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Measurement of visual aftereffects and inferences about binocular mechanisms in human vision

Laurie M Wilcox, Brian Timney¶, Robert St John
Department of Psychology, University of Western Ontario, London, Ontario N6A 5C2, Canada
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Abstract. There is conflicting evidence concerning the characteristics of binocular channels in the human visual system with respect to the existence of a 'pure' binocular channel that responds only to simultaneous stimulation of both eyes. Four experiments were conducted to resolve these discrepancies and to evaluate the evidence for the existence of such an exclusive binocular channel. In the first three studies, tilt aftereffects were measured after monocular adaptation. The relative sizes of the direct, interocularly transferred, and binocular aftereffects were not influenced by the configuration of the adapting pattern (experiment 1), or by the eye used for adaptation (experiment 2). There were also consistent interobserver differences in the relative sizes of the aftereffect seen after monocular adaptation (experiment 3). Taken together, these data raise questions about the appropriateness of a monocular adaptation paradigm for evaluating the presence of a pure binocular channel in observers with normal binocular vision. In experiment 4, in which the paradigm of alternating monocular adaptation was used, data were obtained that are consistent with the presence of a pure binocular channel.

1 Introduction

The interocular transfer of visual aftereffects is strong evidence for the presence of binocular neurons in the human visual system (Blakemore and Campbell 1969; Sutherland 1961). However, there has been little discussion of the characteristics of the binocular units that serve interocular transfer. Recently, several different models of binocular organization have been presented (Cogan 1987; Moulden 1980; Wolfe and Held 1981). Moulden (1980) proposed the existence of three neural channels: two monocular and one binocular. The binocular channel is assumed to respond to stimulation of either eye and may be considered as a logical OR-gate. An alternative model was presented by Wolfe and Held (1981), who proposed an additional binocular channel that behaved like a logical AND-gate, responding only to the simultaneous stimulation of both eyes. Wolfe (1986) has made this distinction between AND and OR channels the basis of a model of binocular rivalry and stereopsis. Cogan (1987) also has proposed a model that contains *only* binocular neurons. In the present paper we shall address only the OR and AND models of Moulden (1980) and Wolfe and Held (1981).

Elsewhere (Timney et al 1989) we have described in detail the predicted results of aftereffect experiments based upon the AND and OR models of binocularity. We will provide only a brief summary of the models and their predictions here. Both models are based on the assumption that the size of an aftereffect depends on the proportions of adapted and unadapted neurons that are stimulated during the testing phase of an experiment. During testing, channels that have been adapted contribute positively to the aftereffect. Channels that are not adapted, but are active in the test phase, serve to dilute the aftereffect. The predictions of the OR and AND models for different adaptation and testing conditions are illustrated in table 1.[(1)] For example, if adaptation

[(1)] The reader should be aware that the absolute magnitude of any transferred aftereffect depends on the weights assigned to each channel. In the original models of Moulden (1980) and Wolfe and Held (1981), the contribution of each channel was weighted equally and the present argument is based on these assumptions.

¶ Author to whom all correspondence should be addressed.

and testing are monocular through the same eye, the effects should be at a maximum, because all of the channels being tested have also been adapted. In the case of interocular transfer, testing of the unadapted eye stimulates the adapted binocular channel, but also an unadapted monocular channel. The result is the well-documented finding (see Mohn and van Hof-van Duin 1983) that the transferred aftereffect is smaller than the direct effect.

The three-channel (OR) model and the four-channel (AND) model make identical predictions for the results of a typical interocular transfer experiment; one would not expect an AND channel to be active during either adaptation or testing. However, these two models make *different* predictions if an additional, binocular, test condition is added. In the case of the three-channel model, binocular testing reintroduces the adapted monocular channel. This channel contributes positively to the aftereffect, making it larger than the interocularly transferred effect. If an additional binocular AND channel is present, this will also be activated during binocular testing. The activity of this unadapted AND channel would presumably reduce or cancel out the contribution of the adapted eye. Under these conditions, one would predict that the binocular aftereffect should be the same size as the transferred effect. Conflicting results have been reported with this experimental paradigm. Moulden (1980) obtained data consistent with the three-channel model (a binocular effect larger than the transferred effect), whereas Wolfe and Held (1981) reported results that they interpreted as being in favour of a four-channel model. In fact, Wolfe and Held found that the binocular effect was *smaller* than the transferred effect.

The major difference between these two studies was in the stimulus patterns used. Moulden (1980) used low-frequency square-wave gratings, similar to those that have been used in other studies of the tilt aftereffect. The subject's task was to judge when the test grating appeared vertical. Wolfe and Held (1981) also used low-frequency square-wave gratings, but they were arranged in a chevron pattern, such that the top half of the pattern could be tilted in one direction and the lower half in the opposite

Table 1. Predicted ranking of the magnitudes of an aftereffect seen after adaptation of the left eye according to a three-channel (OR) model (Moulden 1980) or a four-channel (AND) model (Wolfe and Held 1981) of binocular vision. These models are based on the assumptions that the channels are independent and have equal weights in the generation of an aftereffect, and that it is the left eye that is adapted in this case.

	Adaptation-test condition [a]		
	MON-MON	IOT	MON-BIN
Three-channel (OR) model [b]			
Channels available	M_l, M_r, B_{or}	M_l, M_r, B_{or}	M_l, M_r, B_{or}
Channels adapted	M_l, B_{or}	M_l, B_{or}	M_l, B_{or}
Channels tested	M_l, B_{or}	M_r, B_{or}	M_l, M_r, B_{or}
Proportion of adapted channels tested	2/2	1/2	2/3
Predicted ranking of aftereffect magnitudes: MON-MON > MON-BIN > IOT			
Four-channel (AND) model [b]			
Channels available	M_l, M_r, B_{or}, B_{and}	M_l, M_r, B_{or}, B_{and}	M_l, M_r, B_{or}, B_{and}
Channels adapted	M_l, B_{or}	M_l, B_{or}	M_l, B_{or}
Channels tested	M_l, B_{or}	M_r, B_{or}	M_l, M_r, B_{or}, B_{and}
Proportion of adapted channels tested	2/2	1/2	2/4
Predicted ranking of aftereffect magnitudes: MON-MON > MON-BIN = IOT			

[a] MON-MON, monocular adaptation and testing of the same eye; IOT, interocular transfer, MON-BIN, monocular adaptation and binocular testing.

[b] Channels: M_l, monocular left; M_r, monocular right; B_{or}, binocular OR; B_{and}, binocular AND.

direction. The psychophysical task in this case was the judgment of colinearity of the upper and lower halves.

We have questioned Wolfe and Held's interpretation of their data on a number of different grounds (Timney et al 1989). The most important of these criticisms is that Wolfe and Held's (1981) pattern of results, a binocular aftereffect smaller than that seen with interocular transfer, is not the a priori prediction of a simple AND model based on the ratio of adapted to unadapted channels. As we stated above, binocular testing after monocular exposure introduces an unadapted binocular channel, but it also introduces an adapted monocular channel. Thus, one might expect the transferred and binocular aftereffects to be the same size. In presenting their data, Wolfe and Held did not appear to take into account the positive contribution of the adapted eye during binocular testing.

Although the AND model is an attractive one, the dependence of the pattern of results on stimulus configuration and the logical difficulties of Wolfe and Held's (1981) predictions do not permit a strong claim for its validity to be made on the basis of the data they have presented. The purpose of the series of experiments we report here was to reexamine the factors that might influence the pattern of results in experiments of this nature and also to provide data relevant to the models of binocular organization proposed by Moulden and by Wolfe and Held.

2 Experiment 1: Grating-induced versus chevron-induced tilt aftereffects

2.1 *Introduction*

We were concerned that there should be such a difference in the results of two apparently very similar experiments simply because of the difference in the kinds of stimuli used to test the aftereffect. Although Wolfe and Held (1982) suggested a possible explanation for the difference in terms of Gibsonian 'normalization', it seems unlikely that such a hypothetical mechanism should have selective effects dependent upon which eye was tested. In an attempt to resolve the discrepancies between the two sets of data, we repeated the experiments of Moulden (1980) and Wolfe and Held (1981, 1982) using both chevrons and gratings as the induction stimuli.

2.2 *Method*

2.2.1 *Subjects.* Twenty subjects (aged 18–40 years), including the authors, participated in the experiment. All except the authors were unaware of the purpose of the study, and all had normal or corrected-to-normal acuity and normal stereopsis. Eye preference was determined by means of a sighting task and the preferred eye was always used for adaptation.

2.2.2 *Apparatus.* The stimuli were generated by a commercially available display device (Innisfree, Picasso) operating under computer control. The patterns were displayed on the face of a Tektronix 606 B CRT monitor with a P31 phosphor. Their mean luminance was 20 cd m^{-2} with a Michelson contrast of 0.4 The stimuli were visible through a 5 deg circular mask in the centre of the display. Apart from the light from the display, the testing room was dark. A head rest that wrapped around the temples and a chin rest were used to maintain the subject's head position throughout the experiment. A pair of opaque shutters controlled by the computer permitted viewing of the display with the left, right, or both eyes. A simple sighting task was used to assess eye preference; with both eyes open, the subject was asked to look at the experimenter through a small aperture in a piece of cardboard. The eye aligned with the aperture was taken as the preferred eye.

2.2.3 *Procedure.* The aftereffect was generated by both gratings and chevrons. The gratings were 2.5 cycles deg^{-1} square waves, tilted 10° off vertical. The chevrons consisted of two juxtaposed gratings tilted 10° and 170° off vertical (forming a 160° angle at the apex), separated by a black bar 15 min wide. Observers viewed the display from a distance of 57 cm. The initial exposure period lasted 240 s and was followed by successive readaptation and test intervals of 20 s and 0.5 s respectively. There was an interval of at least 1 week between the grating and chevron sessions, with the order of testing randomised across subjects.

The general procedure was as follows. Before adapting to the tilted line patterns, estimates of perceived vertical or colinearity were obtained for the left eye, the right eye, and both eyes together. During these baseline trials, subjects viewed a blank field of the same mean luminance as the test stimulus and indicated the direction of tilt of a subsequently presented grating or chevron pattern. During the adaptation period, subjects viewed a grating or a chevron pattern. After adaptation, a vertical grating or colinear chevron was presented for 0.5 s to the adapted eye, to the unadapted eye, or to both eyes. Upon hearing a tone, the subject pressed a response button signalling the perceived tilt of the grating pattern, or the direction in which the arrowhead formed by the tilted lines of the chevron pattern appeared to point.

A staircase procedure was used to collect the data. A single independent staircase was run for each of the three testing conditions. The tilt of the pattern was shifted in 0.35° steps in the opposite direction from that signalled by the observer. Once initiated, the test sequence cycled continuously until at least six response reversals had occurred for each staircase. At this point the procedure was terminated. The mean of the reversal points for each staircase was used to determine the observer's perceived vertical. The measure of the magnitude of the tilt aftereffect was the difference between the means of the preadaptation and postadaptation estimates of vertical or colinearity. Within a single session data were gathered for the same-eye monocular adaptation and monocular test (MON-MON) condition, interocular transfer (IOT), and monocular adaptation followed by binocular test (MON-BIN).

2.3 *Results*

Figure 1 shows the average aftereffect for each of the test conditions for the grating and the chevron adapting conditions. In each case, the MON-MON aftereffect is largest, followed by that for the MON-BIN condition, and then that for IOT. A two-way repeated-measures analysis of variance (ANOVA) was carried out on the data. The analysis showed a main effect for the eye tested ($F_{2,38} = 29.75$, $p < 0.0001$) and a main effect for the induction stimulus (gratings versus chevrons; $F_{1,19} = 9.29$, $p < 0.007$).

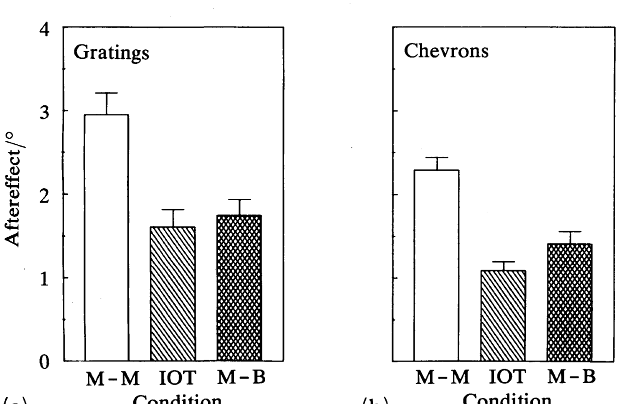

Figure 1. Magnitude of the tilt aftereffect measured with (a) grating and (b) chevron patterns in experiment 1. M-M, monocular adaptation and testing of the same eye; IOT, interocular transfer; M-B, monocular adaptation and binocular testing. The bars represent one standard error.

The grating aftereffect was significantly larger than that generated by the chevrons, but there was no significant interaction that would have suggested differences in the relative sizes of the aftereffects for the two stimuli. A posteriori comparisons were made between the individual means. In all cases the direct effect was larger than either the binocular or the transferred effect with a probability level in each case of less than 0.00001. Neither of the comparisons between the transferred and binocular aftereffects reached significance (gratings, $t_{19} = 0.72$, $p > 0.05$; chevrons, $t_{19} = 1.72$, $p > 0.05$). Given that these two tests failed to reach significance, no corrections for multiple comparisons were necessary.

These results are different from those of Wolfe and Held (1981, 1982). We found no suggestion that the MON-BIN condition produced a smaller aftereffect than the IOT condition. In addition, in contrast to Wolfe and Held (1982), we did not obtain different patterns of results for the gratings and the chevrons.

3 Experiment 2: The influence of eye preference

3.1 *Introduction*

The monocular exposure paradigm requires that one eye be exposed to the inspection pattern while the other eye remains unadapted. In the preceding experiment the subjects always adapted their preferred eye. In his experiment, Moulden (1980) tested each subject twice, in different sessions, adapting both the left eye and the right eye. Wolfe and Held (1981, 1982) did not control for eye preference, but randomly chose the eye to be adapted.

Several authors (eg Anderson et al 1980; Movshon et al 1972) have reported different amounts of interocular transfer depending upon which eye is adapted. In contrast, Moulden (1980), Mohn and van Hof-van Duin (1983), and Wade (1976) found no such differences. Typically, in studies in which differential effects of eye preference have been reported, larger amounts of transfer have been obtained when adapting the preferred eye and testing the non-preferred eye than in the reverse situation. There are a number of potential effects of eye preference on the present experiments, including the possibility that, whereas the size of the transferred effect varies as a function of eye preference, the binocular effect remains constant. Consequently, when the adapted eye is chosen randomly, the *relative* sizes of the aftereffect under the two test conditions could vary across subjects.

This is an important consideration, in that Wolfe and Held (1981, 1982) base their argument for an AND channel on the relative sizes of the transferred and binocular aftereffects. However, in their studies, the eye preference of their subjects is not reported, and consequently its effects on the relative sizes of the aftereffects remains unknown. In the following experiment we examined the possible role of eye preference on the size of the tilt aftereffect in the different test conditions following adaptation of both the preferred and the nonpreferred eye.

3.2 *Methods*

3.2.1 *Subjects.* Ten subjects (aged 18-40 years) were used, eight of whom were naive to the procedures and purpose of the experiment. All had normal or corrected-to-normal acuity and normal stereopsis.

3.2.2 *Apparatus.* The apparatus was the same as that used in experiment 1. Because Wolfe and Held (1981, 1982) reported that their pattern of results can only be obtained when chevron patterns are used to induce the tilt aftereffect, chevrons, rather than gratings, were used.

3.2.3 *Procedure.* Eye preference was assessed as in experiment 1, but two additional tasks were introduced. One was a pointing test, and the other was Miles's A-B-C test

(Porac and Coren 1976). Subjects placed a truncated cardboard cone 10 cm from their faces and viewed the experimenter's nose through the narrow opening. The preferred eye was that one aligned with the apex of the cone. All tasks were repeated three times, and the results were consistent across the three forms of assessment. The experimental protocol was identical to that of experiment 1, and all subjects participated in both adapting conditions. Both the preferred eye and the nonpreferred eye were adapted, in separate sessions, with an interval of at least 1 week between sessions.

3.3 *Results*

Figure 2 shows the size of the aftereffects for the different testing conditions after adaptation of either the preferred or the nonpreferred eye. In each case the pattern of results is the same, and it is also the same as the pattern of results obtained in experiment 1. A repeated-measures ANOVA showed no significant difference between the preferred and nonpreferred adapting conditions nor any interaction. To improve reliability, the results from the two sessions for each subject were pooled and all subsequent analyses were performed on these data. A single-factor repeated-measures ANOVA showed a highly significant effect of testing condition ($F_{2,9} = 30.3$, $p < 0.00001$). A posteriori t-tests (with the Bonferroni adjustment for multiple comparisons) again revealed that the MON–MON effect was significantly larger than that obtained in either the MON–BIN ($t_9 = 7.8$, $p < 0.0001$) or the IOT ($t_9 = 6.6$, $p = 0.0001$) condition, but there was no difference between the latter two conditions. These results confirm the findings of experiment 1 and also show that the eye used for adaptation has no effect on the pattern of results.

In this experiment we used chevrons as adapting and test stimuli to provide a further evaluation of Wolfe and Held's assertion that chevron stimuli are necessary to induce a smaller aftereffect in the binocular test condition than in the transferred condition. However, the results are identical with those of experiment 1 and there is no difference between these two test conditions. This pattern of results, obtained in two experiments, suggests very strongly that the reduced effect in the MON–BIN condition is not a reliable finding.

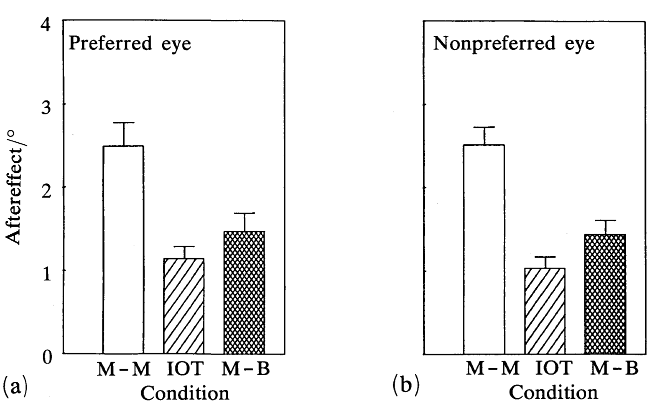

Figure 2. Magnitude of the tilt aftereffect after adaptation of the (a) preferred and (b) nonpreferred eyes for chevron stimuli in experiment 2. M–M, monocular adaptation and testing of the same eye; IOT, interocular transfer; M–B, monocular adaptation and binocular testing. The bars represent one standard error.

4 Experiment 3: Tilt aftereffect measured by the method of constant stimuli

4.1 *Introduction*

The average relative sizes of the MON–BIN and IOT conditions we obtained in the two previous experiments are very similar to those observed by Moulden. But in contrast to Moulden, we found no significant differences between the sizes of the binocular and transferred aftereffects with conventional parametric statistics. When the nonparametric statistic used by Moulden (Wilcoxon signed rank test) is applied to our monocular exposure data, a significant difference between the binocular and transferred test conditions is obtained for some, but not all, of the data. Moulden (1988, personal communication) has provided us with the original data for his tilt aftereffect experiment. We have reanalyzed those data using parametric statistics. Although an overall analysis of variance of his data showed highly significant differences between different test conditions, a posteriori comparisons with the Bonferroni adjustment for repeated measures (Myers 1979) indicated no significant differences between the size of the binocular and interocularly transferred aftereffects. Inspection of Moulden's raw data shows that the binocular aftereffect was larger than the transferred effect in ten out of fifteen subjects. In the part of the present experiment 1 in which grating stimuli were used, fifteen out of thirty subjects showed a larger effect when tested binocularly.

In summary, the analysis of our own and of Moulden's data shows that although the pattern of results averaged over subjects is relatively consistent, there are marked differences between subjects in the relative sizes of the aftereffects across conditions. In both of our experiments, most of the subjects were tested only once or twice, making it difficult to say whether the intersubject variability is simply a reflection of experimental error or is due to true differences in the relative sizes of the aftereffects. To establish the reliability of the individual differences we conducted another experiment in which the data were gathered by the method of constant stimuli.

4.2 *Methods*

4.2.1 *Subjects and apparatus.* Three observers (aged 21–24 years) with normal or corrected-to-normal vision were tested. One was a practiced observer, the remaining two were naive to both the purpose of the experiment and the test paradigm. All were given extensive practice at the task during preliminary sessions. In all essential respects the apparatus was identical to that used in experiment 1. Subjects were seated 90 cm from the display, which was masked to a 3.2 deg circle. The adaptation pattern was a 2.5 cycles deg^{-1} sine-wave grating tilted $10°$ to the right of vertical.

4.2.2 *Procedure.* During each adaptation session an initial exposure period of 120 s was followed by 1 s test and 5 s readaptation periods. The test and readaptation intervals cycled until six observations had been made at each of seven test orientations for the three test conditions (left monocular, right monocular, and binocular). Test orientation and eye tested were randomised. Subjects were asked to indicate whether the top of the grating appeared to be tilted to the left or right of vertical by pressing the appropriate button on the response box.

Prior to the adaptation session, baseline measures of perceived vertical were obtained by the same procedure, with the difference that the adaptation grating was replaced with a blank screen, and the initial grating adaptation period was reduced to 10 s. The number of responses 'to the right' for each test orientation were stored and the data cumulated over successive sessions until a minimum of eighteen trials per datum point had accrued for each test condition.

4.3 *Results*

Psychometric functions were fitted by the method of probits (Finney 1971), and perceived vertical was defined as the 50% point on that function. The aftereffects were defined as the difference between perceived vertical for the preadaptation and postadaptation conditions. In figure 3 we present the psychometric functions that correspond to the aftereffect for each test condition. The data have been normalized by shifting the functions along the abscissa to place the 50% point for each baseline function at 0°. The baseline functions are not shown. For each observer the pattern of results is similar: the MON-MON aftereffect is largest, followed by that for MON-BIN and then IOT. However, the individual psychometric functions illustrate the amount of intersubject variability. For observer AC the MON-BIN aftereffect is substantially larger than the IOT effect, whereas for observers LMW and KK there is virtually no difference between the two functions.

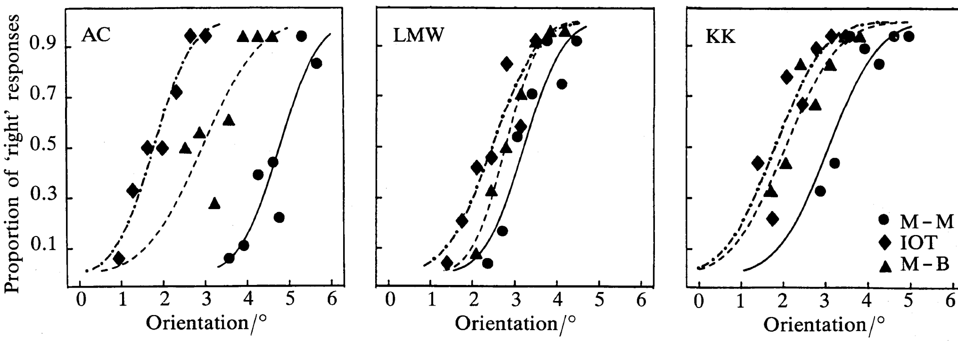

Figure 3. Psychometric functions obtained for the three observers in experiment 3 showing the shifts in perceived vertical after monocular adaptation. M-M, monocular adaptation and testing of the same eye; IOT, interocular transfer; M-B, monocular adaptation and binocular testi.

5 Discussion of experiments 1 to 3

The main purpose of the present series of studies was to reevaluate the claims that have been made for an exclusively binocular channel. Given the data sets of Moulden (1980), Wolfe and Held (1981, 1982), and ourselves, one is directed to the conclusion that the evidence for the presence of an AND channel is equivocal. We will argue here, however, that it is not the inadequacy of the model, but rather the experimental paradigm used to test it, that is at fault. There are two different issues to be addressed here. These are the appropriateness of different stimulus configurations and the validity of the assumptions underlying particular kinds of experiments.

5.1 *Stimulus configuration*

Wolfe and Held (1981, 1982) argued that the differences between their own results and those of Moulden (1980), who did a similar experiment, were a consequence of the particular stimuli that were used to induce and test for the tilt aftereffect. They suggested that only chevrons were appropriate to eliminate the influence of gravity and Gibsonian normalization. In the present experiments we found no evidence that the particular stimulus configuration had any effect on the *pattern* of results obtained, although we did find that gratings tended to induce a larger overall aftereffect than chevrons. Intuitively, this result is a satisfactory one. It seems unlikely that as potentially important a mechanism as one that mediates stereopsis (Wolfe 1986) should not reveal itself under the influence of gravity.

In a separate experiment not reported here (Wilcox 1987), we made another attempt to replicate the pattern of results obtained by Wolfe and Held using the motion aftereffect for drifting vertical gratings. A nulling procedure was used to measure the aftereffect seen after adaptation. Although any potential influence of gravity or normalization was ruled out by this procedure, the pattern of results was identical to that obtained in the present experiments 1 and 2.

5.2 *The monocular exposure paradigm*

The data from all of the experiments with the monocular exposure paradigm suggest that there is a great deal of intersubject variability in the relative sizes of the aftereffects.

One explanation for this variability is that the between-subject variation we observed in all of the monocular exposure studies was not caused primarily by unreliability of the subjects' responses, nor by the psychophysical method, but is a reflection of the weakness of the monocular exposure paradigm.

It has been evident from the earliest studies of the visual cortex that binocular neurons have differing degrees of dominance (cf Hubel and Wiesel 1962). Moulden (1980) acknowledged this fact and described an alternative model that included five classes of binocular neuron, each with different ocular dominance. But he assumed also that the dominance was symmetrical, so that the contribution of the binocular channel to the aftereffects in each eye would be balanced. Although this may be true in general, it is quite likely that the dominance distributions for different individuals vary. If this is so, then the relative contributions of strongly adapted and weakly adapted OR neurons to the size of the binocular aftereffect cannot be predicted.

This difficulty is compounded if one considers the possibility that the contribution of each channel to an aftereffect is not the same. For example, Wolfe and Held (1981) argued that the smaller binocular aftereffect that they observed was a result of a dilution of the effect by the AND channel. But this is possible only if one makes the assumption that the negative effect of the AND channel is stronger than the positive contribution from the adapted eye. In a similar fashion, one could make the argument that the slightly larger binocular effect that we and Moulden (1980) observed was because the diluting effect of an AND channel was insufficient to cancel the contribution of the adapted eye completely. Once weighting factors are introduced, predictions about the *relative* sizes of transferred and binocular aftereffects after monocular adaptation become indeterminate; depending upon the assumptions about the relative contributions of the different channels, a given pattern of results obtained with a monocular exposure paradigm could be regarded as being consistent with both an AND and an OR model.

There is yet another difficulty. If we accept the validity of the assumptions of the predictions outlined in section 1, a binocular aftereffect larger than the transferred aftereffect would be evidence in favour of an OR model, and a nonsignificant difference between the two conditions would be consistent with an AND model. As a result, when using the monocular exposure paradigm, we are attempting to show that there is no difference between the transfer and binocular test conditions—the statistical null hypothesis. The monocular exposure paradigm places us 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.

If these arguments are correct, then the interpretation of any experiment in which monocular adaptation is used to differentiate between different classes of binocular channel is called into question. Is there an alternative?

6 Experiment 4: Tilt aftereffects after alternating monocular adaptation

6.1 *Introduction*

One procedure that does avoid the difficulties described in the last section is alternating monocular adaptation followed by monocular and binocular testing. Both Wolfe and Held (1981, 1983) and Blake et al (1981) have used this procedure, although again with conflicting interpretations. Elsewhere (Wilcox et al 1988), the difficulties associated with Blake et al's (1981) experiment have been pointed out. Wolfe and Held (1981, 1983) used chevron patterns, which they suggest are the only appropriate patterns for revealing the presence of an AND channel. In the following experiment we replicated their study, using both chevrons and grating stimuli. Unlike the monocular exposure procedure, the alternating adaptation paradigm makes positive predictions with respect to an AND channel and avoids the difficulties associated with unequal adaptation of different neuronal populations.

In this procedure, alternating exposure of each eye during adaptation is followed by monocular and binocular testing. The predictions of the AND and OR models differ under these circumstances. The OR model predicts that there should be no difference in the size of the aftereffect for either of these two test conditions because adaptation will have influenced both the monocular and the binocular OR channels. The AND model predicts that there should be equivalent monocular effects and a lowered binocular effect after alternating exposure. The lower binocular aftereffect results from the diluting influence of the AND channel that was not active during the adaptation phase. Thus, this exposure paradigm permits a statistically testable hypothesis: if the AND channel is present, the binocular aftereffect should be significantly smaller than the monocular aftereffect.

6.2 *Method*

6.2.1 *Subjects and apparatus.* Two alternating adaptation experiments were conducted, one with chevrons, the other with gratings, each with a different group of subjects. Twelve subjects (between 18 and 40 years of age) participated in each experiment. All except two were unaware of its purpose, none was stereoblind or had mixed or inconsistent eye preference. The apparatus was the same as that described for experiment 1.

6.2.2 *Procedure.* The general procedure was the same as that for experiment 1. Baseline measures of perceived vertical or colinearity were followed by an adaptation period. The subjects then underwent successive test and readaptation periods until the criterion number of reversals on the psychophysical staircase was obtained for each test condition.

In the baseline condition, measurements of perceived vertical were obtained for each subject by presenting a blank display alternately to each eye for 5 s followed by a test pattern, viewed by either the left eye, the right eye, or both eyes. The test sequence cycled until at least eight reversals were obtained for each staircase. The first two reversals were discarded in the subsequent analysis.

During the initial part of the adaptation phase each eye was exposed to the adapting stimulus alternately for 10 s, which, in combination, produced a total adaptation period of 120 s for each eye. Continuous alternating adaptation to each eye was followed by successive test (0.5 s) and readaptation intervals (12 s). During the readaptation phase the stimulus was presented alternately to each eye for 3 s until both eyes had received a total of 6 s of adaptation. In order to offset any recency effects, the top-up adaptation sequence (left, right, left, right, or right, left, right, left) was alternated between subjects. Measures of the tilt aftereffect were obtained for three test conditions: monocular left, monocular right, and binocular.

6.3 *Results and discussion*

The data for this experiment are presented in figure 4. For both stimulus patterns the binocular aftereffect is smaller than either monocular aftereffect and the two monocular effects are equivalent. We note also that out of the twenty-four subjects tested there was only a single individual for whom the average monocular effect was not greater than the binocular aftereffect, a quite different result from that obtained in the other experiments. An overall analysis of variance showed no significant differences between the grating and chevron conditions ($F_{2,22} = 2.8$, $p > 0.01$) but a highly significant difference between monocular and binocular test conditions ($F_{2,44} = 14.1$, $p < 0.0001$). Subsequent tests of means showed no differences between the monocular conditions for either gratings or chevrons ($p > 0.5$ in each case) but all monocular aftereffects were significantly larger than the binocular aftereffects (for the four monocular-binocular comparisons the two-tailed probability values ranged from 0.005 to 0.01).

Although the results obtained in the monocular adaptation experiments provided weak evidence for the presence of an exclusively binocular channel, the pattern of results obtained in the present study was very reliable and provides much stronger evidence for the presence of such a channel. As mentioned in section 6.1, the use of an alternating adaptation paradigm eliminates the potential difficulties associated with monocular adaptation by ensuring that there is symmetrical adaptation of each channel involved in the production of the aftereffect.

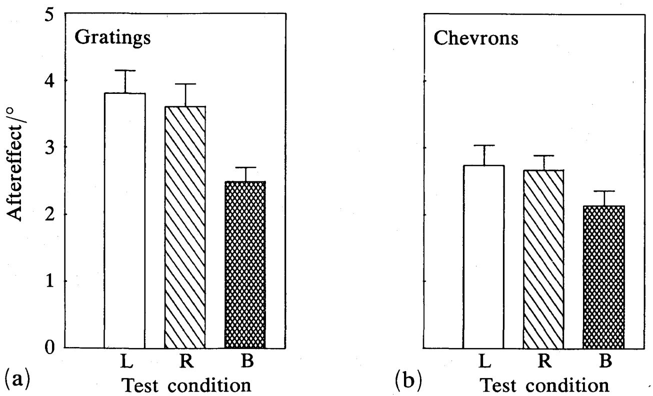

Figure 4. Magnitude of the tilt aftereffect for (a) gratings and (b) chevrons after alternating monocular adaptation in experiment 4. Test conditions: L, left eye; R, right eye, B, both eyes. Bars represent one standard error.

7 General discussion

Our primary purpose in the present studies was to evaluate the evidence for a binocular AND channel. On the basis of the data we have presented here and taking into account the arguments we have put forward with respect to the adequacy of a monocular exposure paradigm, we conclude that the available evidence does favour the existence of two functionally separable binocular channels. But having said that, we point out that a simple model which incorporates independent monocular and binocular channels is not completely adequate. In order to predict the results of a variety of other experiments it seems necessary to invoke inhibitory interactions between the channels.

The notion of interocular inhibition is not a new one. The binocular reduction in brightness known as Fechner's paradox was first described in 1860 (Helmholtz 1909/1962). More recently, others (Legge and Rubin 1981; Pardham et al 1989) have reported contrast versions of Fechner's phenomenon. These data are best explained by assuming that when a 'weak' stimulus is presented to one eye and a 'strong' stimulus to the other, the signal from the weak eye is inhibited.

Other studies, too, suggest that the assumption of a set of independent monocular and binocular channels may be incorrect. Anstis and Duncan (1983) have reported that opposite monocular and binocular motion aftereffects may be generated after monocular adaptation of each eye to motion in one direction and binocular adaptation to motion in the opposite direction. Such a result is not predicted by Wolfe and Held (1981). Their model predicts that the binocular aftereffect should be cancelled by the combined monocular aftereffects. The fact that the binocular aftereffect was not cancelled by the monocularly adapted eyes during testing implies that there is mutual inhibition between the channels. Wade and de Weert (1986) conducted a combination adaptation-rivalry experiment, recording the relative visibility of orthogonal patterns during binocular rivalry after preexposure to one of the test stimuli. They confirmed the results of Blake and his colleagues (Blake and Overton 1979; Blake et al 1980) that the pattern which had not been viewed previously dominated the subject's percept during rivalry. Based upon the pattern of results that they obtained for interocular transfer and binocular adaptation, they proposed a model that incorporated mutual interocular inhibition within the OR channel and direct inhibition of the monocular channels by the AND mechanism.

Although Wade and de Weert's model is consistent with most of the data we have reported, in its original form it cannot account for the pattern of results obtained in the alternating adaptation experiments reported here and by Wolfe and Held (1983). That is, if the AND mechanism inhibits the monocular channels when matched binocular stimuli are viewed, then there should have been no binocular aftereffect after alternating adaptation—this is not the case.

An alternative model incorporating binocular inhibition has been proposed by Cogan (1987). He has argued that there are only two neural channels involved in the integration of monocular information, both of which are binocular. One, the 'either-eye' channel, responds to input from either the left or the right eye, and the other 'fused' channel responds only when similar images are presented to both eyes. According to Cogan, the net binocular response is the sum of the activity of the either-eye and fused binocular channels.

Although the experiments presented here were not designed to test Cogan's model of binocular combination, several of the predictions based on his proposal are similar to those made by a four-channel AND model. In particular, his model incorporates interocular inhibition, but because the pure binocular channel exerts no inhibition on the interocular channel, the model's predictions *are* consistent with the pattern of results obtained with alternating exposure.

Cogan's dual-process model is an attractive alternative to the existing four-channel models. Not only do its predictions agree with the data presented here, but it incorporates mutual inhibition, and therefore is also consistent with Wade and de Weert's (1986) conclusions. However, Cogan's model was developed and tested solely in the luminance domain and it may not be possible to apply his model directly to situations involving more spatially complex stimuli. This question is currently under investigation.

References

Anderson P, Mitchell D E, Timney B, 1980 "Residual binocular interaction in stereoblind humans" *Vision Research* **20** 603-611

Anstis S, Duncan K, 1983 "Separate motion aftereffects from each eye and from both eyes" *Vision Research* **23** 161-169

Blake R, Overton R, 1979 "The site of binocular rivalry suppression" *Perception* **8** 143-152

Blake R, Overton R, Lema-Stern S, 1981 "Interocular transfer of visual aftereffects" *Journal of Experimental Psychology: Human Perception and Performance* **7** 367-381

Blake R, Westendorf D, Overton R, 1980 "What is suppressed during binocular rivalry?" *Perception* **9** 223-231

Blakemore C, Campbell F W, 1969 "On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images" *Journal of Physiology (London)* **203** 237-260

Cogan A I, 1987 "Human binocular interaction: towards a neural model" *Vision Research* **27** 2125-2139

Finney D J, 1971 *Probit Analysis* 3rd edition (Cambridge: Cambridge University Press)

Helmholtz H von, 1909/1962 *Physiological Optics* volume 3 (New York: Dover, 1962); English translation by J P C Southall for the Optical Society of America (1924) from the 3rd German edition of *Handbuch der physiologischen Optik* (Hamburg: Voss, 1909)

Hubel D H, Wiesel T N, 1962 "Receptive fields, binocular interaction and functional architecture in the cat's visual cortex" *Journal of Physiology (London)* **160** 106-154

Legge G, Rubin G, 1981 "Binocular interactions in suprathreshold contrast perception" *Perception & Psychophysics* **30** 49-61
Mohn G, van Hof-van Duin J, 1983 "The relation of stereoacuity to interocular transfer of the motion and the tilt aftereffects" *Vision Research* **23** 1087-1096
Moulden B P, 1980 "Aftereffects and the integration of patterns of neural activity within a channel" *Philosophical Transactions of the Royal Society of London, Series B* **290** 39-55
Movshon J A, Chambers B E I, Blakemore C, 1972 "Interocular transfer in normal humans, and those who lack stereopsis" *Perception* **1** 483-490
Myers J L, 1979 *Fundamentals of Experimental Design* 3rd edition (Boston, MA: Allyn and Bacon)
Pardham S, Gilchrist J, Douthwaite W, 1989 "The effect of spatial frequency on binocular contrast inhibition" *Ophthalmic and Physiological Optics* **9** 46-49
Porac C, Coren S, 1976 "The dominant eye" *Psychological Bulletin* **83** 880-897
Sutherland N S, 1961 "Figural after-effects and apparent size" *Quarterly Journal of Experimental Psychology* **231** 222-228
Timney B, Wilcox L M, St John R, 1989 "On the evidence for a pure binocular process in human vision" *Spatial Vision* **8** 1-15
Wade N, 1976 "On interocular transfer of the movement aftereffect in individuals with and without normal binocular vision" *Perception* **5** 113-118
Wade N, de Weert C M M, 1986 "Aftereffects in binocular rivalry" *Perception* **15** 419-434
Wilcox L M, 1987 *Binocular Channels in the Human Visual System* unpublished master's thesis, University of Western Ontario, Ontario, Canada
Wilcox L M, Timney B, Khan S, 1988 "Does the binocular "and" process operate at threshold?" *Investigative Ophthalmology and Visual Science, Supplement* **29** 411
Wolfe J M, 1986 "Stereopsis and binocular rivalry" *Psychological Review* **93** 269-282
Wolfe J M, Held R, 1981 "A purely binocular mechanism in human vision" *Vision Research* **21** 1755-1759
Wolfe J M, Held R, 1982 "Gravity and the tilt aftereffect" *Vision Research* **22** 1075-1078
Wolfe J M, Held R, 1983 "Shared characteristics of stereopsis and the purely binocular process" *Vision Research* **23** 217-227