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# On the contribution of a binocular 'AND' channel at contrast threshold

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**Abstract.** Three experiments are reported in which an attempt was made to isolate the contribution of an AND channel by measuring aftereffects following alternating monocular adaptation. The first two were designed to test Wolf and Held's proposal that the binocular AND channel does not respond at contrast threshold. In the first experiment the relative sizes of monocular and binocular contrast threshold elevation were compared with the pattern of aftereffects obtained in a study of the suprathreshold tilt aftereffect. Identical patterns of results were obtained under the two adaptation conditions. In the second experiment, the monocular and binocular contrast-reduction aftereffect reported by Blakemore et al was measured over a wide range of reference contrasts. As in the previous experiment, the monocular effect was greater than the binocular effect. This occurred at all reference contrasts. These data support the conclusion that the AND channel contributes to visual performance in the same manner, irrespective of stimulus contrast. In the final experiment an alternative explanation for existing evidence against the existence of an AND channel was assessed.

## 1 Introduction

Since the initial physiological descriptions of binocular neurons in the visual cortex (Hubel and Wiesel 1962) there has been an implicit assumption, in most psychophysical writings, that these neurons constitute a single functional pathway in the visual system (cf Campbell and Green 1965; Moulden 1980) and could account for most aspects of binocular vision. However, it has become clear that, at least in psychophysical terms, it is necessary to assume that there are several binocular 'channels' that may have different functional roles. In several recent models of binocular interaction it has been postulated that multiple binocular channels exist, although opinions on the way in which they are assumed to work differ among authors (Anstis and Duncan 1983; Cogan 1987; Cohn and Lasley 1976; Wolfe and Held 1981).

Wolfe and Held (1981) proposed the existence of two binocular channels. The first was assumed to act as a logical OR gate, responding to input to either eye. Such a channel has been the basis of several explanations for the interocular transfer of visual aftereffects (Blake et al 1981; Moulden 1980). The second channel proposed by Wolfe and Held opperated like a logical AND gate and would respond only when both eyes were stimulated simultaneously. Although there were difficulties with Wolfe and Held's initial formulation (Timney et al 1989), most of the available data do favour the presence of an AND channel (Anstis and Duncan 1983; Wilcox et al 1990; Wolfe and Held 1981, 1983).

Anstis and Duncan (1983) exposed subjects in a single adaptation period to a spiral, rotating in one direction when viewed monocularly, and in the opposite direction when viewed binocularly. They reported independent motion aftereffects for monocular and binocular test trials, a result which they argued could be obtained only if there were two functionally independent binocular channels. Wolfe and Held (1982, 1983) have shown that, after alternating monocular adaptation, the tilt aftereffect obtained monocularly is larger than that found with binocular testing.

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Wolfe and Held argued that during the adaptation period an AND channel, requiring simultaneous binocular stimulation, remained unadapted and served to reduce the size of the binocular aftereffect (see Moulden 1980). More recently, Anderson and Movshon (1989) have argued for a multiple-channel binocular model on the basis of their results with dichoptic contrast-threshold-elevation experiments. Although they do not comment explicitly on the existence of an AND channel, their data are also consistent with its presence.

Most of the relevant data support the existence of an AND channel. However, there have been few attempts to explore its functional characteristics. Only Wolfe and Held (1983; Wolfe 1986) have tried to compare the characteristics of AND and OR channels and to relate them to different aspects of binocular vision. In particular, Wolfe (1986) proposed that the AND channel may be involved in stereopsis whereas the OR channel may be involved in binocular rivalry.

In the present paper we explore one characteristic of the AND channel proposed by Wolfe and Held (1983). Wolfe and Held argued that the AND channel has a higher threshold for stimulation than those of other monocular and binocular channels. In other words, the AND channel does not contribute when the psychophysical task takes place at, or near, contrast threshold. This is a curious proposal which deserves to be explored further, if it is indeed the case that an AND channel is involved in such an important binocular function as stereopsis.

Wolfe and Held (1983) initially proposed that the AND channel has a high threshold to account for the results of Blake et al (1981), who reported evidence against the existence of two separate binocular channels. In an experiment similar to Wolfe and Held's (1982) tilt-aftereffect study, described above, Blake et al measured the binocular contrast-threshold-elevation aftereffect after either alternating monocular adaptation or intermittent binocular adaptation. Blake et al reasoned, in the same way as did Wolfe and Held (1982), that the AND process would not be stimulated during alternating monocular adaptation. Consequently, it should maintain its sensitivity and reduce the binocularly measured aftereffect during testing. In contrast, when adaptation consisted of intermittent binocular exposure, the AND channel would be active both during adaptation and during testing, producing maximum binocular threshold elevation. They predicted that if an AND channel exists, the binocular aftereffect recorded after intermittent binocular adaptation should be greater than the binocular aftereffect produced by alternating monocular adaptation. Blake et al (1981) found no difference between the sizes of the binocular aftereffects obtained in the two exposure conditions. They concluded that "only binocular neurons of the 'OR' type participate in the adaptation process" (Blake et al 1981, page 372).

Wolfe and Held (1983) argued that the discrepancy between their own results and those of Blake and his colleagues (1981) could be attributed to the fact that the tilt aftereffect and the contrast-threshold-elevation aftereffect operate over different contrast ranges. They proposed that the AND channel only responds at suprathreshold levels of contrast, like those used in their tilt-aftereffect experiments. When thresholds are measured, they argued, the channel is not active and therefore cannot contribute to an aftereffect.

Although the experiments of Wolfe and Held (1982) and Blake et al (1981) were superficially similar, procedurally they were quite different. Wolfe and Held made a direct comparison between monocular and binocular aftereffects generated in the same experimental session. Blake et al measured only binocular aftereffects after two different adaptation regimes. In Blake et al's experiments no allowance was made for the possibility that the two types of exposure might have different effects on the overall size of aftereffects, whether measured monocularly or binocularly. We would argue on this basis that the question of whether an AND process might operate at threshold remains unresolved. In the present series of experiments we provide a more systematic evaluation of this issue.

In the first experiment we compared the relative sizes of monocular and binocular aftereffects following alternating monocular adaptation, both for the tilt and for the contrast-threshold-elevation aftereffects. In experiment 2 we examined more closely the possible involvement of an AND channel over a range of contrast values by the use of the contrast-reduction aftereffect. Our results suggest that the AND channel operates at all levels of contrast. In the final experiment we specifically addressed the discrepancy between the conclusions of Wolfe and Held (1982, 1983) and Blake et al (1981). We found that the absolute size of the binocularly measured aftereffect varied with the adapting condition—a factor not considered by Blake et al (1981). We conclude that the similarity of the binocular aftereffects reported by Blake et al (1981) can not simply be attributed to the absence of an AND channel.

## 2 Experiment 1. Alternating adaptation: contrast-threshold-elevation aftereffect versus the tilt aftereffect

### 2.1 *Introduction*

In a number of experiments the alternating-exposure paradigm has been used to examine the activity of a second binocular channel (Wilcox et al 1990; Wolfe and Held 1982, 1983). In these experiments, predictions of the relative sizes of monocular and binocular aftereffects have been based on the assumption that the size of an aftereffect is a function of the combined output of all neural channels driven during testing (see Blake et al 1981; Moulden 1980). Channels that are not involved in the test phase should have no effect on the size of the aftereffect, whereas adapted channels that are driven during testing should increase the size of the effect. Further, when a previously unadapted channel is involved during testing it should weaken the subsequent aftereffect.

The logic of the alternating-adaptation paradigm is as follows: each eye is exposed sequentially to the adapting stimulus. However, the AND channel requires simultaneous binocular stimulation. Consequently, the alternating paradigm should isolate an AND mechanism from the effects of exposure. During subsequent binocular testing, the unadapted AND channel should contribute by reducing the size of the aftereffect. However, this unadapted binocular channel will not be involved in monocular testing, so the monocular aftereffects should be at a maximum. Therefore, after alternating exposure, the two monocular effects should be equivalent but larger than the binocular aftereffect. This prediction has been confirmed in experiments which used the suprathreshold aftereffects of tilt and motion (Timney et al 198Wolf and Held 1981, 1982).

If it is the case that the AND channel is not active at threshold, a different set of predictions would be made for the contrast-threshold-elevation aftereffect. As before, the AND channel will remain unaffected by alternating adaptation to the high-contrast exposure grating, and should not contribute to the monocular aftereffect. However, if the AND channel does not respond at contrast threshold, then it should also remain inactive during the binocular test, and will not dilute the binocularly measured aftereffect. Therefore, the binocular and monocular aftereffects should be equal. We tested these predictions using the contrast-threshold-elevation aftereffect and alternating adaptation. The relative sizes of the monocular and binocular aftereffects were then compared with the results of a procedurally similar suprathreshold-tilt-aftereffect study.

## 2.2 *Method*

2.2.1 *Subjects*. Fourteen subjects participated in the contrast-threshold experiment. Of these, four were practised, whereas the remaining ten were naive to the purpose of the experiment. The tilt-aftereffect data were collected from ten subjects; all but two of these were unaware of the purpose of the experiment. All participants had normal vision or wore their prescribed optical correction. Before testing, the subjects' stereoacuity was assessed with the use of the Randot stereotest and a Bausch and Lomb orthorater. All participants had normal stereopsis.

2.2.2 *Apparatus*. Sine-wave gratings (2.5 cycles $\deg^{-1}$) were generated conventionally with the aid of a Picasso Image Generator (Innisfree), and were displayed on the face of a Tektronix 606B CRT monitor with a P31 phosphor. The gratings had a space-averaged luminance of 20 cd $m^{-2}$. To avoid the formation of afterimages in the threshold experiment, both the adaptation and the test gratings drifted at a constant rate of 1 Hz. The face of the monitor was masked to a 3 deg circular aperture viewed from a distance of 90 cm. Head position was maintained by means of an adjustable chin-and-head rest that partially encircled the subject's head. A microcomputer controlled the stimulus presentation and recorded the subjects' responses. The computer was also used to operate a pair of opaque (black) shutters which restricted the subject's view of the display to the left eye, right eye, or both eyes, as dictated by the viewing condition.

2.2.3 *Contrast-threshold-elevation procedure*. Baseline measures of contrast threshold were obtained by presenting a blank display alternately to each eye for 2.5 s and then a vertical test pattern—to the left, right, or both eyes. Two tones defined a 1 s test interval. The subjects indicated if the grating was visible by pressing the appropriate button on a three-button console. After the baseline session, the subjects adapted each eye alternately (at 2.5 s intervals) to a grating 1.5 log units above contrast threshold, for a total of 120 s. The remainder of the session consisted of successive test and readaptation periods of 1 s and 12 s, respectively. During the readaptation periods the exposure grating was presented alternately to each eye until both eyes had received 6 s of exposure. Recency effects were offset by reversing the adaptation sequence (left, right, left, right or right, left, right, left) from subject to subject. Data were collected by an interleaved-staircase procedure (Levitt 1971). Three single staircases, one for each test condition, were run simultaneously and in random order. After each test interval, the contrast of the test grating was adjusted in steps of 3 dB according to the standard staircase protocol. In pilot trials, we found that any improvement in accuracy afforded by the use of smaller step sizes was offset by increased response variability resulting from fatigue. The adaptation-test sequence cycled until at least 8 reversals occurred on each of the staircases. The first 2 of these reversals were discarded before analysis and the remaining reversal points were averaged to estimate the subject's contrast threshold. We defined threshold elevation as the ratio of the postadaptation to preadaptation thresholds. This measure controls for the differences in binocular and monocular thresholds that result from binocular summation.

2.2.4 *Tilt-aftereffect procedure*. The apparatus and procedure used to collect the data for the tilt aftereffect were similar in all important respects to those described above. The difference between the two procedures was that, in the case of the tilt aftereffect, the subject's task was to indicate the perceived direction of tilt of a grating pattern. Baseline measures of perceived tilt preceded the initial 120 s adaptation to a grating tilted 10° off vertical. After the initial adaptation period there were 0.5 s test and 12 s readaptation periods. Both during the 120 s and during the 12 s adaptation the stimulus was alternated between the two eyes every 3.0 s. There is some evidence that larger tilt aftereffects are obtained when the test stimulus has a lower contrast than the adapting stimulus (Parker 1972). To maximise the strength of the aftereffects, the adaptation and test gratings had Michelson contrasts of 0.64 and 0.25, respectively. The interleaved-staircase procedure, described above, was also used to measure the tilt aftereffect. Three staircases were run simultaneously for the two monocular and the binocular test conditions. The orientation of the test grating was adjusted after each "left"-"right" response in 0.35° steps. Each staircase continued until a maximum of 8 reversals were obtained, and the first 2 reversals on each staircase were discarded. The size of the tilt aftereffect was calculated as the difference between the estimates of perceived vertical before and after adaptation.

### 2.3 *Results and discussion*

An identical pattern of results was obtained both for threshold-elevation and for tilt aftereffect, as shown in figure 1. That is, in both adaptation conditions the monocular aftereffects were equivalent, and were larger than the binocular aftereffects.

A one-way analysis of variance of the threshold-elevation data showed that there were significant differences among the three test conditions ($F_{2,26} = 7.56$, $p < 0.01$). Subsequent tests of means (protected $t$-tests) revealed that the two monocular conditions were statistically equivalent ($t_{13} = 1.21$, $p > 0.05$); therefore we averaged the thresholds for the left and right eyes to provide a single monocular threshold. The binocular aftereffect was significantly smaller than the averaged monocular effect, as determined with a correlated $t$-test ($t_{13} = 3.5$, $p < 0.01$). Analysis of the tilt-aftereffect data produced identical results: again there was a main effect of eyes tested ($F_{2,18} = 30.1$, $p < 0.001$). Subsequent tests of means showed that the monocular effects were equivalent ($t_9 = 1.59$, $p > 0.05$), but greater than the binocular effect ($t_9 = 8.32$, $p < 0.001$). The similarity of the pattern of results obtained with the use of threshold and suprathreshold aftereffects suggests that there is no contrast-dependent change in the contribution of the AND channel. These data are not consistent with Wolfe and Held's (1983) proposal. Instead, they support the notion that the AND channel contributes in the same way at and above contrast threshold.

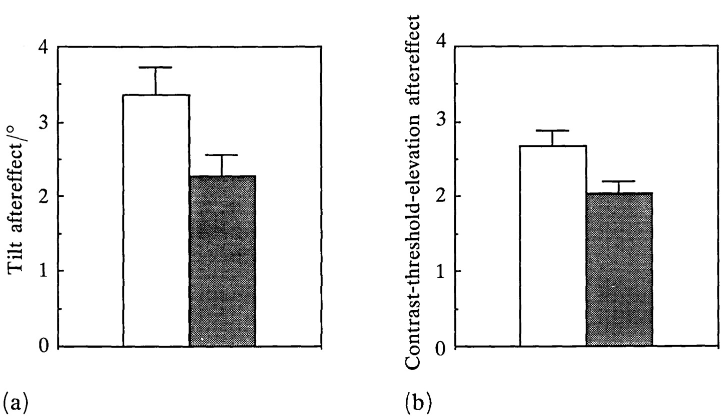


**Figure 1.** Average monocular (open bars) and binocular (filled bars) aftereffects recorded after alternating monocular adaptation. Data present a comparison of (a) the tilt aftereffect and (b) the contrast-threshold-elevation aftereffect. In both adaptation conditions the monocular aftereffects were significantly greater than the binocular aftereffects. Error bars indicate +1 standard error of the mean.

## 3 Experiment 2. Alternating adaptation and the contrast-reduction aftereffect

### 3.1 *Introduction*

The results of the preceding experiment suggest that the contribution of an AND channel to the size of the binocular aftereffect after alternating monocular adaptation is identical for the tilt and contrast-threshold-elevation aftereffects. It does not appear that there is any dependence on how close the test stimulus is to contrast threshold. In the present experiment we looked for additional evidence that stimulus contrast might modulate the influence of an AND process. To avoid the potential complications introduced by using two different types of aftereffects, we chose to use a single one that could be recorded both at and above contrast threshold.

Blakemore et al (1973) reported that after prolonged adaptation to a high-contrast grating, not only was detection threshold for a similar grating elevated, but that the perceived contrast of a suprathreshold grating was also reduced. This is known as the 'contrast-reduction aftereffect'. It is usually measured with the aid of a matching task in which the contrast of a test grating is set to match that of a reference grating, before and after adaptation to a similar high-contrast stimulus. The ratio of the post-adaptation to preadaptation contrast matches is used as an index of the size of the aftereffect. After adaptation the reference stimulus appears to have a lower contrast. Therefore, less contrast is required to match the test grating to the reference grating after exposure.

We reasoned that by using the contrast-reduction aftereffect we could assess any contrast-dependent contribution of an AND channel by varying the range of contrasts of the reference grating. Therefore we were able to test for AND activity along a contrast continuum that included both the threshold and the suprathreshold levels. The experimental predictions were as follows: if the AND channel does not respond at contrast threshold, then it will not continue to lower the size of the binocular aftereffect after alternating adaptation. We would expect that when contrast reduction is plotted as a function of reference contrast, the monocular and binocular functions should overlap at low reference contrasts. As the reference contrast is increased, there should be some point at which the test stimulus becomes visible to the AND channel and will begin to dilute the binocular aftereffect. At this reference contrast the binocular aftereffect should fall below the monocular aftereffect, causing the two functions to diverge. On the other hand, if the AND channel has the same contrast threshold as the other channels, then there should be no overlap of the two functions at the low reference contrasts. Instead, the binocular aftereffect should be consistently lower than the monocular aftereffect at all reference contrasts tested.

### 3.2 *Method*

3.2.1 *Subjects.* Four subjects participated in the experiment. All had some experience with psychophysical tasks. They all had normal visual acuity and stereopsis.

3.2.2 *Apparatus.* The test and adaptation stimuli were generated with the apparatus described for experiment 1. In the present experiment the display was presented within a 6 deg circular aperture in a centre/surround arrangement. During the test phase of the experiment the variable-contrast test grating appeared within a 1.75 deg wide annulus and the fixed reference grating was located in the 2.5 deg centre. During adaptation only the adapting grating was present in the field centre. In a single session, one of six contrast values (0.08, 0.12, 0.16, 0.20, 0.24, or 0.32) was selected as the reference contrast.

3.2.3 *Procedure.* Before adaptation, baseline reference–test contrast matches were taken. After a 10 s exposure to a blank field, the reference and test (the centre and surround, respectively) gratings were presented simultaneously for 1 s. There was then a tone signalling subjects to indicate whether the contrast of the centre grating was higher or lower than that of the surrounding grating. During the adaptation phase the subject adapted each eye alternately (3 s on/off) to a high-contrast grating (0.64) presented in the centre field for a total of 120 s. Maximum adaptation was maintained by using a 12 s readaptation period between trials, and the same 3.0 s alternation rate was used for the initial adaptation and the readaptation periods.

A standard staircase procedure was used to collect the data (Levitt 1971). On the first trial the surround contrast was arbitrarily set 2 dB greater or less than that of the reference grating. On subsequent presentations the contrast of the surround was adjusted in 3 dB steps. Single staircases were run for each of the three testing conditions (left eye, right eye, or both eyes); the three staircases were randomly interleaved. After 8 response reversals, estimates of perceived contrast were calculated from the final 6 reversals for each staircase.

### 3.3 *Results*

To quantify contrast reduction the test contrast required to match the reference grating before adaptation was divided by that required after adaptation; thus a high value represents a greater reduction in perceived contrast. Each threshold was the average of the matches obtained in a minimum of two sessions. Figure 2 shows the contrast-reduction ratio plotted as a function of the contrast of the reference grating.

Overall, the amount of contrast reduction was greater in the monocular test condition than in the binocular test condition at all reference contrasts. In addition, the amount of contrast reduction was greater for low reference contrasts. A two-way analysis of variance supports this observation: the difference between the averaged monocular and binocular threshold elevations was statistically significant ($F_{1,3} = 462.85$, $p < 0.01$). Subsequent protected *t*-tests showed that the two test conditions were statistically different at all reference contrasts. These data are consistent with the conclusion drawn from experiment 1. They do not support Wolfe and Held's (1983) proposal that the AND channel does not respond at contrast threshold. In fact, the slope of the function is in the opposite direction to that predicted if an AND channel did not respond at threshold.

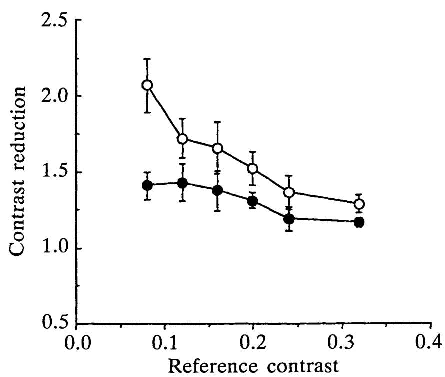


**Figure 2.** Average monocular (open circles) and binocular (filled circles) contrast reduction recorded after alternating adaptation. The amount of contrast reduction was calculated as the contrast required to match the reference contrast before adaptation divided by the contrast needed after adaptation. Each point represents the average of four subjects' data, and the error bars indicate ± 1 standard error of the mean.

### 3.4 *Discussion*

Wolfe and Held (1983) argued that the AND channel "makes no contribution to the perception of near-threshold stimuli" (Wolfe and Held 1983, page 220). However, the results of experiments 1 and 2 support the opposite conclusion—that the AND channel contributes in the same way to the perception of stimuli at and above contrast threshold. Wolfe and Held's (1983) proposal must be rejected. The threshold-response characteristics of an AND channel can not be used to account for the conflicting conclusions of Wolfe and Held (1983) and Blake et al (1981). In experiment 3 we explored an alternative explanation.

## 4 Experiment 3. Intermittent versus alternating adaptation

### 4.1 *Introduction*

As we stated in section 1, there is evidence in favour of a binocular AND channel. Our data are consistent with those of Wolfe and Held (1983), Vidyasagar (1976), and Anstis and Duncan (1983). In addition, evidence for the presence of a second binocular mechanism has been provided outside the aftereffect domain by Cohn and Lasley (1976) and by Cogan (1987). Although these authors do not specifically refer to an AND channel, they do make a strong argument for the existence of two distinct binocular channels, one whose operation is critically dependent on the similarity of the input to the two eyes. Blake et al (1981) argue, on the basis of their contrast-threshold-elevation experiment, that there is no AND channel. Wolfe and Held (1983) attribute the discrepancy between their data and those of Blake et al (1981) to a response characteristic of the AND channel.

Blake and his colleagues compared the absolute size of binocular aftereffects recorded after different adaptation protocols in different sessions. There is no obvious basis for their assumption that, with the same total exposure duration, identical degrees of threshold elevation should be obtained for these two adaptation regimes. When the binocular stimulus is displayed intermittently, there are 'silent' intervals during which there is no stimulation either of monocular or of binocular channels. If we assume that adapted neurons quickly regain sensitivity when the adapting stimulation is stopped (Greenlee et al 1991), recovery during the 'off' portions of the cycle should slow down the growth of the aftereffect. As the 'on-off' interval is lengthened, more recovery will occur, producing a corresponding decrease in the size of the aftereffect.

In comparison, when alternating exposure is used, some part of the binocular OR channel is adapted continuously. Since there are no silent periods there should be less recovery during alternating adaptation. Therefore, we predict that the reduction of the binocular aftereffect induced by the use of intermittent exposure will not take place after alternating adaptation. If this is the case, then the absolute size of the binocular aftereffects after these two types of adaptation will not necessarily reflect the contribution of the AND mechanism.

### 4.2 *Method*

4.2.1 *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 for experiments 1 and 2.

4.2.2 *Procedure.* The data were collected with the use of the contrast-threshold-elevation aftereffect and alternating adaptation as described in experiment 1. In the present experiment we included an intermittent binocular adaptation condition, in which the adapting grating was intermittently presented to both eyes simultaneously. For alternating and intermittent adaptation 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 4.0 s) both for alternating monocular and for intermittent binocular adaptation. The shortest adapting interval used was determined by the timing limitations of the computer interface. For all adaptation intervals the 6.0 s readaptation period was equally divided between the two eyes; however, to obtain equivalent monocular exposure in the 4.0 s condition the readaptation period had to be lengthened to 8.0 s. During 'off' intervals the subjects 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 eye, right eye, both eyes) were run simultaneously, and each staircase was tested until 8 reversals were attained. The final 6 reversals on each staircase, for each test condition, were averaged at the end of a session. Threshold elevation was calculated as the ratio of preadaptation and postadaptation contrast thresholds. All subjects participated in a minimum of two sessions per alternation rate both for alternating and for intermittent exposure.

4.3 *Results*

The amount of threshold elevation at each interval length, for both exposure conditions, is depicted in figure 3. The alternating-exposure data (figure 3a) 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 3b) change as a function of alternation interval, with an apparent decrease both in the monocular and in the binocular aftereffects as the interval is increased.

A two-way randomised-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 test condition (monocular versus 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. Further, comparison of the monocular and binocular aftereffects across intervals revealed that, whereas 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 randomised-blocks ANOVA performed on the intermittent-exposure data are opposite to the pattern described above. That is, there is no effect of eye 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 revealed that, whereas 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.

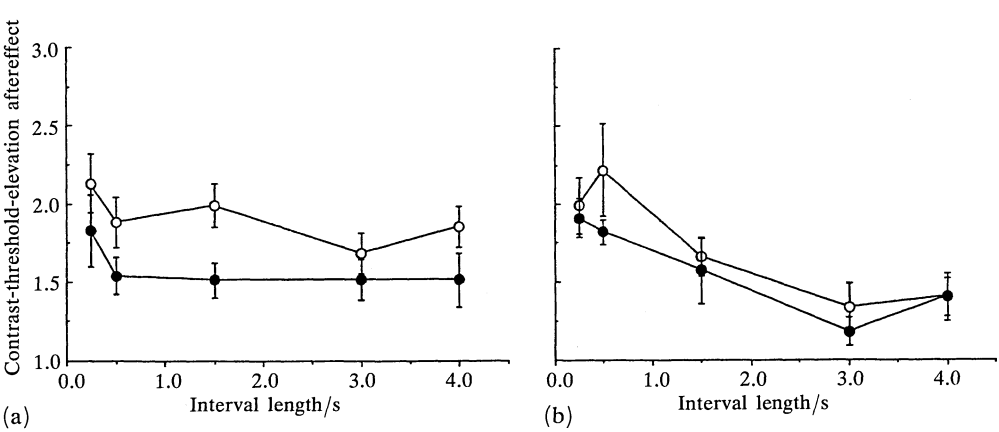


**Figure 3.** Average monocular (open circles) and binocular (filled circles) contrast-threshold-elevation aftereffects recorded after (a) alternating monocular and (b) intermittent binocular adaptation. Thresholds are plotted as a function of on–off interval length (0.25, 0.5, 1.5, 3.0, and 4.0 s). Error bars show ± 1 standard error of the mean.

### 4.4 *Discussion*

As seen in figure 3, the size of aftereffect as a function of on-off rate was quite different in the two exposure conditions. In the alternating-exposure condition there was no significant change in the absolute sizes of the monocular and binocular aftereffects as a function of on-off duration. In the intermittent condition the aftereffects decreased significantly as the on-off interval increased.

The longest on-off duration used here (4 s), is comparable to the 5 s intervals used by Blake et al (1981). At this 4 s duration, the binocular aftereffects recorded after alternating and intermittent adaptation are identical and replicate Blake et al's results. However, if we make the same comparison, using a shorter on-off duration of 0.5 s, we find that the aftereffect in the intermittent-binocular condition is greater than that in the corresponding alternating condition. It seems that the aftereffects measured after intermittent adaptation have been subject to recovery that does not influence the aftereffects of alternating adaptation, as outlined in section 4.1. The presence of this differential recovery confounds the comparison of the absolute sizes of binocular aftereffects made by Blake and his colleagues. Although we do not know precisely the amount of recovery under their experimental conditions, one could argue that the recovery from binocular threshold elevation obscured the predicted positive contribution of the AND channel. We conclude that this comparison is not an appropriate basis for determining the presence of an AND channel. Instead, comparisons between adapting conditions must be based on the relative differences between monocular and binocular aftereffects measured within the same session.

## 5 Conclusions

In experiment 1 we have clearly demonstrated that there is no difference between the pattern of results for different aftereffects recorded at and above contrast threshold. Furthermore, the consistent reduction of the binocular effect relative to the monocular aftereffect at a range of contrast levels (experiment 2) is convincing evidence that the AND channel contributes in the same way, regardless of the overall contrast of the stimulus. It seems clear that the discrepancy between Wolfe and Held (1983) and Blake et al's (1981) results is not due to the contrasts employed. The results of experiment 3 show that intermittent and alternating adaptation are not 'equivalent' forms of adaptation. That is, the off intervals in the intermittent-adaptation condition permit significant recovery from adaptation that does not occur in the alternating-adaptation condition. Thus, the psychophysical data recorded both at threshold and at suprathreshold are consistent in their support of the existence of at least two binocular channels in the human visual system.

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