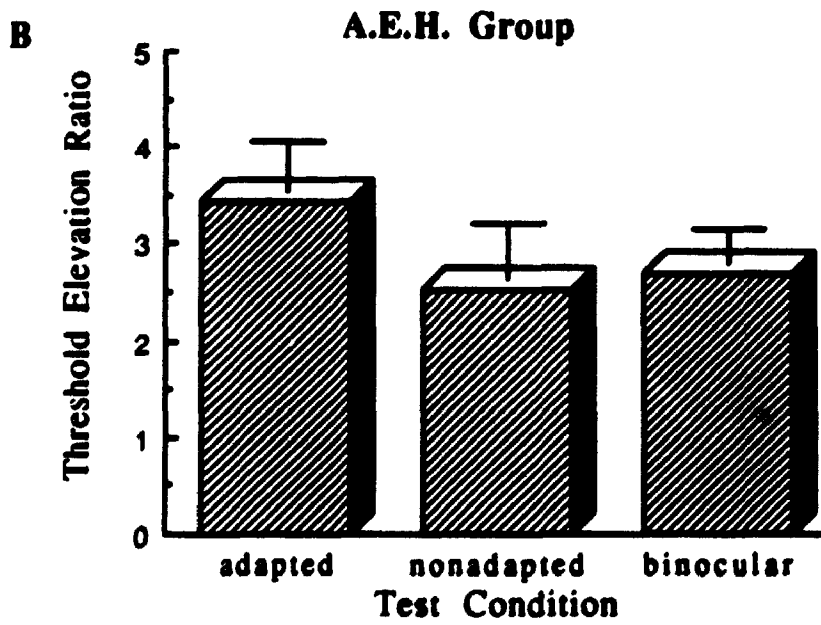
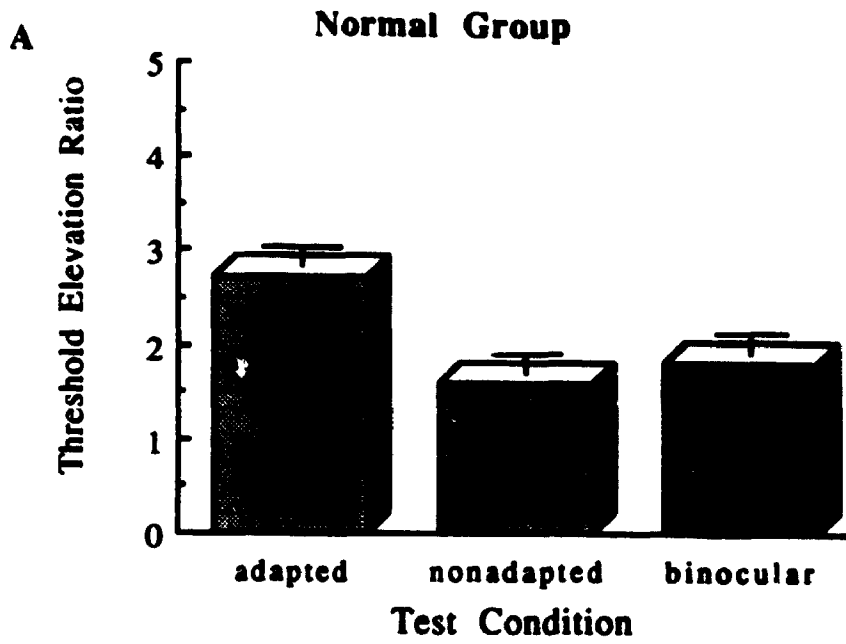


Figure 12: This figure plots the results of monocular adaptation to a high contrast grating. The contrast threshold elevation ratio is plotted for the adapted eye, the nonadapted eye and the binocular condition. The ratio was calculated using the post-adaption and baseline threshold values.

Figure 12A: A.E.H. Stereoblind subgroup

Figure 12B: A.E.H. "3000" subgroup

Figure 12C: A.E.H. ">25" subgroup

Figure 12D: A.E.H. " ≤ 25 " subgroup

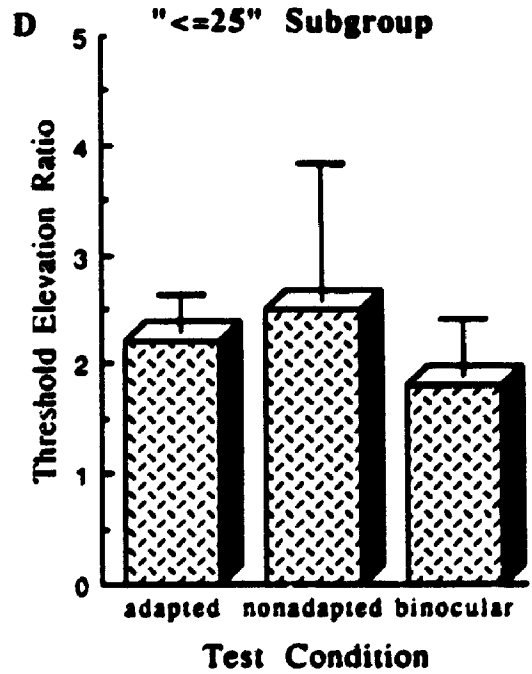
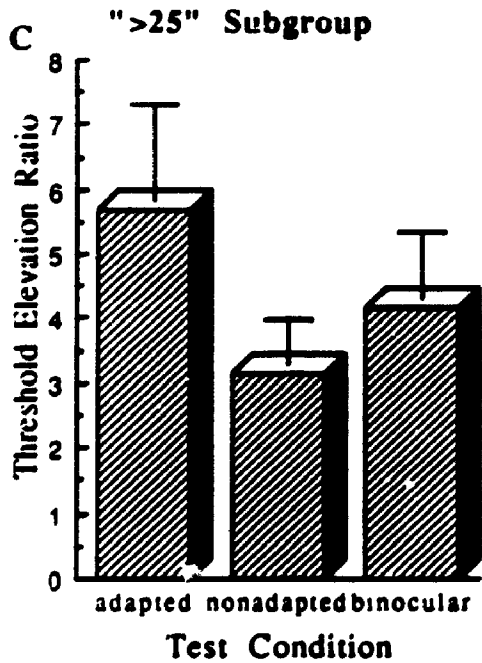
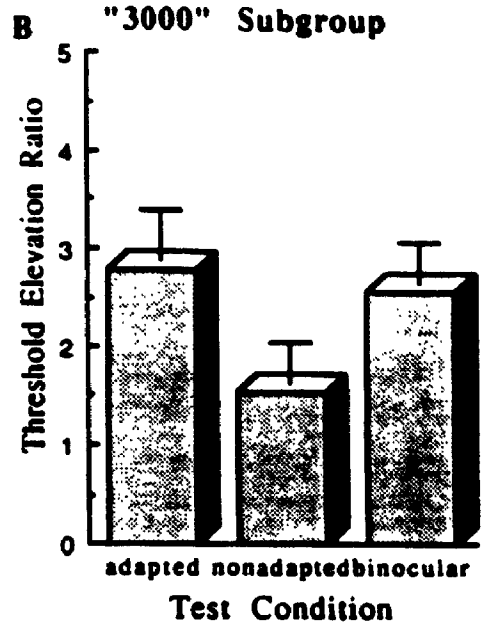
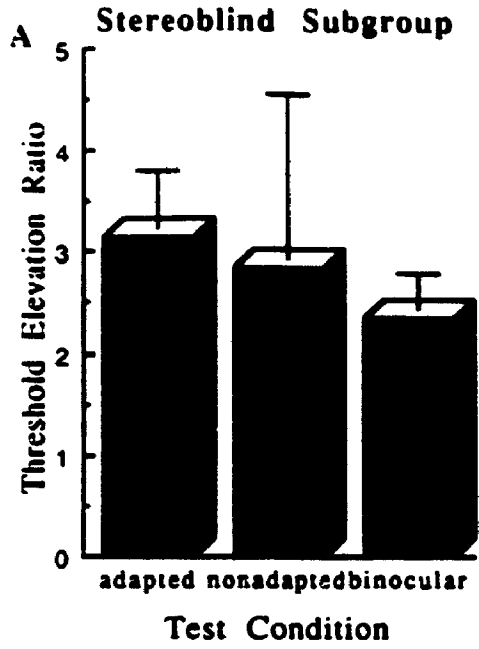
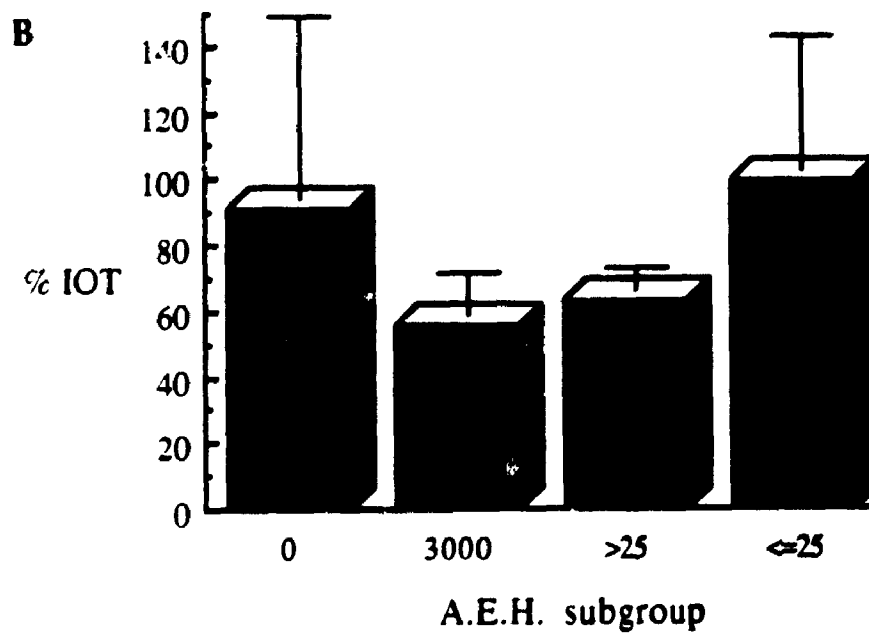
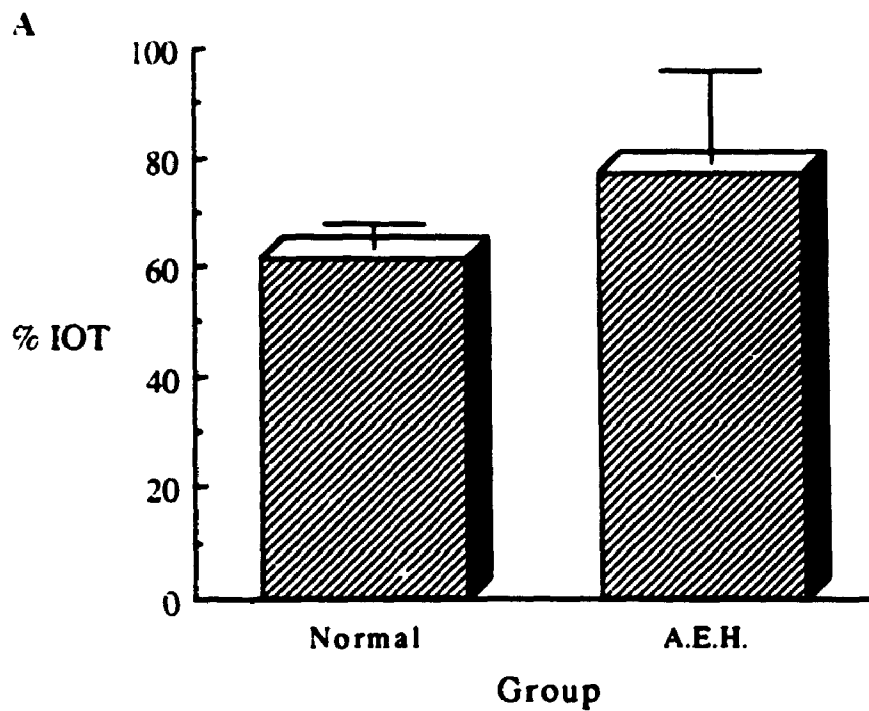


Figure 13: The percent of interocular transfer for the contrast threshold elevation experiment. This value was calculated using the amount of aftereffect in the nonadapted and adapted eyes.

Figure 13A: This figure shows the percent of interocular transfer for the Normal and A.E.H. groups.

Figure 13B: This figure shows the percent of interocular transfer for all four subgroups of the A.E.H. group.

CTE: % IOT for all groups



and the A.E.H. group ($M=77.32\%$) ($t(30)=.99$, $p=.40$). Nor were any differences in the amount of IOT found between the A.E.H. subgroups ($F(3,13)=.32$, $p=.81$). In fact, it is the stereoblind subgroup that show a large amount of transfer to the nonadapted eye ($M=91.26\%$).

Figure 14 shows the relationship between interocular transfer and stereoacuity. As in the last two experiments, a significant correlation did not exist between IOT and stereoacuity ($r=.12$, $p=.52$) during the contrast threshold elevation experiment.

Overview of IOT found during MAE, TAE, & CTE

No relationship was found between stereoacuity and IOT in any of the 3 aftereffect experiments. The following analyses examined the possibility that interocular transfer varies as a result of the type of aftereffect. An additional repeated measures ANOVA grouping all results from the 3 experiments indicated that IOT did vary as a function of the type of aftereffect ($F(2,60)=6.38$, $p<.05$). Post hoc tests, using the Tukey procedure ($p<.05$), showed that the percent of IOT for the MAE ($M=36.5\%$) experiment was significantly lower than both the TAE ($M=60.2\%$) and CTE ($M=68.6\%$). No differences emerged to distinguish the two main subject groups. In other words, all subjects in the Normal and A.E.H. groups showed a smaller amount of IOT for the motion aftereffect.

Figure 15 shows the percent of IOT as a function of stereoacuity for all three aftereffects. It is apparent that no relationship exists between stereoacuity and interocular transfer when all the data from the 3 aftereffects is combined. A multiple

Figure 14: This figure plots the percent of interocular transfer during the contrast threshold elevation experiment. The percent of interocular transfer is plotted individually for each subject depending on their level of stereoacuity.

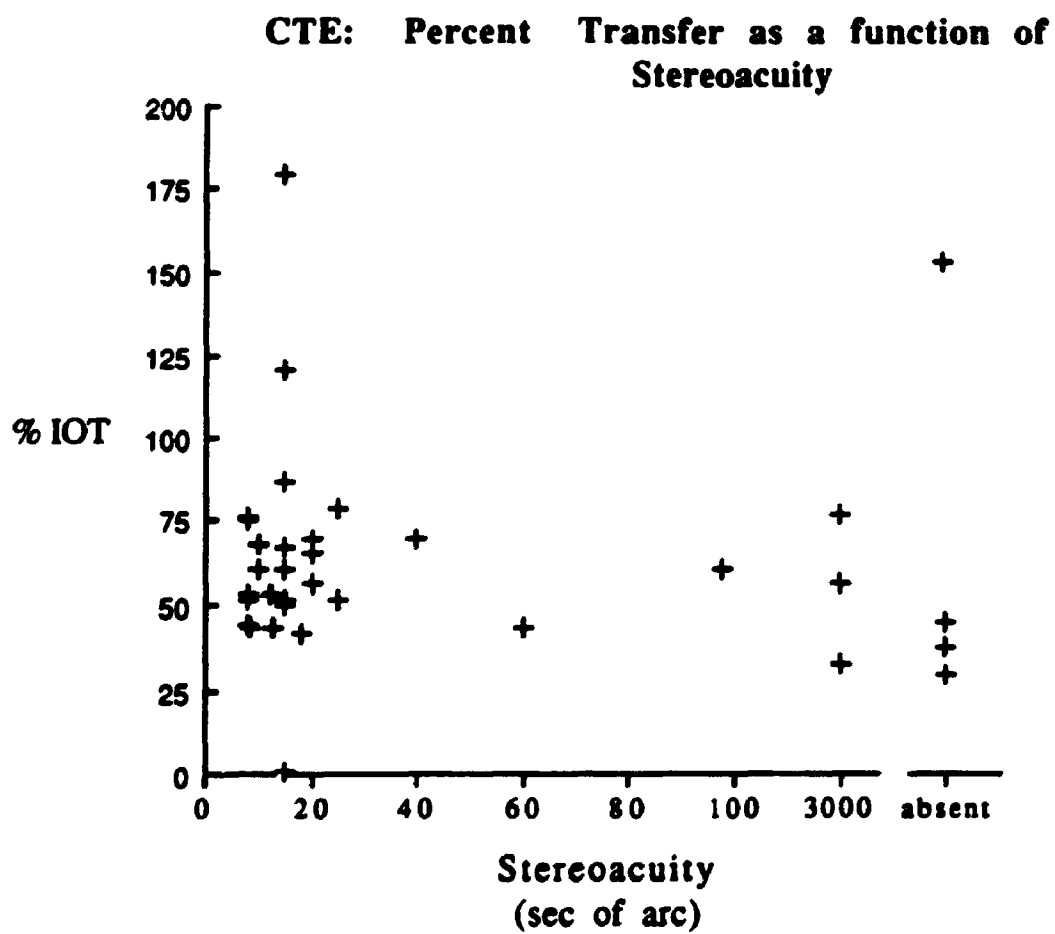
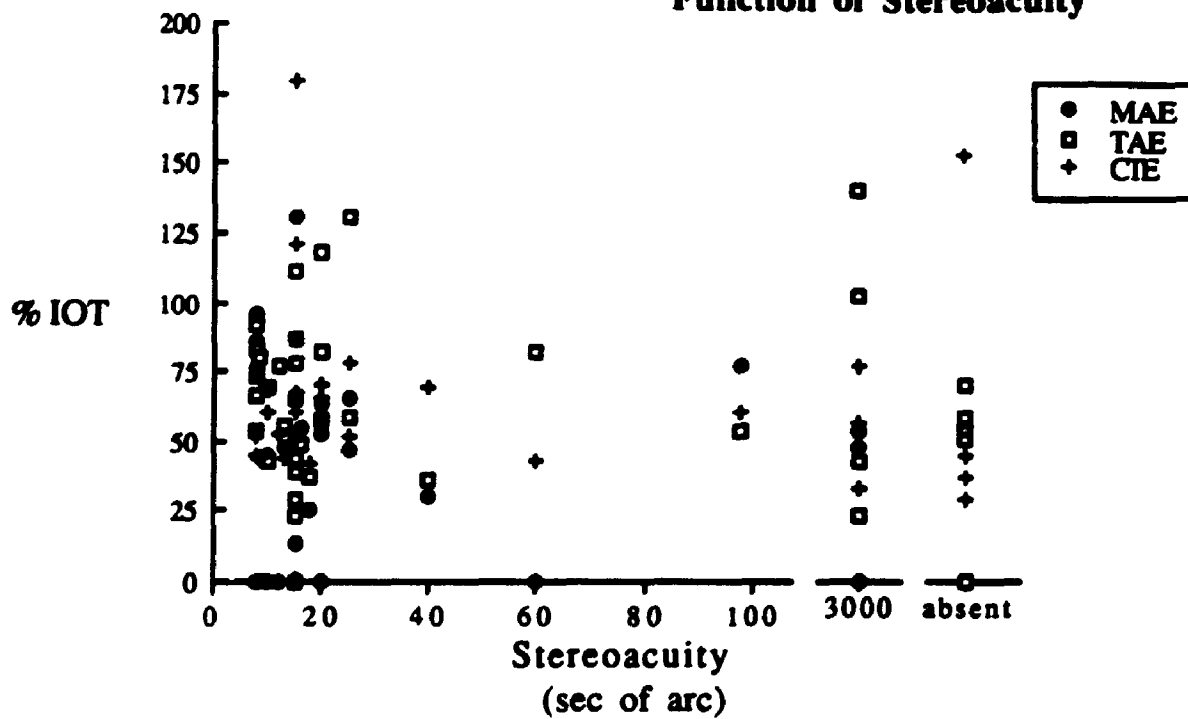


Figure 15: This figure plots the percent of interocular transfer for all three aftereffect experiments (Expt. II, III & IV). The percent of interocular transfer is plotted individually for each subject, and each aftereffect, depending on their level of stereoacuity.

CTE, TAE, & MAE: Percent Transfer as a Function of Stereoacuity



correlation was performed ($R = .37$, $F(3,27) = 1.41$, $p = .26$) which confirms that there is no relationship between stereoacuity and interocular transfer even when all the data points from each aftereffect study are taken into account.

Additional analyses looked at the possibility that the amount of IOT found in one type of aftereffect would be related to the amount of IOT found during another type of aftereffect. However, no significant correlations were found among all combinations of the three different aftereffects (MAE vs TAE, $r = .328$, $p = .07$; MAE vs CTE, $r = .041$, $p = .825$; TAE vs CTE, $r = -.297$, $p = .105$).

Discussion

The outline of this discussion follows the three questions set out at the beginning of this chapter: 1) Do individuals with reduced stereoacuity demonstrate interocular transfer across a range of different aftereffects? 2) Is there a correlation between stereoscopic depth threshold and IOT? and 3) If stereodeficient individuals do show IOT, is it possible that they lack only a subset of binocular neurons? I shall discuss each of these in turn.

Interocular Transfer and Stereodeficiency

With only a few exceptions, the earlier studies of IOT and stereodeficiency measured IOT on only a single aftereffect. The results from all three aftereffect experiments in this study reveal that there is no evidence of a difference between the Normal and the A.E.H. group. The A.E.H. group does in fact, show an amount of

IOT that is considered normal. Even the amount of IOT found for subjects in each A.E.H. subgroup reveals similar findings.

The results from the MAE study provide the only set of data that suggests that a *stereoblind* subject may not exhibit normal amounts of IOT. This subgroup of strabismics with no stereopsis shows minimal (9.0%) amounts of IOT during the MAE. In fact, five of the six subjects in this group showed a complete absence of transfer. On its own, this could be interpreted to reflect a paucity of binocular neurons. It is important, however, to look at this same subgroup's performance on the TAE and CTE since there was no correlation between the percent of IOT in one aftereffect and another. This stereoblind subgroup shows a moderate (43.9%) amount of transfer during the TAE and a large (91.3%) amount of transfer during the CTE experiment. Since interocular transfer implies the presence of binocular neurons, it is clear from these latter results that even stereoblind subjects maintain binocular neurons capable of mediating interocular transfer. Nevertheless, some explanation is required for the results from the MAE.

The low levels of transfer found during the MAE are not unique to the group of stereoblind individuals; all groups and subgroups showed relatively low levels of transfer. Even the Normal group showed low levels of IOT (30.6%) during the MAE. These low values are in contrast to the values stated in the literature which report values between 50 to 80% IOT to be the norm. It is only the " ≤ 25 " A.E.H. subgroup that displays a percentage of transfer much like one would expect from a Normal group. Wade, Swanston and de Weert (in press) have commented on

the variability of aftereffect size during the MAE. They report values from the literature which range considerably depending on the stimulus used and the aftereffect measure. It is conceivable that some combination of the stimulus used and the measuring of the aftereffect in the present study was responsible for the low levels of transfer and not a lack of binocular neurons. Therefore, we are left with the impression that the results from the MAE are still in keeping with the presence of some type of binocular neuron.

Correlation between Stereoscopic Depth Threshold and IOT

In some of the studies mentioned previously in the Introduction, careful measurements of subjects' stereoscopic abilities were not obtained. As a result, it would be difficult to make an unequivocal statement about the relationship between interocular transfer and stereopsis. In the present experiment, great care was taken to examine stereoacuity therefore, it was possible to make a definitive statement regarding stereoscopic ability. In addition, the range of stereoscopic abilities found among individuals in the A.E.H. group allowed us to evaluate a possible correlational relationship.

All three aftereffects tested in the present series of experiments revealed no indication that transfer may vary according to the stereoscopic depth threshold. We are left with the conclusion that there is no evidence of a relationship between IOT and stereoscopic ability. Individuals with relatively poor stereopsis can, and do, show normal amounts of transfer.

The results from the present set of experiments clearly show that subjects with anomalous early visual history are capable of IOT for the aftereffects tested. These findings reinforce and extend the results found by Mohn and van Hof-van Duin (1983). They found that stereoblind individuals showed IOT of the motion and tilt aftereffect. The present study found similar results for the motion, tilt *and* contrast threshold experiments. This implies that although these subjects may not possess a full complement of binocular neurons, the binocular neurons remaining are sufficient enough to handle transfer of information from one eye to the other. It is perfectly reasonable to suggest that these subjects possess binocular neurons responsive to either-eye stimulation, but lack a second type of binocular neuron responsive to simultaneous stimulation.

Amount of Aftereffect and the Number of Binocular Channels

The pattern of the sizes for the adapted, transferred and binocular aftereffects will be discussed in terms of the various models of binocularity. This set of results helps to reinforce the conclusions drawn from the IOT data. That is, individuals with reduced stereoscopic ability may retain binocular neurons in the either-eye channel, but lack binocular neurons which are part of the purely binocular channel. The fact that the A.E.H. group shows evidence of IOT dismisses the possibility of only 2 (monocular) channels and therefore, the results will be discussed in terms of 3 or 4 channels (i.e. 1 or 2 binocular channels).

For both the TAE and the CTE, the Normal group shows a pattern of results

consistent with a four channel model. In both experiments, the Normal group shows a large adapted effect that is greater than the size of the binocular and transferred aftereffects. More importantly, the size of the binocular and transferred aftereffects do not differ. A three channel model predicts a greater binocular aftereffect. The more or less equivalent binocular and transferred aftereffect sizes is an important finding since this pattern of results distinguishes a four channel model from a three channel model.

The pattern of results for the Anomalous Early History group are not as straightforward. As a group, the size of the adapted monocular effect is no different from the size of the binocular aftereffect. This group does show evidence that the binocular effect is greater in size than the transferred effect. As mentioned earlier, the assumption is that the size of an aftereffect is a reflection of the ratio of adapted to unadapted channels where the unadapted channels serve to dilute the size of the aftereffect. In the case of a three channel model, the size of the binocular aftereffect is affected by the adapted ipsilateral monocular and the either-eye binocular channel. The only unadapted channel in this model is the contralateral monocular channel. In comparison, the four channel model also contains the purely binocular channel which would also dilute the binocular aftereffect. In the case of the A.E.H. group, the larger binocular aftereffect in comparison to the transferred aftereffect indicates that, unlike the Normal group, the A.E.H. group shows evidence of only one unadapted channel. One possible explanation is the presence of only one binocular channel in these individuals.

A closer look at the A.E.H. subgroups reveal similar patterns with subtle differences, but the pattern of results are different for the TAE versus the CTE. The pattern of results for the TAE will be dealt with first. The stereoblind subgroup and the ">25" subgroup behave according to a three channel model. In fact, the ">25" subgroup meets the additional prediction that the size of the adapted aftereffect will be greater than the binocular aftereffect.

The other two subgroups show slightly different patterns. It is interesting that the "3000" subgroup does not follow the same pattern as the stereoblind or ">25" subgroups. The "3000" subgroup shows essentially equivalent sizes of aftereffects although the order of size follows the adapted, binocular, and transferred pattern. This is not in keeping with the pattern for a three channel model, nor is it truly characteristic of a four channel model. The subgroup with normal levels of stereopsis show a pattern of results more consistent with a four channel model. This group shows no difference between the size of the binocular and transferred aftereffect.

The pattern of results for the contrast threshold elevation experiment is not as varied. As mentioned previously, the Normal group showed a pattern consistent with a four channel model. In comparison, the A.E.H. group as a whole, and all the subgroups showed no differences in the sizes of aftereffects. It is clear that these individuals with anomalous early visual history behave very differently from individuals with normal binocular vision on this threshold aftereffect study. Nevertheless, the pattern of results always followed the predicted decreasing order of adapted, binocular and then transferred aftereffect size.

The present set of results suggests that the A...H. group may indeed possess fewer binocular channels in comparison to the Normal group, although the results are not equivocal. Taken together with the additional findings from the IOT analysis, these results are strong enough to suggest that stereodeficient individuals do in fact retain functioning binocular neurons.

Freeman and his colleagues have provided physiological evidence that some binocular neurons can survive visual deprivation. Freeman and Ohzawa (1988) have reported that monocularly deprived cats *can* show binocularly interacting cells that are functionally connected to the deprived eye. Previously, it has been shown that the monocularly deprived eye does not show any response to stimulation of the deprived eye or to the nondeprived eye. However, Freeman and Ohzawa (1985) used a different technique of stimulation. Usually, cells are tested with one eye and then the other eye. If the cell responds from stimulation to either eye it is considered binocular. Freeman and Ohzawa (1988) tested their animals binocularly rather than each eye being tested separately. From these results, it appears that it is possible for a monocularly deprived kitten to show binocularly driven cells even though a substantial number of binocular neurons have been lost. These effects will decrease with long term deprivation, but it is important to note that binocular neurons are present even after periods of monocular deprivation.

In another experiment which investigated binocularity, Tsujimoto and Freeman (1981) examined cells in the visual cortex after monocular deprivation and following strabismus. They describe three types of cortico-geniculate cells based on their

axonal conduction velocities: fast, intermediate and slow. Nearly all the cells from the intermediate group were found to be binocularly responsive. Tsumoto and Freeman (1981) found that this group of cells with intermediate axonal conduction velocities were almost entirely missing in strabismic animals and yet both the fast and intermediate cells were affected in monocularly deprived animals. Usually, it is assumed that the reduction in binocularly driven cells is responsible for decreased levels of stereopsis. Tsumoto and Freeman's (1981) work reveals that different subsets of binocular neurons can remain unaffected while others are reduced in number. It is important to note that all binocular neurons are uniform in function.

If we assume that the A.E.H. group do possess binocular neurons of the either-eye type then it is important to rule out the existence of a purely binocular channel. An alternative adaptation paradigm has been suggested as a means of fully adapting all channels but the purely binocular one. If this paradigm, called alternating adaptation, singles out the purely binocular channel, then its absence in individuals with diminished stereo abilities would affect the size of aftereffects expected. The following set of experiments was designed to adapt the two sets of binocular neurons differentially, to determine if, indeed strabismic subjects lack a purely binocular channel.

CHAPTER 3 -- Alternating Adaptation

Introduction

Wolfe and Held (1983) have suggested that the binocular channel affected by simultaneous stimulation of both eyes (the purely binocular channel) is responsible for stereopsis. If this is the case, then strabismic subjects, lacking in stereoscopic abilities, could lack the purely binocular channel but maintain binocular neurons from the either-eye channel capable of IOT. In the previous experiments, strabismic individuals in the A.E.H. group demonstrated IOT. This is evidence that these individuals must possess binocular neurons. Whether or not these subjects might be missing only a subset of binocular neurons was equivocal: the pattern of results following monocular adaptation did not neatly fit the predictions based on a 3 or 4 channel model.

The theory underlying these predictions for aftereffect studies is based upon certain assumptions. The assumptions underlying monocular adaptation and interocular transfer are straightforward; the monocular channels are either adapted or not. The adaptation of the binocular channels, however, may deal with a distribution of adaptation and that becomes more problematic since it is assumed that each channel contributes equally to the size of the aftereffect.

According to the dominance classes of Hubel and Wiesel (1962), the either-eye channel may contain neurons that are more strongly affected by right eye stimulation

and other neurons more strongly affected by left-eye stimulation. Therefore when only one eye is adapted, as in the monocular adaptation paradigm, those neurons most affected by this eye may be strongly adapted whereas other neurons not as affected by this eye may be only weakly adapted. If this is true, then the relative contribution of the strongly adapted or weakly adapted neurons in the either-eye channel during the binocular test condition cannot be predicted with any assurance.

This line of reasoning is also applicable to the Normal group. Their pattern of results does suggest evidence for a second binocular channel since the size of the binocular aftereffect is not significantly different from the transferred aftereffect. In comparison, if only one binocular channel were present, the binocular aftereffect should be greater than the transferred effect. The presence of a purely binocular channel dilutes the size of the aftereffect since it has not been adapted. However, this decrease could also be attributable to the weakly adapted either-eye neurons instead of, or as well as, the second binocular channel. The problem of determining the reason for the size of the binocular aftereffect is exacerbated during the monocular adaptation paradigm because only one eye is adapted.

Blake, Overton and Lema-Stern (1981) have used a different adaptation paradigm, referred to as alternating adaptation, that has been shown to be more appropriate to test for the presence of a second binocular channel (Timney et al., 1989). During alternating adaptation each eye is adapted alternately to the inspection stimulus. This paradigm circumvents the issue of an unknown distribution of adaptation by equally adapting both eyes such that all neurons in the either-eye channel would presumably

be affected. As a result, any decrease in binocular aftereffect size could be attributable to the unadapted purely binocular channel rather than any weakly adapted either-eye neurons.

Due to the strengths of the alternating adaptation paradigm in isolating the activity of the purely binocular channel, it may prove to be a better tool for exploring the relationship between binocularity and stereopsis. In the present experiment, this relationship is explored using the comparison between binocular and monocular aftereffect values (i.e. the ratio of binocular/monocular). Using the four channel model it can be predicted that a purely binocular channel, driven by simultaneous stimulation of both eyes, would not be affected during alternating adaptation and would therefore serve to dilute the binocular aftereffect during post-adaptation testing. During monocular post-adaption testing there would be no diluting influence and both monocular aftereffects should be larger than the binocular aftereffect (see Figure 16).

For individuals with normal vision, the ratio value would be expected to be less than 1 since the monocular aftereffect would always be greater than the binocular aftereffect (see Figure 16B). In comparison, it can be predicted that individuals lacking the purely binocular channel would not possess any unadapted channels to dilute the aftereffect. All three channels would be adapted equally for a result of equivalent monocular and binocular aftereffects. This would lead to a ratio value of 1 (see Figure 16A).

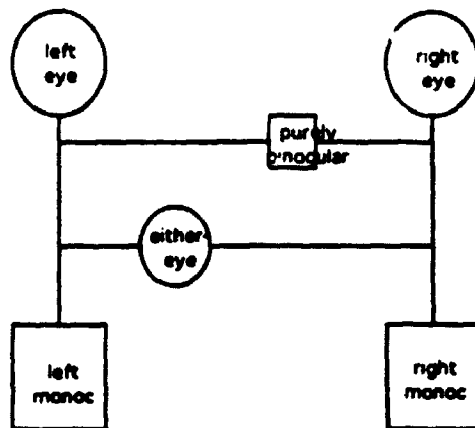
In the following experiments this ratio was examined in both the tilt and contrast threshold elevation aftereffect. The ratio between the size of the monocular and

Figure 16: A schematic drawing showing the pattern of aftereffect sizes following alternating adaptation. The check marks and x's are aligned with the diagram above to indicate the channels affected during adaptation and testing. In this example, the left monocular, right monocular and either-eye channels are adapted. During testing, the contributing adapted neurons are marked with a check. The diluting influence from the unadapted channels, that are driven during testing are marked with an "x".

Figure 16A: Pattern of aftereffect sizes based upon a three channel model.

Figure 16B: Pattern of aftereffect sizes based upon a four channel model.

Alternating Adaptation



<u>Adapt</u>	✓	✓	✓	<u>Proportion of Adapted/Total Channels</u>	<u>Predicted Ratio Value Binoc/Monoc</u>
--------------	---	---	---	---	--

A. Assume influence of 3 channels (no purely binocular channel)

<u>Test</u>	✓	✓	✓	=2/2	} Monoc	=> 1
Pref	✓	✓	✓	=2/2		
Nonpref	✓	✓	✓	=2/2		
Binocular	✓	✓	✓	=3/3		

B. Assume influence of 4 channels

<u>Test</u>	✓	✓	✓	=2/2	} Monoc	< 1
Pref	✓	✓	✓	=2/2		
Nonpref	✓	✓	✓	=2/2		
Binocular	✓	✓	X	=3/4		

binocular aftereffects was used to determine if the A.E.H. group possessed a second set of binocular neurons.

Experiment V -- Tilt Aftereffect

Method

Subjects and Apparatus

All 20 subjects from the Normal group and 17 A.E.H. subjects participated in this experiment. All other details remained as stated for the earlier experiments.

Procedure

The alternating exposure paradigm followed the same general protocol as Experiment III. A baseline measure of the subject's perceived vertical was followed by adaptation to a grating tilted 10° to the right and then successive test and readaptation periods until a criterion number of reversals on the psychophysical staircase were obtained for each test condition.

Baseline measurements were taken for the left, right and both eyes. There were 2 staircases for each eye condition. The test (.5 s) and blank screen (2 s) sequence cycled until 7 reversals were obtained for each staircase, with the first reversal being discarded for the calculation of the perceived vertical. The spatial frequency of the grating was held constant throughout the experiment at 2.5 c deg^{-1}

The initial adaptation period consisted of presenting the adapting stimulus (25% contrast) to each eye for 3 s, alternately, until each eye received 60 s of adaptation

for a total adaptation of 2 minutes. This period was followed by a sequence of test and re-adaptation intervals. The re-adaptation phase was 12 s in total with each eye receiving a total of 6 s. The alternation rate remained at 3 s per eye. Measures of the tilt aftereffect were obtained for three test conditions: preferred eye, nonpreferred eye and binocular.

Results

(i) Amount of aftereffect

Figure 17A shows the pattern of results for the Normal group. Because the comparison of interest was the difference between the monocular and binocular aftereffects, the data for the preferred and nonpreferred eye were collapsed. (An ANOVA was also run on the preferred, nonpreferred and binocular test conditions. If any of these results from the ANOVA are significant they are mentioned.) The t-test comparing the monocular versus binocular aftereffects revealed that the amount of aftereffect in the binocular condition ($M=2.72^\circ$) was significantly less than the aftereffect in the combined monocular condition ($M=3.14^\circ$) ($t(19)=2.7$, $p < .02$). In all cases where t-tests are used, a two-tailed level of significance is applied in order to obtain a more conservative level of significance.

The results for the A.E.H. group are shown in Figure 17B. The combined monocular aftereffect ($M=2.96^\circ$) was slightly greater than the binocular aftereffect ($M=2.54^\circ$) but this difference did not attain significance ($t(16)=1.94$, $p < .10$).

The results for the four A.E.H. subgroups are shown in Figures 18A, 18B, 18C,

Figure 17: This figure plots the results of alternating adaptation to a tilted grating. The amount of tilt aftereffect is plotted for the preferred eye, the nonpreferred eye and the binocular condition. These values were calculated using the perceived vertical measurements found before and after adaptation.

Figure 17A: Normal group

Figure 17B: A.E.H. group

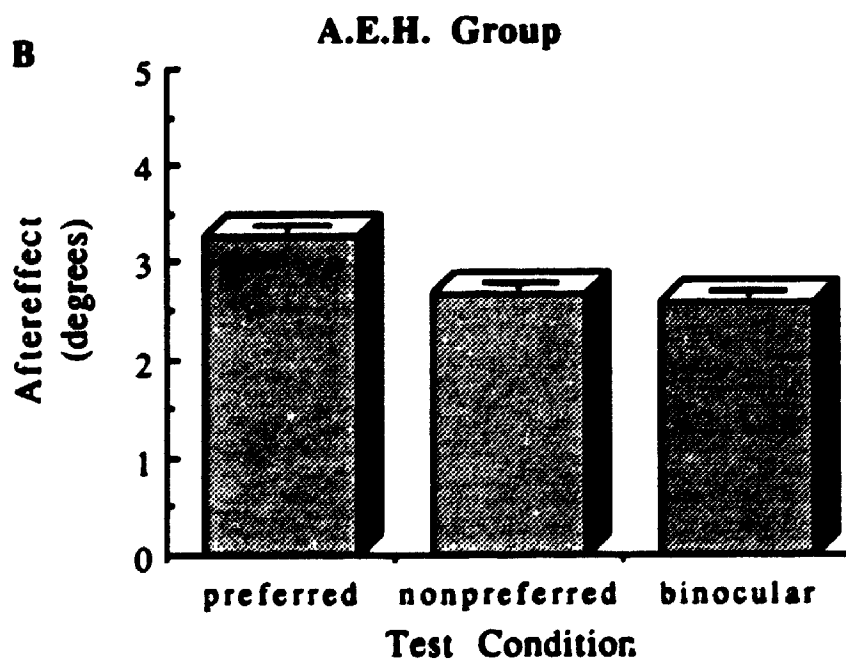
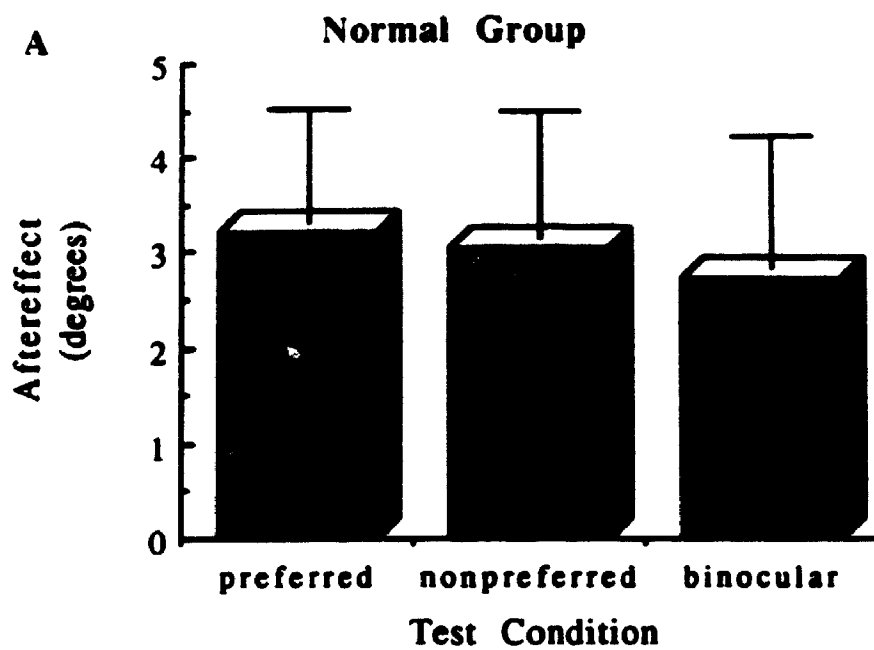
TAE: Alternating Adaptation

Figure 18: This figure plots the results of alternating adaptation to a tilted grating. The amount of tilt aftereffect is plotted for the preferred eye, the nonpreferred eye and the binocular condition. The values were calculated using the perceived vertical measurements found before and after adaptation.

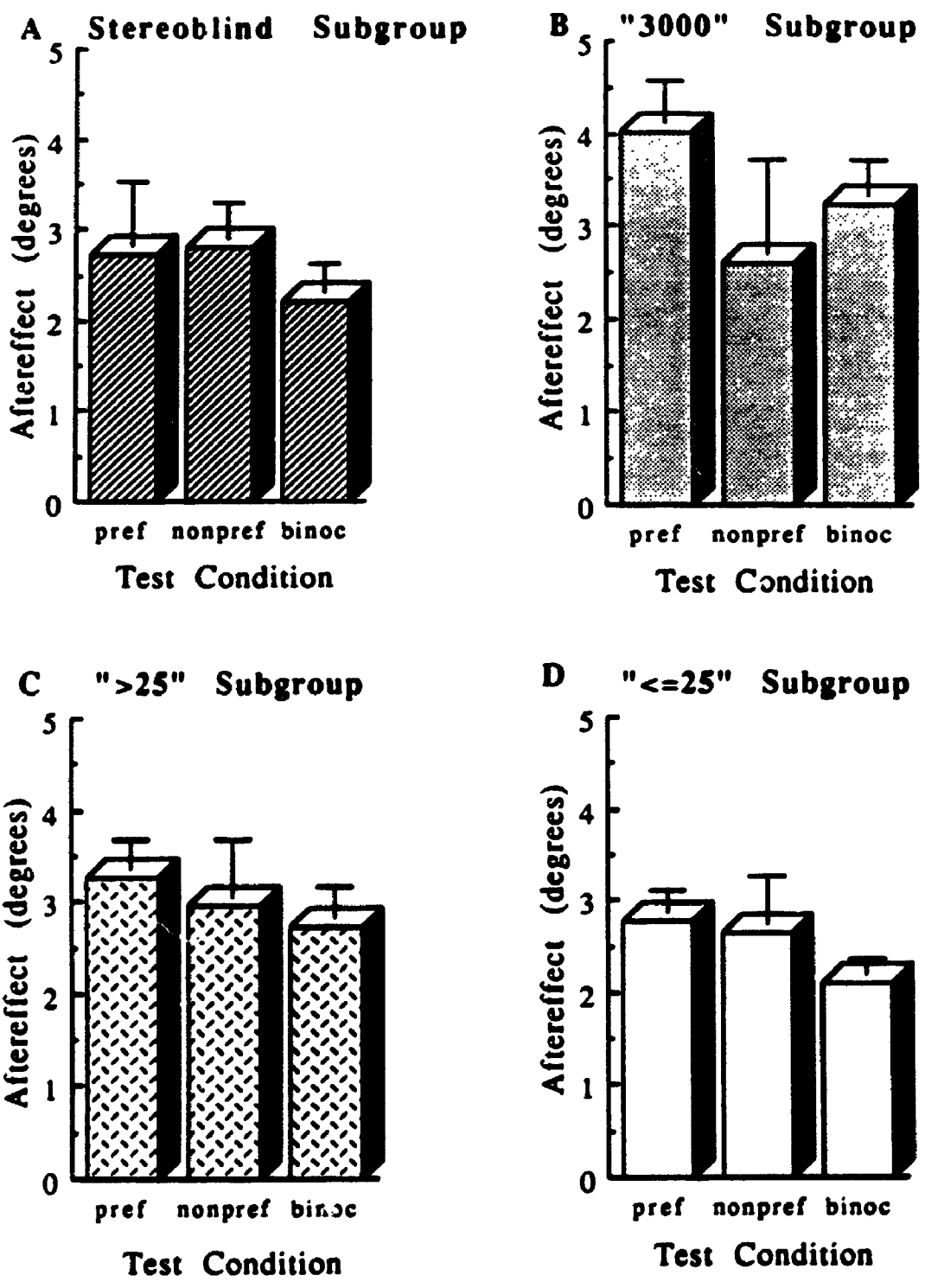
Figure 18A: A.E.H. Stereoblind subgroup

Figure 18B: A.E.H. "3000" subgroup

Figure 18C: A.E.H. ">25" subgroup

Figure 18D: A.E.H. " ≤ 25 " subgroup

TAE: Alternating Adaptation



18D. The stereoblind and "3000" group show no differences in the amount of aftereffect between test conditions ($t(5)=1.17, p=.30$; $t(3)=.10, p=.50$). The other 2 subgroups that have below average to good stereopsis, do show a significant difference ($t(3)=4.84, p<.02$; $t(3)=3.98, p<.05$) between the binocular condition and the combined monocular condition, in the appropriate direction.

(ii) Comparison of monocular and binocular aftereffects

Figures 19A & 19B shows the values for the ratio between binocular and monocular aftereffects (binocular/monocular) for all groups. There were no significant differences between the two main groups in the value of this ratio, nor were there any differences between the subgroups of the A.E.H. group. All groups and subgroups tended to achieve a ratio value hovering around 1.

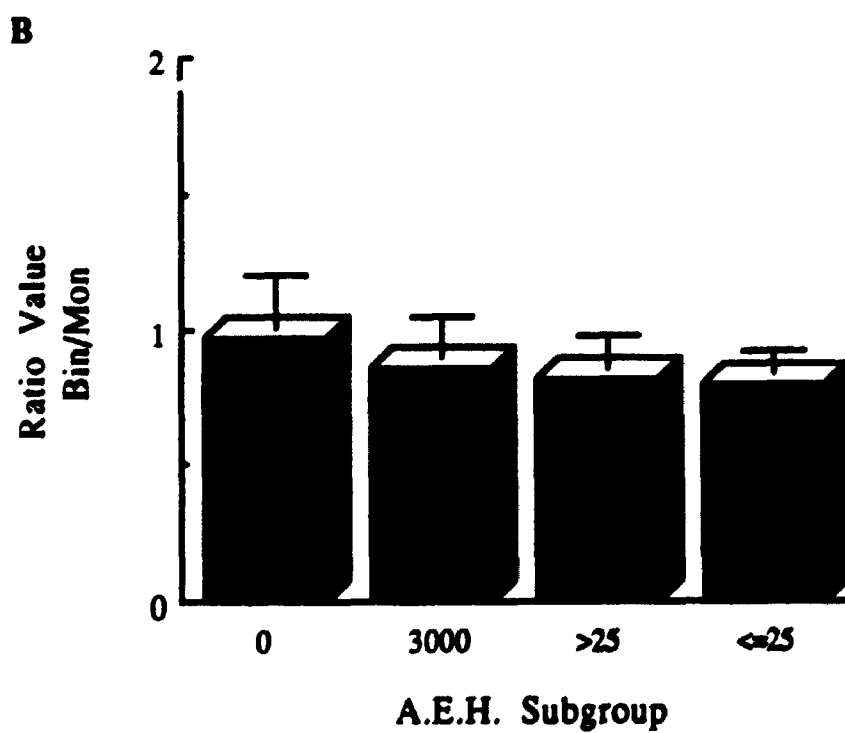
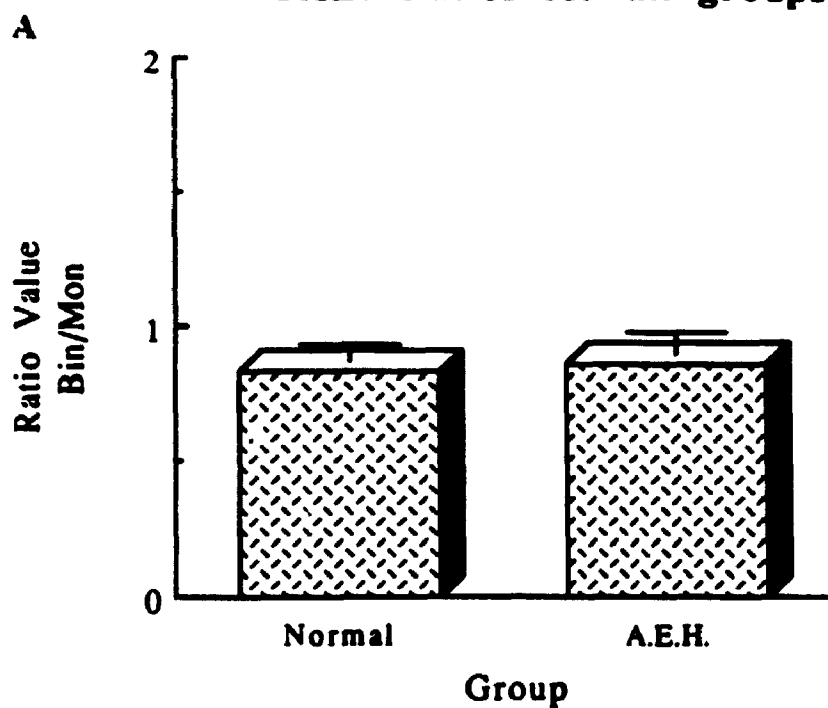
Additional analyses looked at the *a priori* assumption that the Normal group would achieve a ratio value less than 1 whereas the A.E.H.'s value would be more or less equivalent to 1. A single variable t-test revealed that the ratio for the Normal group ($M=.83$) was significantly different from 1 ($t(19)=2.77, p<.02$). The ratio for the A.E.H. group ($M=.87$) did not differ from 1 ($t(16)=1.89, p=.10$).

The ratio value for each A.E.H. subgroup was also compared to the *a priori* value. The only subgroup of the A.E.H. group that achieved a ratio value significantly different from 1 was the " ≤ 25 " group ($t(3)=4.26, p<.05$).

Figure 19: This figure plots a ratio value that reflects the relationship between the size of the monocular and binocular aftereffect. The ratio was calculated using the amount of tilt aftereffect in the binocular and monocular post-adaptation conditions.

Figure 19A: This figure shows the ratio value for the Normal and A.E.H. groups.

Figure 19B: This figure shows the ratio value for all four subgroups of the A.E.H. group.

TAE: Ratios for all groups

Discussion

The pattern of results from this experiment quite clearly show that the Normal group displays evidence of 2 binocular channels whereas the A.E.H. groups' data indicate only one binocular channel. Moreover, the A.E.H. subgroups show a pattern of results that are reflective of their stereoscopic abilities. The subgroups with little or no stereoscopic ability portray the pattern of results consistent with three channels. In comparison, the A.E.H. subgroups with moderate to good stereopsis show a pattern of results just like the Normal group.

The difference between the three and four channel model predictions concerns the relative sizes of the monocular and binocular aftereffects. The smaller binocular aftereffect, in the Normal group and the two A.E.H. subgroups, could be attributed to the diluting effect of the unadapted purely binocular channel. In comparison, the other two A.E.H. subgroups show a lack of a difference in the size of aftereffects which may be indicative of the absence of an unadapted purely binocular channel.

The pattern of results for the ratio of binocular to monocular aftereffect size follows the above results. The ratio of binocular to monocular aftereffect size was expected to be less than 1 for the Normal group, but equivalent to 1 for the A.E.H. group, and this is indeed the pattern of results that is obtained.

Again, it is interesting to note the difference in this pattern of results across the A.E.H. subgroups. The stereoblind and "3000" subgroups show a pattern consistent with the three channel model: equivalent binocular and monocular aftereffects with a

ratio that is no different from 1. The other two subgroups display slightly different findings.

The " >25 " subgroup shows more equivocal results. A smaller binocular aftereffect suggests the presence of the purely binocular channel, but the ratio of binocular to monocular aftereffect size is not significantly different from 1, which suggests only three channels. It is possible that a small proportion of purely binocular neurons are present, but not enough to greatly differentiate the aftereffect sizes.

On the other hand, the " ≤ 25 " A.E.H. subgroup present data that matches the predictions of a four channel model. The smaller binocular aftereffect mentioned earlier is also associated with a ratio value that is significantly less than 1. These individuals had signs of early strabismus and all of these individuals had surgery; two at age 7 and one at age 12. Nevertheless, they have intact stereo abilities and their aftereffect sizes reflect the influence of an additional binocular channel.

Experiment VI -- Contrast Threshold Elevation

Method

Subjects and Apparatus

Eighteen subjects from the Normal group and 14 subjects from the A.E.H. group participated in this experiment. The apparatus was identical to Experiment V.

Procedure

The procedure underlying the alternating exposure paradigm was similar to the

monocular contrast threshold elevation aftereffect in Experiment IV. Baseline measures of contrast threshold were followed by alternating adaptation to an grating of 25% contrast, and then a final set of threshold measurements were taken.

The initial adaptation was 2 min; each eye received 60 s of adaptation. The alternation rate was set at 3 s for the entire experiment. The following test (.5 s) and re-adaptation (12 s) sequence cycled until 7 reversals were met for each of the two staircases in each condition. The experimental protocol and stimulus parameters were as described for Experiment IV. A final threshold elevation factor was calculated for each monocular and the binocular condition.

Results

(i) Amount of Aftereffect

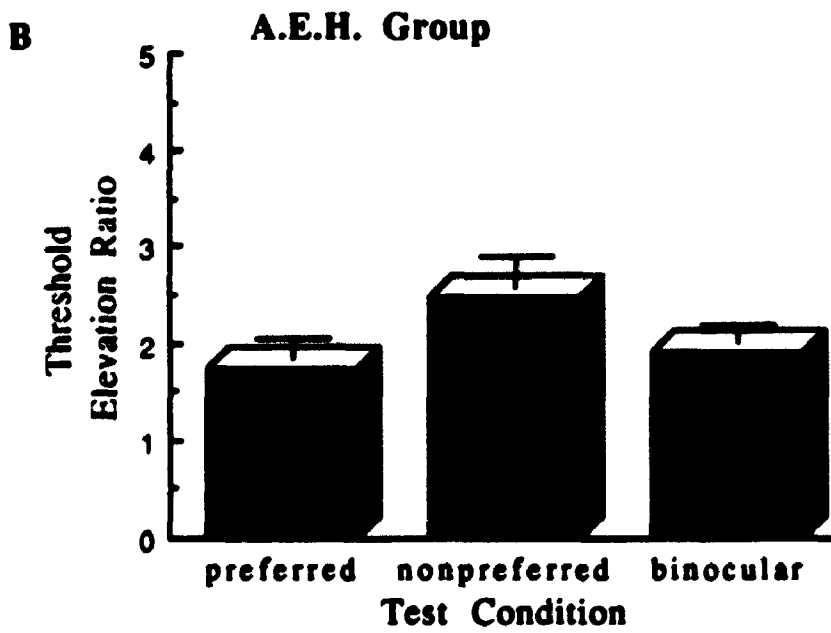
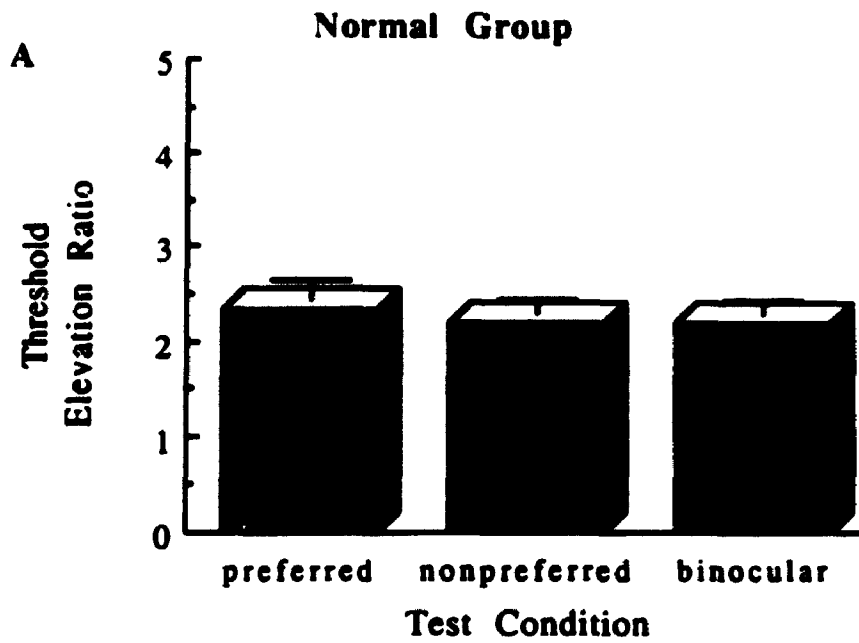
Figure 20A shows the threshold elevation factor for the Normal group. A repeated measures ANOVA revealed no significant differences in the amount of aftereffect between the different test conditions ($F(2,34)=.62, p=.55$), even when the values for both monocular conditions were collapsed ($t(17)=1.08, p=.30$).

The results for the A.E.H. group are shown in Figure 20B. The amount of aftereffect in the combined monocular condition was not significantly different from the binocular condition ($t(13)=1.53, p=.20$). An interesting pattern emerged for this group ($F(2,26)=9.58, p<.001$). The amount of aftereffect in the nonpreferred eye ($M=2.53$) was significantly greater than the amount of aftereffect found in either the preferred eye ($M=1.67$) or the binocular condition ($M=1.90$). Another analysis was

Figure 20: This figure plots the results from alternating adaptation to a high contrast grating. The amount of contrast threshold elevation is plotted for the preferred eye, the nonpreferred eye and the binocular condition. The ratio was calculated using the baseline and post-adaptation threshold values.

Figure 20A: Normal group

Figure 20B: A.E.H. group



performed to determine if the origin of the large nonpreferred aftereffect was due to a larger nonpreferred versus preferred *baseline* threshold value. This analysis showed that the large nonpreferred aftereffect was not reflective of an initially larger baseline threshold value in the nonpreferred eye ($M=.012$) as compared to the preferred eye ($M=.008$) ($t(13)=.85$, $p=.40$).

Figures 21A-21D show all four subgroups of the A.E.H. group. There was no significant difference in the sizes of aftereffects for each subgroup; most notably there was no difference between the binocular and monocular aftereffects. The larger nonpreferred monocular aftereffect is not significantly larger than the preferred or binocular aftereffect in any of the four subgroups but deserves mention as a noticeable trend.

(ii) Comparison of monocular and binocular aftereffects

Figures 22A & 22B display the ratio values for all groups and subgroups. The ratio value did not differ significantly between Normals ($M=1.00$) and the A.E.H. group ($M=1.27$), ($t(31)=1.61$, $p=.12$). In addition, the 4 sub-groups of A.E.H. did not differ in terms of their ratio values.

There were no differences in any of the groups or subgroups when the ratio values were compared against the *a priori* value of 1.

Figure 21: This figure plots the results from alternating adaptation to a high contrast grating. The amount of contrast threshold elevation is plotted for the preferred eye, the nonpreferred eye and the binocular condition. The ratio was calculated using the baseline and post-adaptation threshold values.

Figure 21A: A.E.H. Stereoblind subgroup

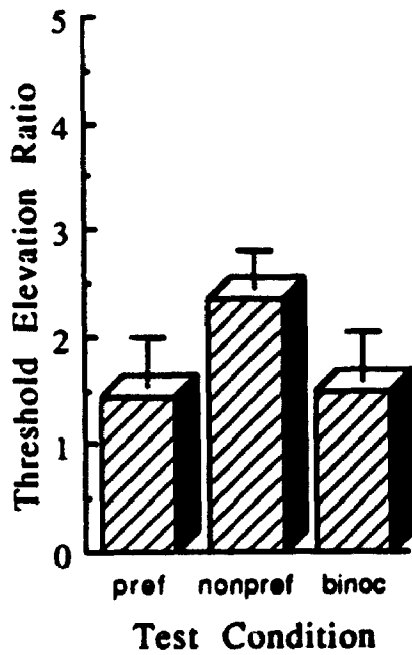
Figure 21B: A.E.H. "3000" subgroup

Figure 21C: A.E.H. ">25" subgroup

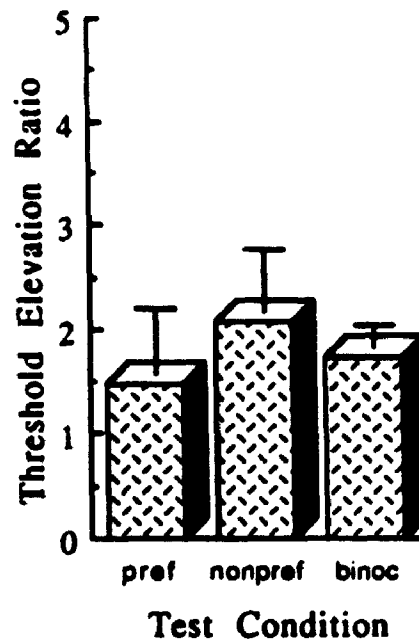
Figure 21D: A.E.H. " ≤ 25 " subgroup

CTE: Alternating Adaptation

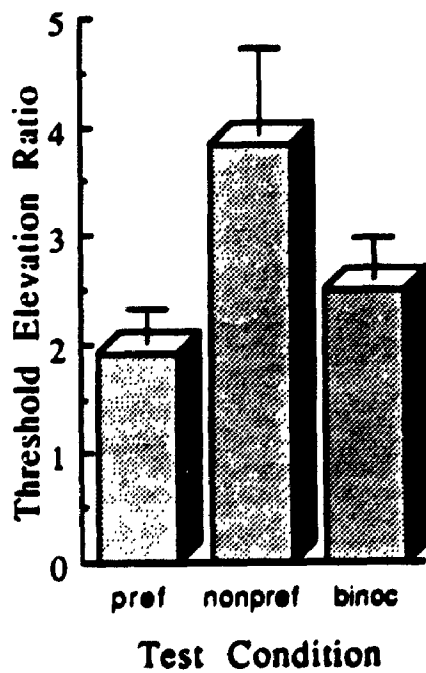
A Stereoblind Subgroup



B "3000" Subgroup



C ">25" Subgroup



D "<=25" Subgroup

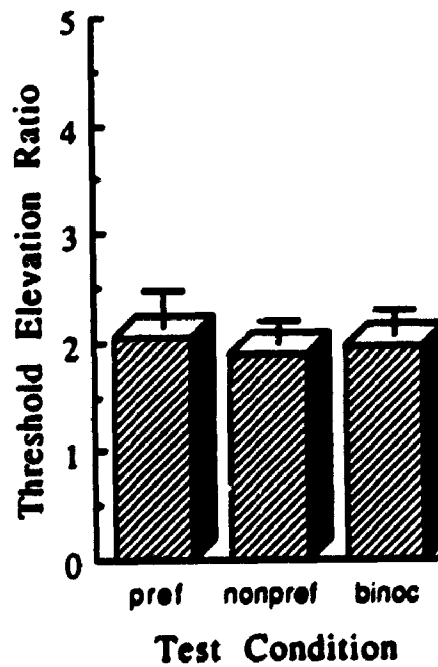
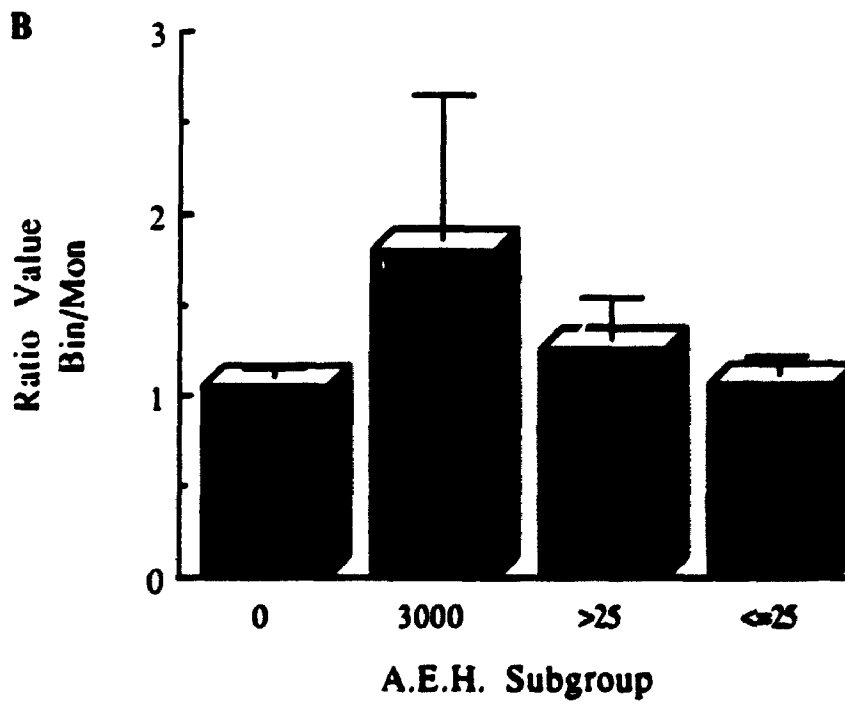
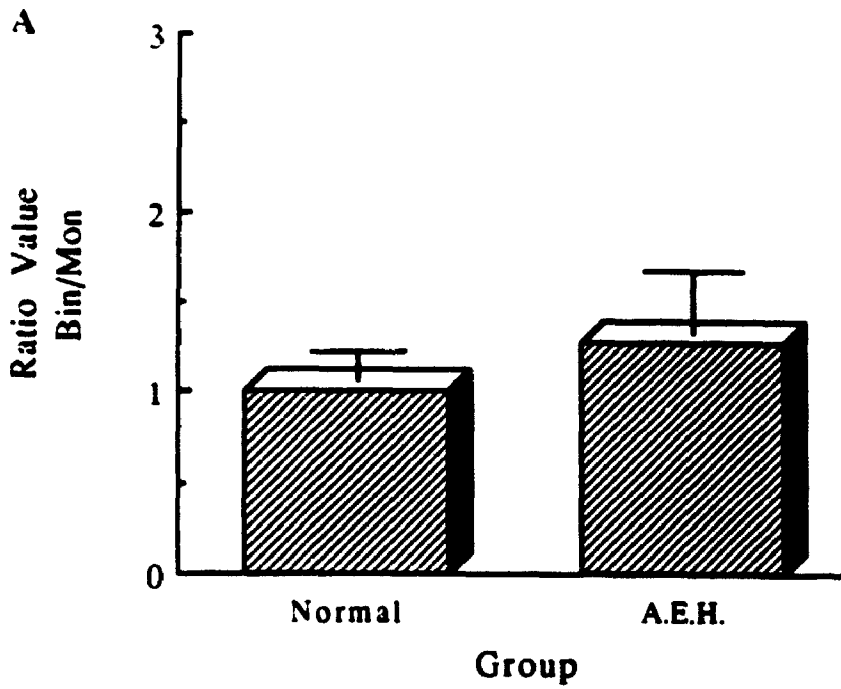


Figure 22: This figure plots a ratio value that reflects the relationship between the size of the monocular and binocular aftereffect. The ratio was calculated using the amount of contrast threshold elevation in the binocular and monocular post-adaptation conditions.

Figure 22A: This figure shows the ratio value for the Normal and A.E.H. groups.

Figure 22B: This figure shows the ratio value for all four subgroups of the A.E.H. group.

CTE: Ratios for all groups

Discussion

The results for the contrast threshold elevation experiment do not follow the same pattern as the tilt aftereffect experiment. In the present experiment both the Normal and A.E.H. groups show no difference between the sizes of the binocular and monocular aftereffects, and none of the ratios are any different from the *a priori* value of 1.

This outcome suggests the possibility that the purely binocular channel may not be in operation at threshold. If the purely binocular channel is not affected at threshold, then it would not exert a diluting influence to reduce the size of the binocular aftereffect. As mentioned earlier, Blake et al. (1981) suggested this distinction, between threshold and suprathreshold stimuli based on their results from a contrast threshold experiment. In addition, Wolfe and Held (1983) have suggested that their data are indicative of a similar distinction. However, Wilcox et al. (1994) have examined this in detail and found consistent evidence for a second binocular channel at threshold. These discrepancies require further attention. The experiments in the following chapter address the presence of a second binocular channel, at threshold, from another perspective.

CHAPTER 4: Binocular Summation

Introduction

The previous chapters used aftereffect studies to investigate binocular channels. The results from the tilt aftereffect experiment suggested that individuals in the A.E.H. group did not possess the purely binocular channel. However, the results from the contrast threshold elevation experiment were not as straightforward. The nature of these results led us to search for other ways in which to examine the binocularity of the visual system. Other researchers interested in the relationship between interocular transfer, stereopsis and binocularity in stereoblinds have also analyzed these subjects' performance on binocular threshold tasks. The present chapter is concerned with such binocular tasks.

Binocular viewing yields a binocular advantage over monocular viewing on a variety of visual threshold tasks (see Blake and Fox, 1973 for a review). In this respect, binocular thresholds are often better than monocular thresholds by approximately 30 - 40%. The superiority of binocular viewing is referred to as binocular summation and is expressed by the ratio of the monocular threshold to the binocular threshold.

Simple *probability* summation refers to a binocular response that is more sensitive than either of the two monocular responses. Pirenne (1943) was the first to report this type of binocular advantage. He suggested that each eye acts as a separate

detector with distinct thresholds, and that the probability of the binocular response is analogous to a single eye that has two independent opportunities (Arditi, 1986). Using probability theory, an equation that represents the probability of binocular detection can be generated. Although many have modified Pirenne's original formula to account for a guessing factor and other assumptions, a commonly reported ratio value for probability summation is approximately 1.25 (Campbell and Green, 1965; Thorn and Boyton, 1974).

Neural summation is said to occur when the binocular advantage is more than would be expected than on the basis of probability summation. Essentially, the two eyes are thought to act like a single detector. In this case, the binocular threshold is greater than the monocular threshold by about 30-40% and the ratio value of 1.4 (or $\sqrt{2}$) has been accepted as a standard for assessing the involvement of neural summation. Campbell and Green (1965) arrived at this value from empirical data. They reasoned that the binocular performance was better than the monocular performance by $\sqrt{2}$ due to the random noise reduction of two inputs. Summation in normal subjects is reported to range from the binocular sensitivity predicted by probability summation to the aforementioned 40% associated with *neural* summation.

There is an interesting comparison between probability and neural summation which deserves mention. Probability summation has been used as a baseline summation value from which to gauge the involvement of additional physiological or neural summation (Blake & Fox, 1973). Although it is assumed that neural summation involves physiological summation between the two eyes and probability

summation does not, there must be a point during probability summation where the two monocular signals are combined. If each monocular signal were completely independent, the binocular threshold would be no better than the best monocular threshold and the ratio of binocular and monocular thresholds would be closer to 1 and not 1.25.

There has been a fair amount of research on the nature of summation in individuals with normal stereopsis and whether or not their data fit the model of probability or neural summation (see Blake and Fox, 1973; Blake, Sloane, and Fox, 1981 for reviews). Those individuals without normal stereopsis have also been examined on binocular threshold tasks. In their review on binocular summation, Blake et al. (1981) state that individuals with stereodeficient capabilities show little, if any, binocular summation. It is assumed that the binocular neurons responsible for stereopsis are also involved in summation and thus individuals with defective stereopsis show a lack of binocular summation. However, there is no *a priori* reason to expect that these individuals would not show at least probability summation. If each eye is functioning properly, then each eye should contribute to the binocular performance. The results have been somewhat mixed regarding the level of summation achieved in stereoblinds, and the next section deals with this issue.

Lema and Blake (1977) found that stereoblind individuals showed no binocular advantage on a contrast detection task. They explored summation over a range of spatial frequencies (2 c deg^{-1} - 6.5 c deg^{-1}) and found that the majority of the stereoblind individuals did not show summation at any of the spatial frequencies.

(One stereoblind did show some summation at a high spatial frequency.) They suggest that their findings lend credence to the notion that there is a common neural mechanism between stereopsis and binocular summation. They conclude that stereoblind individuals do not exhibit summation, not even probability summation. Williams (1974) also found that stereoblind individuals did not achieve a significant difference between monocular and binocular thresholds (i.e. a ratio value close to 1). He suggests that the reason stereoblind subjects do not achieve probability summation may be due to a contralateral inhibition by the dominant eye such that the non-dominant eye is ineffective during binocular viewing.

Von Grunau (1979) has explored the relationship between stereopsis and binocular summation in cats. He reared kittens with alternating monocular occlusion and found that these animals did not show any binocular summation on a contrast threshold task. In addition, he found that congenitally stereoblind Siamese cats do not show summation either. From previous literature it is known that cats raised with alternating occlusion show a depleted complement of binocular neurons and a reduced level of stereopsis (Blake and Hirsch, 1975). Therefore, von Grunau (1979) also concluded that binocular summation and stereopsis may share a common neural mechanism.

Rose, Blake and Halpern (1988) also provide evidence that binocular neural summation is mediated by the same channels that provide stereopsis. They looked at binocular thresholds for stimuli that varied in the amount of disparity present. At zero disparity, the binocular thresholds were approximately 1.4 times greater than the

monocular thresholds but, as the disparity increased the amount of summation decreased to a level associated with probability summation (Rose, Blake and Halpern, 1988). Sometimes the disparity difference was as great as 6° before the summation decreased to probability levels, and this depended on the spatial frequency of the stimulus. Rose et al. (1988) state that their pattern of results mimics the range at which stereoscopic depth sensations occur. The point at which summation drops to probability summation is similar to the point at which stereoscopic depth is no longer present (i.e. the images can no longer be fused).

The data from Levi, Harwerth and Smith (1980) support the association between summation and stereopsis, but Levi et al. (1980) add other binocular functions to this grouping. They investigated normal and stereoblind subjects on binocular summation tasks, interocular transfer abilities and dichoptic masking effects. They suggest that their results reveal two types of binocular interactions; excitatory and inhibitory. In addition to the lack of stereopsis by stereoblind subjects, Levi et al. (1980) found that these individuals did not exhibit binocular summation or interocular transfer. Levi et al. (1980) categorize these behaviours as excitatory interactions in contrast to rivalry and masking which are considered inhibitory interactions. They argued that because the stereoblind subjects show effects from dichoptic masking similar to normals, but do not display binocular summation, it is the excitatory binocular connections that are disrupted while inhibitory interactions between monocular inputs remain unaffected.

The relationship between stereopsis and binocular summation does not hold strong in all investigations. In a study by Sireteanu, Fronius and Singer (1981), strabismic

subjects did not show binocular summation and interocular transfer for stimuli placed in the central region of the retina. However, these same individuals showed both summation and IOT for stimuli in the periphery. Blake, Martens and Di Gianfilippo (1980) also found that stereoblind individuals showed probability summation on a reaction time task.

We are left with a conflicting picture of whether or not stereoblind individuals exhibit summation. As mentioned earlier, there is no *a priori* reason to expect that these individuals would not exhibit probability summation unless there is some form of inhibition from the dominant eye during binocular viewing. The following three experiments investigate different aspects of summation in stereodeficient individuals.

Experiment VII -- Binocular summation: Evidence for neural or probability summation in stereodeficient individuals

This was a retrospective study that included the baseline measurements from Expt's IV and VI. These data provided monocular and binocular contrast threshold values from which to calculate a binocular summation ratio. Our first step was to determine if any, or all, of the subjects in the A.E.H. group displayed probability or neural summation. We expected that the stereoblind subgroup, and possibly other subgroups as well, would show reduced summation.

Method

All of the data from the seventeen Normals and thirteen of the fourteen A.E.H. subjects who participated in experiments IV and VI (both CTE experiments) were used in this study. The remaining A.E.H. subject had extremely deviant baseline thresholds which skewed the results and added a large amount of variability. Although he was included in the previous aftereffect studies, in the present analysis of baseline measurements, his values were excluded. The baseline measurements for both monocular conditions and binocular condition were extracted from the data. Binocular summation values were calculated for each subject (averaged monocular threshold/binocular threshold). Each subject had 2 summation values; one from experiment IV and one from experiment VI. These 2 values were averaged for each subject.

Results

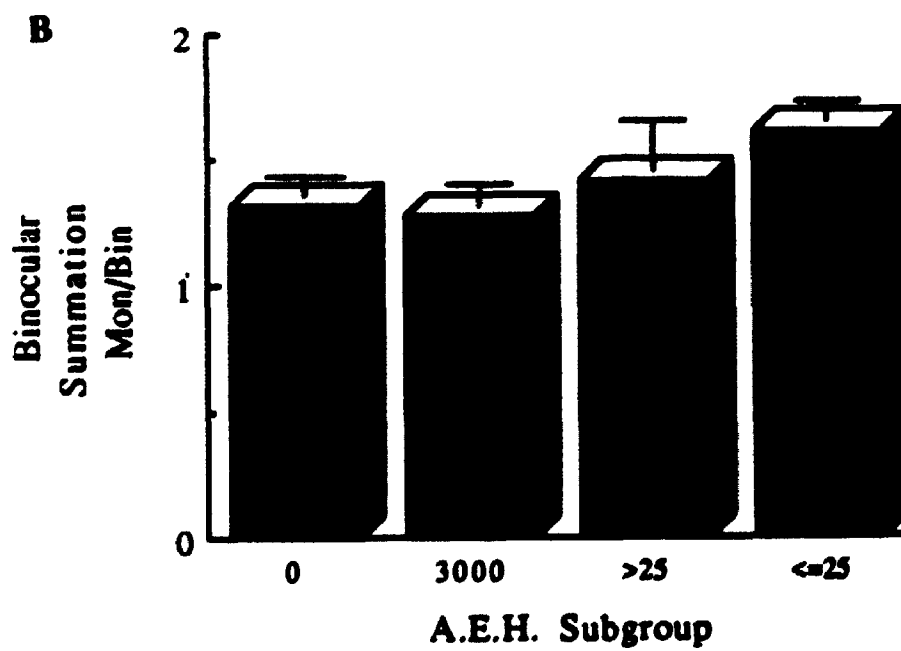
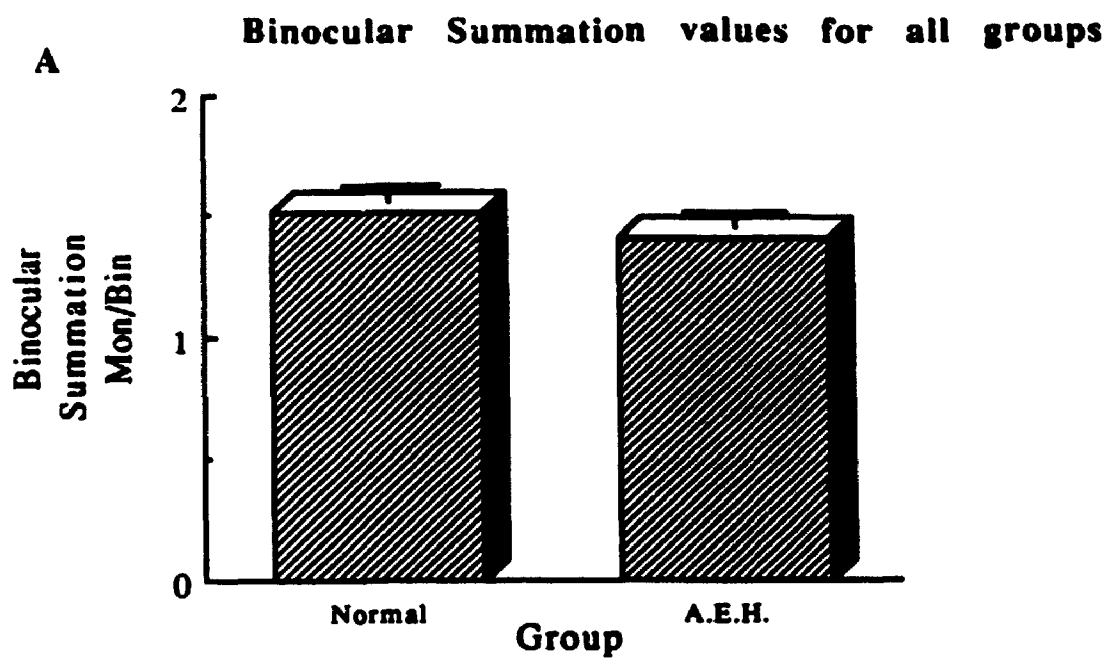
Figure 23A shows the binocular summation values for both the Normal ($M=1.51$) and A.E.H. ($M=1.40$) groups. No significant differences emerged from this analysis ($t(30)=1.52$, $p=.20$). Figure 23B shows the binocular summation values for the 4 A.E.H. sub-groups. A one-way ANOVA revealed that the ratio values were not significantly different from one another ($F(3,9)=1.23$, $p=.355$).

The summation values were compared to the value of 1. A binocular summation value of 1 would indicate that the binocular threshold was equivalent to, and no better than, the monocular thresholds. Both the Normal and A.E.H. groups showed a

Figure 23: This figure plots binocular summation values. These ratios were calculated by comparing the monocular and binocular contrast threshold values taken at 2.5 c deg^{-1} . The threshold values were averaged baseline values from Expt IV & VI.

Figure 23A: This figure shows the binocular summation ratios for the Normal and A.E.H. groups.

Figure 23B: This figure shows the binocular summation ratios for all four subgroups of the A.E.H. group.



significantly greater ($p < .01$) than 1 binocular summation value. The stereoblind A.E.H. subgroup also showed a summation value greater than 1 ($t(2)=5.73$, $p < .05$), as did the " ≤ 25 " subgroup ($t(2)=8.69$, $p < .02$). The other two subgroups, "3000" and " > 25 ", did not have binocular summation values that were significantly different from 1.

A further *a priori* comparison was performed using the predicted probability summation value of 1.25. The summation value for the Normal group was significantly greater than 1.25 ($t(18)=6.62$, $p < .001$), and as a whole, the A.E.H. group showed a significant difference from this value also ($t(12)=2.28$, $p < .05$). However, the only A.E.H. subgroup to show a binocular summation value significantly greater than 1.25 was the " ≤ 25 " subgroup ($t(2)=5.13$, $p < .05$).

An *a priori* comparison was also performed using the value of 1.4 associated with neural summation. Single variable t-tests were used to test for differences. The summation values for the Normal group were significantly greater than 1.4 ($t(18)=2.87$, $p < .02$) but, the summation values for the A.E.H. group were not significantly different from this value. As well, there were no differences within each subgroup from this value.

Discussion

The results from this study very clearly show that individuals with deficient levels of stereopsis show binocular summation. Of particular interest are the stereoblind subgroup who show a binocular summation value of 1.3. This value is greater than

1, but no different from the values associated with probability or neural summation.

These results are at odds with those of Lema and Blake (1977) and Levi et al. (1981) who found that stereoblind subjects did not possess any binocular advantage. In the present study, these individuals do show evidence that both eyes contribute to the binocular threshold since the summation ratio is greater than 1. The fact that the summation ratios are greater than one, indicates that the binocular detection by stereoblinds is not mediated by the most sensitive eye, but rather from a combination of the two eyes. The only A.E.H. subgroup to achieve a summation ratio greater than that associated with probability summation, are those individuals with normal levels of stereopsis (" ≤ 25 "). For this subgroup, the summation value of 1.6 indicates a binocular interaction at the level of neural summation.

As mentioned earlier, a level of probability summation should be expected for the A.E.H. groups unless there is some contributing inhibitory influence from the dominant eye during binocular testing. The fact that three of the four subgroups (all with deficient levels of stereopsis) do not achieve summation values greater than that of probability summation indicates that although both eyes are contributing to the threshold task, the eyes may not be acting together to the same degree as that found in the Normal group or in the " ≤ 25 " subgroup.

These findings aroused an interest in the conditions under which binocular summation will occur. In particular, we were taken with the finding that stereoblind individuals showed levels of summation which fell *between* probability and neural summation. This precluded us from making an unequivocal statement regarding their

summation ability. For this reason, the following experiments explored different aspects of summation in stereoblind subjects.

Experiment VIII -- Binocular summation as a function of interocular phase differences

Introduction

Binocular viewing is better than monocular viewing only under certain circumstances and various researchers have addressed the conditions necessary for binocular summation to occur. In a review, Arditi (1986) mentions the following requirements: spatial correspondence in the 2 retinas (Westendorf and Fox, 1977), temporal correspondence between the two eyes within 100 ms (Matin, 1962), similar size or spatial frequency of the two images as well as the same orientation (Westendorf and Fox, 1975).

Westendorf, Langston, Chambers and Allegretti (1978) used a reaction time paradigm to observe how stereoblind and normal individuals respond to *temporal* differences in stimuli. They showed that normal individuals respond faster when each eye viewed the same stimulus simultaneously (synchronous viewing). The other condition, asynchronous viewing, involved the presentation of stimuli to each eye, separated by 100 ms. The stereoblind individuals in their study did not show the same strong advantage as normals for synchronous viewing, but there was some

indication that these individuals did perform faster during synchronous rather than asynchronous viewing. Westendorf et al. (1978) take this as evidence for the existence of probability summation in stereoblind individuals.

Very little work has been done on the *spatial* patterns necessary for stereoblinds to show summation. Therefore, the present study was designed to look at the effects of spatially modulated stimuli on binocular thresholds for stereoblind subjects. The paradigm used was the same as that of Wilcox (1992) who investigated these effects in normal individuals. She used spatially modulated stimuli, and varied the relative spatial phase between monocular gratings to observe the involvement of the purely binocular channel in a summation task. She found, as have others, that the two monocular stimuli must be matched in-phase (0° phase difference between the two eyes) for neural summation to occur. Wilcox's (1992) experiment was based on Cogan's (1987) model of binocular combination which predicts that when monocular stimuli are of opposite phase, only one binocular mechanism, the either-eye channel, is available to mediate detection. However, if the two images have the same phase, an additional binocular mechanism, the fused channel (equivalent to the purely binocular channel) will contribute to detection. If this proposal is valid, then contrast thresholds for spatially modulated stimuli should be lowest (and binocular summation the highest) when the relative phase of the monocular gratings is 0° and highest when the two gratings are 180° out of phase.

Wilcox (1992) found that as the phase difference between the two monocular images increased, the binocular threshold increased, thereby decreasing the level of

binocular summation. The binocular threshold was at a maximum when the monocular gratings were maximally disparate (180° phase difference). It should be noted, however, that she obtained these results using horizontal gratings, but found a different pattern of results for vertical gratings. Wilcox (1992) attributed the difference in results between horizontal and vertical gratings to the involvement of stereoscopic information present during the vertical gratings.

The present study sought to replicate these results in normal individuals, and to examine the involvement of the purely binocular channel in *stereoblind* individuals when the two monocular images are not phase-matched.

Method

Subjects

The four stereoblind subjects from the original A.E.H. group participated in this experiment (3F,1M). There were four individuals (2M, 2F) with normal levels of stereopsis (20 sec of arc or better) who were not part of the original Normal group. The same test used in the preceding experiments was used to determine this group's preferred eye.

Apparatus

Sine-wave gratings were generated on two Tektronix 608 CRT monitors, as in previous experiments, with a microcomputer interfaced with the Picasso image generator. The two monitors were viewed simultaneously through an adjustable haploscopic mirror system. The subject looked straight ahead as the gratings were

presented to each eye. All conditions for viewing the monitors was as stated in Expt 1. Two sets of stimuli were used for 2 test conditions: a vertical (0°) grating with a spatial frequency of $.4 \text{ c deg}^{-1}$ and a horizontal (90°) grating with a spatial frequency of $.4 \text{ c deg}^{-1}$. The spatial frequency and orientation remained constant for each test condition, ensuring that the test gratings differed only in terms of their relative locations on the two retinae. The Michelson contrast was adjusted to obtain threshold estimates.

The relative phase difference of the gratings presented to each eye ranged between 0° and 180° with a total of 9 phase angles tested at 22.5° intervals. Prior to each trial the absolute position of the gratings was randomly selected to avoid any cues that might have been produced by a constant relationship between the target and the edge of the display.

Procedure

One session consisted of 9 binocular threshold estimates and 1 monocular threshold estimate.

Binocular Threshold Testing

A binocular threshold was obtained for 9 different phase angles. Threshold testing for each phase angle constituted a block and thus there were 9 blocks of trials. Within a block, contrast thresholds were measured binocularly using a randomly interleaved dual-staircase. Each phase angle was tested until 5 reversals were made on both staircases. The final threshold estimates were based on the last 4 reversal points for both staircases. Upon completion of a block, the contrast threshold for that

phase angle was stored by the computer and the next block was initiated. The order of phase angles was chosen randomly at the beginning of each session. Within a single session 9 binocular thresholds, one for each phase angle, were obtained.

Monocular Threshold Testing

Monocular contrast thresholds were also obtained for each orientation. Since it is impossible to generate interocular phase-shifts with monocular gratings, the absolute position of the test grating was varied randomly from trial to trial. Ten threshold estimates were taken of the preferred eye during a single session. The mean of the 10 estimates was calculated.

Each subject completed 3 sessions for each orientation for a total of 6 sessions. The summation ratio for each phase angle was calculated using the binocular threshold for that angle and the monocular threshold.

Results

Figures 24A&B show the results for the Normal group; 24A shows the binocular summation ratios for the horizontal gratings and 24B for the vertical gratings. The summation values appear to decrease as the phase differences increase. Figures 25A&B show the Stereoblind groups results. In contrast to the Normal groups data, the Stereoblind groups summation values do not appear to change as the phase difference increases.

There was a significant difference between the Normal group and the Stereoblind group ($F(8,48) = 12.68, p < .001$) as well as a significant two-way interaction between

Figure 24: Binocular summation ratios are plotted for each phase difference tested. The ratios were calculated using the monocular and binocular threshold values.

Figure 24A: This figure shows the binocular summation ratios for the Normal group when the threshold values were obtained using a horizontal test grating.

Figure 24B: This figure shows the binocular summation ratios for the Normal group when the threshold values were obtained using a vertical test grating.

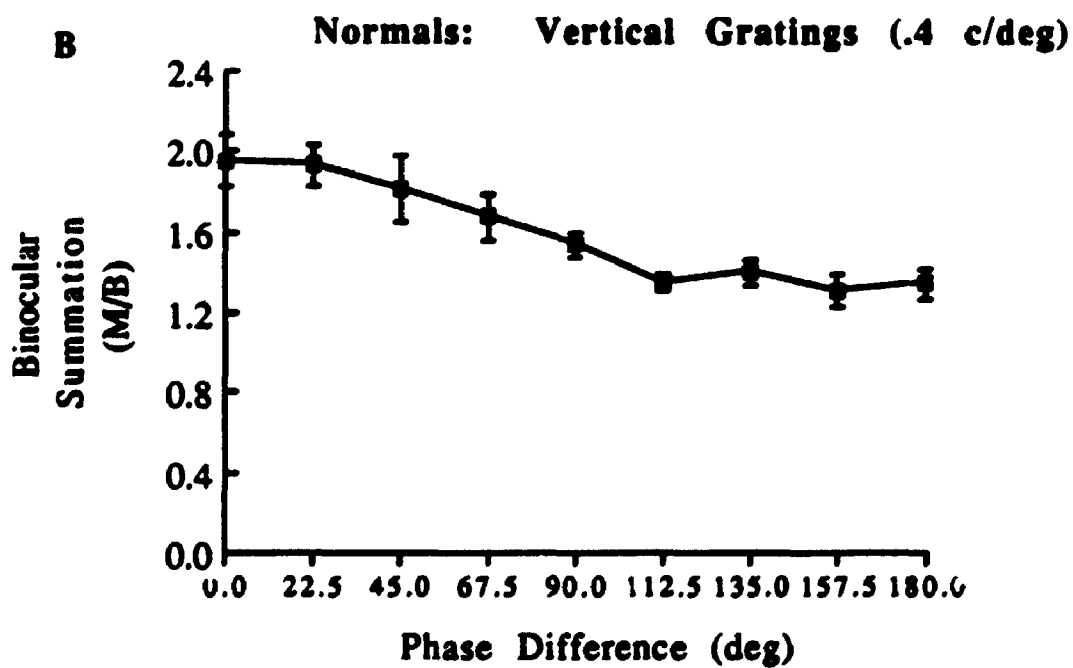
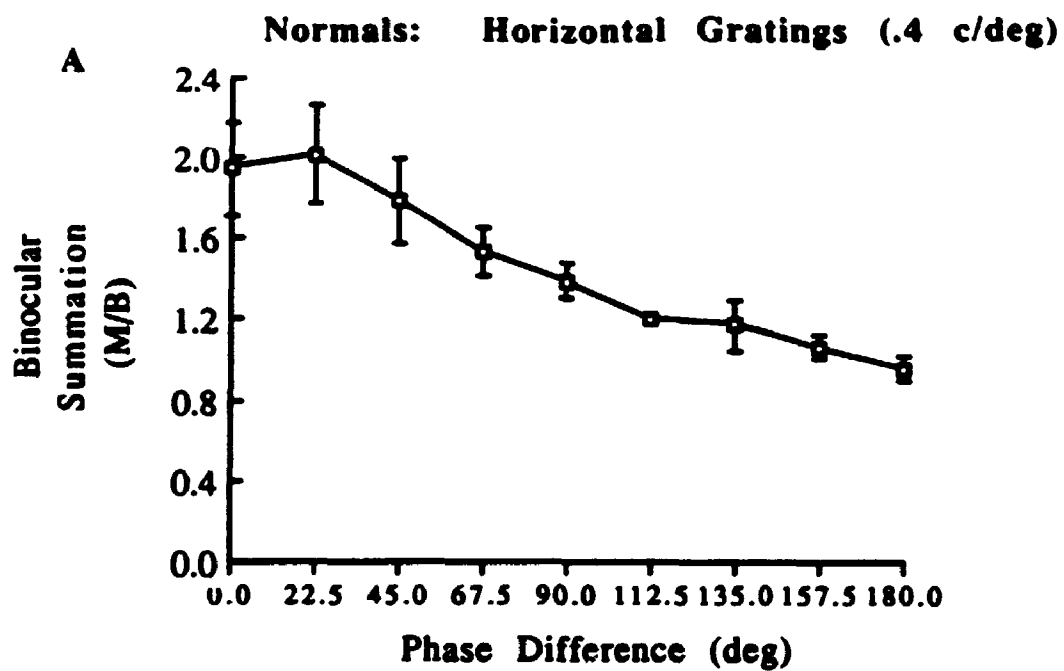
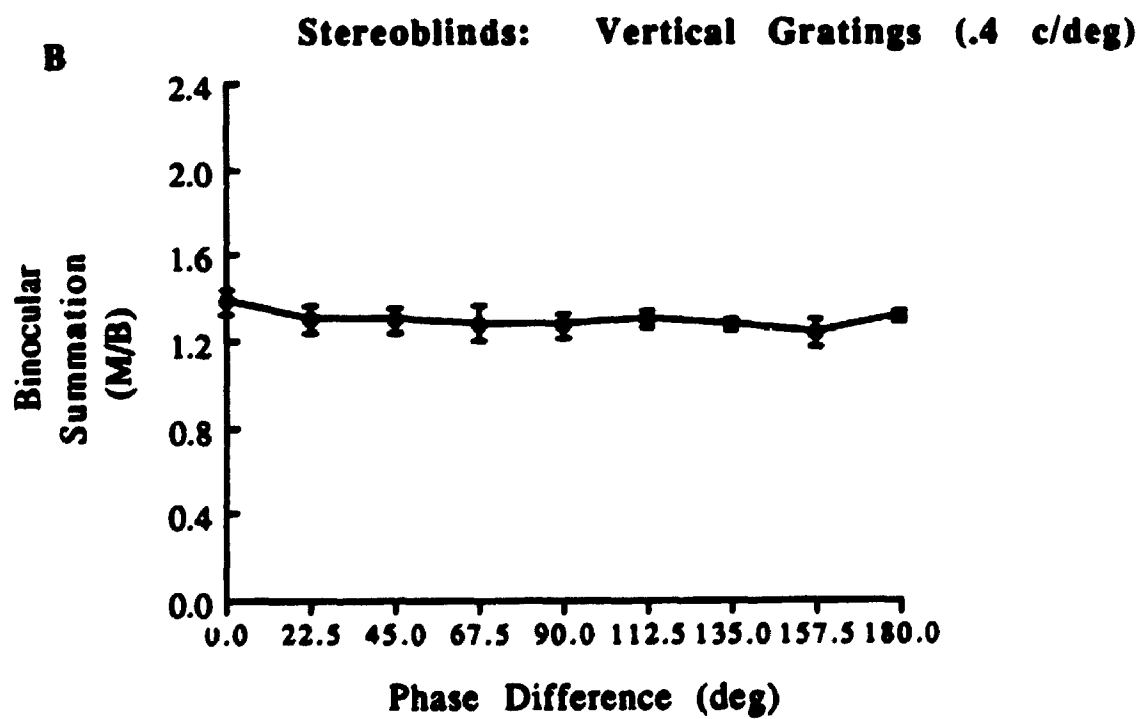
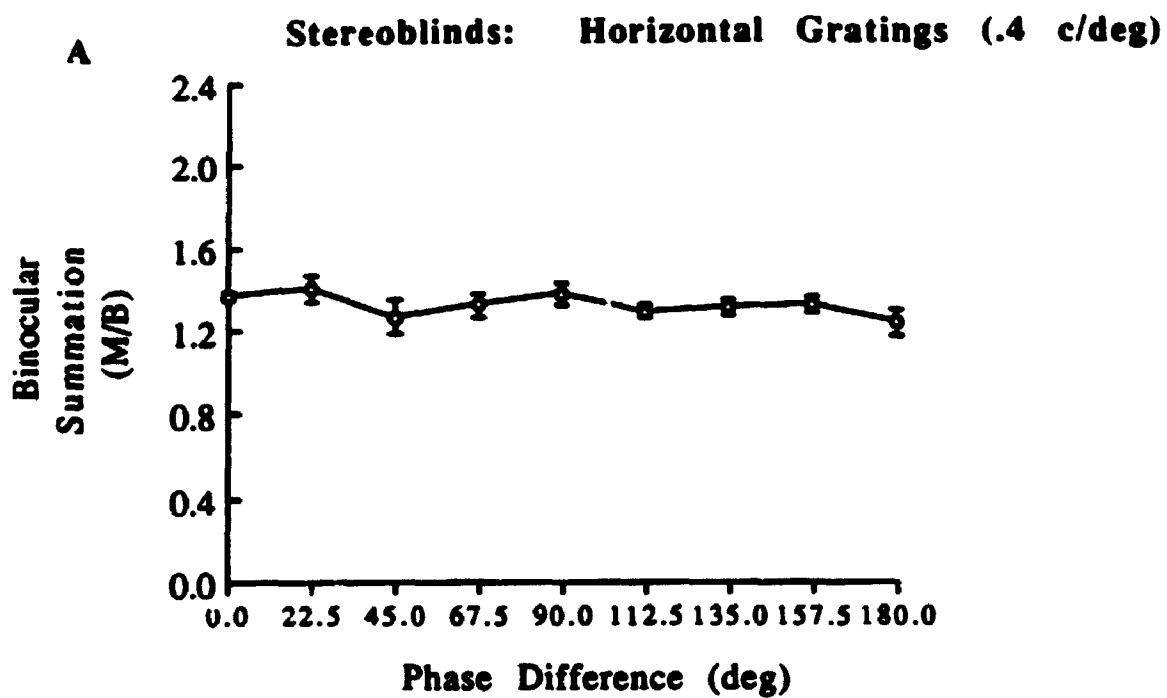


Figure 25: Binocular summation ratios are plotted for each phase difference tested. The ratios were calculated using the monocular and binocular threshold values.

Figure 25A: This figure shows the binocular summation ratios for the Stereoblind group when the threshold values were obtained using a horizontal test grating.

Figure 25B: This figure shows the binocular summation ratios for the Stereoblind group when the threshold values were obtained using a vertical test grating.



the two groups and the phase angle ($F(8,48)=9.15, p < .001$). As no significant differences were found between horizontal and vertical gratings ($t(6)=1.95, p=.10$), all future analyses refer to an average binocular summation value from these two orientations. Figure 26 represents the average summation, for horizontal and vertical gratings, for both groups. This figure nicely summarizes the interactions between the two groups.

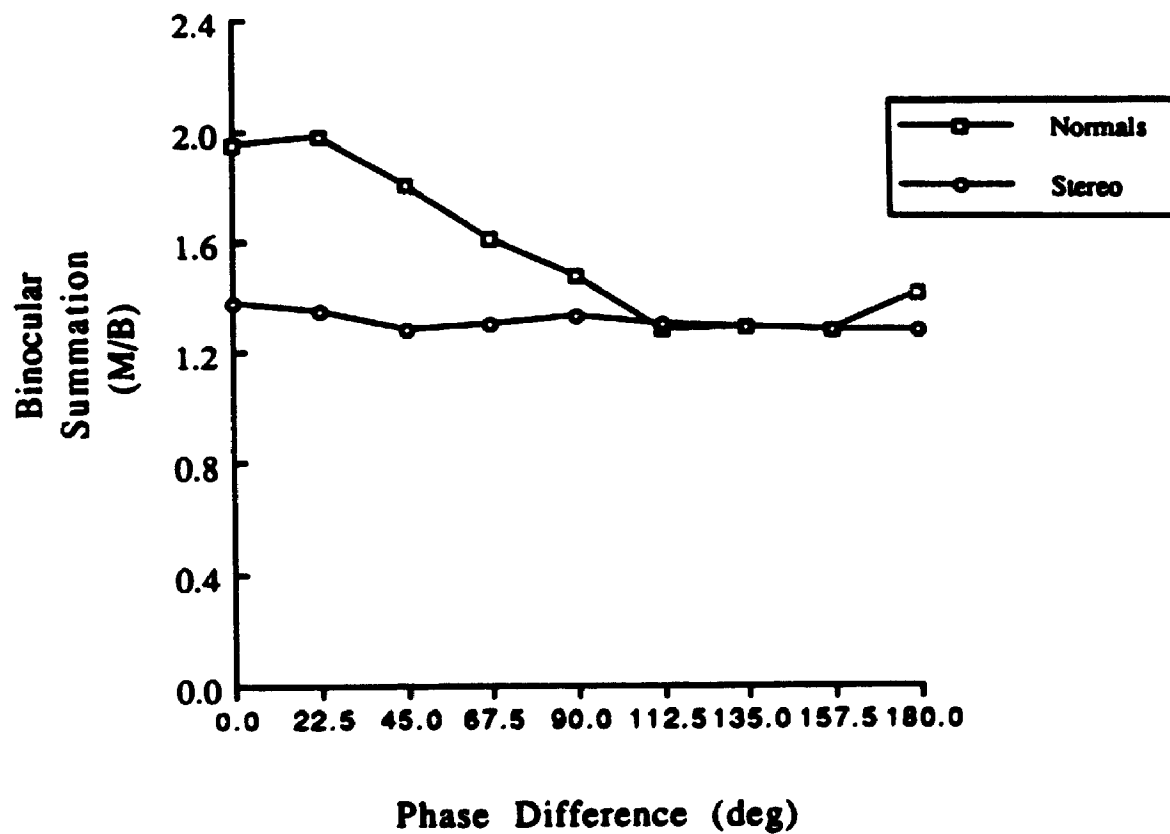
The nature of the above interactions was explored using Tukey's HSD test. Subjects in the Normal group have significantly higher binocular summation values than the Stereoblind group at phase angles of 0° , 22.5° and 45° ($p < .05$) but not at greater angles.

The phase differences between the two monocular images affect the binocular summation values of the Normal group such that the binocular summation values at the larger phase angles of 112.5° , 135° , 157.5° and 180° are all significantly lower ($p < .05$) than the summation values at 0° and 22.5° . In comparison, the different phase angles have no effect on the summation values for the Stereoblind group. The summation value obtained when there are no phase differences between the stimuli, are no different than the summation value when the stimuli are separated by a phase difference of 180° .

Additional analyses looked at the distinction between probability and neural summation. Each of the summation values were compared to the *a priori* values of 1, 1.25 and 1.4 using a single variable t-test to see if either probability or neural summation was in operation over the different phase angles. Both groups show a

Figure 26: This figure shows the binocular summation values that have been averaged from the horizontal and vertical gratings. Both groups are represented at all phase differences.

**Mean Binocular Summation values for
vertical and horizontal gratings**



summation ratio significantly greater than 1 for all phase angles.

The Normal group shows summation values that are significantly greater ($p < .05$) than 1.25 but not significantly different from 1.4 for the phase angles from 0° to 90° . After this point, from 112.5° to 180° , the Normals exhibit summation values significantly less than 1.4 but not significantly different from 1.25.

At all phase angles the stereoblind group shows binocular summation values at least equivalent to, if not greater than, the *a priori* value of 1.25. At phase angles of 0° and 22.5° the stereoblinds show a summation value significantly greater than probability summation, but not significantly different from 1.4; the value associated with neural summation.

Discussion

The robust finding that stereoblind individuals show binocular summation has been upheld in this study. In fact, the stereoblind subjects show evidence of neural summation when the phase difference between the two monocular images is at a minimum. This result could be the influence of a rather low spatial frequency. Holopigian, Blake and Greenwald (1986) report that binocular summation values are at their peak when spatial frequency is low. As the spatial frequency increases the amount of summation decreases. In the previous experiment (Expt VIII), the summation values were obtained with a stimulus spatial frequency of 2.5 c deg^{-1} rather than the present test stimulus of $.4 \text{ c deg}^{-1}$. Thus the high summation values at 0° and 22.5° could be reflective of the low spatial frequency tested.

Wilcox (1992) found differences in the pattern of binocular summation values for vertical versus horizontal mismatched gratings that were not replicated in the present study. Her pattern of results for the vertical gratings followed a completely opposite pattern to those for the horizontal gratings. The results from the present study showed a pattern of results for both the vertical and horizontal gratings that were similar to the pattern of results for Wilcox's (1992) horizontal gratings. Her gratings were presented to individuals with normal stereopsis and she reasoned that the difference was due to stereoscopic information present in the vertical gratings. The design of her apparatus was slightly different and this may be a reason for the differing results. Wilcox's subjects viewed a single monitor and the two fields of the display were physically separated by a nasal septum. Due to this design, the subjects had to wear prisms to maintain fusion. It is possible that vergence movements induced by this setup, may have influenced activity within the stereoscopic system for the vertical stimulus condition, whereas the haploscopic presentations used in the present study may not have led to any enhancement.

It is apparent that the Stereoblind group are showing a binocular advantage. Their binocular summation values are significantly different from 1. However, there are clear differences between the Normals and the Stereoblinds. The Normal group consistently maintains summation values greater than 1.25 whereas the summation values for the Stereoblind group are not significantly different from 1.25 or 1.4. The summation values associated with 0° and 22.5°, for the Stereoblind group, may suggest levels closer to that of neural summation, but the results from the ANOVA

revealed no significant differences in summation values across all of the phase angles tested.

It is obvious that the mismatch of monocular stimuli affects the Normal group such that the level of binocular summation decreases as the mismatch, or phase difference, becomes greater. This effect is not apparent with the Stereoblind group. These results raise the question as to why the stereoblinds do not achieve higher summation values at the smaller phase differences?

To address this issue, the results from the Normal group must be explained. Their results support the argument that the additional purely binocular channel helps mediate detection when stimuli are in phase and thus the binocular summation is high. As the phase differences become greater than 90° , the effect of the purely binocular channel disappears such that the summation decreases. In the case of the Stereoblinds, the additional binocular channel does not appear to operate to mediate detection at the smaller phase differences. This results in a level of summation that is equivalent to the point at which the effects of the purely binocular channel disappear in the Normal group. At the larger phase difference the Normals and Stereoblinds achieve more or less the same level of summation. This must be accomplished by binocular neurons other than those of a purely binocular nature.

Hammond (1991) describes two types of phase related binocular neurons in the cat cortex that are relevant to the present discussion. He presented moving gratings whose interocular positional phase relationship was varied and found neurons responsive to positional phase differences (phase-specific) whereas others were phase-

insensitive. Hammond (1991) suggests that these neurons represent a two-stage mechanism for binocular convergence. The phase-insensitive binocular cells would signal approximate correspondence between the two retinal images. The difference for the phase-specific cells is that they would be more concerned with the finer differences such as those present during stereoscopic viewing. If taken in relation to the present study, Hammond's (1991) results could be interpreted to indicate that the Stereoblind group have the phase-insensitive binocular cells capable of mediating some connections between the two eyes, but not the binocular phase-specific cells necessary for refined match as in stereopsis.

Experiment IX -- Subthreshold Summation

Introduction

The previous experiment on binocular summation has shown that stereoblind individuals show evidence for binocular summation at a level associated with probability summation. In some circumstances, these individuals even exhibit neural summation. Therefore, it is possible that the stereoblind individuals still maintain a level of binocular interaction beyond that of the either-eye channel. The following experiment on subthreshold summation is one way to test if the two eyes are operating collectively when a binocular advantage occurs.

Blake and Levinson (1977) have explored subthreshold summation in normals.

This procedure involves subthreshold stimulus presentations to the non-tested eye in order to affect the threshold in the tested eye. The simultaneous presentation of the subthreshold grating to the other eye significantly lowers the threshold for the tested eye (Blake and Levinson, 1977; Wilcox, 1992). This improvement in threshold, found during binocular testing, has been attributed to a binocular channel sensitive to simultaneous stimulation of both eyes (the purely binocular channel).

Wilcox (1992) has used adaptation techniques, along with subthreshold presentations, to differentially adapt the purely binocular channel. She reasoned that if the purely binocular channel mediated summation, then it should be possible to reduce summation by making this binocular channel less sensitive. Conversely, summation should remain unchanged if the adaptation does not affect the purely binocular channel. This is precisely the pattern of results she obtained.

The following experiment used the pattern of adaptation used by Wilcox (1992). One adaptation condition involved continuous binocular adaptation in order to affect the purely binocular channel. The other adaptation condition did not affect the purely binocular channel, but alternately adapted each eye. It was expected that summation would decrease after binocular adaptation but remain stable after alternating adaptation. Subthreshold summation was measured in individuals with and without stereopsis. If the continuous binocular adaptation condition affected the Stereoblind group in a similar manner to that of the Normal group, it could be concluded that the Stereoblind group retains a set of binocular neurons, capable of functioning at threshold, that reflect the characteristics of a purely binocular channel.

Method

Subjects and Apparatus

Three of the subjects from the Stereoblind group and 2 of the Normal subjects from Expt VIII participated in this experiment. The apparatus was identical to that used in Experiment VIII. The spatial frequency of the gratings was kept constant at 2.5 c deg^{-1} with an orientation of 0° .

Procedure

Each session was divided into four successive stages. After each stage the computer performed the appropriate calculations and initiated the next stage. These stages are summarized in Table 3.

The first stage recorded contrast threshold measurements for the preferred and nonpreferred eyes. This was accomplished using a single-staircase procedure described in preceding experiments. These baseline measurements continued until 15 reversal points were made, fourteen of which were used in the final calculation of the monocular contrast threshold. The threshold for the nonpreferred eye was noted only to be certain that the contrast of the subthreshold grating did not exceed the detection threshold for that eye. The important measure from this stage was the contrast threshold for the preferred eye.

Before initiating the second stage, a subthreshold grating, whose contrast was .15 log units below that of the contrast threshold for the preferred eye, was calculated. This subthreshold grating was presented to the nonpreferred eye while contrast thresholds were recorded for the preferred eye. A dual-staircase procedure was used,

Table 3: The four stages for the threshold measurement and adaptation paradigm of Experiment IX

Stage #	Measurement or Adaptation Paradigm
Stage #1	(i) Measure monocular threshold in the preferred eye (MT_1) and in the nonpreferred eye (ii) Calculate the contrast of the subthreshold grating to be presented to the nonpreferred eye
Stage #2	(i) Measure binocular threshold (BT_1) while nonpreferred eye views subthreshold grating (ii) Calculate preadaptation summation $\text{Pre} = MT_1/BT_1$
Stage #3	(i) Alternating adaptation OR (ii) Continuous binocular adaptation
Stage #4	(i) Measure monocular threshold (MT_2) in the preferred eye while nonpreferred eye views blank screen AND (ii) Measure binocular threshold (BT_2) while subthreshold grating is presented to nonpreferred eye (iii) Calculate postadaptation summation $\text{Post} = MT_2/BT_2$

but the termination point was lowered to 9 reversals on each staircase.

Stage three included adaptation to a grating of 25% contrast for a period of two minutes. There were two types of adaptation. Alternating adaptation consisted of presenting the adapting stimulus to one eye and then the other at an alternation rate of 1.5 s. Continuous binocular adaptation simply presented the adapting stimulus to both eyes simultaneously for the entire adaptation period.

In the final stage, thresholds were recorded for the preferred eye, with and without the subthreshold grating in the nonpreferred eye. Each test condition consisted of two separate sets of randomly interleaved dual-staircases, run simultaneously, until the 9 reversal limit was reached.

The ratio of the contrast threshold for the preferred eye (from stage one) and the subthreshold summation value (from stage two) was used to represent the amount of pre-adaptation summation. Post-adaptation summation was calculated as the ratio of threshold elevation in the preferred eye (without the subthreshold stimulus), to the threshold obtained with the subthreshold grating present (both values from stage 4). The comparison of interest was between the two summation ratios obtained before and after adaptation. Each subject completed 2 sessions of alternating adaptation and 2 sessions of binocular adaptation.

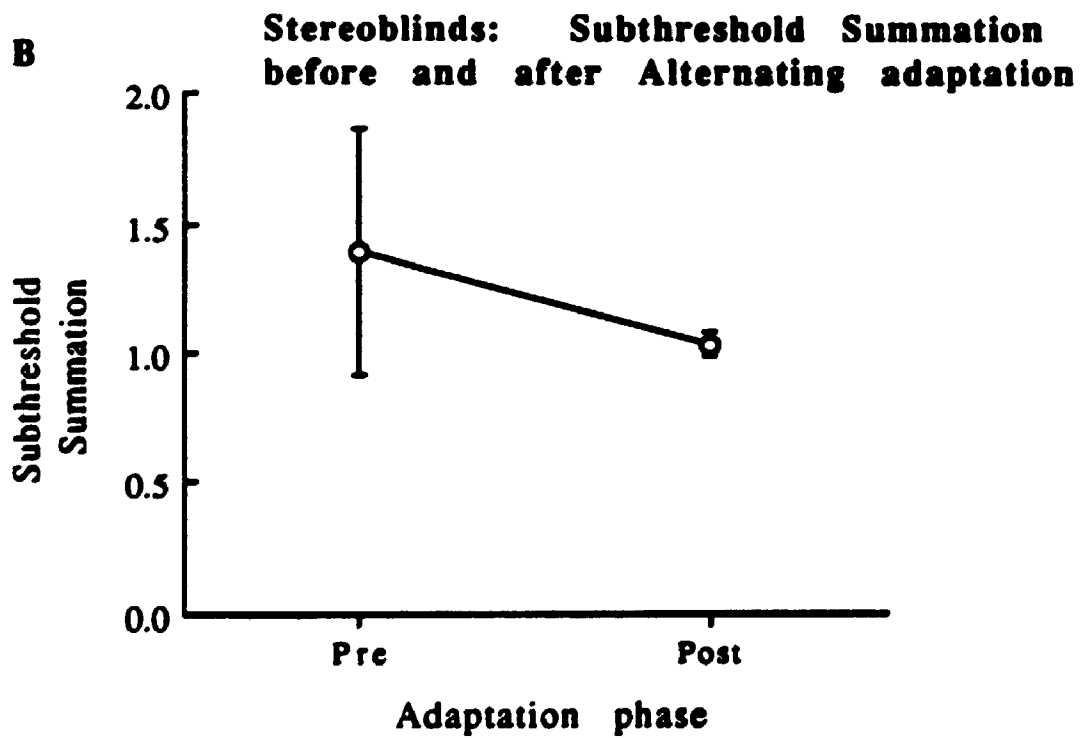
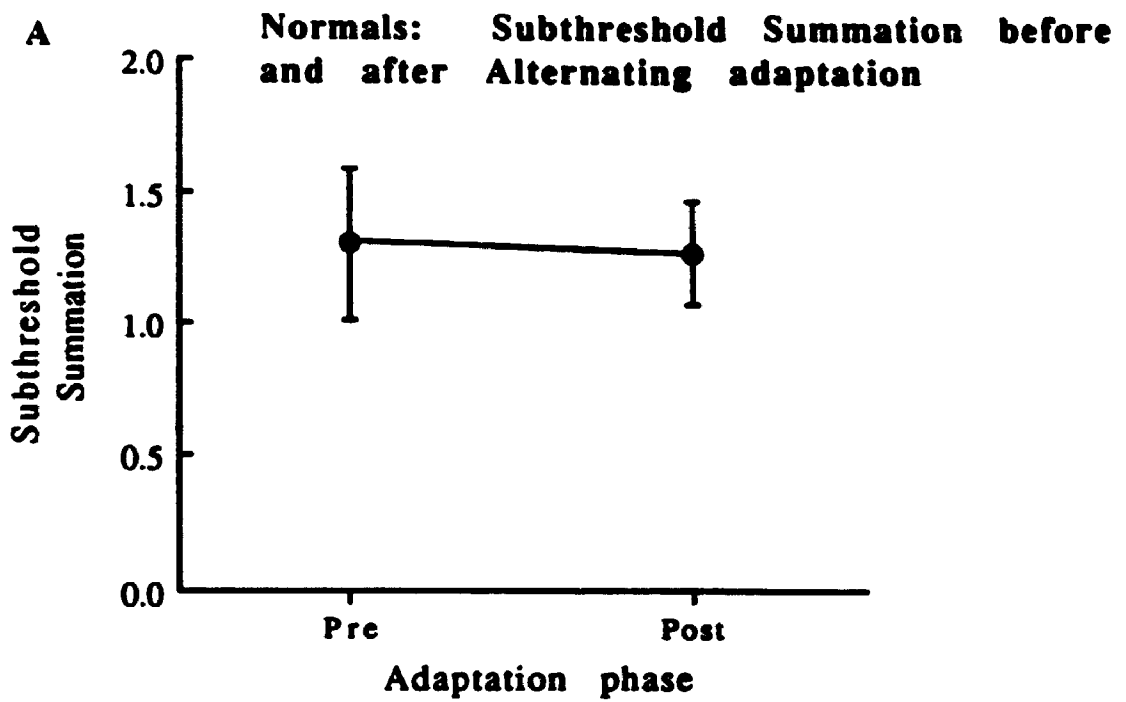
Results

Figures 27A and 27B shows the results from the Normal and Stereoblind group for the alternating adaptation condition. Both groups behave similarly. There is no

Figure 27: This figure shows the pre- and post-adaptation summation ratios for alternating monocular adaptation. The pre-adaptation ratio was calculated as the contrast threshold in the preferred eye divided by the threshold recorded with a subthreshold grating present in the other eye. To calculate the post-adaptation summation ratio, the contrast threshold in the preferred eye (following adaptation) was divided by the threshold measured with the subthreshold grating in the other eye (again following adaptation).

Figure 27A: Normal group

Figure 27B: Stereoblind group



significant difference between the two groups on pre-adaptation summation or post-adaptation summation ($t(3)=0, p=.50$). The same was true for the binocular adaptation condition. This is illustrated in Figures 28A & 28B.

A repeated measures ANOVA revealed a significant interaction between pre- and post-subthreshold summation values and adaptation conditions ($F(1,3)=15.85, p<.05$). Post-hoc tukey tests showed that the difference was because individuals showed a decrease in subthreshold summation after binocular adaptation but not after alternating adaptation.

Discussion

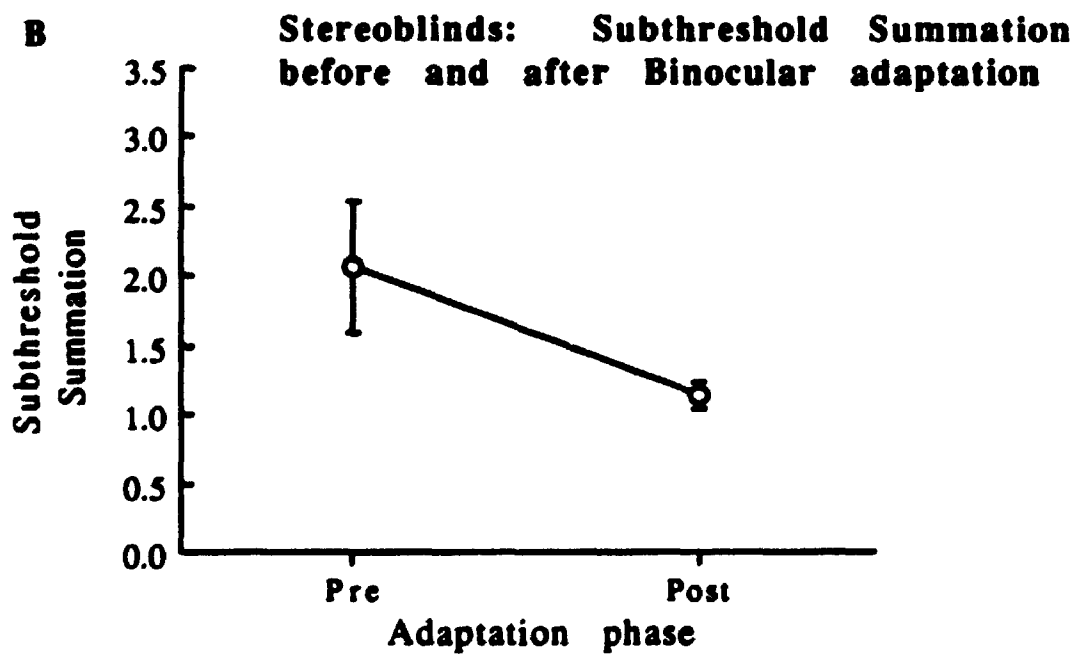
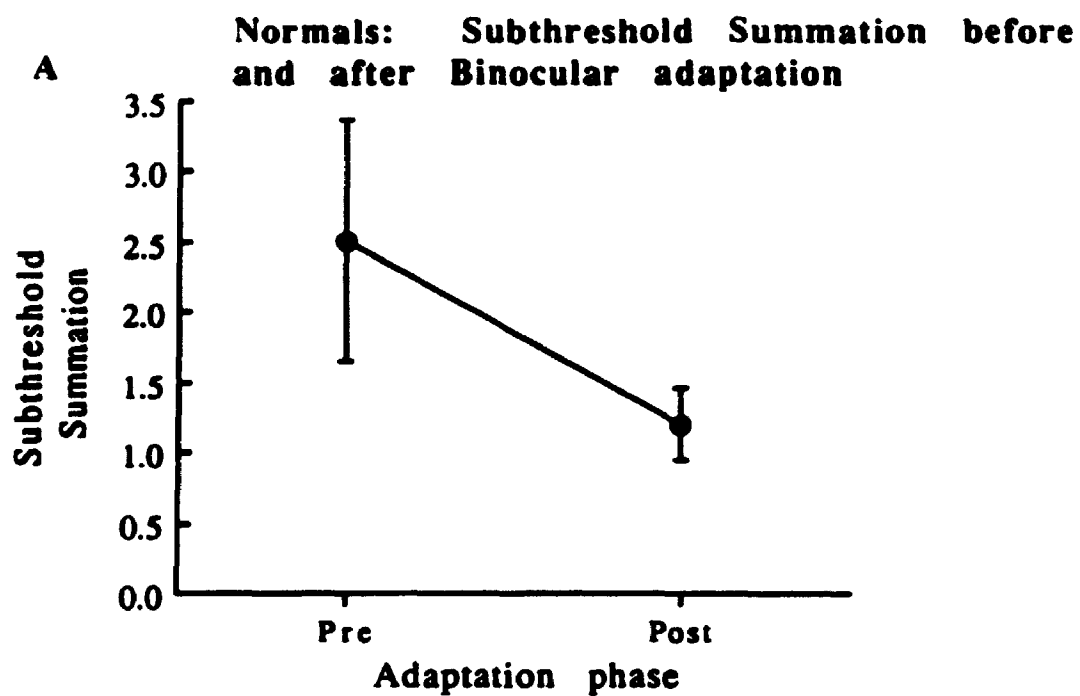
It is clear that both groups exhibit a drop in binocular summation after binocular adaptation but not after alternating adaptation. These data suggest that the purely binocular channel is affected during binocular adaptation. This causes the binocular threshold to increase which results in a decrease in summation for the post-adaptation phase. This was expected for the Normal group. The fact that this occurred for the Stereoblind group reveals that a binocular mechanism sensitive to binocular adaptation is still functioning in these individuals. The data are reinforced by the finding that summation does not decrease after alternating adaptation.

Not only do these results indicate that a purely binocular channel is present in the Stereoblind subjects, but that it is active at threshold. However, its involvement at threshold needs to be clarified. In previous experiments, the eyes were not adapted simultaneously and the Stereoblinds system behaved as though there were no

Figure 28: This figure shows the pre- and post-adaptation summation ratios for continuous binocular adaptation. The pre-adaptation ratio was calculated as the contrast threshold in the preferred eye divided by the threshold recorded with a subthreshold grating present in the other eye. To calculate the post-adaptation summation ratio, the contrast threshold in the preferred eye (following adaptation) was divided by the threshold measured with the subthreshold grating in the other eye (again following adaptation).

Figure 28A: Normal group

Figure 28B: Stereoblind group



contribution from an unadapted purely binocular channel. It could be that this channel does not contribute to mediate detection unless it is first activated by a high contrast adaptation. After the continuous suprathreshold binocular adaptation of the present experiment, the Stereoblinds show evidence of a diluting effect from the purely binocular channel. Thus, the only time that we see signs that such a channel exists is when it is adapted and made *less* sensitive. At threshold, this channel does not exert any influence unless first adapted to a high contrast stimulus. Interestingly, the pre-adaptation measures, which do not include any suprathreshold stimulation, are often more variable than the post-adaptation measures. The variability could be reflective of the unpredictable involvement of the binocular channel at threshold such that the binocular advantage would be altered and thus cause summation to be more variable.

These results augment the findings from the previous experiment to show that stereoblinds retain binocular cells characteristic of the purely binocular channel. Obviously, these binocular cells are not the same as those involved in stereopsis.

Chapter 5 – Summary and Conclusions

The present set of experiments provides very strong evidence for the existence of binocular neurons in individuals with anomalous early visual histories. The following account will summarize the findings of each experiment and comment on the conclusions that can be drawn.

Although the first experiment did not deal directly with binocular organization, it was an important finding in itself. The results from Experiment I revealed that interocular transfer can be considered a reliable measure. It is interesting that this issue has not been dealt with previously. Interocular transfer is a measure commonly used in visual aftereffect studies and its value has played an important role in the quest for knowledge regarding the binocular organization of the human visual system. With this assurance of reliability, a greater level of confidence could be placed in the results from the next three experiments. The fact that IOT remains constant has certain physiological implications as well; it suggests that there is a stable population of neurons that is involved in IOT. This notion will be commented upon in further detail after reviewing the remaining experiments.

It is readily apparent from the results of all three aftereffect studies (MAE, TAE and CTE) that there is no evidence of a difference between the two main groups. Many individuals with anomalous early visual histories display normal levels of interocular transfer. In the present study, there were never any differences in the average percentage of interocular transfer found between the Normal and A.E.H.

groups, although some individuals failed to show transfer in some experiments. In addition, there were no statistically significant differences in the amount of interocular transfer between the four A.E.H. subgroups. Since interocular transfer occurs via binocular neurons, it is evident that the individuals tested were not lacking in this particular subset of binocular neurons.

The fact that there was no relationship between the level of IOT and the level of stereoacuity replicates and extends the findings of Mohn and van-Hof von-Duin (1983). Some individuals with poor stereopsis showed IOT at a level equivalent to that of the Normal group. This reinforces the notion that IOT is not mediated by the same binocular mechanism that subserves stereopsis.

Although the question of interest was the amount of IOT shown by stereodeficient individuals who had a history of early visual problems, we were surprised to find that four of the five individuals in the A.E.H. subgroup, with a stereoacuity equivalent to that of the Normal group (" ≤ 25 "), were strabismic from an early age and all had surgery. Moreover, three of these individuals had surgery at 7 years of age or later (one at age 12). This age is far beyond the sensitive period of 3 years of age suggested by Banks et al. (1975) and Hohmann and Creutzfeldt (1975). In general, people have tended to make the assumption that stereodeficiency is an absolute consequence of strabismus. These results suggest that strabismic individuals can show normal stereoacuity levels.

Having established that IOT is common in stereodeficient individuals, the next step was to evaluate the kinds of binocular channels that might exist in stereoblinds.

This was done in Experiments III - VI by examining the pattern of aftereffect sizes. The pattern of results for the Normal group were quite different from the A.E.H. group for the tilt aftereffect during both monocular and alternating adaptation. This difference was also apparent for the contrast threshold elevation with monocular adaptation. In each case, the Normal groups data was consistent with two binocular channels. For the A.E.H. group the data were more consistent with the presence of only a single binocular channel in the monocular and alternating tilt aftereffect. The results from both the monocular and alternating contrast threshold elevation aftereffects were not as telling. Nevertheless, there was a noticeable difference in the overall pattern of results between these two groups. For the most part, the pattern of results obtained with visual aftereffects suggest the involvement of at least one type of binocular channel.

The implication that the A.E.H. group could have either-eye neurons was readily acceptable. However, up to this point, there did not seem to be any *a priori* reason to assume that this group would have any purely binocular neurons. In Experiment VII the stereoblind subgroup showed evidence of probability summation. Although this finding was to be expected on theoretical grounds, it was at odds with the highly quoted findings of Lema and Blake (1977) and the findings reviewed by Blake, Sloane and Fox (1981). The present results suggest that *strabismic* individuals are capable of using information from both eyes. Nevertheless, the finding that the Normal group maintained a higher level of summation, still points to a less than normal population of binocular neurons for the A.E.H. stereoblind subgroup.

In Experiment VIII, the Stereoblind group showed levels of probability summation across all the interocular phase differences. In fact, there was some indication that these individuals could achieve neural summation. These results also indicated that the Stereoblind group was able to encode information from both eyes, although phase-matched stimuli provided no advantage over stimuli that were not phase-matched. In the Normal group, the additional purely binocular channel helps mediate detection when stimuli are in phase and thus the binocular summation is high. In the case of the Stereoblinds, the additional binocular channel does not appear to operate to mediate detection at the smaller phase differences. At the larger phase differences the Normals and the Stereoblinds maintain a level of probability summation. These findings point to the absence of a purely binocular channel during a threshold task in the Stereoblind group.

The results from Experiment IX came as a surprise. The use of subthreshold summation and binocular adaptation procedures pointed to the presence of purely binocular neurons in the Stereoblind group. In both groups, the binocular summation values are smaller after binocular adaptation. According to the logic of subthreshold summation, this indicates that the Stereoblind group does have binocular neurons characteristic of the purely binocular channel. The fact that they were not evident until this time suggests that the newly introduced adaptation condition could be responsible. Perhaps this channel does not exert a diluting effect unless it is first adapted to a suprathreshold stimulus. However, during monocular adaptation, the purely binocular channel does exert a diluting influence during threshold testing on

Normals but not with the stereoblinds. Therefore, it appears that further testing is required to determine the characteristics of these binocular neurons.

Our findings that stereoblind individuals show evidence for summation points to a separation between binocular summation and stereopsis. Previously, there have been numerous suggestions that the same binocular neurons that mediate stereopsis are also involved in summation (von Grunau, 1979; Levi et al., 1981). In addition, the results from the final experiment suggest that the Stereoblind group does show evidence of binocular neurons thought to be part of the same system that mediates stereopsis. This leads us to suggest that a simple distinction between two types of binocular neurons is not sufficient. What seems more likely, is that of a modular organization. This would include multiple binocular channels, each of which deals with different, or even overlapping functions.

Within the physiological literature, Ferster (1981) has suggested that different neurons tuned to different disparities may be involved in different functions. Moreover, these neurons are found in different areas of the visual cortex. A parallel organization could be suggested for binocular neurons in general. Perhaps it is the case that certain combinations of binocular channels are involved in summation which are distinct from those binocular channels involved in stereopsis.

Anderson and Movshon (1989) suggest a model of binocular organization based on the distribution of ocular dominance channels. Each channel would be different in terms of its relative sensitivity to the two monocular signals. However, there would be no distinctly monocular channels. Anderson and Movshon (1989) do not consider

this a limitation since they postulate channels that are very nearly monocular in nature; a binocular channel may only receive 5-10% of its input from one eye and the majority from the other. This line of reasoning, which implies that the visual system is highly binocular is not uncommon (Gardner and Raiten, 1986).

The present results point to the existence of binocular neurons, previously thought to be absent, in individuals with anomalous visual histories. Nevertheless, it is also clear that these same individuals do not have the same organization as individuals with normal binocular vision since their pattern of results were often different. The present findings point to the complexity of the organization of the visual system. Clearly, simple models of independent channels are inappropriate and it is more likely that the visual system is made up of more than two distinct binocular channels.

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