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PSYCHOPHYSICAL STUDIES OF BINOCULAR INTERACTIONS IN HUMANS

by

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Submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

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ABSTRACT

Psychophysical investigations of binocular interactions have shown that there are at least two binocular channels in the human visual system. In addition to an interocular channel that responds to input to either eye, there is evidence of a binocular channel that acts as a logical AND-gate. This second binocular mechanism will only respond to simultaneous stimulation of both eyes with similar images. Support for the existence of this 'AND' mechanism has been provided by adaptation (Wolfe & Held, 1981, 1982; Wilcox, Timney, & St.John, 1990), and detection experiments (Cohn & Lasley, 1976; Cogan, 1987).

In predicting the results of adaptation experiments several investigators have adopted a 'neural averaging' hypothesis which proposes that the output from all available monocular and binocular channels is averaged to produce the final percept. Experiments I and II evaluated this suggestion and a second proposal that all channels are independent, and that detection is mediated by the most sensitive of these channels. The results of both studies showed that there _is_ interaction between the neural channels.

While there is convincing support for the existence of an AND channel, little is known about its response characteristics. Experiments III through V examined the temporal aspects, threshold sensitivity, and interocular spatial phase sensitivity, of an AND mechanism. Collectively, these experiments support the assumption that the AND channel requires binocular stimuli that are similar along a number of dimensions. The final experiment investigated a potential functional role of the AND mechanism in human vision. In this study, both adaptation and subthreshold summation procedures were used to assess the contribution of the AND channel to binocular summation. The results demonstrated that an AND mechanism makes a significant contribution to binocular summation.

It has been argued previously (Wolfe, 1986) that an AND mechanism is important to stereoscopic vision. Given Wolfe's assertions and the results of Experiment VI, it appears that the output of the AND channel is not necessarily restricted to a single process, but could contribute to several visual tasks, including binocular summation and stereopsis.

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CHAPTER ONE

1.0 Introduction

Prolonged viewing of a visual stimulus will create predictable distortions in subsequently seen stimuli. For example, after gazing at tilted lines for a period of time, vertical lines will appear tilted in the opposite direction. To date, investigators have identified aftereffects of movement (Wohlegemuth, 1911), curvature, (Gibson, 1933), orientation (Gibson and Radner, 1937), size (Kohler and Wallach, 1944), contrast (Blakemore and Campbell, 1969), and spatial frequency (Blakemore and Sutton, 1969). With few exceptions, these aftereffects can be classified as either threshold or contour displacement aftereffects, where the former refers to changes in detectability of near-threshold stimuli and the latter to distortions in the perception of suprathreshold stimuli.

1.1 Neural excitation and aftereffects

The advances made in neurophysiological recording techniques over the past 35 years have made it possible to identify the receptive fields of individual neurons in mammalian visual pathways and to specify their optimal stimulus characteristics (Kuffler, 1953). For example, Hubel and Wiesel (1962) demonstrated that single neurons respond selectively to particular stimulus parameters such as size, orientation, and/or direction of movement. They also noted that the majority of neurons are sensitive to input from either eye and can be categorized with respect to their relative eye dominance (degree of preference for input to one of the eyes).

The selectivity of visual neurons to a number of stimulus characteristics, provides the basis for a physiological explanation of both threshold and contour displacement aftereffects. In the case of the threshold elevation aftereffects, the initial inspection period presumably drives a specific group of cells, or channel, that is optimally responsive to gratings of a particular orientation and spatial frequency. Over time, the neurons within this channel become less responsive, and require a greater amount of excitation in order to reach an activity level sufficient for detection. Thus, when presented with a stimulus of lower contrast or intensity, the adapted channel will not respond - the subject will not see the stimulus.

The same response property, response reduction following prolonged exposure, underlies a neural explanation for contour displacement aftereffects. However, such aftereffects do not rely on the minimal stimulation necessary for detection, but on the combined activity of groups of cells. Consider, for example, the motion aftereffect, where presentation of a stationary test stimulus follows exposure to an identical inspection stimulus, drifting in a single direction. Typically, when viewing the test stimulus, the viewer experiences apparent movement in the direction opposite to that of the adapting grating.

Drawing from both physiological recording from the rabbit retina, and psychophysical observations of human subjects, Barlow and Hill (1963) illustrated a neurophysiological explanation for the motion aftereffect. They proposed that motion is signalled by directionally sensitive pairs of neurons. The members of the pair signal opposite directions of movement; if a rightward-moving stimulus is presented the rightward-sensitive cell increases responding while the leftward-sensitive cell remains at a resting level of discharge, and vice versa. If the channel is continuously activated by movement in one direction its level of activity will eventually drop. When the immobile stimulus is then viewed, the spontaneous activity level of the leftward-sensitive cell is higher than that of the suppressed rightward-sensitive cell; therefore the ratio of firing will erroneously signal movement to the left (the direction opposite to that used for adaptation).

The tilt aftereffect can be similarly explained; cortical cells respond optimally to lines of a given orientation, and the response intensity gradually decreases as the orientation is moved away from the optimal. As a result, the activity profile of a group of cells, each sensitive to a different degree of tilt, forms a distribution with its peak corresponding to the optimal orientation.

Adaptation creates a depression in sensitivity in this distribution that corresponds to the orientation of the adapting stimulus. An asymmetrical activity profile now remains, which resembles the shape normally present when viewing a line tilted in the direction opposite to that of the adapting stimulus. During testing, the physically vertical line will appear to be shifted away from vertical, corresponding to the skew of the activity profile (Sutherland, 1961; Frisby, 1980).

There has been some debate regarding how adaptation is achieved. Early descriptions of the physiological basis of neural aftereffects have assumed that the response reduction following adaptation is due to fatigue or inhibition of the units that are active during testing. An alternative to this explanation is that neural adaptation allows the visual system to adjust its sensitivity in response to prior experience (Greenlee & Heitger, 1988). That is, according to a gain control account of adaptation, the decreased sensitivity to absolute contrast that follows adaptation is a side-effect of obtaining improved sensitivity to contrast differences (Greenlee & Heitger, 1988; Ohzawa, Sclar & Freeman, 1985). According to the preceding account, adaptation serves a functional role in human vision. The precise form of neural activity underlying this gain control mechanism is not fully understood. However, recently Vidyasagar (1990) has proposed that the changes in sensitivity reflect the modification of excitatory connections in co-operative networks of cortical cells.

1.2 Selective adaptation

The preceding descriptions of the neural mechanisms of aftereffects have permitted them to evolve from a phenomenon to be explained, to a useful psychophysical tool. That is, it has become common to use aftereffects, such as those of tilt and motion, as a means of examining the operation of narrowly tuned channels in the human visual system. If the visual system contains functionally distinct groups of neurons with specific response characteristics it should be possible to isolate their activity. Presumably, exposing a subject to a stimulus for an extended period of time will selectively affect similar groupings of cells. Having selectively adapted one class of neuron it should then be possible, by recording the resulting sensory distortion, to determine its perceptual contribution.

A selective adaptation procedure was used by Blakemore and Campbell (1969) to examine orientation and size selective neurons in the human visual system. They reported that the maximum aftereffect was obtained when the adapting and test gratings were of the same orientation and spatial frequency. Exposure to the adapting grating also created a depression in sensitivity for gratings of similar frequencies; this influence decreased as the difference between the spatial frequencies of the adapting and test gratings approached one octave. They concluded that "the adapting pattern is principally depressing the sensitivity of some 'channel' independently of others, and that this channel is adapted by a limited range of spatial frequency" (Blakemore and Campbell, 1969, p.248).

Visual aftereffects and cortical binocularity

Physiological investigations have found that, just as the majority of cortical cells are tuned to a range of orientation and spatial frequencies, many of these cells are affected to different degrees by input to either eye. Visual aftereffects have been used to determine the response characteristics of these binocular channels in the human visual system.

A characteristic of visual aftereffects critical to the study of cortical binocularity is that the majority of aftereffects, such as those of tilt and threshold elevation, will transfer interocularly. That is, following monocular exposure to the adapting stimulus, an aftereffect can be measured in the unadapted eye. Typically the transferred effect is about 50-70% of the aftereffect measured in the adapted eye. The fact that interocular transfer (IOT) takes place has been particularly relevant to the investigation of cortical binocularity, for it is proof of the presence of the neurons that receive and process input from both eyes.

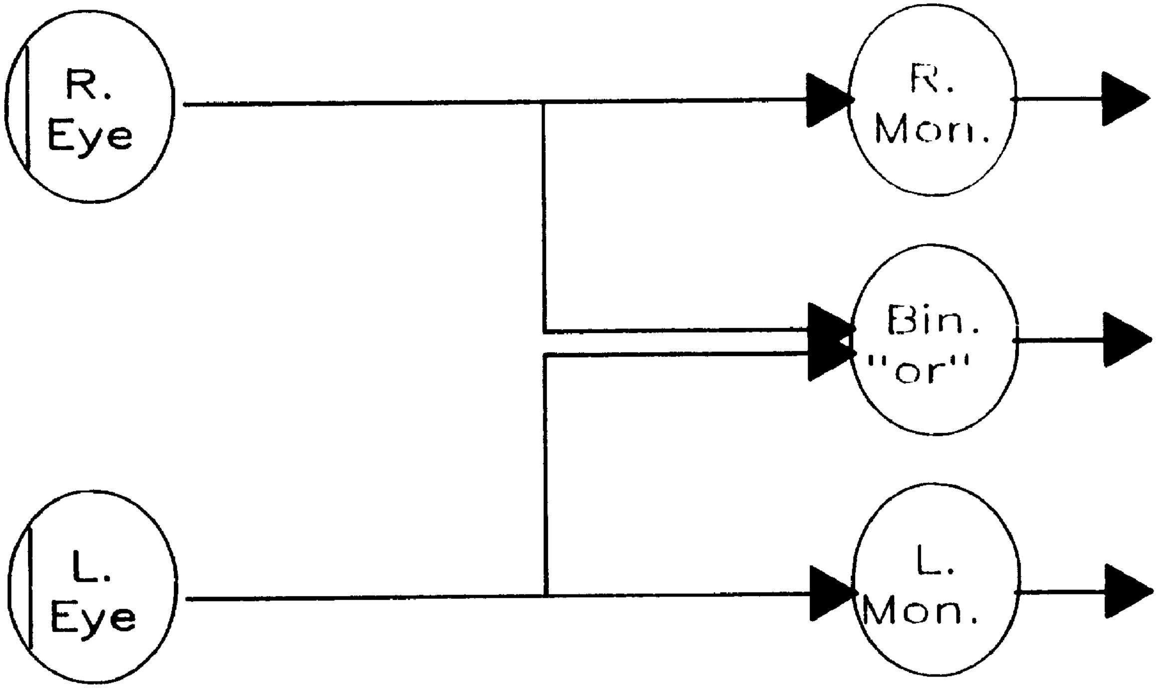
The physical location of the binocular cells, which are responsible for IOT of visual aftereffects, is thought to be the visual cortex, because it is the first binocular centre in the visual system. Proof of the post-retinal location of visual aftereffects has been provided by studies showing that IOT will occur for most aftereffects even when the adapted eye is pressure blinded (motion - Barlow and Brindley, 1963; contrast elevation - Blake and Fox, 1972; and tilt - Ware, 1973).

1.3 The nature of binocular channels: the Binocular 'OR' Model

While the occurrence of IOT is strong evidence of the presence of binocular neurons in the visual system, it says little about the nature of these units. However, it is possible to examine the organization and operation of these channels using procedures such as selective adaptation; the results of these studies can then be used to formulate and test models which describe the properties of various channels. Moulden (1980) constructed one such model, which I will refer to as the OR model (Figure 1). Hubel and Wiesel (1962) classified neurons into seven categories, ranging from exclusively monocular left-eye cells (1) through those activated equally by input to either eye (4) to exclusively monocular right-eye cells (7). For the sake of simplicity, Moulden reduced Hubel and Wiesel's seven channel description of cortical binocularity, dividing the cells into three distinct classes: left monocular (responding to input to the left eye only), right monocular (responding to input to the

Figure 1. Moulden's original three-channel model, with the left monocular (L.Mon), right monocular (R.Mon), and binocular OR ("Or") channels. Lines indicate unidirectional pathways, which represent visual input/output. The model assumes independent, equally weighted channels whose activity is pooled when more than one channel is driven.

The "OR" Model



right eye only), and binocular (responding to input to either the left eye, or the right eye, or both eyes simultaneously).

In formulating predictions of the operation of these various channels Moulden made two assumptions; that the three sets of neural units operate independently of one another, and that the size of the aftereffect is a function of the proportion of cells that have been adapted and are then driven during testing. Therefore, the aftereffect represents the pooled activity of all the cells driven during testing. Units that are adapted during the inspection period, but not activated in the test period do not contribute to the aftereffect. Also, the output of unadapted neurons driven in the test period, serves to reduce the aftereffect (Moulden, 1980; p.43).

The channels proposed by Moulden's OR model, and the assumption of neural averaging, provide an explanation for the reduced size of interocular transfer. When one eye is exposed to a stimulus, the corresponding monocular and the binocular processes are adapted. When testing the adapted eye, only the adapted channels are activated, creating a maximum effect. But when measuring the aftereffect in the unadapted eye (IOT), the output of the monocular units of the unadapted eye combine with the adapted binocular processes, producing a lowered aftereffect (Moulden, 1980). It should be noted that the predicted incompleteness of IOT is consistent with the majority of the aftereffect data (Mitchell and Ware, 1974; Blake, Overton, and Lema-Stern, 1981).

The preceding logic can also be used to predict the relative sizes of aftereffects when a third, binocular, test condition is introduced to the monocular adaptation paradigm. As outlined above the direct effect will be larger than the transfer effect because in the latter condition only half of the tested channels will have been adapted. In comparison, during binocular testing, all three available channels will be active, two of which have been adapted (one monocular and the binocular OR). Thus two-thirds of the tested channels have been adapted, producing a larger binocular than transfer effect.

It should be noted that these predictions specify the **proportions** of channels contributing to the size of an aftereffect, therefore, although one-half of the available channels are activated in the transfer condition, the size of that aftereffect is not necessarily fifty percent of the direct effect. In fact, the actual magnitude of the transferred effect has been cited as being anywhere from fifty to one-hundred percent of the direct effect (Movshon, Chambers, and Blakemore, 1972).

Moulden (1980) used the monocular exposure paradigm to examine aftereffects induced by tilt and motion. His interpretation of the data appeared to be both qualitatively and quantitatively consistent with the simple binocular OR model. The pattern of results for both experiments showed a large direct effect, and the aftereffect in the binocular condition was greater than the transfer condition.

Moulden's results were consistent with an OR model, moreover, his conclusions were supported by independent investigations of a link between IOT and binocularity. At this time, it was generally assumed that there was only one binocular channel that processed all binocular information. Thus researchers such as Movshon, Chambers and Blakemore, (1972) argued that both stereopsis and IOT of aftereffects should be mediated by the same population of cells. Further, assuming that deficits in stereopsis result from a paucity of binocular cells, they predicted that stereoblind individuals would show significantly less IOT than subjects with a normal complement of binocular neurons. Initial measurements of IOT using stereoblind subjects confirmed these predictions, encouraging researchers to assume that a single binocular channel existed to mediate all binocular activity. It was later argued that not only were IOT and cortical binocularity related, but IOT could be used as an index of binocularity, as a means of assessing a subject's cortical binocularity (Mitchell and Ware, 1974).

In response to data from a variety of adaptation and detection/discrimination experiments, a number of researchers have started to question the completeness of the 3-channel OR model. These experiments, which will be described in more detail in subsequent sections, have led to the recent formation and evaluation of an alternative model (Blake et al., 1981; Wolfe and Held, 1981), which has been labelled an "AND model".

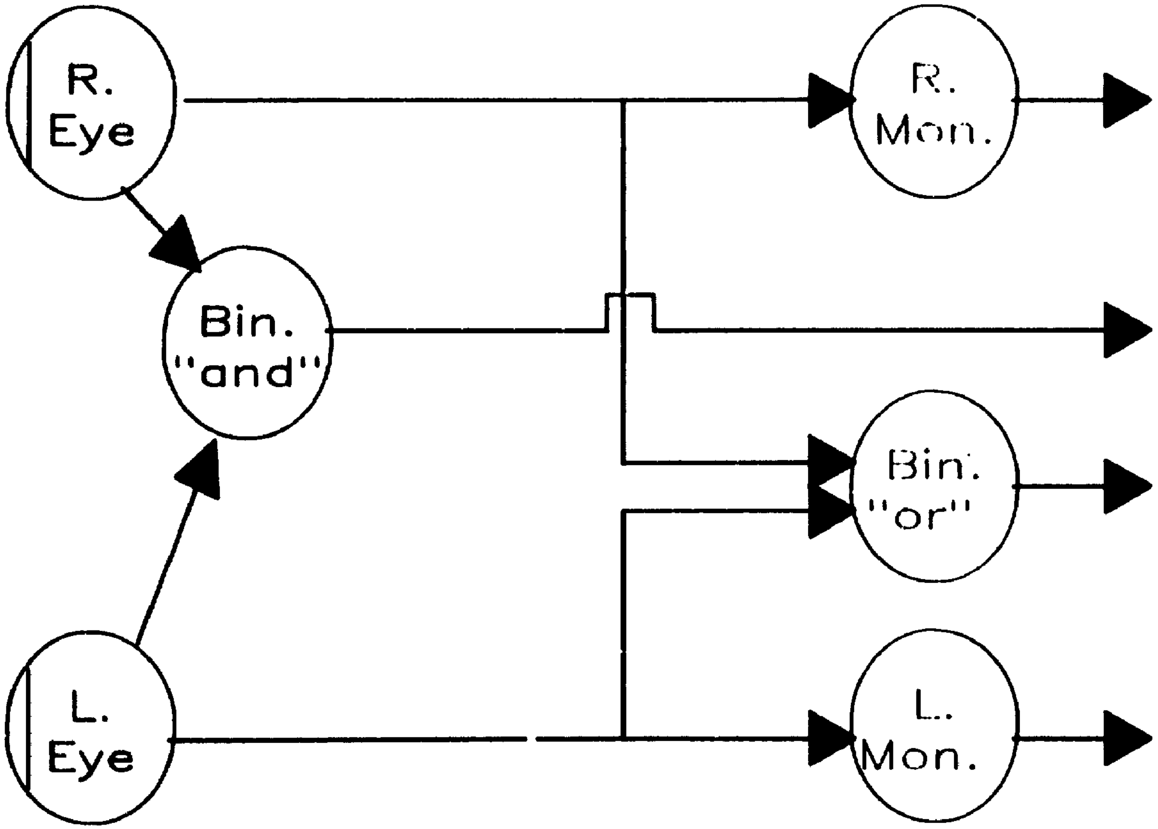
1.4 The nature of binocular channels: the Binocular 'AND' Model

The AND model is similar to the OR model in that it includes Moulden's (1980) original three neural channels, and makes the same assumptions about the combined activity of the various processes. The difference between the two is the presence of a fourth process, a exclusively binocular channel which acts as a functional AND-gate, for it will only respond to simultaneous binocular stimulation (Figure 2).

Wolfe and Held (1981,1982,1983) conducted a series of studies exploring the contribution of the AND channel to binocular vision. At the same time, several investigators had reported that, not only did some stereoblind subjects exhibit IOT, but often there was no consistent relationship between the degree of stereodeficiency and IOT (Hess, 1978; Buzzelli, 1981; Mohn and van Hof-Van Duin, 1983). Wolfe and Held (1983) interpreted this separability of stereopsis and IOT as support for their proposal that there are at least two binocular mechanisms in the human visual system. They argued that the AND channel forms the neural substrate of stereopsis, while the OR channel mediates IOT. Using their logic we could argue that stereoblind individuals who are unable to transfer visual aftereffects have neither the AND

Figure 2. Wolfe & Held's four-channel model "AND" model. The key is as for figure 1 with the addition of the And channel, representing the pure binocular process.

The "AND" Model



or OR channels. Those who do exhibit IOT must have interocular OR cells, but their AND cells are absent or deficient.

Wolfe and Held (1981) initially attempted to find evidence of the operation of an AND channel using the monocular exposure paradigm. Because their data confirmed their predictions, Wolfe and Held (1981) concluded that a second binocular channel does exist in the human visual system. However, Timney, Wilcox and St.John (1989) pointed out that neither Wolfe and Held's predictions nor their data were consistent with the AND model that they described. In response to this contradiction, Wilcox, Timney, and St.John (1990) replicated and extended these experiments, and found consistent support for the modified predictions, based on the AND model. In addition, the pattern of results obtained in their experiments replicated those of Moulden (1980). The discrepancy between the pattern of results reported by Wolfe and Held (1982) and those found by Moulden (1980), and Wilcox et al. (1990) is difficult to resolve. However, as Wilcox and her colleagues (1990) pointed out, a large portion of the problem may be attributed to the monocular adaptation protocol. That is, when the monocular exposure paradigm is used to study the contribution of the AND channel, the experimenter must show that there is no difference between the transfer and binocular test conditions - the statistical null hypothesis. Therefore, when using the monocular exposure paradigm to assess the activity of the AND channel, the experimenter is at a statistical disadvantage; unless the binocular and transfer test conditions are significantly different, no definite claims can be made about the status of the AND model. When trying to obtain evidence for an AND model it would be preferable to generate a positive prediction about the pattern of results which would support the presence of an AND channel.

Another problem, specific to the monocular exposure paradigm, is posed by the nature of the exposure and test conditions. During monocular exposure, different classes of binocular OR neurons will be affected to varying degrees, depending on their sensitivity to input from the exposed eye. Therefore, during binocular testing some of the unadapted or "less-adapted" OR cells could serve to dilute the aftereffect. The diluting influence of the proposed AND channel then will be confounded by the contribution of partially adapted OR cells.

Wolfe and Held (1982) also used an **alternating** monocular adaptation paradigm and the tilt aftereffect to test for the AND channel. The authors adapted subjects to a tilted line pattern first to one eye, then to the other, and this sequence cycled for the duration of the exposure period. During alternating adaptation the subject never views the exposure stimulus with both eyes simultaneously, therefore, the AND channel should not be affected by the exposure.

Subsequently, when the aftereffects are measured monocularly, the aftereffect should be strong because all of the channels involved in detecting the test stimulus were adapted (monocular and binocular OR). In contrast, when testing is binocular, the AND channel will respond, thus the aftereffect will reflect the combined activity of the two adapted monocular channels, the adapted interocular channel as well as the unadapted AND channel. Because it has not been adapted, the AND channel will signal the true position of the test stimulus and dilute the size of the aftereffect. According to the preceding logic, following alternating monocular adaptation the binocular aftereffect should be lower than each of the monocular aftereffects. This pattern of results has been obtained repeatedly, in Wolfe and Held's experiments, and in subsequent investigations (Wilcox et al., 1990).

Timney et al. (1989) have argued that alternating monocular exposure is preferable to monocular exposure for isolating the activity of the AND channel. As outlined above, the AND model predicts equivalent monocular effects and a lowered binocular effect following alternating exposure. Thus, this exposure paradigm is more powerful because a statistically testable hypothesis can be generated: if the AND channel is present there should be a significant difference between the monocular and binocular test conditions.

1.41 Evidence for an AND channel: Opponent adaptation experiments

A number of other aftereffect experiments provide evidence of the presence of two binocular channels in the human visual system. For example, Vidyasagar (1976) conducted an aftereffect study using the standard orientation-contingent color aftereffect technique (McCollough, 1965), but presented **opposite** color-orientation pairings under monocular and binocular conditions. For example, if the left and right eyes viewed green horizontal and red vertical, then both eyes viewed red horizontal and green vertical. If the binocular cells were limited to an interocular OR channel, the monocular adaptation would cancel or null the binocular exposure condition and there would no binocular aftereffect. However, if there is an exclusive binocular channel, then there should have been a measurable binocular aftereffect.

Vidyasagar's (1976) results showed opposite color-orientation aftereffects in the monocular and binocular test conditions, and he interpreted the data in terms of the involvement of exclusively binocular cells in the McCollough effect. It is obvious that the binocular aftereffect could not have been generated within a binocular OR channel, as it would have been nulled by the monocular adaptation. The data are consistent with the adaptation of a binocular channel that is unaffected by monocular input - an AND channel. More recent studies of the McCollough effect, have replicated

Vidyasagar's results (Seaber and Lockhead, 1989· Savoy, 1984).

Vidyasagar's (1976) logic was also used by Anstis and Duncan (1983) in a motion aftereffect (MAE) experiment. These authors adapted each eye monocularly to a clockwise-rotating spiral and then binocularly to anticlockwise motion. Following this adaptation sequence, subjects reported independent monocular vs binocular aftereffects; they all saw anticlockwise motion when tested through either eye alone, and clockwise movement when both eyes were tested simultaneously.

Again, if a simple three-channel model accurately described the human visual system then we would expect no independent binocular aftereffect because monocular exposure to opposite rotation should have nulled the apparent motion seen binocularly. However, there was a measurable MAE under the binocular test condition, so Anstis and Duncan (1983) concluded that in the human visual system there exists a second binocular channel, one that operates as a logical AND-gate.

Anstis and Duncan's (1983) description of the organization of the binocular visual system includes two binocular channels, an interocular binocular OR channel and an AND channel. They argued that the interocular channel consists of mutually inhibitory cells that are excited by input to one eye, but inhibited by stimulation of the other eye. These "eye-opponent" cells replace the exclusively monocular channels present in models such as those presented by Blake et al. (1981) and by Wolfe and Held (1981,1982) and could provide a neural basis for binocular rivalry (Anstis and Duncan, 1983).

Anstis and Duncan's experiments have other implications for their organizational scheme. That is, during the binocular exposure phase, each eye's monocular channel is adapting to movement opposite to that viewed in the individual monocular adaptation conditions. This presentation of equal and opposite directions of movement should null the monocular aftereffects resulting in no independent monocular aftereffect. However, as noted above, both Anstis and Duncan (1983) and Vidyasagar (1976) did find significant monocular and binocular aftereffects. There are several plausible explanations for presence of the monocular aftereffects, one option is that the model presented by Anstis and Duncan (1983) is sufficient with just two binocular channels: the AND and the interocular channel with eye-opponent inhibition. The cells within the interocular channel will be adapted during monocular exposure, but will not be affected during binocular adaptation because they will have been 'shut-down' by mutual inhibition.

Another possibility involves an AND channel and either the eye-opponent process described by Anstis and Duncan, or the retention of exclusively monocular channels and the interocular OR channel. Regardless of the nature of the monocular processing, inhibition from the AND cells to the mechanism that receives monocular information, during binocular adaptation would spare these inputs from the opposing adapting motion, and leave the monocular aftereffect intact. In Anstis and Duncan's final depiction of their model they incorporated both mutual eye-opponent inhibition and AND-mediated inhibition of the eye-opponent channel, and discarded the monocular channels.

Although Anstis and Duncan's description does account for their data, when taken to the extreme it is not consistent with existing psychophysical data. For example, following binocular adaptation, monocular and binocular aftereffects are equivalent (Moulden, 1980; Wolfe and Held, 1982). If there were no independent monocular channels, and the interocular channel cancelled its own activity when similar stimuli are presented to the two eyes, only the AND mechanism will be available to generate the aftereffect. Because the AND channel does not respond to monocular stimuli, there should be <u>no</u> monocular aftereffect following binocular adaptation. Obviously, this conflicts with the existing aftereffect literature. To be consistent with the known characteristics of monocular and binocular adaptation, Anstis and Duncan's model would have to be modified slightly such that the inhibition responsible for silencing the monocular response during binocular adaptation is not complete. This would provide not only for independent monocular aftereffects in the dichoptic adaptation experiments, but because there would be some degree of nulling of effects, it also accounts for the reduced size of these dichoptic aftereffects (Savoy, 1984).

1.42 Evidence for an AND channel: Detection and discrimination data

To this point I have concentrated on adaptation/aftereffect experiments, and their implications for cortical binocularity. However, support for a dual-binocular model of the visual system has also been provided by simple detection and discrimination experiments. For example, prior to Vidyasagar's experiment's and Wolfe and Held's 4-channel proposal, Cohn and Lasley (1976) presented a convincing argument against the assumption that there is only one binocular channel in the human visual system. They measured thresholds for detection of positive and negative luminance changes in point sources of light. In some of the test conditions positive or negative changes in one eye were paired with like changes in the other (matched) while in the remaining conditions the changes were in opposing directions (dichoptic).

The resulting thresholds were consistently lower when stimuli of like sign were viewed by the two eyes, regardless of the direction of change, than when the monocular combinations were dichoptic. The shape of the function predicted by models assuming a single binocular combination site (probability and energy summation models) were not compatible with their data set (cf. Cohn and Lasley 1976). However, their pattern of results was consistent with the activity of two independent binocular processes, one that uses synaptic summation and the other, inhibition. The summation mechanism signals the presence of like-signed stimuli, while the differencing (inhibitory) mechanism detects local contrast.

In a subsequent test of their dual-binocular hypothesis Cohn, Leong, and Lasley (1981) showed that subjects could readily discriminate between matched and opposite -polarity stimuli. Further, they found that thresholds for matched monocular stimuli were more affected by correlated binocular noise while unmatched monocular signals were best masked by uncorrelated noise. Cohn et al. (1981) argued the observed relationship between interocular polarity and masking effectiveness was another demonstration of the inadequacy of single channel models of binocularity. Instead, their results support the presence of dual binocular channels wherein "a binocular summing and a binocular differencing mechanism supply information to higher decision centres and that information in the two mechanisms may be separated by the observer" (Cohn and Lasley, 1976; p. 1022).

Cogan (1987) also found differences in dichoptic increment-decrement thresholds, using full-field luminance changes, which suggested that single-channel models of binocularity do not accurately represent the human visual system. From his data and those of Cohn and Lasley (1976) and Cohn et al. (1981), he developed a binocular model which assumes that the summing and differencing mechanisms described by Cohn and Lasley represent two distinct binocular combination sites. The differencing or 'either-eye' channel is an interocular mechanism which consists of cells responsive to both monocular and binocular input. The activity of this interocular channel is not dependent on the relative orientation and spatial frequency, or luminance polarity of the monocular images.

The second set of binocular neurons, which Cogan (1987) calls a 'fused' channel, is the summing site where cells only respond to monocular stimuli that are matched for polarity. An example of the separation of function of these two channels is as follows, the either-eye channel would be active if the left eye viewed a dark field, while the right eye viewed a light field, but the fused channel would remain silent. Thus, in Cogan's (1987) model the characteristic that differentiates the interocular and fused channels is their sensitivity to the relative polarity of the images in each eye.

A feature of Cogan's model that distinguishes it from those presented by Moulden (1980) and Wolfe and Held (1981, 1982) is the absence of independent monocular channels. Cogan

(1987), like Anstis and Duncan (1983), argued that within the either-eye channel there are cells excited by stimulation of one eye, but inhibited by input to the other eye. Although the final output of these interocular units would be indistinguishable from monocular cells, he argues that there is no independent monocular activity, so all visual stimuli are processed by these two binocular mechanisms. In the interest of clarity, in subsequent sections I will refer to the either-eye mechanism as the interocular OR channel and the fused channel as the AND channel, unless specific points about Cogan's model need to be addressed.

The weight of the psychophysical data favours a visual system with at least two distinct binocular channels; one which operates as a logical OR-gate, the other as an AND-gate. While there is evidence for the existence of an exclusively binocular channel, little is known about the response characteristics of this mechanism. As noted in the Introduction, when using visual aftereffects to examine the response characteristics of neural channels it has become common to make the assumption that the output of the various channels is pooled or averaged in some way. The first two experiments were performed to compare the pooling hypothesis with the proposal that all the channels are independent.

After establishing that the channels do not appear to operate independently, Experiments III through V used a variety of adaptation protocols to determine how the response of an AND mechansim varies with changes in the temporal alternation rate, contrast level, and interocular spatial phase characteristics of the stimulus. The ultimate goal of studying the activity of neural channels is to determine their functional role in human vision. The final study examined the contribution of an AND channel to one such process, binocular summation.

CHAPTER TWO - THE ASSUMPTION OF NEURAL POOLING

2.0 Experiment I - A test of Independence vs. Neural Pooling

2.1 Introduction

In developing the logic for his studies of the mechanisms of color vision in humans, Stiles (1949) made explicit the assumption that of all the units available, the neural mechanism with the greatest sensitivity will signal the presence or characteristics of a visual stimulus. This Most Sensitive Unit hypothesis has since been applied (both implicitly and explicitly) to other areas of visual processing. For example, Barlow (1972) presented a convincing argument for the critical role of the most sensitive unit in the absolute threshold for detection. He reviewed evidence from a variety of fields of research: ranging from the specificity of sensory nerve fibers, to the inherent reliability and sensitivity of individual units, and the direct link between single unit activity and fixed-action patterns in the frog. Barlow's (1972) thesis was that single units can individually signal sensory stimuli, and that the human system is organized to exploit this capacity. He argued that

> the important point is that quantitative knowledge of the noise level and reliability of single retinal ganglion cells enables one to see that the performance of the whole visual system can be attributed to a single cell: averaging is not necessary.
>
> (Barlow 1972;p.378).

In Barlow's paper, he considers primarily the operation of single cells at the initial stages of detection ie. retinal ganglion cells. While there is little question that single cells play a critical role in the detection of light quanta, and consequently in determining the absolute threshold for the detection of spots of light, as one moves through the stages of processing in the human visual system, the neurons become more specialized and can be divided into classes of units according to their response characteristics. For example, cells are grouped according to their orientation preference, spatial frequency tuning, sensitivity to direction of motion, and eye preference. Thus, when moving from describing the minimum quanta necessary for detection of light, to the contrast threshold for grating stimuli, the most sensitive unit hypothesis must be revised to accommodate the fact that groups of cells each with different response characteristics now process the visual stimulus. The logical extension of the most sensitive unit hypothesis is a most sensitive mechanism (MSM) hypothesis which proposes that detection of visual stimuli is dependent on the activity of the most sensitive group of cells.

In one respect, the statement "the most sensitive mechanism mediates detection" is a truism, obviously the group of units that detects a stimulus must be the most sensitive mechanism. However, this assumes that all available mechanisms are able to detect the stimulus independently, that there is no interaction among the channels. If activity in one channel was able to modulate the output of another channel, then the channel with the lowest threshold may not be available or capable of mediating detection. Thus, a critical, and often implicit, requirement of the most sensitive mechanism proposal is that the channels involved in detection be independent. Therefore, in future references to the MSM hypothesis I will use the more relevant term, 'Independence' hypothesis. Specifically, Independence means that the mechanisms under consideration do not interact in any way, and as a result the most sensitive of these will signal the presence of a visual stimulus.

Blake and his colleagues performed a series of experiments, using the contrast threshold elevation aftereffect, to examine the properties of monocular and binocular channels in the human visual system. These authors pointed out (after Anderson, Mitchell, and Timney, 1980), that conflicts arise when an Independence hypothesis is considered in the context of the contrast threshold elevation aftereffect. It is well documented that contrast threshold elevation induced in one eye will show sizable transfer to the other (Blakemore and Campbell, 1969; Blake et al., 1981), and that IOT is consistently less than the direct effect.

The widely accepted explanation of the contrast threshold elevation aftereffect is that monocular adaptation to a high contrast grating decreases the sensitivity of a population of monocular cells optimally sensitive to this pattern. When adapting and testing the same eye, all units that receive input from the adapted eye have been made less responsive. As a result, it takes more stimulus contrast to surpass their threshold, which is reflected in an increase in the subject's contrast threshold. However, when the unadapted eye is tested, presumably the monocular neurons that are stimulated are cells that have not been previously adapted. An Independence theory would predict that because these monocular cells were not exposed to the adapting pattern, they should be able to detect the stimulus at normal contrast levels, resulting in no interocular transfer of contrast threshold elevation.

The Independence account of visual detection leaves two important questions unanswered: why does interocular transfer of contrast threshold elevation occur, and why is it lower than the direct effect? To date there have been two efforts to resolve this issue. The first approach attempted to reconcile the Independence hypothesis and the IOT data by proposing that the monocular and binocular channels have unequal sensitivities (Blake et al., 1981; Brown and Woodhouse, 1986). The second approach abandoned the Independence theory and proposed instead that thresholds are the result of pooling of the output of groups of cells which may vary in their sensitivity to the stimulus (Blake et al., 1981).

2.11 Differential Sensitivity Proposal

Blake et al. (1981) proposed that an Independence hypothesis could be consistent with the IOT of contrast threshold elevation, but only if the monocular channels are less sensitive than the binocular mechanism. The logic is as follows: under normal viewing conditions the binocular OR channel detects all visual stimuli at threshold. However, during monocular adaptation to a high contrast grating the binocular channel is made less sensitive, and as adaptation continues its threshold is eventually raised above that of the unadapted monocular cells. Subsequent testing of the adapted eye involves monocular and binocular channels, both of which have been adapted, producing a relatively high threshold. However, when testing the unexposed eye, the unadapted monocular cells will signal the presence of the stimulus. Thus, adaptation of the binocular channel reveals the unadapted (lower) sensitivity of the monocular channel resulting in a greater aftereffect in the adapted eye than in the non-adapted eye.

2.12 Neural Pooling

As noted in the Introduction, the application of pooling to the results of aftereffect experiments was first done explicitly by Moulden (1980). His predictions based on pooling have been confirmed using the suprathreshold aftereffects of tilt and motion. In response to the conflict between Independence theory and IOT of contrast threshold elevation, Blake et al. (1981) adopted Moulden's description of pooling, and applied it to the contrast threshold elevation aftereffect. They argued that the post-adaptation detection thresholds are decided by the ratio of tested to adapted channels with each test condition.

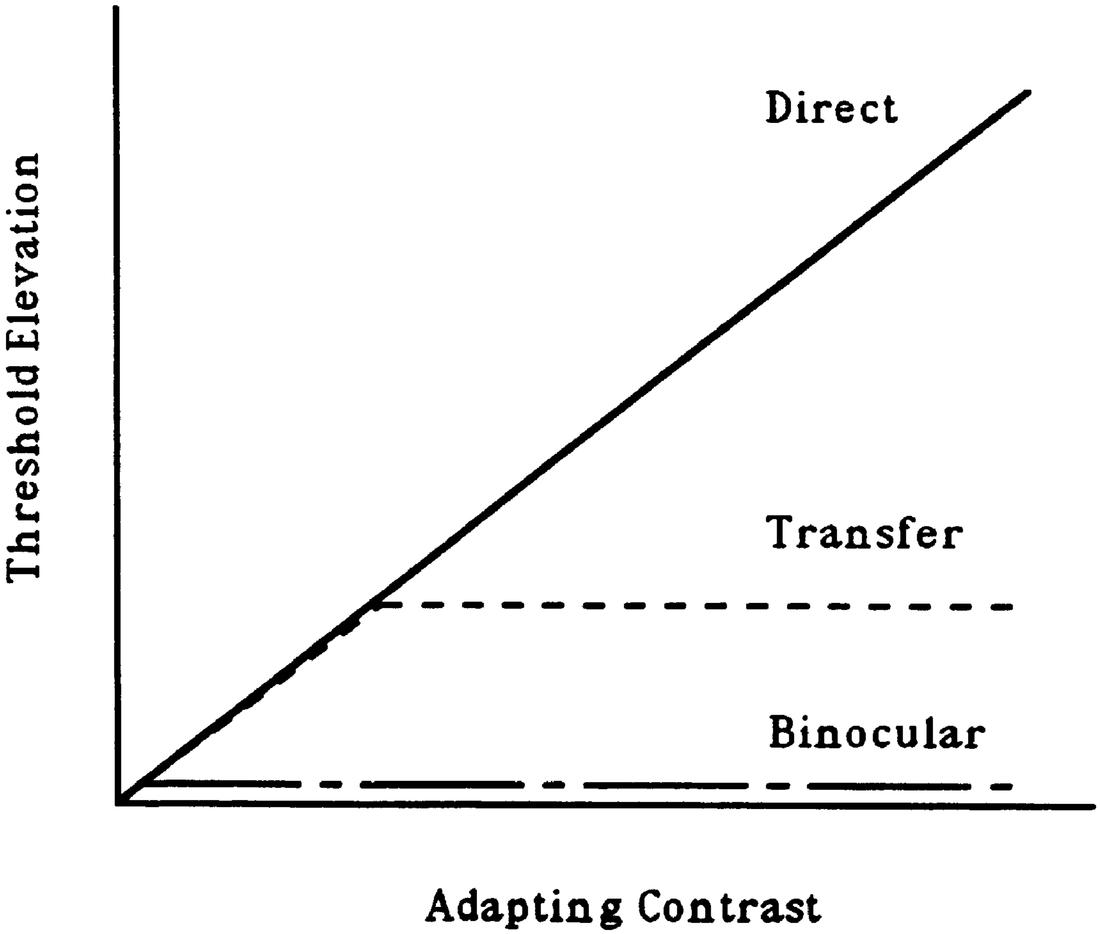
It should be noted that neural pooling, as it is described by Moulden (1980) and by Blake et al. (1981), involves groups of cells or channels, differentiated by their sensitivity to monocular and binocular input. However, the most sensitive unit hypothesis (as detailed by Barlow 1972) was designed to describe the activity of single cells at the earliest stages of detection in the visual system. In fact, Blake et al. (1981) argued that neural pooling is a more economical and efficient method of stimulus detection than one based on the activity in single units. Their logic is that if detection were based on the activity of a single cell there would be a high false alarm rate which could be best compensated for by an increase in response threshold. Thus Blake and his colleagues propose to replace the most sensitive unit hypothesis with neural pooling, but in doing this they adopt the language of a most sensitive mechanism (Independence) hypothesis. However, the argument that they presented applies only to the detection tasks described by Barlow (1972) where detection thresholds were measured for single points of light using dark-adapted subjects, it does not apply to the task that they use. As mentioned earlier, measurement of contrast threshold using spatially modulated stimuli involves channels whose ultimate level of activity depends on the combined responses of many such units.

It is important that such assumptions be made explicit. Blake et al.'s (1981) subtle jump from single cells to channels does not affect the reasoning presented for the existence of IOT of contrast threshold elevation, however, it does become problematic when trying to understand the physiological basis of pooling at contrast threshold. This issue will be discussed further in the General Discussion.

In a test of neural pooling vs. an Independence hypothesis (assuming monocular and binocular channels have different sensitivities), Blake et al. (1981) recorded contrast threshold elevation in the adapted and non-adapted eye using a range of adapting contrasts. Existing threshold elevation data show that when adapting and testing the same eye (the direct condition), the aftereffect gradually increases with adapting contrast, and levels off at some high contrast value. It was predicted that if the monocular cells are less sensitive than the binocular, then the aftereffect recorded in the non-adapted eye (transfer condition) should follow this pattern but should reach an asymptote before the aftereffect measured in the adapted eye (direct condition).

Blake et al. (1981) also posited that there should be a range of low adapting contrasts, at which the binocular channel is only partially adapted (see Figure 3). At these

Figure 3. A hypothetical diagram of direct (adapt-test same eye), transfer (test unadapted eye), and binocular contrast threshold elevation recorded following monocular adaptation. Predictions are made on the basis of an Independence hypothesis, and its corollary that monocular mechanisms have higher detection thresholds than the binocular channels.


Direct
Transfer
Binocular
Threshold Elevation
Adapting Contrast

near-threshold contrasts the direct and transfer effects will both be determined by the activity of the binocular OR channel, and should overlap. The results of their study showed that both the direct and IOT functions started to asymptote at an adapting contrast 1.5 lu above threshold. Furthermore, the direct aftereffect was consistently greater than the IOT aftereffect at all adapting contrasts. In their interpretation of these results, Blake et al. (1981) rejected the Independence hypothesis and argued instead for neural pooling.

In an independent threshold elevation experiment, also designed to assess the putative differential sensitivity of the monocular and binocular channels, Brown and Woodhouse (1986) measured changes in the direct and transfer effects as a function of adaptation duration. Because contrast and duration are known to have similar effects on threshold elevation, their logic and predictions were essentially the same as those of Blake et al. (1981). Brown and Woodhouse (1986) reported that IOT peaked at 6 min adaptation, while the direct effect continued to increase up to 16 min. They argued, as outlined above, that the response recorded using the non-adapted eye represents the normal (unadapted) threshold of the monocular units. In a more recent set of experiments Oduwaiye and Woodhouse (personal communication, 1991) found similar results using a different testing procedure. Although Oduwaiye and Woodhouse's data confirmed their predictions, they never obtained the 100% transfer at low adapting contrasts that was predicted by Blake et al. (1981). Instead the IOT function was always less than the binocular effect.

2.13 Experimental Predictions

The results of the experiment performed by Blake et al., conflict with those of Brown and Woodhouse (1986). The following experiment was designed to examine this discrepancy using a paradigm similar to that of Blake et al. (1981). Blake and his colleagues (1981) based their predictions on the existence of only one binocular channel. As outlined in the Introduction, there is reason to believe that humans have a dual-binocular visual system. Therefore, the following predictions and subsequent interpretations assume a 4-channel model with both binocular AND and OR channels; a hypothetical diagram of the outcome is presented in Figure 3.

Contrast threshold elevation was measured monocularly and binocularly following monocular adaptation, using a range of adapting contrasts. If the binocular OR channel has a lower threshold than the monocular channels, there should be a range of low adapting contrasts at which it is more sensitive than the unadapted monocular channel. Until the adapting contrast is strong enough to raise the binocular channel's threshold above that of this monocular mechanism, the same groups of cells are responsible for the thresholds measured in the direct and transfer conditions, therefore the thresholds should be identical. When the adapting contrast is high enough to make the binocular channel less sensitive than the unadapted monocular channel, the two functions should diverge; the direct effect will continue to rise until it reaches some high contrast saturation point, while the transfer effect will flatten immediately, and stay at a constant level regardless of the adapting contrast. In the binocular test condition, the most sensitive channel will be the unadapted AND channel. Given that it has not been adapted, the AND channel should detect the test stimulus at its normal threshold, producing no binocular aftereffect.

The relative positions of the direct and transfer functions will be quite different if the Independence hypothesis does not accurately describe the detection process, and some form of neural pooling, like that proposed by Blake et al. (1981), does occur. To simplify the predictions of the pooling hypothesis, I will present them in terms of ratios of tested:adapted channels. The pooling hypothesis assumes that there is a direct relationship between the size of an aftereffect and proportion of channels tested that have been adapted. For example, consider monocular testing following the same-eye adaptation. In this situation all of the tested channels have been adapted (test:adapt ratio = 1:1), therefore the aftereffect should be at a maximum. In contrast, the ratio drops to 2:1 when the unadapted eye is tested. Now only half of the channels tested have been adapted, and the aftereffect should be lower.

As the adapting contrast is raised the direct effect will increase, as will the IOT effect. However, because of the test:adapt ratio, the IOT aftereffect should always be less than that measured in the adapted eye. Further, because the unadapted monocular channel is never affected by adaptation, it should have a constant diluting effect on the transferred condition. However, as the reference contrast is raised, increasing adaptation within the adapted monocular and binocular OR channels will result in a pronounced improvement in the direct effect. Therefore, the slope of the IOT function should be more shallow than that of the function representing the direct effect. During binocular testing, the presence of the unadapted AND channel also results in a test:adapt ratio of 2:1. Thus neural pooling predicts that the binocular function will be similar in shape and position to the IOT function.

2.2 Methods

2.21 Subjects

Four female subjects with normal or corrected to normal vision were tested repeatedly over a period of several months. Two of these subjects were naive to the purpose and procedures involved, while the two remaining subjects were practiced observers. All subjects exhibited normal levels of stereopsis, and the preferred eye was always used for adaptation.

2.22 Apparatus

Essentially the same apparatus was used for Experiments I - VI so a thorough description will be provided here, and details specific to individual experiments will be reported where appropriate. Gratings were displayed using conventional television techniques, on two Tektronix 608 CRT monitors with green (P31) phosphors. A micro-computer was used to drive a CED1401 interface to 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 11.0 cd/m^2. Contrast was defined in Michelson terms as ((Lmax - Lmin)/(Lmax + Lmin) x 100), and the maximum contrast used was 60%.

For all experiments, the adaptation and test gratings were sinusoidal, and depending on the experimental conditions, could be varied in orientation, spatial frequency, temporal frequency, or relative phase. In this first experiment the spatial frequency of the adaptation and test gratings was 2.5 c deg^{-1} and they drifted at approximately 0.3 Hz, to minimize the formation of afterimages during adaptation. The two monitors were viewed simultaneously through an adjustable mirror system. The mirrors used in our haploscopic system were calibrated and adjustable in three dimensions, providing precise control over the alignment of the two fields. Both circular fields were 5 deg in diameter, and surrounded by a matte black mask. For most experiments (including Experiment I) the displays contained a 2.0 deg central fixation square; one side of each square was constructed to create nonious lines which allowed the subject to gauge the accuracy of his/her fusion.

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

2.23 Procedure

Contrast threshold elevation was measured, following adaptation to one of seven adapting contrasts, for the left, right and both eyes, using a conventional aftereffect protocol. Baseline measures of contrast threshold were followed by adaptation to an identical grating of a higher contrast, and then a final set of threshold measurements were taken. During the baseline phase, subjects viewed a blank screen for 10s, followed by a test interval (0.5s) delimited by two tones. After the second tone, the subject pressed the appropriate button on the response box; the contrast of the test stimulus was varied according to this response. The remaining trials were preceded by 3s blank intervals. If on one trial the subject did not see the grating, then on subsequent presentations the contrast was increased in 3db steps until her response changed to 'yes' and then reduced until the response returned to 'no'.

Testing proceeded according to a standard staircase procedure (Levitt, 1971) in which a series of response 'crossover' points define a staircase. One staircase was tested for each of the test conditions (left, right, binocular). The starting point for each of the staircases was determined initially by using staircases with large step-sizes to provide rough estimates of the thresholds for each eye. These reversal points were not used in the final calculation of thresholds but the estimate increased the efficiency of the procedure by reducing the amount of time required at the beginning of each session to reach threshold. After the initial threshold estimate, the three staircases were run simultaneously, and on a given trial, the staircase (test condition) was selected randomly. Each session continued until 9 reversals were obtained on each staircase; a staircase was tested only until its quota of reversals was attained.

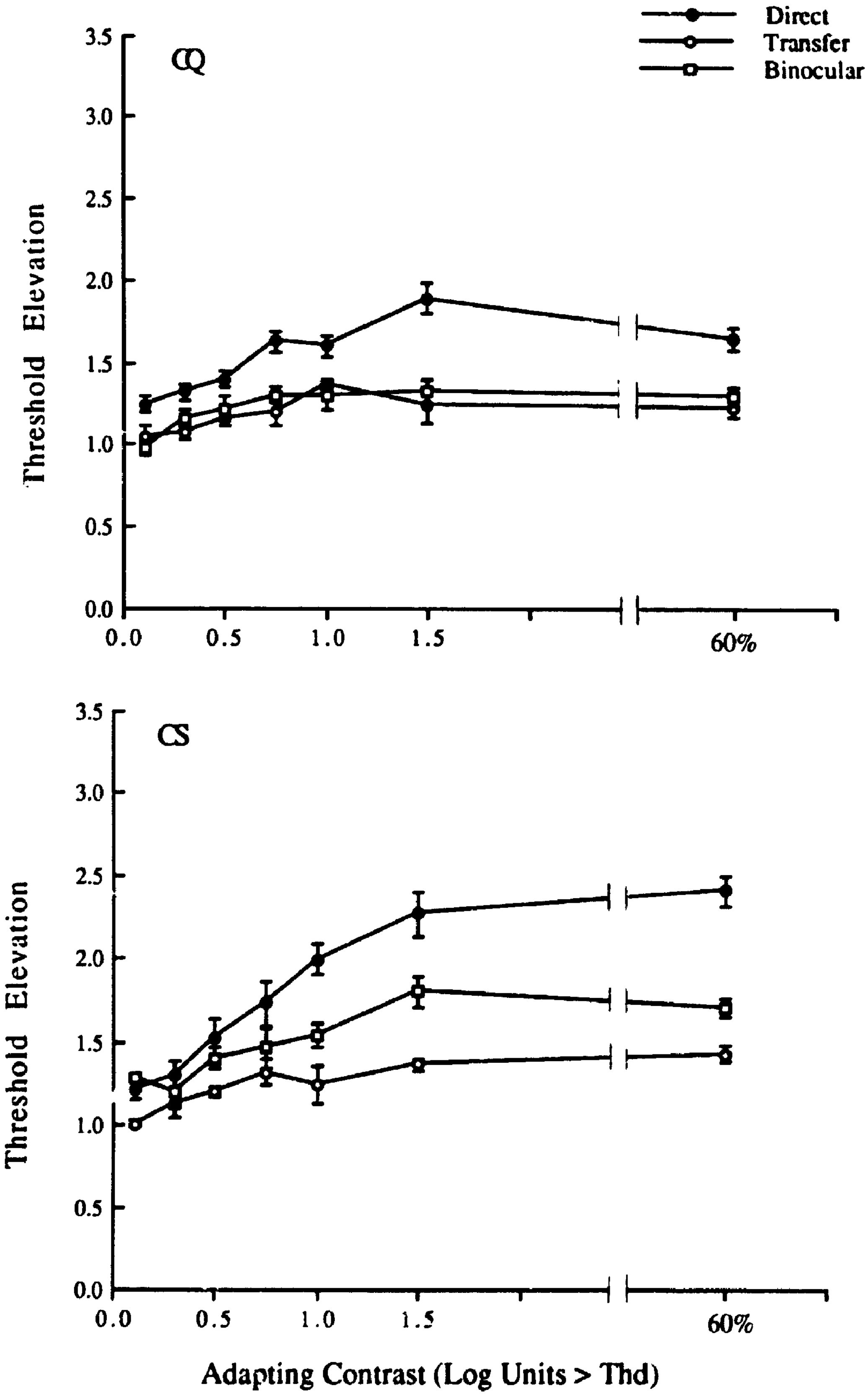
After baseline data were collected, subjects viewed the monocular adaptation grating for 2 min, and were then tested as described above. The 3s blank interval between trials in the baseline period, was lengthened to a 12s readaptation interval to ensure that a constant level of adaptation was maintained throughout the session. Again, the readaptation and test periods cycled until the required number of reversals were obtained for each staircase. Seven adapting contrasts were presented over a number of sessions, six of these were 0.1, 0.3, 0.5, 0.75, 1.0, and 1.5 log units above the subject's baseline threshold, while the seventh contrast was the maximum available (60%). Thus for five of the adaptation conditions, the relative contrast was held constant for all subjects while for the final condition the physical contrast remained unchanged.

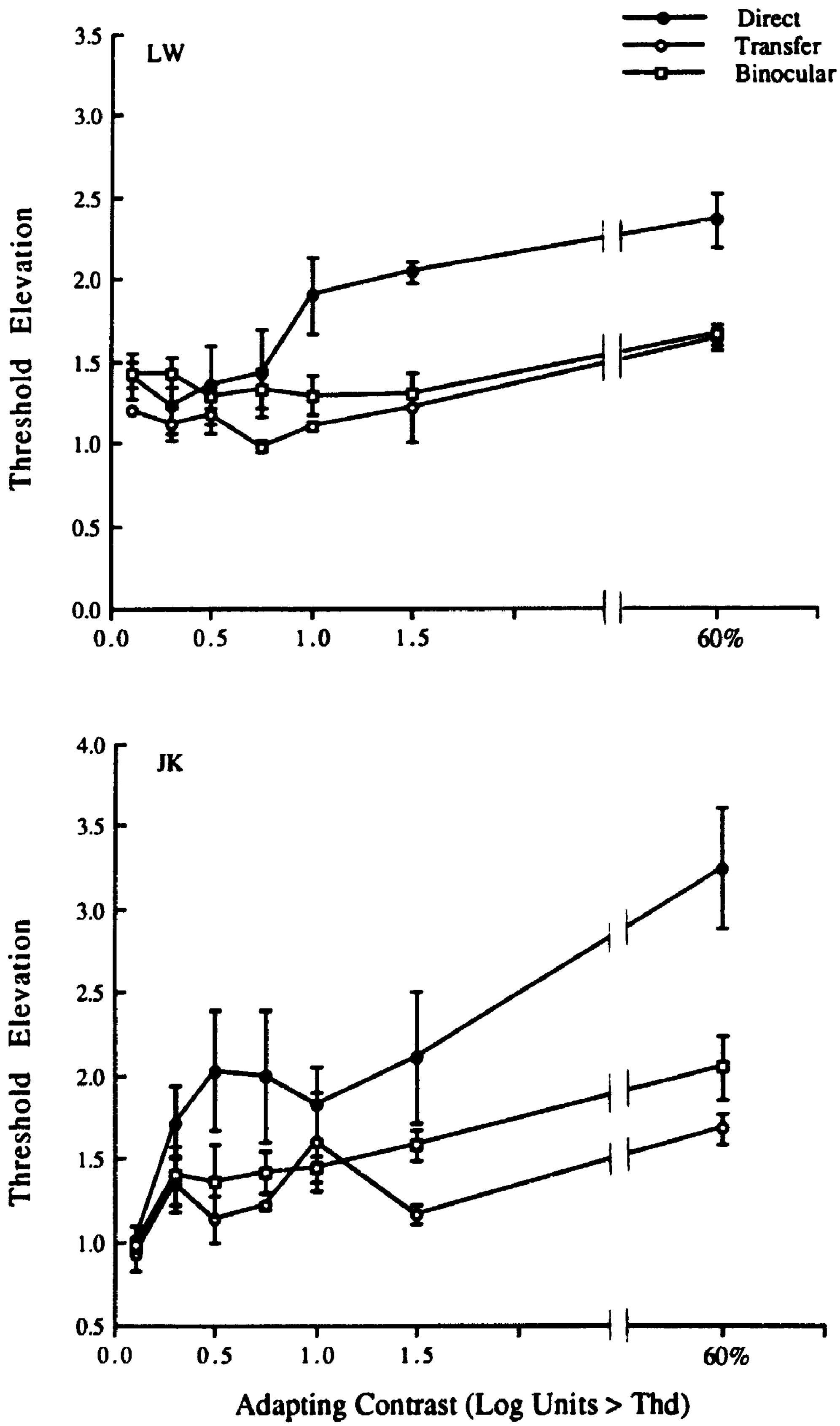
Baseline and adaptation thresholds were calculated separately by taking the average of the final 8 reversals on each staircase. The first reversal was always discarded. The magnitude of threshold elevation for each test condition was calculated by taking the ratio of adaptation/baseline thresholds. In a single session threshold elevation was measured for all three test conditions for a single adapting contrast. At least two such sessions were run for each subject in each of the adaptation conditions.

2.3 Results

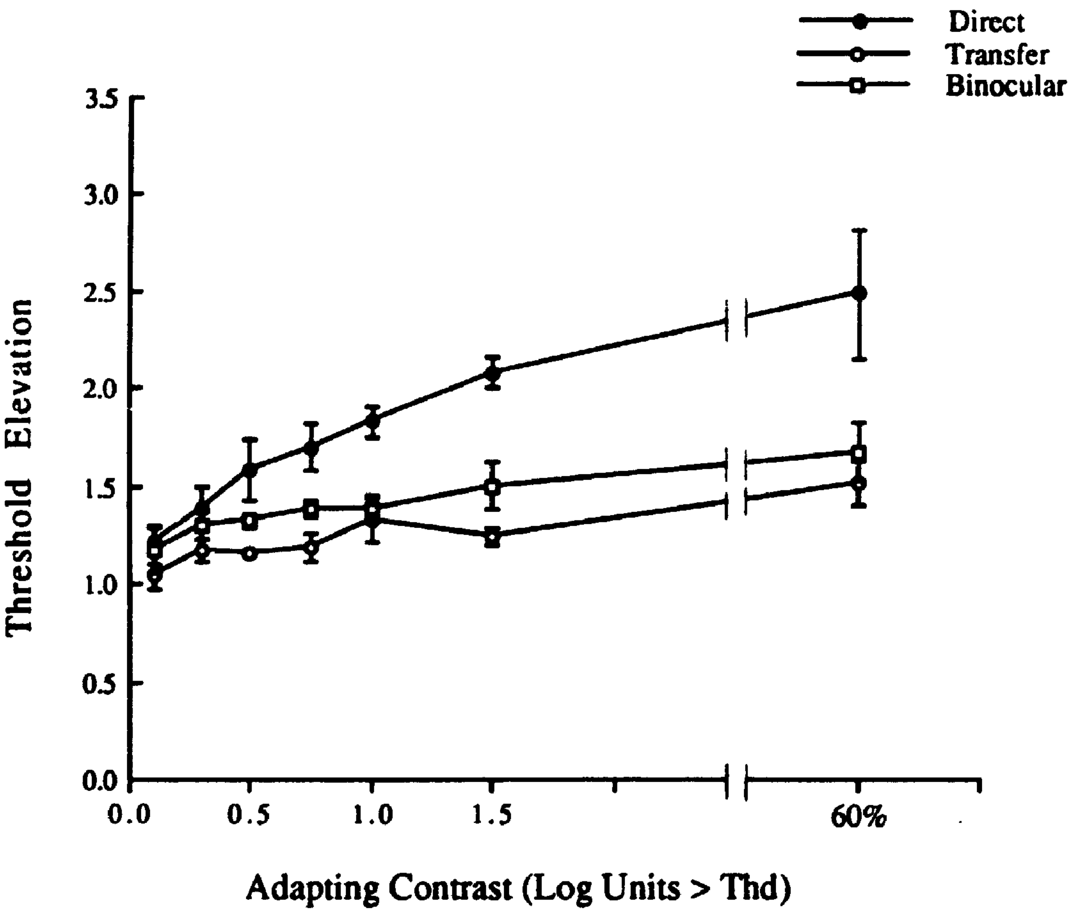
The threshold elevation data, obtained from individual subjects are shown in Figure 4; Figure 5 depicts the average of these data. Notice that the direct effect rises with increasing adapting contrast until it levels off at 1.5 log units above threshold. At the lowest adaptation contrasts, the transferred effect is consistently below the direct effect, and continues to increase as the adapting contrast is raised. The binocular function consistently falls below the direct effect, and above or near the transferred effect.

Figure 4. Monocular (direct and transfer) and binocular contrast threshold elevation is shown here for each of the four subjects in Experiment I. Aftereffects were recorded following monocular adaptation. A range of seven adapting contrasts were used, the first six of these were 0.1, 0.3, 0.5, 0.75, 1.0, and 1.5 log units above the subject's baseline threshold, while the seventh contrast was the maximum available (60%). Error bars represent +- 1 standard error of the mean.


Direct
Transfer
Binocular
CQ
CS
Threshold Elevation
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.5
1.0
1.5
60%
Adapting Contrast (Log Units > Thd)


Direct
Transfer
Binocular
LW
Threshold Elevation
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.5
1.0
1.5
60%
JK
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.5
1.0
1.5
60%
Adapting Contrast (Log Units > Thd)

<u>Figure 5.</u> The data presented in figure 4 was averaged to generate the three functions depicted here. Again, monocular and binocular aftereffects were recorded following monocular adaptation, using seven adapting contrasts. Error bars represent +-1 standard error of the mean.


Direct
Transfer
Binocular
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Threshold Elevation
0.0
0.5
1.0
1.5
60%
Adapting Contrast (Log Units > Thd)

A randomized blocks ANOVA showed significant main effects of both the reference contrast ($F_{6,18} = 8.42$; $p < .001$) and eye tested ($F_{2,6} = 44.10$; $p < .001$). The interaction was also significant ($F_{12,36} = 5.30$; $p < .001$). Subsequent tests of means showed that the direct and transferred aftereffects were significantly different even at the lowest adapting contrasts used. The difference between the binocular and transfer functions was significant at only two adapting contrasts. Although the increase in the IOT function is modest, protected t-tests showed that the thresholds at adapting contrasts of 0.1 and 0.3 were significantly smaller than the maximum contrast at ($t_4 = -2.82$; $p < 0.01$) and ($t_4 = -3.37$; $p < 0.01$) respectively.

2.4 Discussion

2.41 IOT vs Direct Aftereffects

Our data do not support the predictions of an Independence hypothesis. For three of the four subjects, at all adapting contrasts the direct and IOT functions were separate. Only one subject had similar direct and IOT effects at the lowest adapting contrast. However, even for this subject the two functions diverged immediately afterwards and for the remainder of the adapting contrasts the IOT function was consistently below the direct function. In all four of the data sets, the direct and IOT curves both increase with adapting contrast to approximately 1.5 lu. Notably, this is also the adaptation contrast level that Blake et al. (1981)

report as the saturation point for their direct and IOT effects. These results are also very similar to those of Bjorklund and Magnussen (1981) who measured contrast threshold elevation using a range of adapting contrasts. Their direct and IOT functions are identical in form to those obtained in this experiment; as soon as the adaptation gratings were visible, the direct aftereffect exceeded that measured in the unadapted eye, and they began to asymptote at roughly the same point. Thus, neither of these experiments support the putative shift in the detection mechanism from adapted binocular neurons to less sensitive monocular cells.

2.42 IOT vs Binocular Aftereffects

The location of the binocular function, relative to the other two curves, strengthens the argument against an Independence hypothesis. That is, all subjects showed significant binocular threshold elevation, at levels equal to or greater than that recorded in the IOT condition. Although the binocular and IOT functions overlap completely for only one of the three subjects, data from the remaining subjects shows that the binocular curve is always closer to the transfer than the direct curve. This is consistent with the presence of an unadapted AND channel that dilutes the size of the binocular aftereffect.

The binocular and IOT functions are not identical as a simple pooling hypothesis, and the AND model, would predict. Instead there is a trend in the individual data for the binocular effect to exceed the transferred effect. Wilcox et al. (1990) performed a series of monocular exposure experiments to test the validity of three vs four-channel models of the visual system. They reported that the IOT and binocular aftereffects were statistically equivalent and therefore supported the AND model; however, the pattern of IOT vs binocular aftereffects were highly variable both within and across subjects. The binocular effect was either equal to or greater, but was never lower, than the transferred effect.

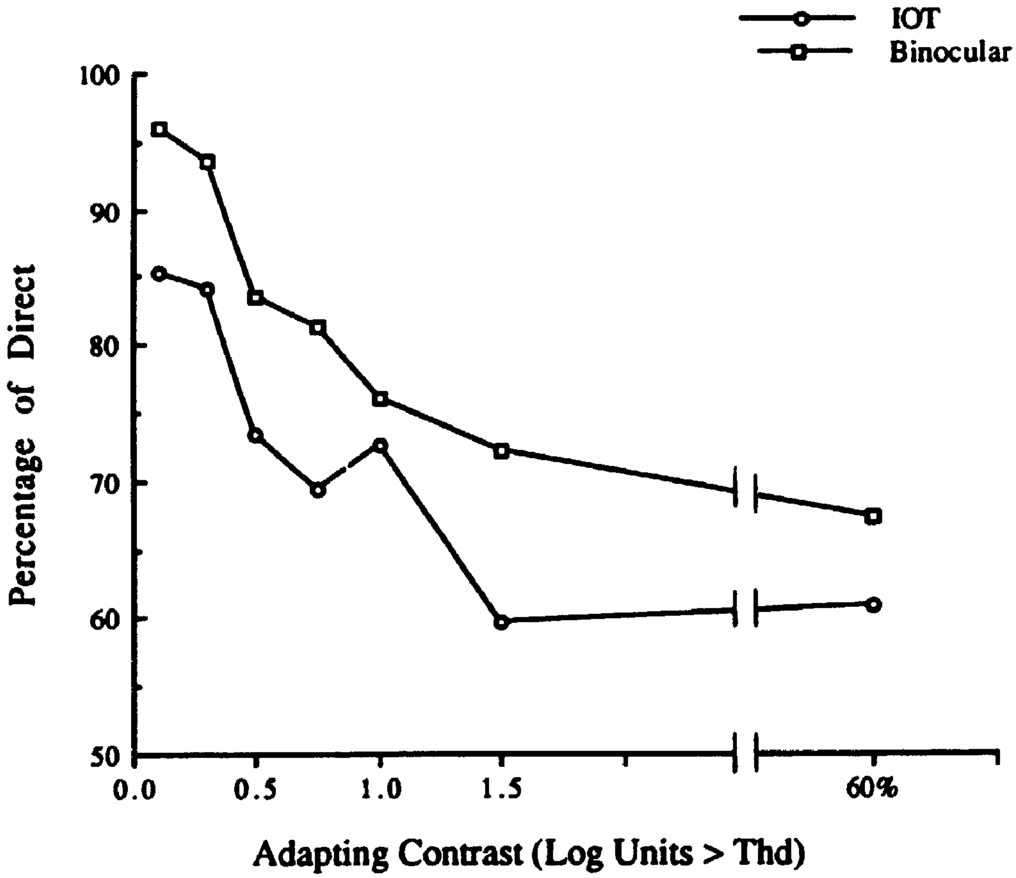
Wilcox et al. (1990) posited that this variability is the result of the nature of binocular cells within the OR channel. That is, during monocular exposure, different classes of binocular OR neurons will be affected to varying degrees, depending on their sensitivity to input from the exposed eye (ocular dominance). Therefore, during binocular testing some of the unadapted or "less-adapted" OR cells could serve to dilute the aftereffect. The diluting influence of the proposed AND channel would then be confounded by the contribution of partially adapted OR cells. As commented in the Introduction, Wilcox et al. (1990) concluded that the monocular exposure paradigm is not the method of choice for assessing the activity of the AND channel. The issue under investigation here is not the appropriateness of the AND model. However, these data replicate results of Wilcox et al. (1990) and support their argument against the use of the monocular exposure paradigm in such experiments.

2.43 Percent IOT of Direct Effect

It is obvious from Figure 5, that the IOT effect is not a constant proportion of the direct effect at all adapting contrasts. This result is consistent with Blake et al.'s (1981) simple pooling proposal. As noted previously adaptation of the monocular and binocular OR channels will rise with increasing adapting contrast, while the diluting effect of the unadapted monocular channel will remain constant across all adapting conditions. Because of this, the direct effect shows a marked growth as a function of adapting contrast, while the transferred effect increases more slowly.

The differential growth rate of the direct and IOT functions is predicted by the pooling hypothesis, but raises an important issue when interpreted in terms of the proportion of transferred vs the direct effect. That is, it has become common practice to express the amount of transfer as a percentage of the direct effect (%IOT = IOT/Direct x 100). Obviously, any difference in the rate of growth of the two aftereffects could have dramatic effects on this percentage. The averaged data depicted in Figure 5 shows that the direct effect rises more quickly than the IOT effect, and Figure 6 illustrates that as the adapting contrast is increased to a maximum, %IOT drops from approximately eighty five to sixty percent of the direct effect. Results presented by Bjorklund and Magnussen (1981) also exhibit this

Figure 6. The two functions shown here are the IOT and binocular aftereffects expressed as a percentage of the direct effect (IOT/Direct x 100). Both functions represent the averaged data from four subjects.


IOT
Binocular
Percentage of Direct
100
90
80
70
60
50
0.0
0.5
1.0
1.5
60%
Adapting Contrast (Log Units > Thd)

trend.

The dependence of the percent IOT on the adapting contrast is an important observation, for it is common practice to express the amount of IOT as a percentage of the direct effect. Increases in adaptation contrast could produce misleading improvements in %IOT and, unless the adapting contrast is carefully controlled, comparisons of the %IOT across experiments will not be valid. The preceding concerns are emphasized by another study reported by Bjorklund and Magnussen (1980) in which they used the same IOT paradigm but manipulated the adapting duration. The functions generated using this method showed an increase in %IOT with increasing adapting duration, the opposite pattern to that obtained in the variable adapting contrast IOT experiments (Bjorklund and Magnussen, 1980). It seems that %IOT is an even less reliable index than initially thought, for it can vary independently with at least two characteristics of the adapting stimulus.

2.5 Conclusion

The results of Experiment I clearly do not support the claim that the binocular mechanisms have lower thresholds than monocular. Given this, the assumption that the neural channels are independent, and the most sensitive mechanism mediates detection, fails to explain the presence of IOT of contrast threshold elevation. In contrast, the data presented here are consistent with a pooling hypothesis which suggests that the detection threshold is determined by the collective sensitivities of all available channels (Moulden, 1980; Blake et al., 1981).

3.0 Experiment II - The Independence hypothesis vs neural pooling

3.1 Introduction

Experiment I showed that an Independence hypothesis does not predict the relative sizes of contrast threshold elevation following monocular adaptation. Instead, a description based on interaction between channels, similar to a pooling process, seems to provide a better account for the overall pattern of results. Sloane and Blake (1981) also assessed the plausibility of neural averaging, but used a different experimental paradigm. These authors attempted to manipulate the sensitivity of the left monocular, right monocular, and binocular channels, independently and record the resulting aftereffects. To control the amount of adaptation within each channel, Sloane and Blake (1981) used alternating monocular adaptation and varied the proportion of time that each eye viewed the adapting stimulus during the exposure interval. A range of right-eye:left-eye temporal ratios were used, but the total adaptation period was held constant. Adaptation intervals were divided into 10 s bins, and during each bin the adapting grating was visible alternately to either eye for one of five duration conditions (3:1, 2:1, 1:1, 1:2, 1:3). In the 3:1 condition, in each 10 s bin, the right and left eyes were exposed for 7.5 s and 2.5 s respectively. At the end of the 60 s adaptation period, the right eye received a total 45 s adaptation, while the left eye was adapted for only 15 s.

Sloane and Blake (1981) argued that if pooling does occur, then aftereffects measured monocularly should decrease directly with the reductions in exposure duration. However, because the total adaptation period was held constant, the binocular OR channel should exhibit the same amount of threshold elevation across all test conditions. In contrast, if an Independence hypothesis is adopted, then the binocular threshold should be determined by the least adapted (most sensitive) monocular channel. Thus the binocular function should trace the lower ends of the two monocular functions, forming an inverted U-shaped curve that peaks where the monocular curves intersect. Sloane and Blake's predictions, based on neural pooling, were confirmed by their data. Monocular threshold elevation declined directly as the temporal ratio was decreased, while the binocular aftereffect remained constant across all temporal ratios.

Although Sloane and Blake (1981) assume a three-channel model of the visual system which has only a single binocular combination site, the data obtained in the binocular test condition are consistent with the presence and contribution of an exclusively binocular channel. That is, in three of their five subjects' data, the binocular function sits well below the intersection point of the two monocular functions.

This constant reduction in the binocular effect, relative to the monocular effect, would be expected given the diluting contribution of the AND channel during binocular testing, following alternating exposure.

The results of Sloane and Blake's (1981) experiment support a neural pooling hypothesis, however, the manner in which they manipulated the sensitivity of the various channels may have introduced an experimental confound. That is, the gradual reduction of the monocular aftereffects could also be ascribed to aftereffect decay during other-eye adaptation. At the most extreme ratio, while the left eye was exposed for 7.5 s, the right eye viewed a blank screen, then received only 2.5 s adaptation. Further, the blank interval in the less-adapted eye was lengthened by the 5s response period that immediately followed the test interval.

There is some evidence that visual aftereffects decay in two stages, that there is an initial fast drop followed by a plateau where the effect declines at a slower rate. Oduwaiye and Woodhouse (personal communication, 1991) have argued that in the traditional adapt-test-adapt paradigm the degree of threshold elevation has been measured during the unstable, fast portion of the fast-decay interval which lasts up to 30s after 2 min adaptation. They warned that in such experiments, unless the adaptation length and contrast are carefully controlled, it will be difficult to obtain an accurate measure of the effects of exposure.

Concerns about the effects of this fast decay are minimal when aftereffects are recorded immediately following exposure to the adapting stimulus, as is the case in the experiments reported here. However, in Sloane and Blake's (1981) experiment, the total blank interval produced by the non-adapting periods and the 5s response interval, place their measurements within this quick-decay period. As a result, as the blank interval in the non-adapting eye was increased, the probability of decay also increased.

The potential seriousness of the effects of decay is underscored by another, related, characteristic of Sloane and Blake's (1981) adapt-test paradigm. Recall that the total adaptation duration was held constant across all adaptation ratios. Therefore, as the adaptation ratio was made more extreme, and the blank interval in the less-adapted eye increased, there was a corresponding decrease in the subsequent top-up period for that eye. Greenlee, Georgeson, Magnussen, and Harris (1991) have demonstrated that the rate of decay of the contrast threshold elevation aftereffect is directly related to adaptation duration; threshold elevation decays faster following short adaptation periods than it does after long adaptation periods. In sum, as the temporal ratio is increased, not only does the less-adapted eye have more time to recover from adaptation, but this recovery occurs at a faster rate. Therefore it is possible that this decay alone could have been responsible for Sloane and Blake's (1981) results.

In light of the preceding concerns, I decided to assess the independence of the monocular and binocular channels using a paradigm that is free from the decay confound. As noted in Experiment I, in their study of threshold elevation, Greenlee et al. (1991) demonstrated that contrast threshold elevation also increases as the adapting contrast is raised. Therefore, instead of varying the monocular exposu durations, the relative contrast of the adapting grating in the two eyes was manipulated during simultaneous binocular exposure.

Given the direct relationship between adapting contrast and aftereffect strength, the logic outlined by Sloane and Blake (1981) should also be applicable here. That is, assuming that there is interaction among the monocular and binocular channels, the two monocular functions should exhibit a gradual decline with the reduction of adapting contrast in that eye. The binocular function should intersect the two monocular curves at the 1:1 ratio, where the interocular contrasts are matched. If there is interaction among the neural channels the remaining binocular thresholds should fall between, but not below, the monocular functions.

The preceding description assumes that there is interaction among the various channels, however a different outcome is to be expected if the channels are independent. The monocular functions should follow the same pattern as described for neural pooling. The binocular and monocular aftereffects should be equivalent when the contrast is the same in the two eyes, for the threshold of all channels will have been increased by adaptation. As the interocular contrast ratio increases, the AND channel will cease to be affected by adaptation, and during binocular testing will detect the stimulus at contrast levels equivalent to those required prior to adaptation. Therefore, at these extreme adapting ratios, there should be no binocular threshold elevation. Therefore, if there is no pooling of output, the binocular function should peak sharply at the 1:1 ratio, but on either side of this point it should drop below the two monocular functions, to non-adapted threshold levels.

3.2 **Method**

3.21 Subjects & Apparatus

Three experienced psychophysical observers participated in Experiment II. All had normal visual acuity and stereopsis. The apparatus used to generate the stimuli, and to store the data, was the same as that described in Experiment I. Subjects were required to detect stationary 2.5 c deg^{-1} sine-wave gratings which were identical in the two eyes. Seven ratios of, 11:1, 3:1, 2:1, 1:1, 1:2, 1:3, 1:11, corresponding to contrasts of 0.56:0.05, 0.45:0.15, 0.40:0.20, 0.30:0.30 in the left and right eyes, were used to induce threshold elevation.

3.22 Procedure

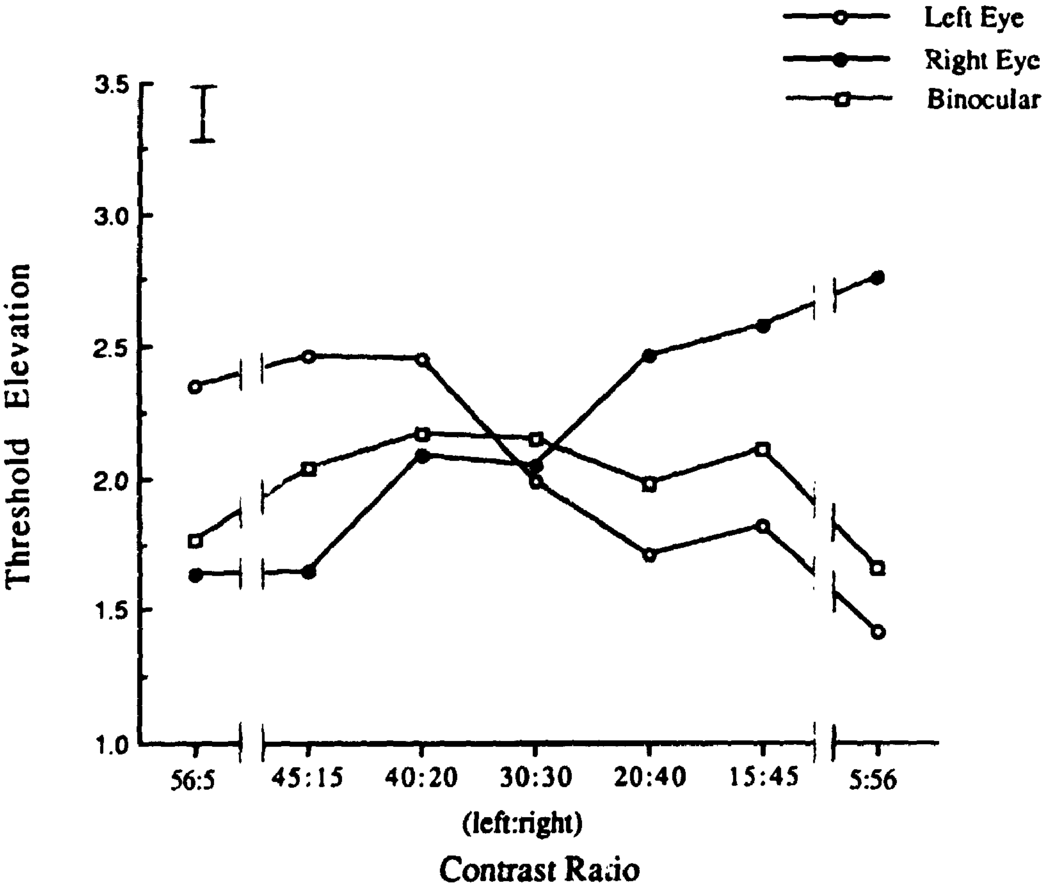
The standard adaptation paradigm was used to record contrast threshold elevation in the left, right, and both eyes following binocular adaptation. In the baseline phase the initial exposure to the blank field was 10s, and the inter-trial interval was 3s. These durations were increased to a 2 min exposure and 12s top-up, during the adaptation phase. At the beginning of each session, the adaptation contrast ratio to be used to induce threshold elevation was selected at random.

A conventional staircase procedure, identical to that described for the preceding experiment, was employed. Three independent staircases (one for each test condition) were interleaved, and on each trial the staircase was selected randomly to eliminate any effects of test order. Each staircase was tested until nine reversals were attained; the final eight reversals were averaged to provide the threshold estimate for each session. Threshold elevation was taken as the ratio of adaptation to baseline contrast thresholds. The final estimates of threshold elevation represent the average of at least three such sessions, for each of the seven interocular ratios.

3.3 Results & Discussion

Figure 7 displays the results of Experiment II. The magnitude of threshold elevation, for each test condition, is plotted as a function of the contrast ratio of the adapting

Figure _7._ Monocular and binocular contrast thresholds are plotted here as a function of interocular contrast ratio. One of the following seven contrast ratios were presented during binocular adaptation, 11:1, 3:1, 2:1, 1:1, 1:2, 1:3, 1:11. The average standard error (+-1) is shown in the upper left-hand corner.


Left Eye
Right Eye
Binocular
3.5
3.0
2.5
2.0
1.5
1.0
Threshold Elevation
56:5
45:15
40:20
30:30
20:40
15:45
5:56
(left:right)
Contrast Ratio

gratings. As predicted by a neural pooling model, the two monocular functions show that threshold elevation is greatest when the contrast in that eye is high, and decreases gradually as the contrast is reduced. The binocular function crosses the two monocular functions at their midpoints and never drops below them on either side of the 1:1 ratio.

A Randomized blocks ANOVA showed that there is a significant interaction effect ($F_{12,24} = 12.1$; $p < 0.0001$). Subsequent Protected t-tests showed that for the monocular thresholds, the change in elevation from 56:5 to 5:56 was significant. Further, as predicted by an averaging hypothesis, the binocular function never dropped below either of the monocular curves.

Protected t-tests applied to the binocular thresholds showed that the threshold obtained using a contrast ratio of 45:15 is greater than at 56:5 ($t_2 = 4.47$; $p < .05$). Also, the binocular threshold obtained with a contrast ratio of 40:20 is greater than with a ratio of 5:56 ($t_2 = 7.28$; $p < .05$). Thus it appears that there is a trend in the binocular function for the aftereffect to increase as the monocular contrasts are made more similar. Although the pattern is not strong, its direction is consistent with the assumption that an AND channel is affected by matched interocular contrasts, but not by the extreme adapting ratios. Presumably, when the contrasts are matched, the AND channel contributes to improve performance. However, as the contrast ratio is made more extreme, an unadapted AND mechanism begins to reduce the size of the binocular aftereffect.

The results of Experiment II are compatible with those reported by Sloane and Blake (1981). The monocular threshold elevation dropped with decreasing contrast in that eye. Importantly, an Independence hypothesis could not be used to predict the pattern of results because the binocular threshold elevation was never less than the monocular threshold elevation.

3.4 Conclusion

The results of Experiments I and II reject the Independent channels hypothesis in favour of interaction between the monocular and binocular channels. Also, Experiment I illustrated that there is no reason to suspect that the monocular and binocular OR channels have different detection thresholds. Therefore, those who would argue in favour of the independence of the neural channels must provide yet another explanation for the presence and reduced size of interocular transfer of threshold elevation. In contrast, an interaction-based neural averaging account requires no such proviso for it describes the outcome of a wide variety of adaptation-aftereffect experiments, both at and above contrast threshold. To this point, neural pooling has been used to describe this interaction process, and is one way of conceptualizing the integration of information across channels. However, while pooling can be used to predict the relative sizes of visual aftereffects, it may be too simplistic to give any insight into the details of the neural interaction. This issue will be discussed in more detail in the General Discussion.

4.0 Experiment III - Temporal characteristics of alternating adaptation: effects on the AND Channel

4.1 Introduction

In their descriptions of an AND mechanism, Wolfe and Held (1981,1982) and Cogan (1987) have made casual reference to the need for simultaneous stimulation of both eyes in order to affect the AND channel. In fact, this requirement is the basis for the logic of the alternating exposure paradigm; when using alternating exposure it is assumed that sequential presentation of the monocular images permits adaptation of all the channels except the AND mechanism.

A number of variations of the alternating adaptation paradigm have been used to study the activity of the AND mechanism (Wolfe and Held, 1982; Blake et al., 1981; Wilcox et al., 1990). However, the choice of alternation interval has been an arbitrary one; there has been no systematic investigation of the effect of varying the alternation rate on the contribution of the AND channel. This concern is especially relevant to one of Blake et al.'s (1981) studies (described in Experiment IV) in which they compared the absolute sizes of only the binocular aftereffects for alternating monocular vs intermittent binocular adaptation. In this experiment no control studies were performed to determine the effects of varying the 'on-off' interval on the results of either of the types of adaptation. It is obvious that if the alternating adaptation paradigm is to be used to study the operation of the exclusively binocular channel, we need to know more about how the temporal characteristics of alternation affect this mechanism.

Typically, following alternating adaptation the monocular aftereffect is greater than the binocular aftereffect; this difference has been attributed to the diluting effect of the unadapted AND channel during binocular testing (Wolfe & Held, 1981; Wilcox et al., 1990). There are two obvious effects of varying the alternation rate on the contribution of the AND channel following alternating adaptation; there could be either optimal or minimal isolation of the AND channel. Optimal isolation would occur if the AND channel was completely unaffected by alternating exposure. Subsequently, during binocular testing the AND channel's diluting influence would be at a maximum, thus resulting in a large monocular-binocular difference. On the other hand, it is possible that under some adaptation conditions the AND channel will not be perfectly isolated. For example if the alternating rate is too fast, then the AND channel might respond to the adapting stimulus, and subsequently contribute positively during the binocular test. This situation would be manifest by significant reduction or elimination of the monocular-binocular difference. At this point, without any empirical evaluation of the effects of varying the alternation rates, the status of the intervals currently being used is unknown. That is, one can not state with any certainty whether or not the standard alternation rates are actually the best ones for optimal isolation of an AND channel, or indeed, if the rate of alternation makes a difference to the activity of the AND channel.

Recall that alternating exposure adapts all channels except the AND channel, while binocular exposure affects all channels including the AND mechanism. A binocular test condition was included to provide an estimate of the size of the binocular aftereffect when the AND channel is adapted during the exposure phase. To make the two adapting conditions comparable, the binocular adaptation stimulus was presented intermittently, using the same on-off rates as in the alternating adaptation condition.

4.2 Method

4.21 Subjects and Apparatus

Four subjects, with normal or corrected vision, participated in the experiment. All subjects were experienced psychophysical observers, but only two were aware of the purpose of the study. The apparatus was identical to that described in Experiment I.

4.22 Procedure

The data were collected using the standard aftereffect paradigm; assessments of subjects' contrast threshold were made before and after adaptation to alternating monocular or intermittent binocular gratings. The pre- and post-adaptation stages were identical except that during the adaptation stage subjects viewed the grating for 2 min, and then test intervals were interleaved with 6s readaptation.

For both adaptation conditions the total length of exposure was held constant, but the 'on-off' rate was varied. Five alternation intervals were tested (0.25, 0.5, 1.5, 3.0, or 4.0s) for both of the exposure conditions, and one interval length was selected at random for each session. The shortest adapting interval used was determined by the timing limitations of the CED1401 interface. For all adaptation intervals the 6.0s readaptation period was equally divided between the two eyes; however, to obtain equivalent monocular exposure in the 4.0s condition the readaptation period had to be lengthened to 8.0s. For all adaptation conditions, during 'off' intervals the subject's viewed homogeneous fields of the same mean luminance as the adapting grating.

A randomly interleaved, dual-staircase procedure was used to gather the data. All three test conditions (left,right,both) were run simultaneously, and each staircase was tested until seven reversals were attained. The final six reversals on each staircase, for each test condition, were averaged at the end of a session. Threshold elevation was calculated as the ratio of pre- and post-adaptation contrast thresholds. All subjects participated in a minimum of two sessions per alternation rate for both alternating and intermittent exposure.

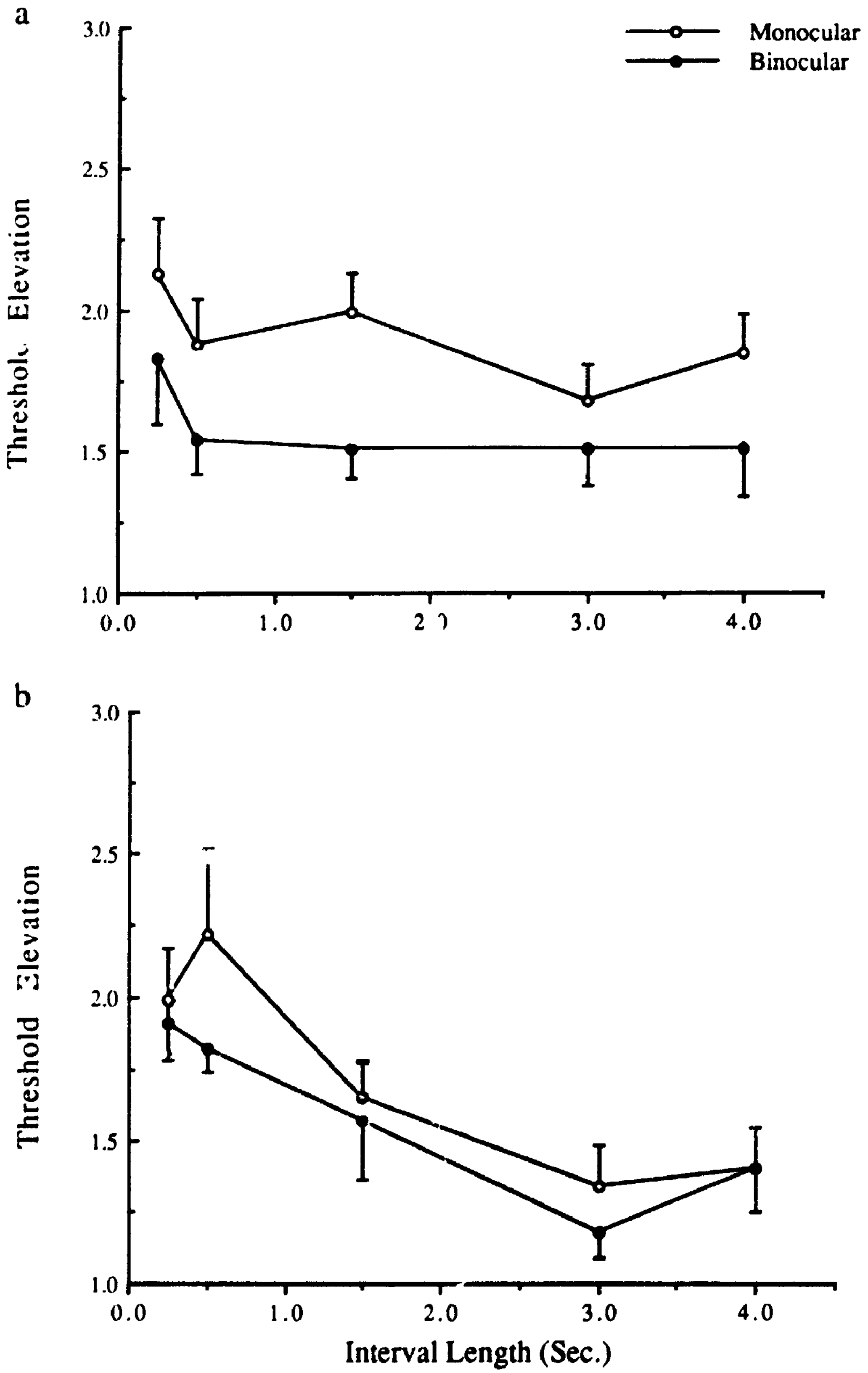
4.3 Results

The amount of threshold elevation at each interval length, for both exposure conditions is depicted in Figure 8a & b. The alternating exposure data (Figure 8a) show the typical alternating adaptation pattern; the monocular effect is greater than the binocular effect, at all interval lengths. In contrast, the intermittent binocular results (Figure 8b) change as a function of alternation interval, with an apparent decrease in both the monocular and binocular aftereffects as the interval length is increased.

A two-way randomized blocks ANOVA was performed on each of the data sets. The analysis of the alternating exposure data showed that there is a main effect of whether testing was monocular or binocular ($F_{1,3} = 19.99$; $p < 0.05$), but no effect of interval length ($F_{4,12} = 3.079$; $p > 0.05$). Subsequent tests of means, protected t-tests, confirmed that for all five of the intervals the monocular aftereffect was significantly greater than the binocular aftereffect at the 0.05 level. Further, comparison of the monocular and binocular aftereffects across intervals revealed that while there were small fluctuations in the size of the monocular effect, the binocular effects did not vary as a function of interval length.

The results of the randomized blocks ANOVA performed on the intermittent exposure data are opposite to the pattern described above. That is, here there is no effect of eye

Figure 8. _a_ & _b_ Monocular and binocular contrast threshold elevation was recorded following a) alternating monocular adaptation and b) intermittent binocular adaptation. In both figures, thresholds are plotted as a function of 'on-off' interval length 0.25, 0.5, 1.5, 3.0, or 4.0 s. Partial error bars show + or - 1 standard error of the mean.


a
Monocular
Binocular
Threshold Elevation
3.0
2.5
2.0
1.5
1.0
0.0
1.0
2.0
3.0
4.0
b
Threshold Elevation
3.0
2.5
2.0
1.5
1.0
0.0
1.0
2.0
3.0
4.0
Interval Length (Sec.)

tested ($F_{1,3} = 4.41$; $p > 0.05$) but there is a main effect of interval ($F_{4,12} = 25.23$; $p < 0.05$). The protected t-tests reveal that, while the monocular and binocular aftereffects are equivalent at all interval lengths, there is a significant drop in the amount of threshold elevation as the alternation interval is increased. The tests of means also show that while there are no differences between the two fastest alternation conditions (0.25 and 0.5 s), for either monocular or binocular test conditions, these conditions are both statistically greater than the 3.0 and 4.0s conditions. In sum, there is a decrease in threshold elevation as the interval is lengthened, that levels off at 3.0s.

4.4 Discussion

The results of this experiment show that there is no significant change in the diluting influence of the AND channel as the alternation rate is varied. It was predicted that if one alternation rate was optimal for isolating the AND channel, then the monocular-binocular difference would be at a maximum at this point. However, the binocular aftereffect did not decrease at any alternation rate, indicating that the five alternation rates are equally effective in isolating the AND channel.

The consistency of the binocular aftereffect relative to the monocular aftereffect provides empirical support for the assumption that the range of alternating rates currently used are safely above the temporal integration limits of the

AND channel. Thus, even at the fastest alternation rates, the AND channel is still excluded from the adaptation process and, in the binocular test condition, continues to dilute the size of the aftereffect. I acknowledge that if shorter intervals could have been generated, at some point the AND channel would begin to respond during adaptation. Unfortunately, because of equipment limitations I was unable to identify this alternating rate here, but the question is currently under investigation.

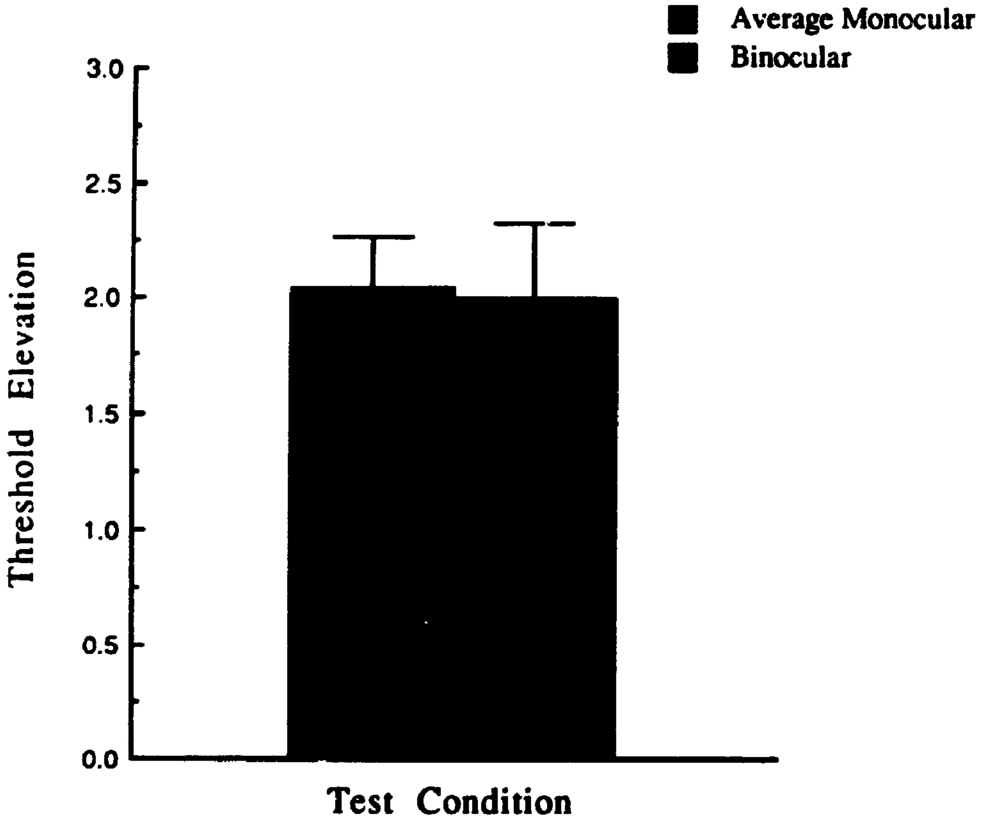
The intermittent binocular adaptation condition was included as a reference, to provide an estimate of the size of binocular aftereffect produced after adapting all channels, including the AND channel. However, it appears that these data are affected by another factor, as they show a systematic decrease as a function of interval length that does not occur when using alternating adaptation. The most straightforward explanation for this phenomenon is that during the blank 'off' intervals during intermittent adaptation, the monocular and binocular channels begin to regain their sensitivity; the aftereffect decays. Initially, the reduction in the size of the effect with increasing off time may seem surprising, especially given that the maximum interval length is still relatively short (4s). Indeed, when contrast thresholds are measured using the method of adjustment paradigm subjects are routinely allowed up to 5s to make their judgments (Blake et al., 1981).

Recovery from threshold elevation has been studied in detail by Greenlee et al. (1991); they found that the characteristics of the decay of the aftereffect depended differentially on the contrast and duration of the adapting stimulus. For example, as the adapting duration was increased the aftereffect took longer to decay. In comparison, as the adapting contrast was raised, the recovery function became steeper because the initial level of aftereffect was raised, but the time taken to recover remained constant. Therefore, the rate of decay is not a simple function of the length of adaptation, but depends on the interaction of the duration and contrast of the exposure stimulus. Directly relevant to the decay issue is their Figure 2 (1991; p.227) where Greenlee et al. show that following adaptation to a grating of 81% contrast, the size of the aftereffect drops by a full log unit in less than 5.0s. Blake et al. (1981) do not report the physical contrast of their adaptation stimuli, however, the data provided by Greenlee and his colleagues support concerns about the effects of decay which occurs within the initial 5.0s following adaptation.

To provide a basis for the assessment of decay that occurs during intermittent adaptation, threshold elevation was measured fc several subjects binocularly, without the blank intervals. The data were collected using the same apparatus and procedure as in the intermittent condition, and the total adaptation time was held constant. The results are illustrated in Figure 9. Notice that the monocular and binocular aftereffects are identical, and that threshold elevation is a factor of 2.0. Comparison of the aftereffects of continuous and intermittent binocular exposure (Figures 8b and 9) show that at the shortest intervals, the aftereffects in the intermittent condition are identical to those in the continuous condition. However, as the interval is lengthened, in the intermittent condition, the monocular and binocular aftereffects are diminished.

Indirect support for the existence of the binocular OR channel is provided by the decay that occurs during intermittent binocular adaptation, but not during alternating monocular adaptation. That is, when the binocular stimulus is displayed intermittently, there are 'silent' intervals during which there is no stimulation of the OR channel. Assuming that sensitivity begins to recover when the adapting stimulation is stopped, then decay during the 'off' portions of the cycle will cause the aftereffect to grow at a reduced rate. It is reasonable to assume that as this interval is lengthened, more decay will occur, and there will be a corresponding decrease in the size of the aftereffect. In contrast, when the adapting stimulus is alternated monocularly between the two eyes, some portion of the OR channel is being adapted continuously. Therefore, because in the alternating exposure condition the OR channel does not have to undergo any 'silent' periods, I would not predict,

Figure 9. Shown are the levels of monocular and binocular contrast threshold elevation recorded following continuous binocular adaptation. Error bars indicate +1 standard error.


Average Monocular
Binocular
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Threshold Elevation
Test Condition

and did not observe, a reduction in the binocular effect with increasing interval length.

4.6 Conclusion

The data reported here replicate our previous suprathreshold and threshold alternating adaptation results. More important, the results demonstrate that the range of alternation rates used in previous alternating adaptation experiments (1.5-3.0s) should be equally effective in isolating the exclusively binocular channel. Finally, the results of this experiment allow us to state with certainty that monocular stimuli that are alternated as quickly as 0.25s will remain invisible to the AND mechanism.

5.0 Experiment IV - The responsiveness of the AND mechanism at threshold

5.1 Introduction

Experiment III used the contrast threshold elevation aftereffect to examine the temporal limitations of the AND channel. However, Wolfe and Held (1983) have argued that the AND channel is inoperative when the psychophysical task takes place at, or near contrast threshold. These authors initially made this suggestion (Wolfe and Held, 1983) in response to a contrast threshold elevation experiment performed by Blake et al. (1981) that looked unsuccessfully for evidence of a second binocular combination site. In their experiment Blake et al. (1981) used the threshold elevation aftereffect and alternating adaptation to determine if there is more than one class of binocular neuron. Subjects were exposed to the adapting stimulus with each eye alternately for a specified period of time, or to both eyes intermittently for equivalent durations. Following both types of adaptation, the aftereffects were measured binocularly. Blake et al. (1981) reasoned that the AND process would not be driven during alternating adaptation, and should subsequently dilute the binocularly measured aftereffect. In the intermittent exposure condition the AND channel would be active during both stages, producing maximum binocular threshold elevation. They predicted that if an AND channel exists, then the binocular aftereffect recorded following alternating adaptation would be smaller than the binocular aftereffect resulting from intermittent binocular adaptation. Blake et al. (1981) found that there was no difference between the magnitude of the aftereffects obtained in the two exposure conditions, and concluded "that only binocular neurons of the 'OR' type participate in the adaptation process" (p.372).

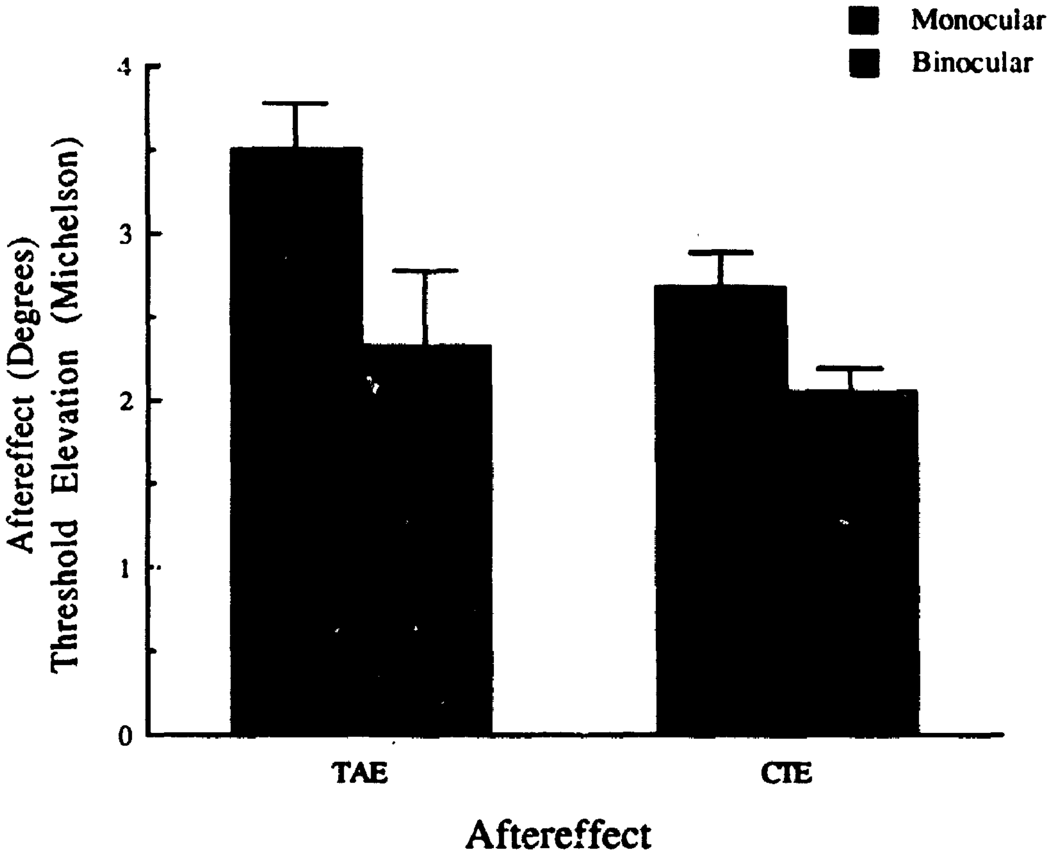
In a series of suprathreshold tilt aftereffect experiments, Wolfe and Held (1981, 1983) found support for a dual-binocular visual system. In response to the apparent discrepancy between their results and those of Blake et al. (1981), Wolfe and Held (1983) suggested that the threshold elevation aftereffect does not involve the AND channel. That is, they argued that the AND channel does respond to suprathreshold stimulation, like that used for the tilt aftereffect, but does not respond to threshold levels of contrast used in threshold elevation experiments. Consequently, the diluting influence of the AND channel would be apparent when alternating adaptation was used with the tilt aftereffect, but not when used with the threshold elevation aftereffect.

In addition to the results of Experiment III, evidence for an AND channel has been provided, outside the adaptation/aftereffect domain, using a variety of detection tasks. It is of relevance here that some of these discrimination and masking experiments assessed subjects' detection thresholds, a task which Wolfe and Held claim does not involve the AND channel. Clearly, there is a conflict between Wolfe and Held's proposal and the existing data. The experiments performed by Cohn and his colleagues (1976, 1981) and by Cogan (1987) have been presented as evidence of a dual-binocular system. However, if the AND channel does not participate in threshold tasks, then their data reflect the contribution of a process other than the AND channel and must be reinterpreted.

As a preliminary test of the putative insensitivity of the AND channel, I performed a simple alternating adaptation experiment using the contrast threshold elevation aftereffect, and compared the results with the pattern found in the corresponding suprathreshold tilt aftereffect experiment (Wilcox et al., 1990). The logic and predictions for the relative sizes of monocular and binocular aftereffects obtained following alternating adaptation are outlined in the Introduction. To summarize, the monocular aftereffects should be at a maximum because in both test conditions all the tested channels have been adapted. However, the binocular aftereffect should be significantly lower than the monocular aftereffects because of the diluting influence of the unadapted AND channel. To be consistent with Wolfe and Held's (1983) proposal, the lowered binocular effect should be obtained for the tilt aftereffect, but not for the threshold elevation aftereffect. The data did not confirm Wolfe and Held's proposal; the monocular aftereffects were larger than the binocular effect, for both the threshold and suprathreshold adaptation conditions (see Figure 10). These data suggest that the AND channel does contribute at detection threshold, and in the same manner as it does above threshold.

The preceding alternating adaptation study involved a comparison of two different aftereffects, one operating at threshold and the other at suprathreshold. However, these two aftereffects are believed to result from different patterns of neural activity (see Introduction). Therefore, I decided to test the hypothesis more rigorously using a single aftereffect, contrast reduction, which could be measured both at and above contrast threshold. An advantage of this aftereffect is that it provided evidence of AND activity

Figure 10. Suprathreshold tilt (TAE) and contrast threshold elevation (CTE) aftereffects were recorded monocularly and binocularly after alternating monocular adaptation. The averaged monocular, and the binocular aftereffects are illustrated here. The vertical axis represents the degree of tilt aftereffect as well as the ratio of pre- and post-adaptation contrast thresholds.



Monocular
Binocular
4
3
2
1
0
Aftereffect (Degrees)
Threshold Elevation (Michelson)
TAE
CTE
Aftereffect

along a contrast continuum. Therefore, if the AND channel is insensitive at contrast threshold, the monocular and binocular functions should overlap at low reference contrasts. When the reference contrast is increased the test stimulus should become visible to the AND channel, and at this point the binocular aftereffect will fall below the monocular aftereffect. On the other hand, if the AND channel has the same contrast threshold as the other channels, then there should be no overlap at the low reference contrasts; the binocular aftereffect should always be lower than the monocular aftereffect.

5.2 **Method**

5.21 Subjects

Four subjects, 22 - 40 years of age, participated in the experiment. All subjects were practiced psychophysical observers with normal visual acuity and stereopsis.

5.22 Apparatus

The apparatus used to generate the test and adaptation stimuli was identical, in all important respects, to that described in Experiment I. Sine-wave gratings (2.5 c deg^{-1}), with a space-averaged luminance of 20 cd m^2 were used throughout the experiment. The contrast of the adapting stimulus was held constant at 40%, while the contrast of the test gratings was varied to match that of the reference. A pair of opaque shutters, under software control, restricted the subject's view of the monitor according to the viewing condition. The display consisted of two concentric circular fields, formed by two independent outputs from the image generator. The reference stimulus (fixed contrast) was presented in the center field (radius of 2.5^0) and the test grating (variable contrast) appeared within the outer ring (width of 1.75^0). For each test session one of six reference levels (8%, 12%, 16%, 20%, 24%, 32%) was selected for the contrast of the centre field.

5.23 Procedure

Exposure to the adaptation stimulus was preceded by baseline measures of reference-test contrast matches. During the pre-adaptation period the reference and test gratings (the center and surround respectively) were presented for 1s followed by a tone. Upon hearing the tone the subject indicated whether the contrast of the inner-most grating was higher or lower than that of the surrounding grating. On the first trial the surround contrast was arbitrarily set 2 db greater or less than the reference intensity. Over subsequent trials the contrast of the surround was adjusted according to the standard staircase procedure. Three single staircases, one staircase for each of the viewing conditions (left, right, and binocular) were tested simultaneously and in random order. Estimates of perceived contrast were calculated by averaging the final 6 reversals on each staircase.

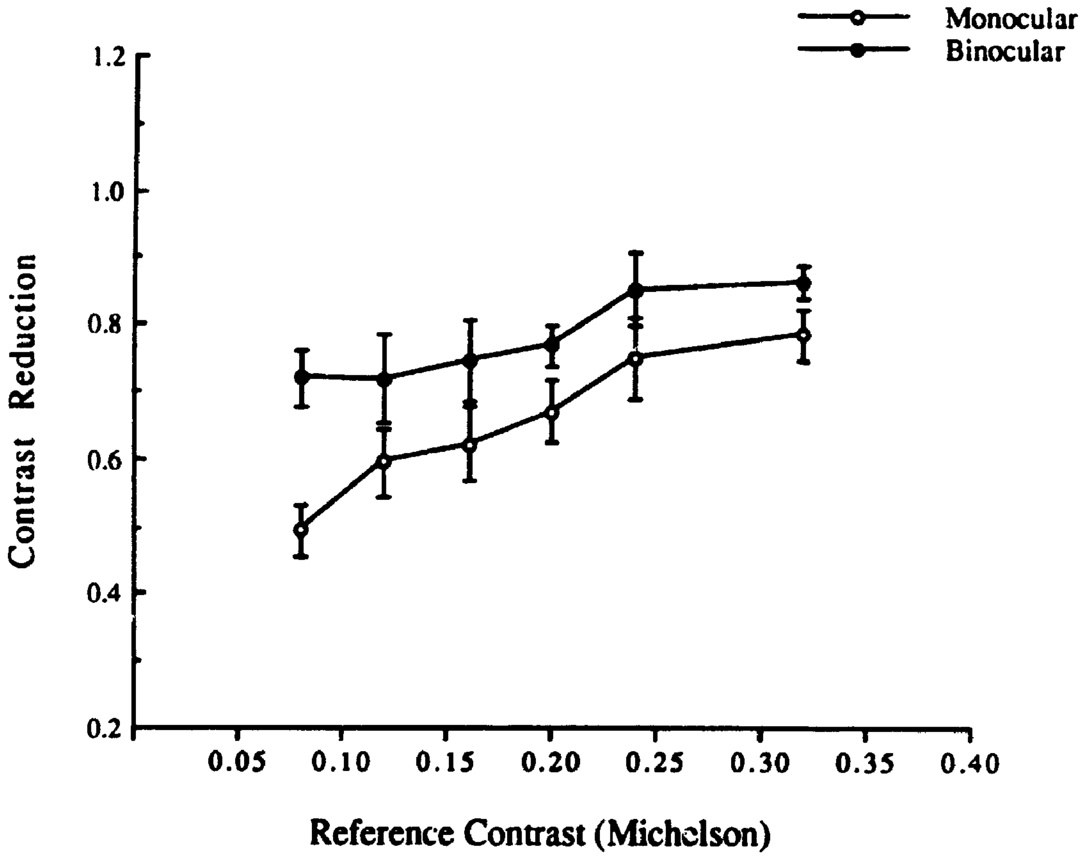
Essentially the same procedure was used during the adaptation stage. Subjects adapted each eye alternately to a high contrast grating presented in the center field. The alternation rate was 2.5s and the initial exposure duration was 120s; the level of adaptation was maintained using a 6s readaptation period between trials. To quantify the amount of contrast reduction, the average test contrast required to match the reference grating after adaptation, was divided by that required before adaptation. Therefore, the amount of contrast reduction was represented as a ratio that varied from 0.0 - 1.0, with scores nearing 1.0 indicating little or no aftereffect. Each threshold represented the average of the matches obtained in a minimum of two sessions.

5.3 **Results**

The change in apparent contrast as a function of the contrast of the reference grating, the average of four subjects, is plotted in Figure 11. It is obvious that the amount of contrast reduction was greater in the monocular test condition than in the binocular test condition, at all reference contrasts. The individual subjects' data consistently show the same monocular advantage.

A two-way randomized blocks ANOVA supports the preceding observations; the difference between the binocular and monocular threshold elevation was significant ($F_{1,3} = 462.85$; $p < .001$). Subsequent protected t-tests showed that the monocular and binocular test conditions were statistically different at all reference contrasts (df = 3, p

Figure 11. Centre-surround contrast matches were made monocularly and binocularly after alternating monocular adaptation. The reduction in perceived contrast of the test grating is plotted as a function of the contrast of the reference grating. Because the effect of adaptation was to lower perceived contrast, a value of 1.0 on the ordinate indicates no change in perceived contrast. The monocular function shown here represents the average of the two monocular test conditions, and the error bars indicate +-1 standard error of the mean.


Monocular
Binocular
Contrast Reduction
1.2
1.0
0.8
0.6
0.4
0.2
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
Reference Contrast (Michelson)

< 0.01). The main effect of reference contrast and the interaction term were also significant at ($F_{5,15} = 8.4461$; $p < .001$), and ($F_{5,15} = 4.676$; $p < .01$) respectively.

5.4 Discussion

Wolfe and Held (1983) argued that the AND channel "makes no contribution to the perception of near-threshold stimuli" (Wolfe and Held; 1983, p.220). However, the results of Experiment IV support the opposite conclusion, that the AND channel contributes to the perception of stimuli at and above contrast threshold.

Subsequently, I have reexamined Wolfe and Held's argument in an attempt to clarify the discrepancies between their conclusions and those of Blake et al. (1981). After doing so, I must question the validity of Wolfe and Held's (1983) proposal; both the evidence that Wolfe and Held (1983) present in support of their position, and Blake et al.'s (1981) results, are subject to reinterpretation.

In the study that they presented as evidence of the threshold insensitivity of the AND channel, Wolfe and Held (1983) used alternating adaptation, and measured the magnitude and decay of the MAE. They then compared the pattern of monocular and binocular aftereffects obtained in the two test conditions. Wolfe and Held (1983) classified the magnitude estimation condition as a suprathreshold task, and the decay condition as a threshold task. They reported that the binocular effect was less than the monocular effects when the measure was a magnitude estimate, but that monocular and binocular effects were the same size when duration was measured. They attributed the difference in the pattern of results to the absence of the diluting influence of the AND channel when testing the duration of the MAE.

Although it is reasonable to propose that different results might be obtained under threshold and suprathreshold conditions, it is difficult to understand how measurement of duration of an aftereffect can be classified as a threshold task of the type proposed by Wolfe and Held (1983). It is obvious that in threshold elevation studies the contrast threshold of the subject, the point at which the stimulus is just visible, is being manipulated and recorded; this does require a threshold judgment. However, when judging the duration of an aftereffect, the threshold for detection is not being measured; rather than recording the minimum stimulation necessary for detection, one is recording the point at which the adapted cells return to their normal rate of discharge, or the moment that the firing distribution becomes symmetrical. Clearly the duration of the MAE can not be classified as a threshold detection task as argued by Wolfe and Held.

A second, and perhaps more fundamental, reason for questioning Wolfe and Held's (1983) proposal is that Blake et al.'s (1981) results do not conclusively reject the AND model. Therefore Wolfe and Held's (1983) attempt to reconcile the two experiments may have been unnecessary. Recall that Blake and his colleagues (1981) measured only the binocular aftereffects following two different types of adaptation; they did not record the monocular aftereffects. Thus their comparison was between the absolute sizes of the binocular aftereffects obtained under the alternating monocular and intermittent binocular adaptation conditions.

Experiment III reports the results of alternating and intermittent adaptation measured monocularly and binocularly with a range of alternation rates (see Figure 8a and b). Because Experiment III uses both alternating and intermittent adaptation, and includes a binocular test condition, data obtained at the longest test interval (4.0s) replicate and extend Blake et al.'s (1981) study. The data show that at this test interval, the absolute sizes of alternating and intermittent binocular aftereffects are equivalent ($t=1.19$; $p = 0.32$). However, the relative sizes of the monocular and binocular effects obtained following the two adaptation conditions are quite different. The data obtained after alternating adaptation show the expected pattern ($Ml = Mr > B$), but monocular and binocular test conditions are equivalent in the intermittent condition ($Ml = Mr = B$). The difference in the overall pattern of results for the two types of adaptation conditions suggests that there is some additional factor involved.

Comparison of the sizes of the monocular and binocular aftereffects across interval lengths reveals one such factor. In the intermittent condition both test conditions show significant amounts of decay as the blank interval is increased from 1.0 to 4.0 min. However, no such decrease in the size of the aftereffects is observed in the alternating condition. As discussed in Experiment III, this recovery of sensitivity, in the intermittent adaptation condition only, is easily explained by the nature of intermittent adaptation and the assumption that the binocular OR channel is influenced by either of the eyes.

During intermittent binocular adaptation there are blank periods during which neither eye is stimulated. These non-adapting intervals provide an opportunity for all the channels to recover from adaptation, consequently, longer blank intervals would result in less threshold elevation. This factor does not influence the alternating data because during alternating adaptation one of the two eyes is always stimulated, therefore while the effect might decay in the monocular channels during the 'off' periods, the OR mechanism is given no opportunity to recover from adaptation.

It appears that the equivalent binocular effects that Blake et al. (1981) obtained following alternating and intermittent adaptation could be a function of decay of the binocular effect during intermittent adaptation. It is likely that in Blake et al.'s (1981) study, the AND channel did reduce the binocular effect following alternating adaptation.

But, because the binocular effect recorded following intermittent adaptation was also reduced, there was no difference in the absolute sizes of the two test conditions.

5.5 Conclusion

The results of this experiment are unambiguous: the diluting influence of the AND mechanism is consistent regardless of test contrast. Given these data, and the considerations presented above, there is no support for Wolfe and Held's (1983) suggestion that the AND channel is less sensitive than the remaining monocular and binocular mechanisms.

6.0 Experiment V - Interocular phase sensitivity of the AND Channel

6.1 Introduction

As noted in the Introduction, Cogan (1987) has proposed a model of the visual system that consists of two channels which can be equated, in many respects, with the AND (Fused channel) and OR (Either-eye channel) mechanisms. In a study designed to assess his model, Cogan (1987) measured binocular luminance thresholds for binoptic or dichoptic full-field luminance changes. In some conditions the monocular changes were in the same direction (both increments or decrements), while in others the changes were in opposite directions (an increment in one eye and a decrement in the other). He, like Cohn and Lasley (1976), found that detection performance was markedly improved when like shifts were viewed by the two eyes, regardless of their sign. However, when the luminance phase-shifts were dichoptic, detection performance dropped. Cogan's interpretation of these results was that the dichoptic (unmatched) pairs were detected by one group of binocular cells, while the binoptic (matched) pairs activated a second binocular mechanism.

On the basis of his data, as well as the results obtained by Cohn and Lasley (1976) and Cohn et al. (1981), Cogan (1987) argued that the critical response characteristic that distinguishes between the Either-eye and Fused channels is their sensitivity to interocular luminance phase (polarity) differences. That is, the Either-eye channel will respond to input to either of the two eyes, in spite of interocular differences in phase. However, the Fused channel will not respond if the monocular stimuli have different phase relationships. Therefore, when a bright stimulus is shown to one eye while the other views a relatively dark stimulus, only the OR channel will respond, but the AND channel will remain silent.

The experiments performed by Cogan (1987) and by Cohn and Lasley (1976) used relatively simple visual stimuli to find evidence of two binocular channels. Typically, visual information is more complex, and there are generally large variations in luminance across a scene. Most likely with this consideration in mind, Cogan (1987) stated at the conclusion of his paper that his model could be applied to "any visual task for which monoptic, binoptic, and dichoptic responses can be measured, eg. at the contrast threshold" (Cogan, 1987; p. 2134).

We used sine-wave gratings to determine if Cogan's model could be applied to simple testing of contrast thresholds using a spatially modulated stimulus. The following experiment uses Cogan's (1987) logic to predict the relative sizes of monocular and binocular thresholds for grating detection. Whereas Cogan (1987) manipulated the relative luminance phase of monocular fields, this experiment uses spatially modulated stimuli, consequently I varied the relative spatial phase of monocular gratings.

If Cogan's luminance increment/decrement results can be generalized to spatially modulated stimuli, then one would expect the AND channel to contribute to detection when the two monocular gratings are phase-matched (0^0 phase relationship), thus yielding relatively low thresholds. As the phase-angle between the two gratings is increased, the contribution of the AND channel to detection should diminish, such that when the monocular gratings are maximally disparate (180^0 phase relationship) thresholds should be at their highest.

In designing the preceding experiment, I used horizontal gratings to avoid any potential effects of introducing stereoscopic depth into the detection situation. However, Part II of the study was performed specifically to assess the effect of these horizontal retinal disparities, generated using vertical gratings, on the activity of the AND channel. Fusion of monocular stimuli that have been laterally displaced on the two retinae creates a sensation of depth; the stimulus will appear to lie off the fixation plane. Further, within a range of approximately 0^0-0.5^0 (Rose, Blake, and Halpern, 1988), the sensation of depth will increase as the interocular stimulus disparity is increased. Therefore, if vertical gratings were used, it is possible that subjects would be able to use information from the stereoscopic system to signal the presence of the test stimulus. If this signal was salient, it might disrupt or obscure the contribution of the AND and OR channels to detection.

6.2 **Method**

6.21 Subjects

Data were collected using three female subjects. Two of the subjects were practiced psychophysical observers who were aware of the purpose of the experiment. The third subject was naive to both the purpose and procedures involved and was included as a control to corroborate the data obtained from the experienced subjects. Where required, the subjects wore corrective lenses.

6.22 Apparatus

Sine-wave gratings were generated, as in Experiment I, with a microcomputer and a CED1401 interface to a Picasso image generator. The visual display was slightly different from that used in Experiment I, in that gratings were presented on a single Tektronix 606a monitor with a green (P31) phosphor. The space-averaged luminance was held constant at 13.0 cd/m^2 while the Michelson contrast was adjusted to obtain threshold estimates. Three spatial frequencies were tested (3.0, 0.80, 0.53 c deg^{-1}) and within each test condition the contrast and spatial frequency of the two monocular stimuli were identical, ensuring that the test gratings differed only in terms of their relative locations on the two retinae.

The relative phase of the two gratings ranged between 0^0 and 360^0 with a total of 20 phase angles tested at 18^0 intervals. For the control subject the test interval was doubled to 36^0 so that every second phase-shift was tested. 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.

To maintain stable convergence subjects wore base-out prisms housed in light-weight spectacle frames. The minimum prism strength necessary to comfortably achieve and maintain fusion was determined individually, therefore, different prism strengths were required for each subject (HBS - 14 D, LMW - 3 D, NG - 7 D). During testing the subject's head position was maintained using a combination chin and head rest. The two fields of the display were physically separated by a matte black nasal septum, which extended 57.0 cm to the viewing monitor. The divider served to restrict each eye's view of the display to a single field (5^0 x 4^0). Four small squares (each subtending approximately 0.25^0), were positioned at the corners of a 1.0^0 deg central square region. The subjects reported that this arrangement was effective in maintaining constant fusion of the monocular fields.

6.23 Procedure

Within a single 45 min session, one threshold estimate was obtained for each of the twenty phase angles, in twenty sequential blocks of trials. Prior to each test session the order of testing for the 20 phase angles (blocks) was chosen randomly to avoid any effects of test sequence. Within a block, contrast thresholds were measured binocularly using a randomly interleaved dual-staircase.

Each phase angle was tested until five reversals were accumulated on both staircases. Upon completion of a block of testing, the arithmetic mean of the final four reversal points on each staircase was calculated and stored by the computer. At least five sessions were run for each spatial frequency. Therefore, the final threshold estimates for each phase angle, within each of the test conditions, represented the average of at least forty reversals.

Monocular contrast thresholds were also recorded at each spatial frequency. Essentially the same dual-staircase procedure was used, but because 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. Each eye was tested individually, and ten threshold estimates were obtained during a single session. The mean of the ten estimates was calculated and later used to compare binocular to monocular threshold performance, in the form of summation ratios.

6.3 Results

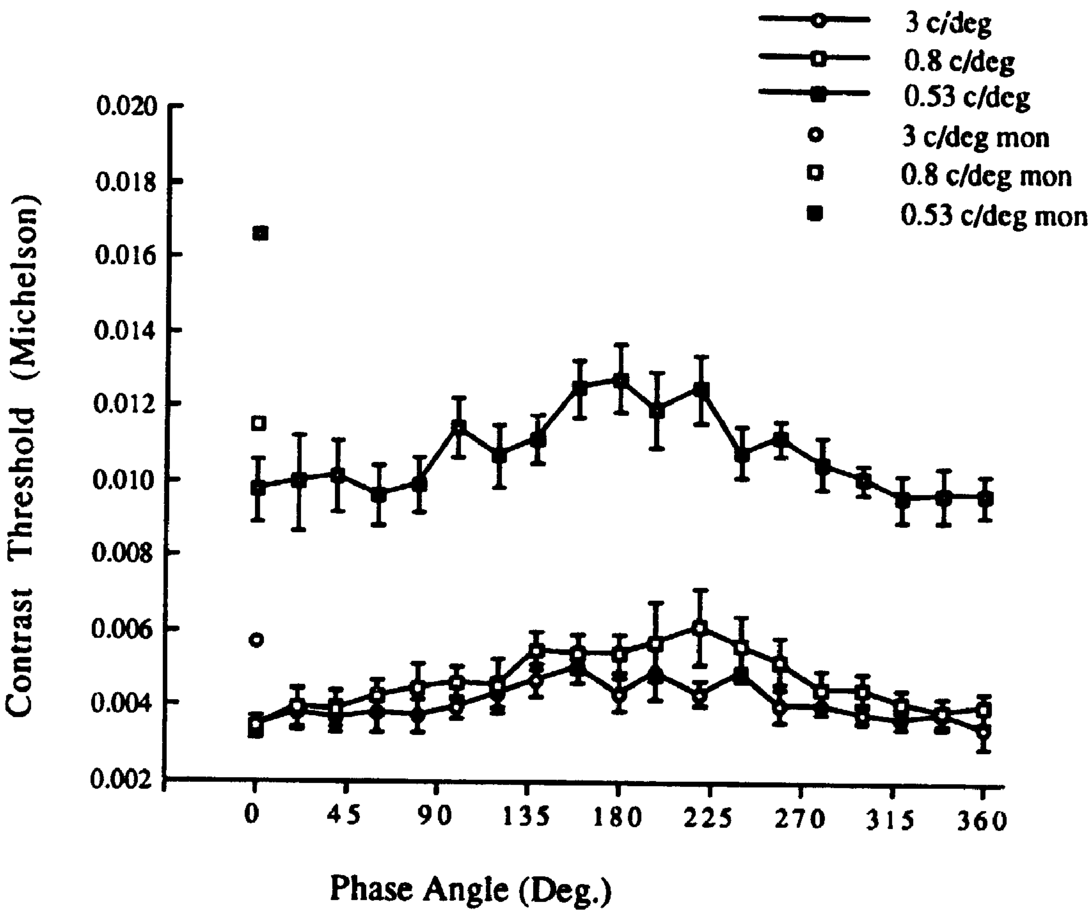
Part I - Horizontal gratings

Contrast thresholds, plotted as a function of phase angle, are depicted in Figure 12; each point represents the average of two subjects' data. The data obtained from the third subject showed the same pattern of effects, but were not included here because she was tested in only half of the conditions. The average of the monocular thresholds, for each frequency, is indicated along the vertical axis.

The function relating contrast threshold to phase-angle has a similar shape at all three frequencies; the subjects' thresholds are relatively high when the phase of the two stimuli is disparate, but decrease as the relative phase is made more similar. This pattern was unaffected by spatial scale; i.e., it was obtained at all frequencies.

Binocular summation was calculated by dividing monocular by binocular thresholds. The resulting summation

Figure 12. Contrast thresholds were recorded monocularly and binocularly using horizontal gratings and a range of interocular phase angles. The graph shows changes in threshold obtained for three frequencies (3.0, 0.8, and 0.53 c deg^{-1}) as a function of phase difference. The three isolated points along the vertical axis show the average of the monocular thresholds for each of the frequencies. The error bars show +-1 standard error of the mean.

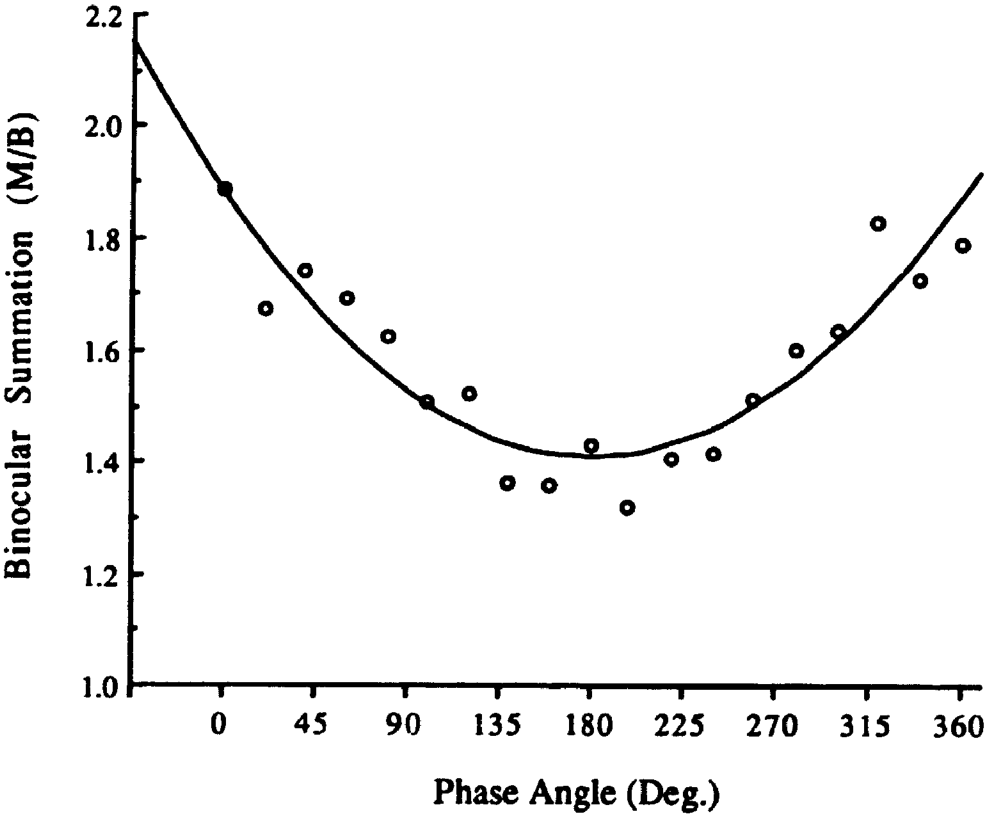

3 c/deg
0.8 c/deg
0.53 c/deg
3 c/deg mon
0.8 c/deg mon
0.53 c/deg mon
Contrast Threshold (Michelson)
0.020
0.018
0.016
0.014
0.012
0.010
0.008
0.006
0.004
0.002
0
45
90
135
180
225
270
315
360
Phase Angle (Deg.)

contours illustrate how binocular performance varies relative to monocular performance as a function of the interocular phase relationship. Figure 13 displays the average of the binocular summation contours, and illustrates that as the interocular phase-angle was increased, binocular summation decreased dramatically. Specifically, the average summation in the 0^0 phase condition was 1.84, this dropped to 1.43 when the phase was shifted by 180^0.

In the binocular summation literature, a summation ratio near 1.2 is thought to be evidence of simple probability summation (Campbell and Green, 1965); the improvement in binocular relative to monocular performance resulting simply from having two independent detectors. However, investigators generally report that improvement in binocular performance is near a factor of $\sqrt{2}$, and this value has been accepted as a standard for assessing neural summation.

The ratios presented here exceed that predicted by probability summation at all interocular phase differences. Even when the stimuli are 180^0 out of phase, and the AND channel should be silent, the binocular summation ratios are equivalent to that predicted by neural summation. This implies that the OR channel should be credited with some amount of facilitative activity in response to binocular stimulation. Further, as Cogan has proposed, the contribution of the OR channel occurs irrespective of the interocular

Figure 13. Binocular summation ratios are plotted here as a function of the interocular phase angle. Binocular summation was calculated by taking the ratio of the monocular and binocular contrast thresholds displayed in figure 12. This graph depicts two subject's data, averaged across three spatial frequencies (3.0, 0.8, and 0.53 c deg^{-1}).



2.2
2.0
1.8
1.6
1.4
1.2
1.0
Binocular Summation (M/B)
0
45
90
135
180
225
270
315
360
Phase Angle (Deg.)

phase relationship of the monocular gratings.

It is significant that the summation ratio increases to 1.84 as the interocular phase difference is reduced. This improvement is much greater than predicted on the basis of single binocular channel models (Campbell and Green, 1965). Therefore, it appears that as the two gratings become better aligned, another class of binocular cells contributes to improve performance.

Part II - Vertical Gratings

As noted earlier, lateral displacement of vertical gratings in the two eyes creates a horizontal retinal disparity which can be used by the stereoscopic system to signal relative depth. I was interested to see what effect this disparity information would have on detection performance. If there was no effect of introducing horizontal disparity, then the relationship between contrast threshold and phase-shift should be identical to that obtained using horizontal gratings. However, if the subjects were able to use information from the stereoscopic mechanism to signal the presence of the test stimulus, this pattern would not be present.

The procedure and test conditions used to record contrast thresholds were identical to those described above, except that the gratings were rotated to 0^0, and the lowest frequency was 0.48 instead of 0.53 c deg^{-1}. The resulting thresholds are plotted as a function of phase angle in Figure

14. The two higher frequency curves show no consistent relationship between interocular phase-shifts and contrast thresholds. In comparison, the 0.48 c deg^{-1} function exhibits a pattern that would be predicted if the subjects used disparity information to detect the gratings; thresholds fall as the phase-shift is increased, and reach a minimum when the gratings are 180^0 out of phase.

The binocular summation ratios calculated from the data obtained using vertical gratings, are very different from those reported for the horizontal test condition. Because there was no change in the two higher frequency functions, their summation ratios are correspondingly invariable. However, comparison of the low frequency summation contours from Parts I and II illustrates a dramatic effect of introducing disparity information. Figure 15 shows that the shape of summation contour for the 0.48 c deg^{-1} vertical grating is the reverse of that obtained using horizontal gratings.

6.4 Discussion

6.41 Horizontal Gratings

Cogan's (1987) model of binocular combination predicts that when monocular stimuli are of opposite phase only one binocular mechanism, the OR channel, is available to mediate detection. However, if the two images have the same phase an additional binocular mechanism, the AND channel, will contribute to detection. If this proposal is valid, then

Figure 14. Contrast thresholds were measured as in figure 10, using vertical gratings. Thresholds are plotted as a function of interocular phase angle and the three isolated points show the monocular thresholds for each spatial frequency. The error bars represent +-1 standard error of the mean.

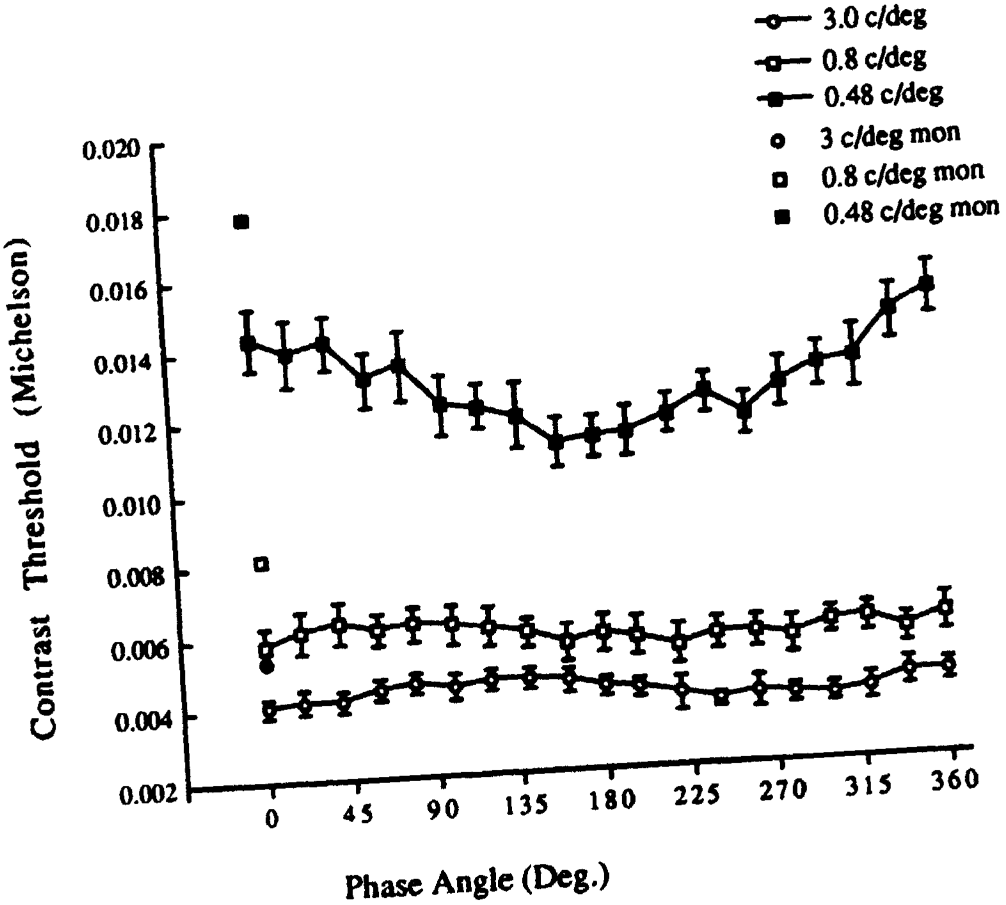
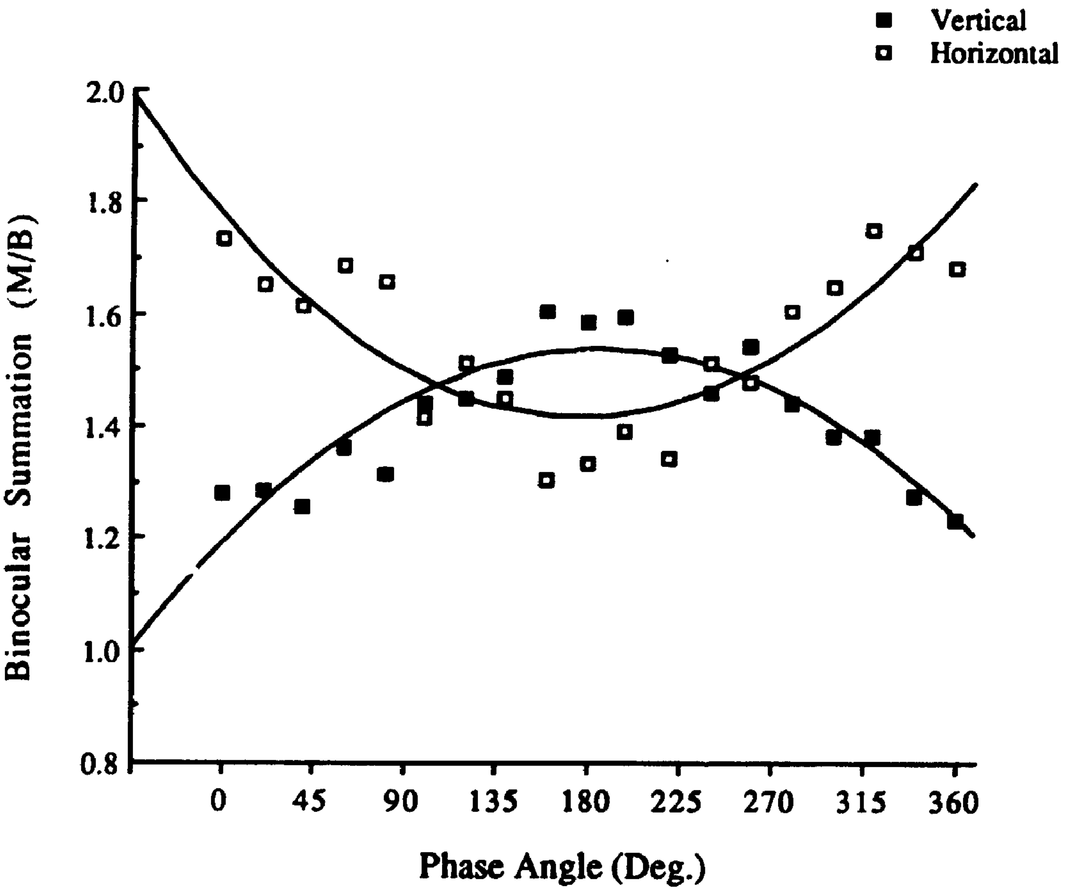

3.0 c/deg
0.8 c/deg
0.48 c/deg
3 c/deg mon
0.8 c/deg mon
0.48 c/deg mon
Contrast Threshold (Michelson)
0.020
0.018
0.016
0.014
0.012
0.010
0.008
0.006
0.004
0.002
0
45
90
135
180
225
270
315
360
Phase Angle (Deg.)

Figure 15. Binocular summation ratios were calculated, as in figure 12, using the monocular and binocular threshold data obtained with vertical gratings (figure 14). For comparison, the data for the lowest frequency, at both orientations, are graphed as a function of interocular phase angle.


■ Vertical
□ Horizontal
Binocular Summation (M/B)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0
45
90
135
180
225
270
315
360
Phase Angle (Deg.)

contrast thresholds for luminance modulated stimuli should be lowest when the relative phase of the monocular gratings is 0^0 and highest when the two gratings are 180^0 out of phase. This pattern of results was obtained at all three spatial scales when horizontal gratings were used, and supports Cogan's (1987) proposal, that the AND channel is sensitive to phase differences.

6.42 Vertical Gratings

When vertical gratings were detected, the contrast thresholds obtained using 3.0 and 0.8 c deg^{-1} did not change as a function of phase-angle, while the 0.48 deg^{-1} data follow a pattern opposite to that predicted by Cogan's model. It is likely that the difference in the pattern of thresholds obtained using horizontal and vertical gratings can be attributed to the presence of disparity information. This proposal most obviously applies to the low frequency test condition, where thresholds vary directly with the amount of stereoscopic information present. That is, as the relative phase-angle was increased the amount of disparity present also increased, and detection thresholds improved. Thus it appears that subjects were able to use some disparity-contingent information to signal the presence of the test grating.

Vergence errors are the most obvious reason for the absence of disparity-contingent variation at both 3.0 and 0.8

c $\deg^{-1}$. Normally, vergence eye movements are used to quickly bring the monocular fields into alignment allowing perceptual fusion of the two fields. This vergence is relatively precise. However, once the monocular stimuli are fused the human visual system can tolerate substantial misalignment, up to 2^0 for random-element stereograms, before signalling that two stimuli are not accurately fused (Fender and Julesz, 1967). In the display used here, subjects' fusion was guided by a set of four small markers which, in retrospect, may not have been adequate to maintain precise alignment of the two fields. Therefore, fluctuations in vergence could have introduced discrepancies in the relative positions of the monocular fields that, while changing the phase relationship of the gratings, were not large enough to be noticed by the subjects. The end result is that the physical disparity could have been varying randomly within a block of trials, in spite of efforts to hold the interocular position constant.

These small deviations in the alignment of the two fields would create shifts in the locations of the monocular gratings on the two retinae. This is a concern especially with the 3.0 and 0.8 c $\deg^{-1}$ frequencies because of the close spacing of the bars, for example, when using the 3.0 c $\deg^{-1}$ grating, the maximum phase-shift corresponded to 10 min arc disparity. Consequently, an error of only 10 min arc would create a 180^0 phase-shift. Although the potential for these vergence errors would still be present at lower frequencies, their effect on the disparity would be markedly reduced because of increased distance between adjacent bars; now for 0.48 c deg^{-1}, a displacement of 180^0 would require a disparity shift of 60 min arc. If the preceding account is valid, then when testing 3.0 and 0.8 c deg^{-1} the true positions of the gratings on the two retinae were highly variable, so that any pattern of results depending on the phase-relationship will have been lost.

6.5 Conclusion

The results of Part I demonstrate that when horizontal gratings are used, contrast thresholds vary as a function of interocular phase-angle. The improvement in detection performance as the position of the stimuli in the two eyes becomes more similar, is consistent with Cogan's (1987) proposal. That is, dichoptic images are detected by the OR channel only, but as the stimuli are made more similar, an AND mechanism contributes to improve performance. The low-frequency data obtained in Part II show that the introduction of stereoscopic information disrupts the preceding pattern of effects. It is possible that subjects were able to use additional disparity information to signal the presence of the stimulus.

CHAPTER FOUR - THE FUNCTIONAL ROLE OF AN AND CHANNEL

7.0 Experiment VI - The AND Channel and Subthreshold Summation

7.1 Introduction

The ultimate goal of studying the response characteristics of the exclusively binocular channel is to determine what contribution it makes to human vision. The studies reported here illustrate that the AND channel will respond to simultaneous monocular stimuli that have the same contrast and phase; the AND channel requires closely-matched monocular stimuli.

There is a striking similarity between these response requirements, and the conditions necessary for binocular summation. As noted previously, binocular summation refers to the fact that for a variety of visual tasks binocular detection is better than monocular by a factor of at least √2 (see Blake and Fox, 1972). This enhancement is greater than would be predicted by simple probability summation (Pirenne, 1943), and has led several investigators to conclude that it results from true neural facilitation. The fact that this binocular advantage is absent when more complex tasks, such as letter recognition are used, (Frisen and Lindblom, 1988) argues for the relatively low level of this processing. Further, the improvement in detection or performance is obtained only if the monocular stimuli are similar along a number of stimulus dimensions. In contrast to the AND mechanism, a great deal is known about the limitations of binocular summation. For example, binocular summation can be eliminated by introducing, a 1/2 octave difference in spatial frequency, a temporal delay of greater than 100 msec, out-of-phase flicker, or more than 15^0 orientation difference (Arditi, 1986). The dependence of both the AND channel and summation on the similarity of monocular images, suggests that the AND mechanism is a good candidate for the neural substrate of binocular summation. However, while correlational evidence may suggest a causal relationship, on its own it can not prove that one exists. Instead, what is required is a more direct test of the relationship between summation and the activity of the AND channel.

The following experiment assessed the contribution of the AND channel to binocular summation using a combination of two psychophysical paradigms, the selective adaptation procedures described earlier and subthreshold summation. The latter refers to the fact that the contrast threshold for a monocular grating is significantly lowered by simultaneous presentation of a subthreshold grating to the other eye. The logic of this experiment is as follows. If the AND channel mediates summation phenomena, such as subthreshold summation, then it should be possible to reduce summation by making the AND channel less sensitive. Conversely, if a treatment does not affect the exclusively binocular channel then summation should also remain unchanged.

In the following experiment binocular summation was recorded before and after alternating monocular and continuous binocular adaptation. Recall that when alternating adaptation was used, all channels should have been active in the exposure phase, except for the binocular AND mechanism. According to the preceding logic, the AND mechanism should have been equally responsive before and after alternating exposure, consequently subthreshold summation should remain unchanged. In the second condition, binocular adaptation was employed, ensuring that all available channels, including the AND channel, were adapted. Thus, following this exposure condition, the AND channel would be less sensitive and summation should be correspondingly reduced.

7.2 Method

7.21 Subjects and Apparatus

Six subjects, all of whom were experienced psychophysical observers, participated in this study. Prior to testing, the hole-in-paper test was used to determine each subject's preferred eye. This eye was used for measuring subthreshold summation throughout the session, and optical correction was worn when necessary.

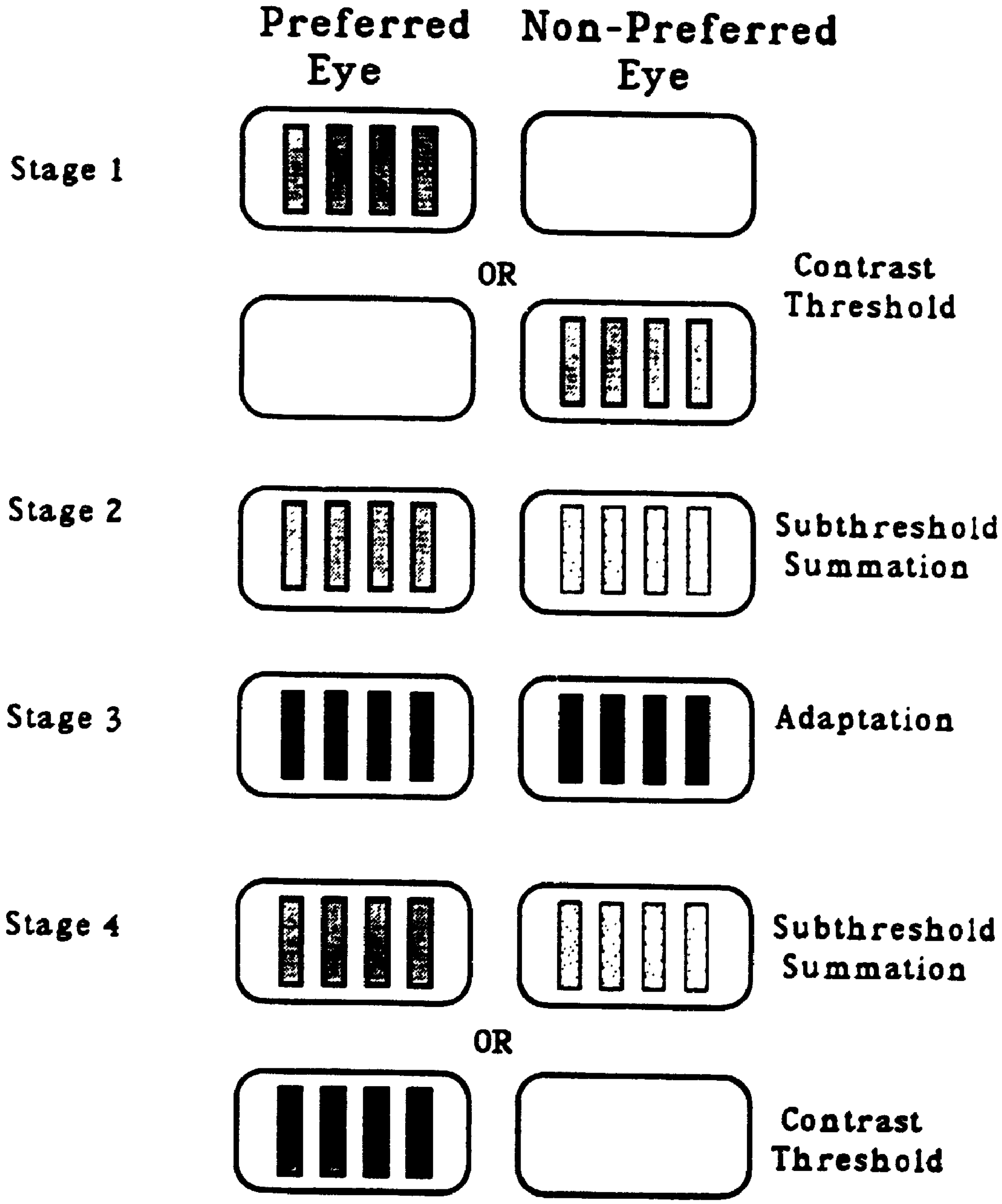
The standard apparatus was used, with a minor adjustment to the face of the display. A single black circle, approximately 15' in diameter, was positioned in the centre of the two fields replacing the 2^0 square fusion pattern. In subsequent checks of fusion subjects indicated that the dot, combined with the black edges of the circular apertures, provided sufficient contour information for accurate and stable fusion of the two fields.

7.22 Procedure

Contrast thresholds were recorded using the staircase procedure and a forced-choice task, as described in the preceding experiments. Each session was divided into four stages which are illustrated in Figure 16; after each stage the computer performed the appropriate calculations, and initiated the next set of trials. At the start of each session, baseline estimates of contrast threshold were measured for each eye, using two randomly interleaved single-staircases. Both staircases were tested until fifteen reversals were obtained on each; the final fourteen reversals were averaged independently for each staircase to provide estimates of the monocular contrast thresholds. The contrast threshold in the preferred eye was used to calculate the contrast of the subthreshold grating (0.15 log units below contrast threshold) to be presented to the other eye during subthreshold summation testing. Although Blake and Levinson (1977) recommended a reduction of 0.10 log units for the subthreshold stimulus, in pilot testing I found that a 0.15 reduction in contrast consistently produced greater summation. The contrast threshold for the non-preferred eye was recorded to be certain that the contrast of the

Figure 16. The four stages of Experiment VI are depicted here. The darkness of the filled bars represents the relative contrast of the test or exposure gratings. In the first stage contrast thresholds were assessed for both eyes. In the second stage, the threshold for the preferred eye was measured with a subthreshold grating presented to the partner eye. Following alternating monocular or continuous binocular adaptation (stage 3), thresholds were recorded again for the preferred eye with and without the subthreshold grating in the other eye (stage 4).

Figure 16


Preferred Eye
Non-Preferred Eye
Stage 1
OR
Contrast Threshold
Stage 2
Subthreshold Summation
Stage 3
Adaptation
Stage 4
Subthreshold Summation
OR
Contrast Threshold

subthreshold grating did not exceed the detection threshold for that eye. This did not occur in any of the test sessions.

In the second stage, contrast thresholds were recorded for the preferred eye with the subthreshold grating presented simultaneously to the other eye. Again a dual-staircase procedure was used, but the termination point was lowered to 9 reversals on each staircase. Measures of sub-threshold summation were followed by 2.0 min of alternating monocular (1.5s alternation rate), or continuous binocular adaptation.

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

For each session the ratio of baseline contrast threshold (stage 1) to the summation threshold (stage 2), in the preferred eye, was used to represent the amount of pre-adaptation subthreshold summation. Post-adaptation summation was calculated as the ratio of threshold elevation without the subthreshold grating in the partner eye, to the threshold obtained with the subthreshold grating present (stage 4). The critical comparison was between the two summation ratios obtained before and after adaptation (averaged across five sessions). In the summation literature reports of summation ratios greater than 2.0 are rare. Therefore, the few scores that were greater than 2.0 were classed as artifacts and discarded, regardless of the adaptation condition.

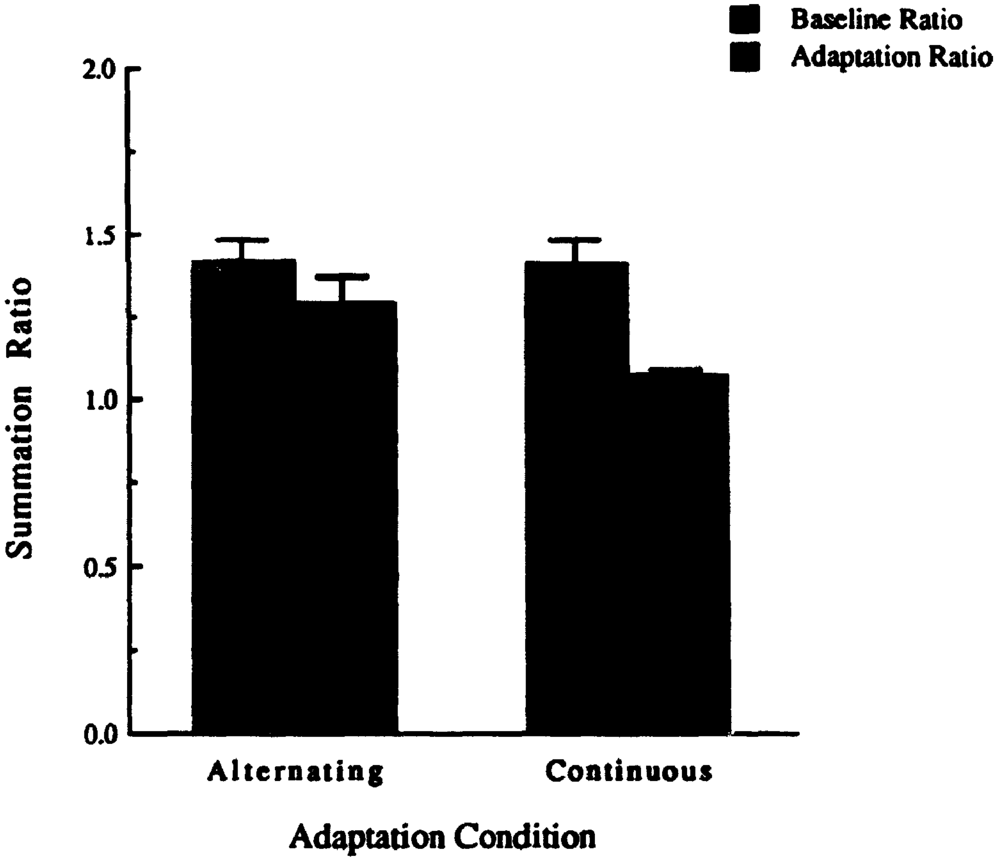
7.3 Results & Discussion

The ratios of pre- and post-adaptation subthreshold summation were calculated for the alternating monocular and binocular adaptation conditions. These summation ratios are illustrated in Figure 17; values near 1.0 indicate an absence of summation, while ratios greater than 1.0 correspond to increased summation. While alternating adaptation appeared to have little effect on subthreshold summation, binocular adaptation virtually eliminated it.

The preceding observations were confirmed using a randomized blocks ANOVA. The analysis showed no effect of adaptation regime ie. alternating monocular vs. continuous binocular adaptation ($F_{1,5} = 3.53$; $p > 0.05$), but there was a significant main effect of whether summation ratios were recorded before or after adaptation ($F_{1,5} = 80.82$; $p < 0.05$). The interaction between the two conditions was also statistically significant ($F_{1,5} = 10.75$; $p < 0.05$). Subsequent protected t-tests showed that while there was no difference between the pre- and post-adaptation ratios for alternating adaptation ($t_5 = 2.08$; $p > 0.05$), the two were statistically different in the binocular adaptation condition ($t_5 = 6.72$; $p < 0.05$).

As predicted, subthreshold summation was not affected by alternating adaptation, but was eliminated by binocular

Figure 17. The pre- and post-adaptation summation ratios for alternating monocular and continuous binocular adaptation are depicted here. 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). Summation ratios near 1.0 represent an absence of summation. Error bars indicate +1 standard error of the mean.

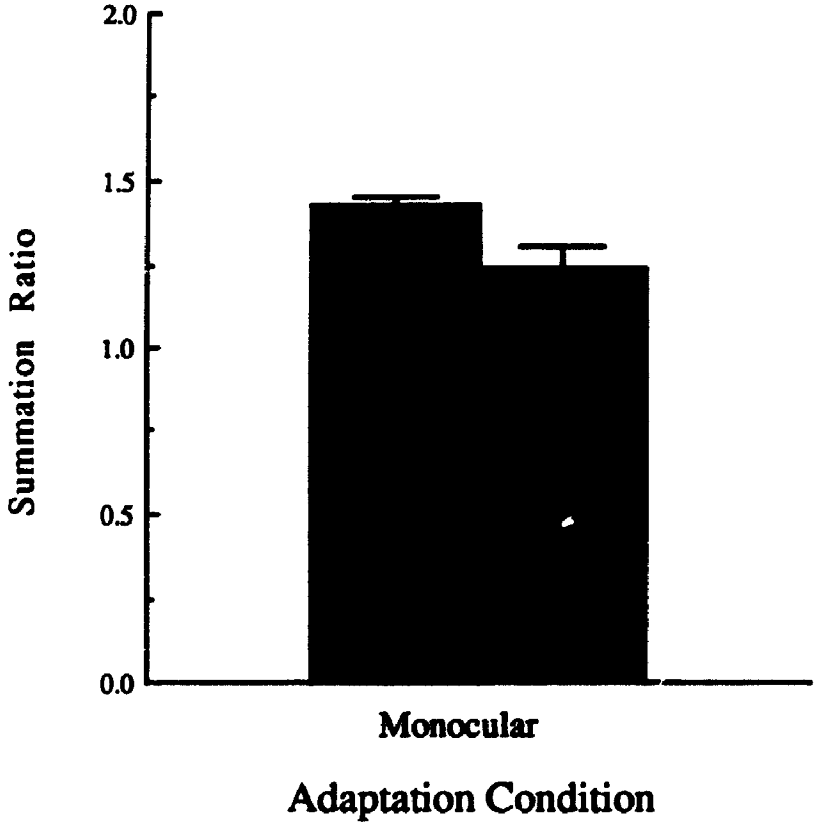

■ Baseline Ratio
■ Adaptation Ratio
2.0
1.5
1.0
0.5
0.0
Summation Ratio
Alternating
Continuous
Adaptation Condition

adaptation. Not surprisingly, the pre-adaptation summation ratios are identical in the two exposure conditions, therefore the significant interaction is caused by the drop in summation following binocular adaptation; a drop that does not occur after alternating adaptation.

The subthreshold summation ratios obtained in the two adaptation conditions confirm the experimental hypothesis and so support the proposed role of the AND channel in binocular subthreshold summation. To determine if the similarity of the pre- and post-adaptation summation ratios in the alternating adaptation condition was not due to factors specific to that form of adaptation, a follow-up condition was run. This adaptation condition was identical to the preceding two, except that subthreshold summation was assessed before and after monocular adaptation. As in the alternating adaptation condition, monocular exposure should not affect the AND channel. Consequently, if only the AND mechanism contributes to binocular summation, subthreshold summation should not be influenced by monocular adaptation.

The summation ratios recorded before and after monocular adaptation are depicted in Figure 18 and are identical to those obtained in the alternating exposure condition. A Student's t-test for correlated observations showed no difference in the pre and post -adaptation summation ratios ($t_5 = 2.17$; $p > 0.05$).

Figure 18. The summation ratios shown here were calculated as described for figure 17, but before and after monocular adaptation. Error bars indicate +1 standard error of the mean.


2.0
1.5
1.0
0.5
0.0
Summation Ratio
Monocular
Adaptation Condition

7.4 Conclusion

The results of this study are straightforward. When the exclusively binocular mechanism was made less sensitive binocular summation was eliminated, indicating that the AND channel contributes to binocular summation. In Experiment V binocular summation was measured under all testing conditions, irrespective of the interocular phase angle. This was interpreted as evidence of a facilitatory contribution of the binocular OR channel that was not phase-specific.

In the preceding experiment there was opportunity for adaptation of the OR channel in the alternating and continuous monocular adaptation conditions. However, in neither of these conditions was there evidence of binocular summation in the OR channel. It seems that the subthreshold summation recorded here is somehow different from the summation measured in Experiment V in that it involves the AND but not the OR channel.

CHAPTER FIVE - REVIEW OF EXPERIMENTS AND DISCUSSION

8.0 General Discussion

The psychophysical experiments presented here were designed to study the response characteristics of a binocular channel that acts as a logical AND-gate, in that it will only respond to matched binocular input. The common objective of these experiments was to explore the contribution of this binocular channel to human vision.

Monocular adaptation and the contrast threshold elevation aftereffect were used in the first experiment to assess whether monocular and binocular mechanisms are independent. I also tested the proposal that the monocular channels have a higher threshold for stimulation than the binocular channels. In this study, I varied adapting contrast and recorded changes in monocular and binocular thresholds. The data showed not only that the monocular and binocular channels have the same threshold for detection, but, an interaction-based explanation provided a better account of the data than did an Independent channels hypothesis. A similar conclusion was reached in Experiment II where interocular contrast ratios were varied during binocular adaptation, and threshold elevation was recorded monocularly and binocularly. Again, the data were not consistent with the assumption that the channels are independent.

Experiments III through V were designed to examine the response characteristics of an AND channel. In Experiment III we varied the temporal characteristics of alternating adaptation to determine if there are optimal alternating rates that can be used to exclude the AND channel from adaptation. I concluded that alternating rates between 0.25 and 4.0 s are equally effective at isolating AND cells. In addition, the data revealed that the 3-4 s blank intervals present during intermittent binocular adaptation permitted significant decay of the contrast threshold elevation aftereffect. Thus, intermittent binocular adaptation is not the appropriate binocular control for alternating monocular adaptation. The fourth study demonstrated that contrary to Wolfe and Held's proposal (1982, 1983) an exclusively binocular channel does not have a higher threshold for stimulation than the other channels. The AND channel appears to function in the same manner both at and above contrast threshold.

Experiment V was performed to assess the effect of interocular phase differences on the activity of the binocular AND channel. Cogan (1987) varied only the polarity of the stimuli using full-field luminance changes. To place this experiment in the wider context of spatial vision, I used spatially modulated stimuli and varied their interocular position, or relative phase. The results were dependent on the orientation of the gratings. That is, when vertical gratings were used to record thresholds, the phase-dependent contribution of the AND channel observed when horizontal gratings were used, was absent. From these data I concluded that when stereoscopic information is available it affects detection thresholds, making the facilitatory contribution of an AND channel difficult to isolate. It appears that the relationship between the AND channel and stereopsis is not straightforward, therefore, an AND channel should not be identified directly with the stereopsis mechanism. Finally, Experiment VI was performed to assess the functional role of the AND channel in binocular summation. The results suggested that the AND channel plays a significant role in binocular summation.

8.1 Neural Pooling

The models that have been forwarded to describe classes of cells in the human visual system have often used the terms independent and/or distinct in reference to individual mechanisms (Moulden, 1980; Wolfe and Held, 1981, 1982; Cogan, 1987). In fact, when describing how these channels operate, both Moulden (1980) and Blake et al. (1981) explicitly state that visual information is carried by three independent channels. However, a closer examination of the data actually reported by Blake and his colleagues (Blake et al., 1981; Sloane and Blake, 1981), as well as the results of Experiments I and II, suggest just the opposite conclusion, that it is not accurate to describe the monocular mechanism and binocular AND and OR channels in this manner. That is, the psychophysical data show consistently that there is interaction among these groups of cells.

Blake et al. (1981) argue that the individual channels are independent but their output is eventually combined, such that detection performance is determined by the pooled activity of all available channels. Unfortunately, while their description of pooling provides a way of conceptualizing the final output of the combination process, it provides no insight into how it takes place. A closer study of their proposal (see Blake et al., 1981; Sloane and Blake, 1981) reveals that they assume that pooling occurs within the visual cortex, that each of the channels is equally weighted, and the final output depends on the proportion of the channels contributing to the pool (channels tested) that have been adapted. From their description, it is possible to produce a general overview of the pooling process. First, we can assume that pooling occurs serially; the outputs of the AND, OR and monocular mechanisms converge on a group of cells at a subsequent stage of processing. It also follows from their description that detection performance should be based solely on the degree of excitation at this pooling site; when its activity exceeds some threshold level of intensity the pooling cells will signal that a stimulus is present.

The preceding description is intuitively appealing, however, it raises some logical concerns. As mentioned above, in describing the activity of the various groups of cells, Blake et al. (1981) argued that the activity of the monocular and binocular mechanisms is pooled, but they also assumed that the channels are independent. These two statements are contradictory; if the output of all available channels is pooled at a single detection site, then the channels can not be independent. The pooling site is simply a group of cells with a constant threshold, therefore, many different combinations of input to this site will generate the same response. For example, there would be no way of distinguishing between a large contribution made by a single mechanism, or a lesser contribution provided by two different channels. Thus, if Blake et al. (1981) argue that pooling occurs, they cannot also describe the individual channels as independent.

As noted earlier, the results of Experiments I and II support the conclusion that the monocular and binocular mechanisms are not independent. While it is clear that some form of interaction does occur, neural pooling may not be the most accurate description of this interaction. That is, Blake et al. (1981) adopted the notion of pooling from Moulden's (1980) discussion of suprathreshold aftereffects. They then applied it directly to their contrast threshold elevation experiments. When a task involves contrast levels that are well above threshold, perception often depends on the combined activity of cells that vary along some response dimension (ie orientation). Therefore, it is not difficult to accept that pooling of activity can affect how that stimulus is perceived.

However, when this logic is applied to the sensitivity of the visual system at contrast threshold it is difficult to understand how or why pooling occurs. That is, pooling requires that when one adapted and one unadapted channel contribute to detection, the threshold represents the combination of the two sensitivities. Therefore, the end result is subtractive in nature; the system is less sensitive than it would be if only the unadapted channel mediated detection. It is not clear why information regarding the presence of a stimulus would be combined in this manner, especially when the consequence of this pooling is to lower the overall sensitivity of the visual system.

Blake et al. (1981) argued that pooling is advantageous to the visual system because when activity of single units is combined, variability is reduced, making detection more reliable. In their explanation they explicitly refer to the activity of single-units. However, in the aftereffect experiments conducted by Sloane and Blake (1981) and by Blake et al. (1981) performance is determined, not by individual cells, but by groups of units. Presumably, these channels have already performed the initial averaging that the authors refer to (Blake et al., 1981). Thus Blake et al.'s (1981) justification of neural pooling is not relevant to their proposal.

An alternative way of thinking about the integration of information across channels is in terms of inhibitory interactions between these channels. Blake et al. (1981) do not mention inhibitory activity in their description of pooling, however, psychophysical and electrophysiolgical experiments have demonstrated that there are inhibitory interactions between the monocular and binocular mechanisms. For example, both Anstis and Duncan (1983) and Cogan (1987) have argued from psychophysical experiments that purely monocular channels should be replaced by eye-opponent or mutually inhibitory activity between binocular OR cells. Their proposals are corroborated by a number of electrophysiological experiments which found virtually no pure monocular activity, but did record substantial interocular inhibition in the striate cortex (Gardner and Raiten, 1986; Maske, Yamane, and Bishop, 1984).

There is some preliminary evidence of a second inhibitory connection, this one between the exclusively binocular cells and the monocular mechanism. In Vidyasagar's (1976) study of the McCollough effect he adapted subjects to opposite color-orientation pairings, and found independent monocular and binocular aftereffects. This study, and a number of other dichoptic adaptation experiments, have shown that even though the monocular mechanism is exposed to equal and opposite adaptation during binocular exposure, its aftereffect is not nulled. Pooling can not easily accommodate this result. The monocular mechanism could be kept immune from the effects of binocular adaptation if the exclusively binocular mechanism inhibits the monocular channel(s) during binocular adaptation.

These are just two potential forms of inhibitory interaction, given the pervasiveness of inhibitory interactions in the visual cortex, there may be many others. It is conceivable that this sort of inhibition between channels is the neural basis of what Blake et al. (1981) have labelled 'pooling'. That is, inhibitory connections permit activity in one channel to modulate the activity of the others. Because these inhibitory interactions occur as the visual information is processed, the need for a pooling site which combines output from all of the channels is eliminated. One advantage of this proposal is that, although the channels interact, their output is not combined in such a way that the origin of the information is lost. Instead, eye of origin information is maintained, and could used subsequently by other visual processes.

8.2 The functional role of the AND channel in human vision

Investigators have argued that stereo-anomalous populations, such as people who had childhood strabismus, are binocularly deficient and as a result show little or no interocular transfer of visual aftereffects (Movshon et al., 1972; Mitchell and Ware, 1974; Levi, Harwerth and Smith, 1980). Some have taken the argument further and suggested that because there is a direct relationship between the degree of stereopsis and extent of IOT, that IOT can be used as an index of cortical binocularity (Ware and Mitchell, 1974). However, a number of investigators have demonstrated significant IOT in stereoblind individuals (Wade, 1976; Hess, 1978; Buzzelli, 1981; Anderson, Mitchell and Timney, 1981). This evidence of a dissociation between stereopsis and IOT is important for it highlights the point that the binocular visual system is not composed of a single, homogeneous group of binocular cells. To the contrary, the fact that the two may exist independently suggests strongly that they are served by different channels. One possible way of organizing the system is to assume that an AND channel contributes to stereo-processing, while the OR channel mediates IOT. Therefore, subjects who lack stereopsis, but still show IOT of visual aftereffects might have binocular OR cells, but do not have a normal complement of exclusively binocular cells. Results showing that stereoblind individuals do not transfer visual aftereffects interocularly are also consistent with the proposed functional dissociation of the AND and OR channels. Subjects who fail to exhibit either IOT or stereopsis might have a more severe binocular deficit, and lack both binocular channels.

Some evidence of a relationship between the activity of an exclusively binocular channel and stereopsis has been provided by Wolfe and Held (1982, 1983). In one set of experiments, Wolfe and Held (1982) demonstrated that the effects of cyclopean adaptation can not be measured monocularly. They argued that this is proof that the effects of adaptation to random-element stereograms are restricted to the AND channel. Wolfe and Held (1983) also presented data from a series of experiments designed to illustrate some of the shared characteristics of an AND channel and stereopsis. They reasoned that the identification of such similarities would strengthen the argument that exclusively binocular cells are critically involved in stereopsis. Some of Wolfe and Held's (1983) data do support their position. For example, in two of their experiments they used an alternating adaptation paradigm and induced artificial anisometropia during the adaptation and test periods. Wolfe and Held concluded that because the monocular and binocular aftereffects were equivalent in the anisometropic test condition, the dichoptic blur was effective at eliminating the contribution of an AND channel. Further, the degree of anisometropia used to exclude exclusively binocular cells was the same as that previously shown to disrupt stereopsis.

In a subsequent publication, Wolfe (1986) elaborated on their four-channel model and argued that the AND channel is the neural substrate of stereopsis. However, several of Wolfe and Held's (1982, 1983) studies have been criticized on logical and methodological grounds (Burke and Wenderoth, 1989; Timney et al., 1989; Blake and O'Shea, 1988), and as a result, more evidence is needed to uphold the proposal that an AND channel should be identified with the stereoscopic mechanism.

Although it is reasonable to suggest that an AND channel contributes to stereopsis, there are additional reasons to question whether or not it is the only type of cell that contributes to stereopsis. For example, interocular positional differences are necessary for depth to be generated stereoscopically. Therefore, for an AND channel to satisfy Wolfe and Held's (1986) description, it would have to be composed of different classes of binocular cells that are sensitive to a range of interocular phase-differences. There is both psychophysical (Richards, 1970) and electrophysiological (Poggio and Fischer, 1977) evidence that disparity processing takes place in three general types of disparity-sensitive groups of cells which are tuned for zero, crossed, and uncrossed disparities. If an AND channel is to be solely responsible for stereopsis, it must incorporate each of these cell types. It is possible that an AND mechanism consists of classes of units which respond optimally to different interocular phase-angles, however, to this point there is no empirical support for this proposal. Furthermore, if the AND mechanism were subdivided into these different cell types, then its contribution to detection would not be contingent on interocular phase differences. However, the results of Experiment V, using horizontal gratings, demonstrate that the AND mechanism responds differently as a function of the interocular stimulus position. Therefore, it does not seem likely that the exclusively binocular channel is composed of different classes of disparity-tuned units.

It is well documented that stereopsis is resistant to a number of interocular stimulus differences. An example of the resiliency of stereopsis was provided by Ogle (1950; as cited by Graham, 1965) who reported that a qualitative sense of stereopsis could be maintained with as much as 7^0 disparity, when the images were clearly diplopic. Fender and Julesz (1967) reported a similar phenomenon using random-element stereograms; depth was perceived even when the disparity in the monocular images was increased beyond the point where the images were initially fused. Fender and Julesz (1967) have reported that this effect can be induced for up to a 2^0 increase in disparity beyond the point of perceptual fusion. Again, the characteristic that distinguishes a binocular AND-gate from an OR-gate is its sensitivity to interocular stimulus differences. It is unlikely that a channel whose distinguishing response characteristic is that it requires matched input to the two eyes would respond when the interocular positional differences exceeded the fusional limit. This suggests that some other neural channel contributes to stereoscopic vision in humans.

It appears that Wolfe and Held's (1983; Wolfe, 1986) proposal needs to be modified; an alternative is to assume that an AND channel processes one type of stereoscopic information, but it is not the only type of cell that contributes to stereoscopic vision. Investigations of the conditions necessary to affect the activity of an AND channel have revealed that its response is contingent on the similarity of the monocular stimuli. These response characteristics are very similar to those that would be necessary for a mechanism to signal when stimuli lie on the horopter. Thus, the 'matched' signal originating within the AND channel could be used by the visual system to indicate when images lie the fixation plane. According to this proposal the AND mechanism would constitute just one of the three classes of cells identified by Richards (1970), the zero-disparity units, which signal when an object does not lie in depth.

There are single-unit data which support the presence of cells that respond optimally to zero disparity, in both the cat and monkey. For example Poggio and Fischer (1977) reported tuned excitatory and tuned inhibitory units that respond best to images that stimulate corresponding retinal areas. In addition, Poggio, Gonzalez, and Krause's (1988) investigation revealed large numbers of cells optimally sensitive to zero disparity which they called "tuned zero units". While facilitated by correlated monocular stimulation the activity of these tuned zero units was completely suppressed in response to uncorrelated monocular images. In as much as these cells require 'matched' stimulation of both eyes, these cells fit the description of an AND channel.

Richard's (1970) depiction of the stereoscopic system includes two other classes of cells, one which process crossed disparities and the other uncrossed disparities. Electrophysiological investigations have also identified groups of cells that correspond nicely to these classes. Poggio and Talbot (1981) recorded from "near and far" cells in the monkey striate cortex that were differentially sensitive to crossed and uncrossed disparities respectively. Furthermore, Poggio and Fischer (1977) pointed out that the vast majority of the near/far units are dominated by one eye (ocularly unbalanced). They also commented on the strong relationship between ocular dominance and disparity sensitivity; those units showing extreme dominance by one eye, were most sensitive to depth in the image. The obvious connection can be made between these near/far units, that are best suited for processing disparity information, and the binocular OR channel.

In conclusion, an alternative to Wolfe and Held's proposal is to assume that no one neural channel is completely responsible for processing stereoscopic information. That is, instead of forming the sole neural substrate of stereopsis, it seems more reasonable to assume that the AND channel is one of several classes of cells that contribute to stereoscopic depth perception. Albeit speculative, one way of organizing the stereoscopic system, is to assume that the AND channel signals when stimuli lie on the horopter, and cells belonging to the OR channel indicate when an object is in front of, or behind, the fixation point.

8.3 AND channel and binocular summation

The improvement in detection performance provided by binocular viewing is dependent on the relative frequency, orientation, contrast and temporal properties of the monocular stimuli (Arditi, 1986). As noted in Experiment VI, this dependence of binocular summation on the similarity of the monocular images is reminiscent of the response characteristics of an AND channel. Experiment VI was performed to assess this relationship, and the results suggested that exclusively binocular cells are necessary for binocular summation. Given the proposed relationship between an AND channel and stereopsis, and the interpretation of Experiment VI, it appears that the exclusively binocular channel contributes to both binocular summation and stereopsis.

The notion that there is a population of binocular cells common to stereopsis and binocular summation has been forwarded on the basis of psychophysical investigations of binocular summation in normal and stereoblind humans (Lema and Blake, 1977; Levi, Harwerth and Smith, 1980). In both of these experiments, subjects with normal levels of stereopsis exhibited summation levels at or above a factor of √2. In comparison, the summation ratios for individuals with abnormal binocular experience oscillated near 1.0 (no summation).

Levi et al. (1980) also reported that while their stereo-deficient subjects showed no binocular summation, their performance in suprathreshold dichoptic masking experiments was comparable to that of the visually normal subjects. These authors suggested that the explanation for this functional dichotomy is that there is a separation between excitatory and inhibitory processing in the visual cortex. That is, disruptions in coincident binocular stimulation degrades excitatory connections within the cortex, ie. the AND channel. However, inhibitory interactions remain and are able to mediate dichoptic masking.

The proposal that binocular summation and stereopsis have a common neural basis was also supported recently in set of behavioural (Harwerth, Smith, Paul, Crawford, and von Noorden, 1991), and electrophysiological experiments (Crawford, Pesch, von Noorden, Harwerth, and Smith, 1991). These authors found that in monkeys, binocular occlusion from birth to 2-16 weeks had dramatic effects on measures of binocular summation and on the perception of depth in random dot stereograms. These deficits were specific in that the deprivation had little effect on temporal modulation sensitivity, or spectral sensitivity. Furthermore, the negative behavioural effects were accompanied by significant changes in the ocular dominance characteristics of cells in the striate cortex of the binocularly deprived animals. Crawford et al. (1991) reported that in the visually normal monkeys 76% of the cells in the striate cortex were binocularly innervated. However, in the treatment group, the binocular complement was reduced to 18%.

The preceding observation demonstrates that binocular cells are common to both stereopsis and binocular summation. More specifically, Crawford et al. (1991) noted that, in the visually deprived animals, inhibitory interconnections between extreme ocular dominance classes were maintained; the most striking effect of binocular deprivation was in the reduction of excitatory binocular activity. This restriction of the effects of deprivation to excitatory binocular activity suggests that although some portion of the OR channel may also be affected, binocular deprivation has its strongest effect on AND-like cells.

This section has presented evidence for the role of AND cells in both stereopsis and binocular summation. Independent investigations have demonstrated a close association between deficits in stereopsis, and reduced or absent binocular summation. Further, it has been suggested that these deficits can be attributed to a disruption of excitatory binocular activity, which is characteristic of the AND channel. One conclusion that can be drawn is that the concurrent losses of stereopsis and binocular summation could be ascribed to a defective or deficient AND mechanism.

8.4 Conclusion

I have reviewed evidence from a variety of experiments illustrating that an exclusively binocular channel could contribute to both stereopsis and binocular summation. If this is true then the output of the AND channel is obviously not restricted to a single visual process. Instead, its role in human vision should be described in more general terms. That is, an AND channel might signal the presence of binocular stimuli that are temporally and spatially matched. Subsequently, this information could be used by a number of visual processes, including binocular summation and stereopsis.

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