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The Effect of Dark and Equiluminant Occlusion on the Interocular Transfer of Visual Aftereffects

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Lehmkuhle and Fox [(1976) *Vision Research, 16,* 428–430] reported that interocular transfer (IOT) of a translational motion aftereffect (MAE) was greater if the non-adapting eye viewed an equiluminant field than if it viewed a dark field. They recommended equiluminant occlusion of the non-adapted eye when measuring IOT of aftereffects. We tested this proposal in three experiments. First, we assessed IOT with equiluminant and dark occlusion for three different classes of aftereffects. Although transfer was greater with equiluminant occlusion for the translational MAE, there was no significant difference in the amount of transfer for the tilt aftereffect or the contrast threshold elevation effect. Second, we tested the hypothesis that spuriously large IOT could be the result of an aftereffect from tracking eye movements in the non-adapting eye. When potential tracking movements were reduced by using rotating spokes, a rotating spiral or contracting concentric circles, there was a corresponding reduction in the occlusion-dependent transfer. Third, we found that luminance shifts had no influence on the amount of transfer when all contours were eliminated from the non-adapting eye. We conclude that the type of occlusion used for measuring IOT of the translational MAE is important only when visible contours in the non-adapting eye contribute to the adapting process.

Aftereffects Contrast threshold elevation Interocular transfer Motion Tilt

INTRODUCTION

Lehmkuhle and Fox (1976) reported that the magnitude of interocular transfer (IOT) for a translational motion aftereffect (MAE) was influenced by the kind of occlusion used for the non-viewing eye during adaptation. They measured the duration of the MAE for drifting gratings under two conditions. In one, the non-viewing eye was occluded by an opaque shutter that prevented light from reaching that eye; we refer to this as dark occlusion. In the second, the non-viewing eye saw a blank display screen matched in luminance to that of the adapting eye; we refer to this as equiluminant occlusion. Although they found no difference in the size of the monocular aftereffect, IOT was greater in the equiluminant than in the dark occlusion condition. Lehmkuhle and Fox argued that the lower IOT in the dark-occlusion condition may have been caused by the disruptive effect of the sudden change in retinal illumination that occurred when the partially dark-adapted eye was exposed to the test stimulus. On the basis of this interpretation of their data they argued that equiluminant occlusion provided a more valid measure of aftereffects and recommended it be used in studies of IOT.

Lehmkuhle and Fox's study was limited to the measurement of the duration of the translational MAE for drifting gratings, but their recommendation has been taken to apply to other aftereffects (cf. Moulden, 1980; Wade & Wenderoth, 1978). Although this may be a valid generalization, it has not been tested empirically. Although visual aftereffects may share common physiological substrates, they differ in several respects. For example, the MAE is thought to be the result of a shift in the distribution of neural activity (Barlow & Hill, 1963; Mather, 1980; Wade, 1994) while the threshold elevation effect is assumed to result from a shift in the overall level of activity (Frisby, 1980). Given the potential for differences across aftereffects, it becomes important to test the generality of the differential IOT before accepting Lehmkuhle and Fox's recommendations. In Experiment 1 we tested their explanation of the differential aftereffects by measuring IOT for three different aftereffects—the translational MAE, the tilt aftereffect, and the contrast threshold elevation effect. Preliminary reports of these studies have been presented elsewhere (O'Shea, Timney, Wilcox & Symons, 1990; Timney, Wilcox & Symons, 1989).

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EXPERIMENT 1: GENERALITY OF DIFFERENTIAL IOT METHODS

Subjects

Six subjects participated in Experiment 1. All had normal stereopsis (assessed using the Randot Stereotest) and corrected-to-normal acuity. Sighting dominance was determined using a simple pointing task and the sighting dominant eye was adapted.

Apparatus

Sinusoidal gratings (3.0 c $\deg^{-1}$) were generated using a Picasso Image Generator (Innisfree Inc.) driven by a microcomputer. They were displayed on Tektronix 608 CRT monitors with green (P31) phosphors. The face of each monitor was covered by a black mask containing a 5 deg circular aperture and was viewed from a distance of 57 cm. The space-averaged luminance of the monitors was matched at 11 cd m^{-2}. To be consistent with Lehmkuhle and Fox's (1976) study, the gratings used in the MAE experiment had a Michelson contrast of 0.3. To maximize the size of the tilt aftereffect, both the adaptation and test gratings had a contrast of 0.68. For the threshold elevation aftereffect, the adapting grating also had a contrast of 0.68.

Two different kinds of occlusion were used. In the first (dark occlusion), we used a single monitor, located directly in front of the subject. The subject's view of the display screen was obstructed by opaque black shutters mounted in a large black screen and controlled electronically by the microcomputer. In the second (equiluminant occlusion), two monitors were used and a mirror arrangement permitted each eye to view a single display. The alignment of the monitors and the presence of the masks around the screen permitted stable fusion of the two display screens. During adaptation and testing, the non-viewing eye was exposed to a blank display screen with the same mean luminance as the monitor viewed by the adapting eye. The subject's head position was maintained using a combination chin- and head-rest that wrapped around the subject's head at the temples. The testing room was dark, with the stimulus display as the only source of illumination.

Procedure

Translational motion aftereffect. In this condition, subjects adapted to a grating drifting to the left or right at 3 Hz. No fixation point was present, although subjects were instructed to maintain fixation near the centre of the screen. The drifting adaptation grating was presented for 45 sec then the movement was stopped. Concurrently, the experimenter started a timer; it was stopped when the subject reported that the apparent movement had ceased. On the next trial the direction of adapting movement was reversed to avoid contamination by the preceding adaptation condition. The duration of the illusory motion in the adapted and non-adapted eyes was measured on alternate trials, and within a single session two trials were run for each eye under the two occlusion conditions. Each subject participated in six sessions.

Tilt aftereffect. Before adaptation, a baseline measure of perceived vertical was obtained for each eye. The data were gathered using a staircase procedure. Two independent single staircases were run concurrently, one for each eye tested, and the two eyes were tested alternately from trial to trial. On each trial the test grating was presented for 0.5 sec, followed by a 2 sec blank inter-trial interval. The orientation of the grating was set initially to vertical and then was shifted in 0.35 deg steps in a direction determined by the observer's response. That is, if the subject reported clockwise tilt on one trial, then on the next trial for that eye the orientation would be shifted counterclockwise. The test sequence continued until there were six reversals on each staircase. These reversal points were averaged to provide a pre-adaptation estimate of perceived vertical.

After the baseline measures were obtained, subjects viewed an adapting grating tilted 10 deg to the right for 120 sec; a vertical grating was then presented for 0.5 sec to the adapted eye or the unadapted eye, and the subject pressed a response button signalling its perceived tilt. A response was followed immediately by 6 sec of top-up adaptation. Data were accumulated using the same staircase procedure as for the baseline condition. The measure of the size of the tilt aftereffect was the difference between the means of the pre- and post-adaptation estimates of perceived vertical. Each subject completed two sessions for each of the occlusion conditions.

Contrast threshold elevation aftereffect. Data for the threshold elevation experiment were gathered using the same psychophysical procedures as for the tilt aftereffect. The subject's detection threshold was measured before and after adaptation. Following the initial 120 sec adaptation period, the contrast of the test stimulus was set initially at 2 dB above or below the subject's baseline threshold. The test contrast was then increased or decreased in 3 dB steps in the direction opposite to that indicated by the subject's response and the staircase was run until there were six reversals on both of the staircases. The size of the aftereffect was taken as the ratio of post- to pre-adaptation thresholds. Each subject participated in at least two sessions for each of the occlusion conditions and the data were averaged.

Results

Motion aftereffect

The results of this part of the experiment are presented in Fig. 1(A). For easier comparison with the data of Lehmkuhle and Fox (1976) we have presented our results in the same format as those authors. As one might expect, the transferred aftereffect was smaller than that in the adapted eye for both occlusion conditions. The result of relevance to the present study, however, is that although the aftereffect measured in the adapted eye was slightly larger for equiluminant than for dark occlusion, the amount of IOT was much greater. Statistical analysis confirmed this pattern of results. A two-way, repeated measures ANOVA gave a significant main effect for eye

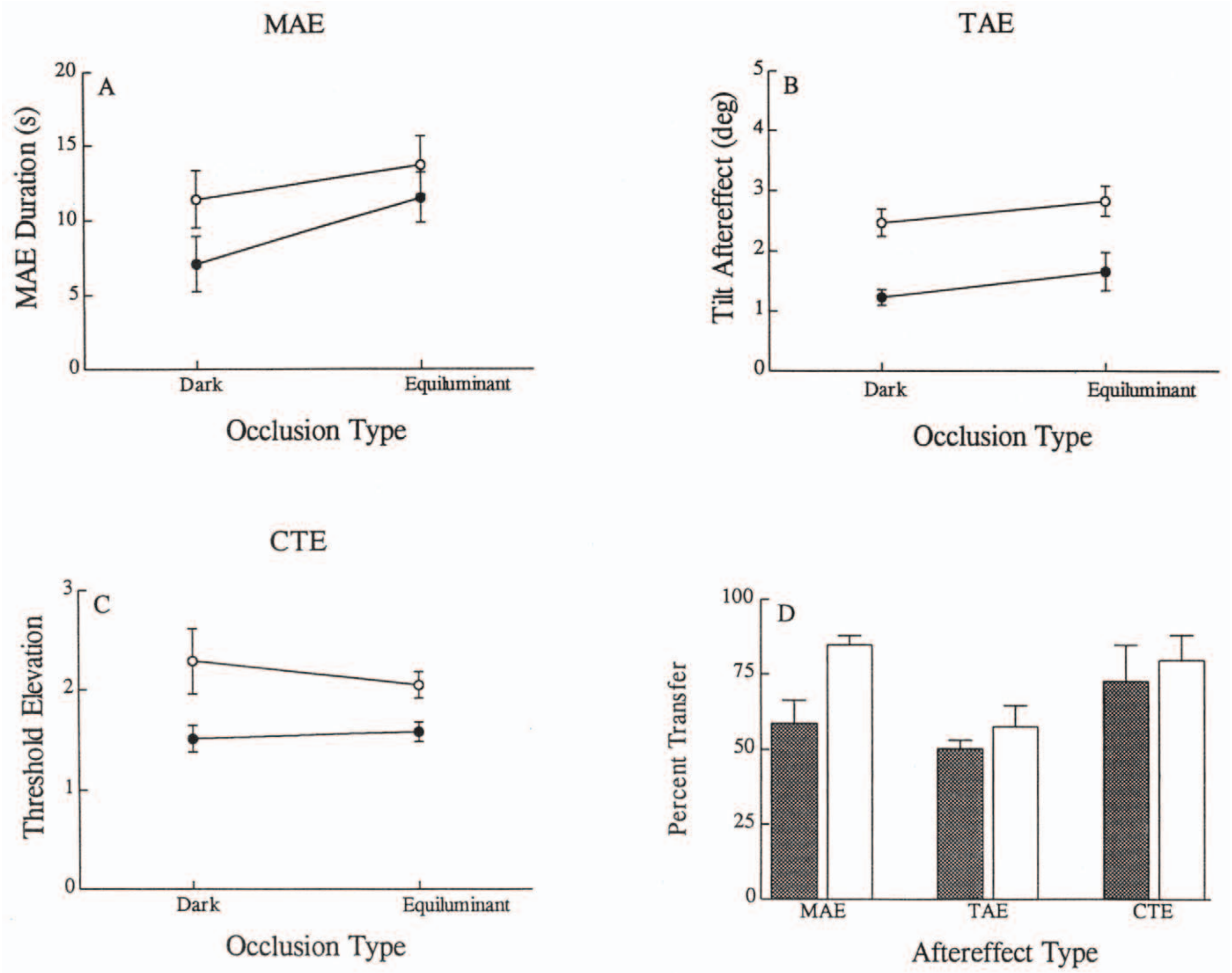

FIGURE 1. Magnitude of three different aftereffects under dark and equiluminant occlusion conditions. Open circles indicate the monocular effect; solid circles indicate interocular transfer. (A) The duration of the motion aftereffect. (B) The shift of perceived vertical in the tilt aftereffect. (C) The increase in contrast threshold following adaptation, expressed as the ratio of post- to pre-adaptation thresholds. (D) The percentage of interocular transfer for each of the aftereffects under the two occlusion conditions. Solid bars indicate dark occlusion; open bars indicate equiluminant occlusion. Error bars equal ±1 SE.

tested ($F_{1,5} = 63.34$; $P < 0.01$); that is, IOT was smaller than the direct effect. There was a significant main effect for type of occlusion ($F_{1,5} = 23.52$; $P < 0.01$); that is, the combined equiluminant aftereffects were larger than those for dark occlusion. Finally, the interaction between occlusion condition and amount of interocular transfer was significant ($F_{1,5} = 8.40$; $P < 0.05$). As Lehmkuhle and Fox (1976) had reported, IOT was greater in the equiluminant condition.

Tilt aftereffect

The data from this part of the experiment are shown in Fig 1(B). Again, the monocular effects are largest and similar in size for the two conditions. In this case, however, there is no differential transfer. Results of a two-way repeated measures ANOVA show a significant main effect of eye tested ($F_{1,5} = 218.79$; $P < 0.01$), but no significant interaction between the type of occlusion and amount of transfer.

Contrast threshold elevation

Threshold elevation following adaptation is shown in Fig. 1(C). The monocular effects are similar in size and greater than interocular transfer. There is very little difference in the size of the transferred effects under the two occlusion conditions. Statistically, there was a main effect for eye tested ($F_{1,5} = 7.20$; $P < 0.05$), but no significant interaction.

The question of interest in this study was the amount of transfer obtained using the two types of occlusion, for the different aftereffects. We calculated the percentage transfer for each of the aftereffects by taking the ratio of the monocular to the transferred effect and these data are plotted in Fig. 1(D). For the MAE, the amount of transfer was substantially greater in the equivalence condition than in the dark occlusion condition, while there was only a slight difference for the tilt aftereffect and the threshold elevation effect. There was a significant difference in the percentage transfer for the MAE

($t_{\text{movement}} = 2.65$, d.f. = 5, $P < 0.05$), replicating the findings of Lehmkuhle and Fox (1976). However, there was no statistical difference between the percentage transfer for the two viewing conditions for the tilt and threshold effects ($t_{\text{tilt}} = 1.06$, d.f. = 5, $P > 0.3$; $t_{\text{contrast}} = 0.70$, d.f. = 5, $P > 0.5$).

Discussion

In their experiment, Lehmkuhle and Fox (1976) showed that IOT of the MAE from a drifting grating is greater if the non-adapting eye is exposed to a blank display screen of the same space-averaged luminance as that of the adapting stimulus. We have replicated this result. However, the present extension of the Lehmkuhle and Fox study indicates that this differential transfer does not apply to other aftereffects. Lehmkuhle and Fox argued that the sudden change in illumination of the dark occluded eye disrupted transfer in some fashion. While there may be a slight disruptive effect of dark occlusion, we did not find large differences in the amount of transfer as a function of adapting condition for the tilt or contrast threshold elevation aftereffects.

It could be argued that the failure to find differences between the two occlusion conditions for the tilt and threshold elevation aftereffects was because different measures of each aftereffect were used. An alternative measure of the motion aftereffect may have eliminated the difference. Although we did not test this possibility directly, the results from Experiment 2, presented below, argue against it. In that experiment we were able to reduce the dark/equiluminant occlusion difference by using different adapting stimuli, even though we used the same duration measure of the aftereffect.

These results raise an interesting question about the interpretation of the existing interocular transfer data. It is generally accepted that the presence of IOT provides strong evidence for binocular neurons in human visual cortex. More important, several investigators have suggested that the amount of transfer may be taken as an index of binocularity on the grounds that there is a significant relationship between IOT and stereoacuity (Mitchell & Ware, 1974; Movshon, Chambers & Blakemore, 1972). However, others have failed to find this relationship (Mohn & van Hof van Duin, 1983). If IOT may be influenced by the kind of adapting occlusion for some aftereffects, the use of different aftereffects and different methods of occlusion could account for some of the conflicting results.

The fact that occlusion type does not markedly affect IOT for the tilt aftereffect and threshold elevation effect implies that it is not the sudden change in illumination at the eye suggested by Lehmkuhle and Fox (1976) that modulates the amount of interocular transfer. The following experiment was designed to examine an alternative possibility.

EXPERIMENT 2: THE ROLE OF EYE MOVEMENTS

An explanation for differential IOT based on intrinsic differences between occlusion conditions runs into difficulty when it can not be applied to all classes of aftereffect. An alternative explanation for the MAE data is suggested by the results of a study by Morgan, Ward and Brussell (1976). These authors reported an aftereffect of tracking eye movements. Subjects who tracked a drifting grating across an aperture, thereby eliminating movement of the grating stripes over the retina, nevertheless experienced a MAE when they viewed a stationary grating.

Morgan *et al.* argued that the aftereffect was due to induced movement. They suggested that as the eyes tracked the grating, the objectively stationary contours of the edge of the stimulus display would move across the retina in a direction opposite to that of the gratings. At the end of the adaptation period, there would be an aftereffect of the surround retinal motion in the same direction as that of the original grating drift. This tracking aftereffect leads to induced apparent movement of the stationary grating in the opposite direction. Similar results have been reported by Anstis and Reinhart-Rutland (1976). Day and Strelow (1971) also found that the motion aftereffect is strongly dependent on the presence of contours surrounding the moving display. In a second experiment, Morgan *et al.* (1976) measured the MAE after subjects had tracked the grating with one eye while the other viewed the blank field. The transferred aftereffect was as large as that in the adapting eye. They proposed that conjugate eye movements resulted in similar retinal stimulation of both eyes and a subsequent aftereffect. In support of this argument they reported that when the subjects fixated during adaptation, the interocular transfer was much reduced.

If one considers the role of occlusion in the context of Morgan *et al.*'s (1976) and Anstis and Reinhart-Rutland's (1976) studies, another possible explanation for the larger transfer in the equiluminant condition emerges. In both the study described above and that of Lehmkuhle and Fox (1976) the drifting grating was presented through an aperture whose contours would move across the retina with any eye movements. In addition, Lehmkuhle and Fox provided a distinct black line on each side of the display screen to serve as fusional aids. They did not report using a fixation point. In our own study, although subjects were instructed to look at the centre of the screen, there was also no fixation point. Murasugi, Howard and Ohmi (1986, 1989) have reported that foveal fixation of stationary contours, with attention, is required to reduce optokinetic responses effectively.

We propose that, as a result of tracking eye movements during adaptation, there would have been movement of the surround contours on the retina of the non-adapting eye, thus generating an induced MAE of the kind described by Morgan *et al.* (1976), Anstis and Reinhart-Rutland (1976), and more recently, by Swanston and Wade (1992). If the tracking eye movements were not present consistently throughout adaptation, it is likely that this induced aftereffect would not be as large as that reported by Morgan *et al.* (1976). However, it would be indistinguishable from the conventional transferred effect, and could have been responsible for a spuriously large aftereffect in what we assumed to be the *unadapted* eye. This interpretation is strengthened by Symons' (1994) observation that in the absence of a fixation point, even when subjects are instructed to fixate, they are unable to do so. Symons recorded eye-movements directly during adaptation to a 3 c deg^{-1} grating drifting at 3 Hz. OKN-like movements were present throughout the recording period.

If our argument is correct, we would expect the induced aftereffect to produce an increased amount of interocular transfer only in the equiluminant occlusion condition. In the dark condition, where the black shutters completely blocked the subjects' view of the surround contours, an induced motion aftereffect could not occur. It follows that if the opportunity for tracking eye movements was reduced or eliminated, so too would the enhanced interocular transfer.

To test this proposal we ran an additional series of MAE experiments in which the opportunity for conjugate tracking eye movements was reduced or eliminated. We used three different adapting stimuli: rotating spokes, a rotating spiral, and continuously contracting concentric circles. These three stimuli should, to varying degrees, reduce conjugate tracking movements.

Method

Subjects

Six experienced subjects were tested with the spokes, spirals, and concentric circles. All had normal visual acuity and stereopsis, and used their dominant eye for adaptation. An additional 10 naive subjects were tested with the spiral. Their data showed the same pattern as those of the experienced subjects and we have not included them in the present study.

Apparatus

Three adapting stimuli were used: an 11 deg disk containing eight radiating spokes with a bar-width of 1.2 deg, an Archimedes spiral with an 11 deg radius and a line width of 1.8 deg, and a set of concentric circles with an outside diameter of 18.5 deg and a spatial frequency of 0.7 c deg^{-1}. For the spokes and spiral, the patterns consisted of black lines painted onto a white background. Black and white contracting concentric circles were computer-generated and displayed on a VGA monitor screen. All of the stimuli had a Michelson contrast of greater than 90% and a space-averaged luminance of approx. 20 cd m^{-2}. The spoke pattern rotated at a constant speed of 25 rpm during the adaptation period; for spiral adaptation, the disk rotated at 110 rpm and appeared to be contracting during adaptation. The concentric circles contracted towards the centre of the display at a velocity of 2.5 deg/sec.

Two types of occlusion were used during adaptation: the non-adapting eye viewed either a blank field of approximately the same luminance as the rotating pattern, or a black shutter. A combined chin and head rest was used to keep the subjects' head position constant.

Procedure

The subject was asked to fixate the centre of the adaptation stimulus throughout the 45 sec exposure period. The direction of rotation was alternated from trial to trial in the spoke condition. For the spiral and the circles, only contracting motion was used because of the reported asymmetry in the size of the aftereffect with expanding and contracting spirals (Scott, Lavender, McWhirt & Powell, 1966). In all cases, the order of testing (monocular vs IOT) was alternated, as was the type of occlusion (dark vs equiluminant). After the adaptation period, the aftereffect was measured using either the adapted or non-adapted eye. The subject kept his or her gaze in the centre of the pattern and indicated verbally when the apparent movement stopped.

In the rotating spoke condition, subjects were tested in six sessions. During an individual session two aftereffect estimates were obtained for both the monocular and transferred aftereffects. In the spiral condition, each of the subjects participated in a minimum of two sessions. Within each session both occlusion conditions were tested twice, providing a total of four aftereffect estimates for each test condition. The same procedure was followed for the concentric circles.

Results

Spokes

The duration of the MAEs following adaptation to a rotating spoke are displayed in Fig. 2(A) for both dark and equiluminant occlusion. The monocular effects are approximately equal and the transferred effect is smaller than the monocular effect. The amount of transfer is lower for the dark-occlusion condition, but the difference is less pronounced than when gratings were used to induce the MAE [cf. Fig. 1(A)]. A two-way repeated measures ANOVA showed that the monocular effect was significantly larger than the IOT ($F_{1,5} = 21.77$; $P < 0.01$). There was also a significant interaction between the amount of transfer and occlusion condition ($F_{1,5} = 8.43$; $P < 0.05$). Subsequent protected *t*-tests showed that this significant interaction can be attributed to a significant increase in the IOT in the equiluminant test condition.

Spiral

Figure 2(B) shows the duration of the MAE for spiral adaptation. Again, IOT is smaller than the monocular aftereffect, but the size of this difference is constant across the two types of occlusion. A two-way ANOVA showed a significantly larger monocular effect ($F_{1,5} = 34.28$; $P < 0.05$); and no significant interaction between transfer and occlusion type. There was no significant effect for occlusion type ($F = 1.16$).

Concentric circles

Figure 2(C) illustrates the duration of the MAE for the concentric circle adaptation condition. As in the preceeding conditions, IOT is smaller than the monocular effect, but there is no apparent change in amount of transfer as a function of the type of occlusion. A two-way

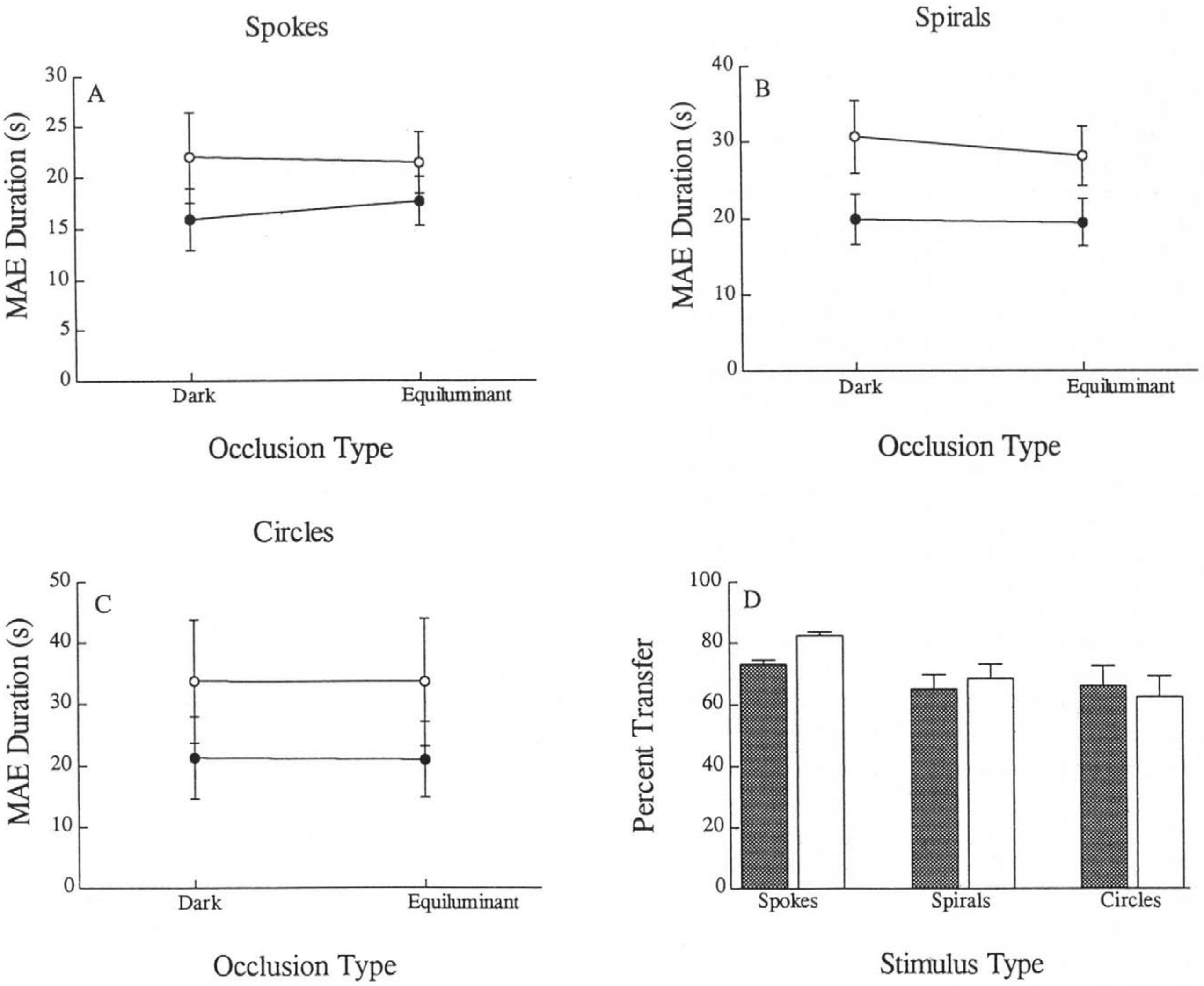

FIGURE 2. Duration of the motion aftereffect for rotating spokes (A), contracting spiral (B) and contracting concentric circles (C). (D) shows the percentage of interocular transfer for each of the aftereffects under the two occlusion conditions. Solid bars indicate dark occlusion; open bars indicate equiluminant occlusion. Conventions as for Fig. 1.

ANOVA confirmed these observations with a main effect of eye tested ($F_{1,5} = 8.36$, $P < 0.05$) and non-significant occlusion and interaction terms ($F = 0.01$ and 0.02 respectively).

The magnitude of IOT for the different occlusion conditions is shown in Fig. 2(D). In this case it may be seen that there is relatively little difference in the amount of transfer for each of the three stimulus conditions. As we mentioned above, however, *t*-tests on the percentage IOT showed that there was significantly more transfer in the equiluminant condition for the spokes.

Discussion

The results of the present study are consistent with the eye-movement hypothesis. That is, when rotating stimuli are used, providing less opportunity for tracking eye movements, the occlusion-dependent differential IOT is reduced. This is most evident in the concentric circle condition, when it is impossible to track all directions of movement simultaneously. In this condition the amount of IOT is virtually identical for both types of occlusion. This result is not consistent with the proposal that sudden shifts in the light-adapted state of the eye with dark occlusion reduces IOT.

For the spoke conditions there was more IOT when equiluminant occlusion was used, although the absolute size of this difference was less than that obtained with the drifting gratings. It is possible that in this condition torsional eye-movements were induced. There is evidence that this may occur. Seidman, Leigh and Thomas (1992) have shown that rotating spokes will produce torsional optokinetic nystagmus during the adaptation period following which there are slow phase movements in the direction of the aftereffect. If we assume that conjugate eye movements were generated in the non-adapting eye during adaptation to the spokes, then it is possible that IOT could be enhanced by an aftereffect of eye movements. We might expect that this effect would be reduced in the case of the spoke pattern because the potential OKN effects are quite small. In the case of the spiral it is uncertain whether it can produce an OKN response at all (Seidman *et al.*, 1992). For the contracting concentric circles, as we have said, the possibility of conjugate eye movements should be completely absent, as there is no consistent translational or rotational movement for any single direction of motion.

In a separate series of MAE experiments (Symons, Pearson & Timney, in preparation) we found greater interocular transfer when the non-adapting eye viewed a display with a 1 deg textured annulus surrounding a blank 3 deg central region than when the non-unadapting eye viewed a 5 deg blank display. In each case the blank fields were equiluminant. The adapting eye viewed translational motion in a 3 deg diameter circular area with a stationary textured surrounding annulus. The enhanced interocular transfer was reduced when a stationary central fixation dot was added to the display, suggesting that the enhancement resulted from eye-movements in the unadapted eye that generated a motion aftereffect to the surrounding contours in that eye.

While the results of these experiments support the eye-movement hypothesis, they have not ruled out the possibility that the differential transfer observed under dark and equiluminant occlusion conditions could be due to the change in the light-adapted state of the eye. In the final experiment we explored this possibility.

EXPERIMENT 3: REDUCTION OF SURROUND CONTOURS

The results of Experiments 1 and 2 provide strong evidence for the hypothesis that conjugate tracking of the non-adapted eye generates an induced MAE, inflating the apparent transfer of the translational MAE. Lehmkuhle and Fox (1976) originally argued that the decreased transfer of the aftereffect in the dark condition might be due to the abrupt change in luminance brought about by the opening and closing of the shutters. They suggested that the sudden onset of the dark occlusion in the adapted eye in the transfer test condition might cause a masking effect, disrupting the aftereffect. While the results of Experiments 1 and 2 suggest that the induced MAE to the surround contour in the equiluminant condition produces increased apparent IOT, we have not tested the luminance shift hypothesis of Lehmkuhle and Fox (1976) directly. Our third experiment controlled for the presence of surround contours while assessing the effects of shifts of luminance on the original MAE for drifting gratings. By using full-field translucent occluders to create ganzfeld-like conditions, we were able to introduce changes in luminance while eliminating virtually all contours to the occluded eye.

Method

Subjects

Four experienced subjects were used for both conditions. All subjects had normal or corrected to normal visual acuity and stereopsis and used their dominant eye for adaptation.

Apparatus

Apart from the occluders, the apparatus for this experiment was identical to that used in the MAE study of Experiment 1. The occluders were two halves of a table tennis ball, sculpted to fit the subject's orbit. Each was mounted on a short handle that permitted the subject to hold the translucent occluder against the eye. In the equiluminant condition, a beam of light from an optical fibre lamp was adjusted to back-illuminate the occluding semisphere to a luminance equivalent to that of the display monitor (11 cd m^{-2}). In the dark condition, only ambient illumination from the monitor was present. The luminance within the ganzfeld was below that which we were able to measure with our photometer (<1 cd m^{-2}). The occluders were controlled manually by the subject and the light source in the equiluminant condition was controlled manually by the experimenter. When the occluders were in position, no surround contours could be seen, creating a functional ganzfeld for the non-adapting eye.

Procedure

Each subject participated in four sessions for each equiluminant and dark occlusion condition. Unlike Experiment 1 subjects held the occluders over their eyes and switched them manually when instructed by the experimenter. In other respects the procedure was identical to the MAE study of Experiment 1.

Results

The results for Experiment 3 are shown in Fig. 3. The monocular aftereffect was larger in the equiluminant condition but the size of the transferred effect did not change at all. A two-way repeated measures analysis of variance assessed the influence of luminance level and eye tested on these data. As can be seen in the figure, the duration of the MAE was larger for the adapted eye for both occlusion conditions ($F_{1,3} = 23.13$, $P < 0.05$). However, there was no significant interaction between level of illumination and eye tested ($F_{1,3} = 4.93$, NS). There was a significant main effect for occlusion type resulting from the large aftereffect in the monocular equiluminant occlusion condition ($F_{1,3} = 13.19$, $P < 0.05$).

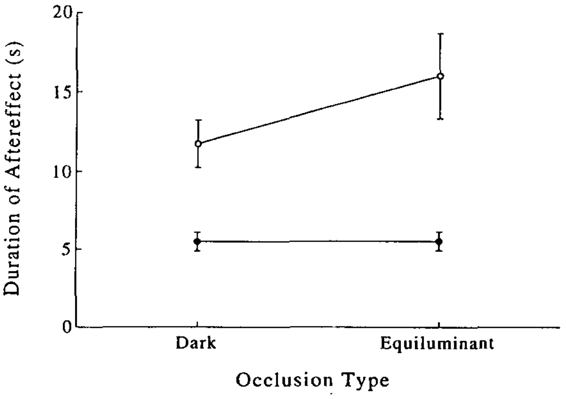

FIGURE 3. Duration of the translational motion aftereffect under dark and equiluminant ganzfeld occlusion. Open circles indicate the monocular effect; solid circles indicate interocular transfer.

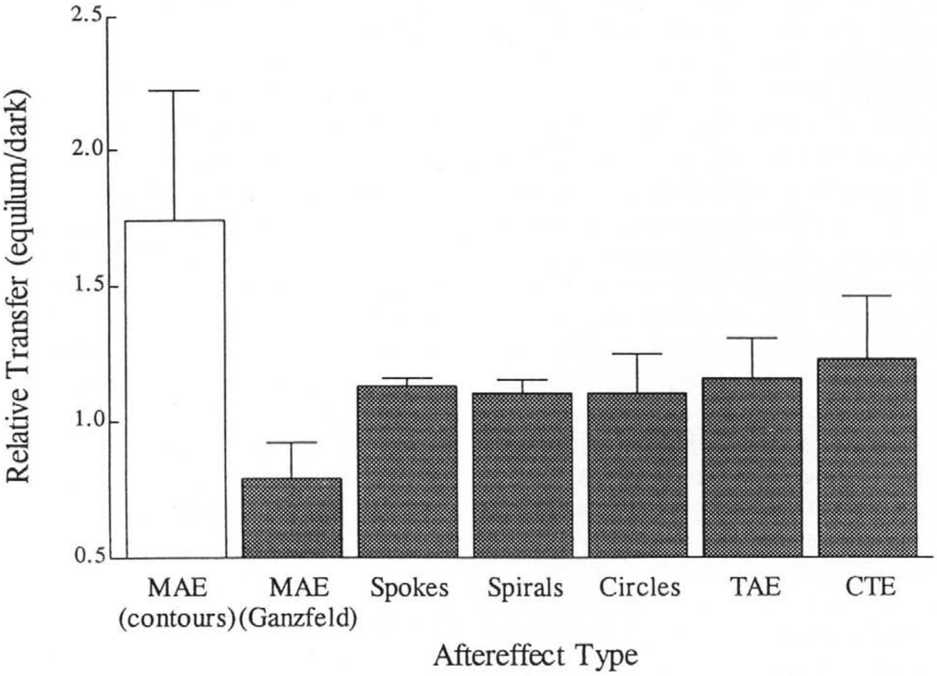

FIGURE 4. Relative amount of transfer for the different occlusion conditions for all aftereffects tested. Relative transfer was calculated by dividing the percentage transfer for equiluminant occlusion by the percentage transfer for dark occlusion for each adapting stimulus. A value greater than 1.0 signifies that the amount of transfer was greater in the equiluminant condition.

Discussion

By using translucent ganzfeld-like occluders, this experiment controlled for the influence of contours in the non-adapted eye while assessing the effect of luminance changes. Under these conditions we observed no interaction between luminance level and eye tested. When contours in the non-adapting eye are eliminated, so too is the differential transfer found by Lehmkuhle and Fox (1976). We have confirmed this result in a related series of experiments (O'Shea & Timney, in preparation) showing that it is critical to eliminate the visible contours during adaptation, rather than during testing. Recently, Wade, Swanston and de Weert (1993) have provided additional evidence for the importance of a visual framework in determining the size of the transferred aftereffect. They comment that when their stimuli were presented on an illuminated screen they obtained almost twice as much IOT as when a dark surround was present.

The present data are also pertinent to an issue recently raised by Mack, Hill and Khan (1989) and Chaudhuri (1991). These authors suggest that tracking eye movements alone can account for some MAE phenomena. Chaudhuri (1991) proposes that the MAE might be due in part to the registration of corollary discharges from the eye muscles attempting to counteract the optokinetic nystagmus that results from adaptation. Mack *et al.* (1989) offer a similar proposal and further suggest that this process plays a critical role in the generation of the MAE. Both these authors suggest that retinal motion is a less important factor in the MAE.

The data from Experiment 3 suggest that eye movements alone do not play as important a role as might be inferred from Chaudhuri (1991) and Mack *et al.* (1989). The large reduction in interocular transfer of the MAE in the conditions where surround contours were eliminated suggests that the retinal motion of the surround contours in the Experiment 1 equiluminant condition was a much more important factor for the generation of the aftereffect than just eye movements. It remains to be seen whether the transferred aftereffect in the contourless adaptation conditions results from transferred retinal motion information or from eye movements.

One curious feature of the results of Experiment 3 is that the size of the monocular aftereffect is larger for the equiluminant condition than for dark occlusion. We are uncertain as to why this should be so.

CONCLUSIONS

The present study has replicated the original finding of Lehmkuhle and Fox (1976) in showing that the magnitude of interocular transfer may be influenced by the kind of occlusion used for the non-viewing eye. However, this occurred only when the adapting stimulus was a drifting grating and the non-adapting eye viewed objectively stationary surround contours. It did not occur for aftereffects with stationary contours, for the MAE for spirals or concentric circles, nor for a translational MAE when the non-adapted eye did not see any contours. These results are all summarized in Fig. 4 where we have calculated the relative transfer for the dark and equiluminant IOT. It may be seen that the only condition in which the amount of transfer is substantially greater in the equiluminance condition is for drifting gratings when the non-adapting eye views a screen with distinct border contours. This difference disappears even for drifting gratings when the non-adapting eye views a ganzfeld.

Lehmkuhle and Fox (1976) argued that the reduced transfer obtained with dark occlusion resulted either from changes in light adaptation when switching from adaptation to test or from the disruptive effect of a sudden change of luminance when the shutter was lifted from the unadapted eye. On the basis of this interpretation they suggested that equiiuminant occlusion gave a more valid measure of interocular transfer. The present data suggest just the opposite conclusion, that the large amount of transfer found with drifting gratings may be an artifact of conjugate tracking eye movements and that the optimum occlusion is one in which no contours are visible to the non-adapting eye (regardless of luminance level). It is important to note, however, that differential transfer is limited to the translational MAE and that for other aftereffects, the type of occlusion used does not seem to have a significant effect.

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