The Effects of Contrast Reversal on the Direct, Indirect, and Interocularly-transferred Tilt Aftereffect

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We compared the size of the tilt aftereffect (TAE) when the adapting and test stimuli were of opposite contrast (OC) to that of the traditional TAE in which both stimuli were the same contrast (SC). For example, one sort of OC adapting stimulus was a dark bar on a mid-luminance ground, and the test stimulus was a light bar on a mid-luminance ground; the comparison SC adapting and test stimuli were both light on a mid-luminance ground. We were able to map the usual function relating the size of the TAE against orientation of the adapting stimulus, but found no differences between OC and SC stimuli. This replicates the finding of Magnussen and Kurtenbach (1979), and extends it over a full range of adapting orientations to include the indirect TAE. In a second experiment we tested interocular transfer of OC and SC TAEs. Again we found no difference in size of the TAE between OC and SC conditions. We conclude that the TAE is mediated at a site in the visual system at which contrast polarity is unimportant.

Gibson and Radner (1937) reported that if one looks for some time at a line that is titled from vertical, what we will call the *adapting* stimulus, when one then looks at an objectively vertical line, the *test* stimulus, it appears tilted slightly in the opposite direction. Gibson and Radner termed this the *direct tilt afteraffect* (TAE). When the adapting stimulus is a line tilted about 75 degrees, say clockwise, from vertical, they found the vertical test stimulus to appear tilted slightly in the same direction. Gibson and Radner termed this the *indirect* TAE. The TAE has proved to be an important phenomenon for understanding human perception of orientation.

Carpenter and Blakemore (1973) proposed the most generally accepted explanation of the direct TAE in terms of lateral inhibition between cells in the striate cortex broadly tuned to particular orientations. For example, perception of a vertical line would be mediated by activity in cells tuned not only to vertical, but also by cells with orientation tunings up to 30 degrees clockwise and anticlockwise from vertical. The algebraic sum of all the cells' activity would specify vertical. Adaptation to a line tilted, say, by 15 degrees clockwise from vertical would depress the activity of some of the cells that normally respond when a vertical line is presented. When a vertical test line is subsequently presented, these adapted cells contribute less to the algebraic sum, shifting it away from vertical in the anticlockwise direction.

It is not obvious how to apply Carpenter and Blakemore's explanation to the indirect TAE. To do so, Wenderoth and Johnstone (1987) proposed that the indirect TAE is mediated in a different part of the brain, an extrastriate area, processing global orientation properties such as axes of symmetry and interactions between widely separated stimuli. For example, Wenderoth and Johnston hold that adaptation to a line titled 75 degrees from vertical affects a vertical test contour through a "virtual line" (p. 699), formed by an axis of symmetry orthogonal to the adapting line, that is at 15 degrees anticlockwise from vertical. This

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allows Carpenter and Blakemore's explanation to apply to the indirect TAE at this extrastriate site. To appreciate how, imagine a real adapting contour substituted for the virtual line: it would produce a direct TAE in the clockwise direction, exactly what is perceived in the indirect TAE. Wenderoth and Johnstone explained the differences in strength of direct and indirect effects through summation of effects in the striate and extrastriate areas: with the direct effect, the real and virtual lines coincide allowing summation in striate and extrastriate areas; with the indirect effect, only the virtual line is close enough in orientation to the test contour to influence its perceived orientation within the extrastriate area. Wenderoth and van der Zwan (1989) reviewed experimental support for the notion that the indirect TAE arises from axes of symmetry. For example, they confirmed that the indirect TAE is abolished by surrounding the adapting and test stimuli with a square frame, this frame offering many, competing, virtual lines to that of the adapting contour.

There are at least two ways of addressing where in the visual system the TAE might be mediated. The first involves using stimuli of opposite contrast polarity. For example, O'Shea and Mitchell (1990) found that vernier acuity, a task thought by some to depend on orientation processing (e.g., Sullivan, Oatley, & Sutherland, 1972), is worse when one stimulus is light on a mid-luminance ground and the other is dark, compared with when both stimuli are dark. O'Shea and Mitchell suggested that this form of processing occurs relatively early in the visual system. Magnussen and Kurtenbach (1979), however, measured the TAE with adapting stimuli that were either the same contrast (SC) as the test stimuli, or were of opposite contrast (OC). They found no difference in the direct TAE between OC and SC conditions, suggesting that the TAE is mediated at a later stage in the visual system at which contrast polarity is unimportant. In Experiment 1, we will attempt to replicate this finding and extend the investigation of the influence of contrast polarity to the indirect TAE.

The second means of locating the site of processing of the TAE in the visual system dates back at least to Gibson and Radner (1937): *interocular transfer* (IOT). With this technique, the adapting stimulus is presented to one eye, and the test stimulus to the other. The TAE occurs under such conditions, suggesting that its site must be at or after binocular convergence. We present a simplified model, in the form of a flow chart, in Figure 1.[1] In the model, we assume that information in separate channels, in this case separate eye-channels, needs to be combined for an aftereffect to occur. We call this the stage of binocular combination (BC) and have placed the TAE mechanism after BC for clarity. The logic remains the same if the two processes occur at the same site.

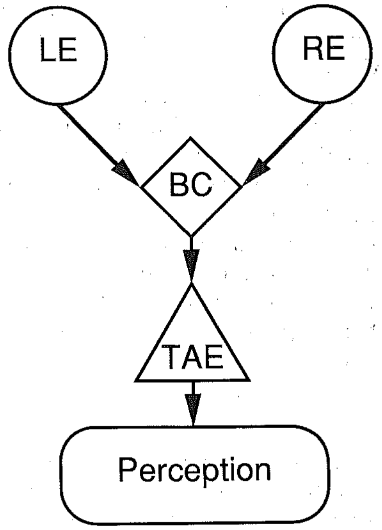

Figure 1. Flow chart illustrating the relationships between left-eye (LE) and right-eye (RE) channels (circles), the site of the TAE (triangle) and perception. As the TAE shows IOT, information from different-eye channels must be combined before the TAE mechanism. Combination takes place at the site of binocular combination (BC, diamond).

Binocular phenomena, however, are usually degraded when the stimuli are of opposite contrasts for the two eyes. Stereopsis is abolished, to be replaced by rivalry, in both line (Levy & Lawson, 1978) and random-dot stereograms (Julesz, 1963). As well, binocular summation is degraded to probability summation by OC half-images (Westendorf & Fox, 1974). In Experiment 2, we will assess whether IOT of TAE is also disrupted by making the stimuli opposite contrast.[2]

Experiment 1

Magnussen and Kurtenbach (1979) studied the TAE with OC stimuli. In one experiment they used stimuli that were either white or black bars on a gray ground, generating four possible combinations of adapting and test stimuli. Adapting stimuli ranged in orientation from 7.5 degrees to 60 degrees in six steps. While both subjects showed a clear relationship between the amount of TAE and the orientation of the adapting stimulus, with a maximum at about 15 degrees, neither subject showed any significant differences between SC and OC conditions.

In Magnussen and Kurtenbach's (1979) second experiment, they adapted to black-white edges of two sorts of polarity (i.e., black on the left, white on the right, WB, and vice versa, BW) and tested with a WB edge. Again they found the usual function relating adapting orientation to TAE magnitude, but no difference between the two edge-polarity adapting conditions. In pilot experiments, we found the same independence of edge polarity on the TAE. Magnussen and Kurtenbach tested adapting orientations only to a maximum of 60 degrees from vertical, thereby excluding the indirect TAE. We decided to repeat their Experiment 1 over a full range of orientations.

Method

Subjects

Seven students volunteered for the experiment to gain credit for a course in introductory psychology. All had normal or corrected-to-normal vision.

Apparatus

Stimuli were presented in separate channels of a Gerbrands two-field tachistoscope. Viewing distance was 76 cm. Stimuli were single lines of either white or black, with dimensions of 2.25 degrees by 0.10 degrees, presented on a green background. Adapting stimuli could have one of seven orientations clockwise from vertical to horizontal in 15 degree steps. An additional "adaptation" condition was included that consisted of a blank field of background luminance. The test stimulus was a single line mounted on a rotating platform, allowing its orientation to be set at any value.

The luminance of the background was 0.30 Cd/m^2. Michaelson contrast of the white lines was 0.20, and of the black lines was 0.13.

Procedure

Subjects were first given 10 minutes of dark adaptation. On each trial, the subject used a hand-held button to present the adapting stimulus for 1 s. Following a dark interstimulus interval of 100 ms, the test stimulus appeared for 100 ms. Subjects were required to judge whether the test stimulus was tilted clockwise or anticlockwise from vertical. The inter-trial interval was at least 4 s.

Adapting orientation, contrast-polarity and test contrast-polarity conditions were blocked. Points of subjective vertical were found by a staircase procedure. On the first trial of a new set of conditions, the orientation of the test stimulus was set at random to any one of nine values over a ± 2-degree range around vertical in 0.5 degree steps. The orientation of the test stimulus on the next trial was changed by a 0.5 degree step opposite to the direction of the subject's response. Trials continued in this way until the subject reversed judgement. The test orientation was then changed by 0.5 degrees in a random direction and trials continued until the subject made another reversal. This sequence of trials was continued until four reversals had occurred.

Order of testing adapting conditions and contrasts was approximately counterbalanced for order and serial position by a Williams square. All possible conditions of contrast of adapting and test lines were tested for the eight adapting conditions for a total of 32 conditions per subject.

Results and Discussion

Points of subjective vertical were determined for each condition and for each subject by averaging the four values over which subjects reversed their judgements of the tilt of the test line. Orientations at which reversals occurred were scored as positive if clockwise and negative if anticlockwise, making direct TAEs have positive values.[3] For each subject, means for the blank-field adaptation condition were subtracted from means for the conditions in which the adapting stimulus was a line. These data were analysed by a three-way, within-subjects analysis of variance. This found the orientation of the adapting stimulus to be the only significant effect, $F(6, 36) = 13.69$, $p < .01$. Whether the test stimulus was white or black was not significant nor did it have any significant interactions. Critically, whether the contrast relationship between the adapting and test stimuli was the same or different was not a significant effect, nor did it have any significant interactions. These results are graphed in Figure 2.

Figure 2 shows that all conditions produced a reliable direct TAE. At an adapting orientation of 15 degrees, the direct TAE is about 1.42 degrees. The indirect effect is weaker; at 75 degrees orientation of the adapting stimulus, it is about .034 degrees. The indirect effect is usually about a third of the size of the direct effect (e.g., Muir & Over, 1970). What is apparent is that SC conditions do not differ markedly from OC conditions for either the direct or indirect TAEs.

The results of Experiment 1, taken together

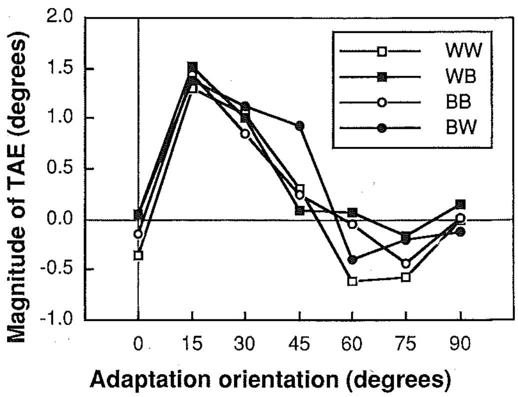

Figure 2. Plot of the magnitude of the TAE against orientation of the adapting stimulus for the four conditions of adapting and test contrasts (WW, both adapting the test lines were white; WB adapting line white, test line black; BB, both adapting and test lines black; BW, adapting line black, test line white). Positive values on the Y-axis show direct TAEs; negative values show indirect TAEs.

with the results of Magnussen and Kurtenbach (1979), allow us to conclude that if there are any differences between SC and OC adaptation on direct TAEs, they are quite weak. The minimal effect of contrast polarity on the direct TAE suggests that it is mediated higher up the visual pathway than effects that are contrast dependent (see General Discussion, for a summary).

Our results allow us to make the same conclusion about the indirect TAE; contrast polarity has very little, if any, effect. This suggests that the indirect effect is mediated at either the same or a higher site than the direct effect, a conclusion consistent with Wenderoth and Johnstone's (1987) proposal.

We can use an alternative strategy to locate the site of TAE processing by combining our contrast-polarity manipulation with interocular transfer. We will do so in Experiment 2.

Experiment 2

Interocular transfer of the TAE is consistent with the idea that the site of TAE processing is cortical. Also supporting this notion is the finding that IOT of TAE is reduced in observers with compromised binocularity (Mohn & van Hof-van Duin, 1983). As we discussed earlier, reversing the contrast of stimuli presented dichoptically essentially abolishes binocularity, indexed by stereopsis and binocular summation, in normal observers. What might be the effect on IOT of TAE by reversing the contrast of adapting and test stimuli?

Method

Subjects

Seven students participated in the experiment to gain credit for a course in introductory psychology. All had Snellen acuities of 6/6 or better in each eye and no problems with binocular vision.

Apparatus

Stimuli were presented in separate channels of a Gerbrands four-field tachistoscope. Viewing distance was 79 cm. Stimuli were single lines of either white or black, with dimensions of 5.22 degrees by 0.22 degrees, presented on a gray background. Adapting stimuli were a blank field, a vertical line, or a line tilted anticlockwise from vertical by 15 degrees. The test stimulus was mounted on a rotating platform allowing its orientation to be set to any value.

Polarizing filters in the body of the tachistoscope and in the eyepiece allowed the test stimulus to be visible only to the right eye. By changing the filters in the field containing the adapting stimulus, it could be made visible to either eye. The fourth field of the tachistoscope contained a small, luminous fixation point, optically superimposed on the centre of all stimuli. It was unfiltered, so was always visible to both eyes, serving as a stimulus to binocular alignment.

The luminance of the background was 0.25 Cd/m^2. Michaelson contrast of the white and black lines was 0.63

Procedure

The procedure was essentially the same as in Experiment 1 with the following changes: Subjects were first given 5 minutes of dark adaptation; the interstimulus interval was 10 ms; and there were a total of 20 conditions that were randomly ordered.

There were five sorts of adaptation stimuli: a blank field, a vertical black or white line, and a 15-degree black or white line. These adapting stimuli could be presented to either the left or the right eye. Test stimuli were either the same contrast or opposite contrast to the adapting lines, and were always presented to the right eye. The 20 conditions represented the full combination of all these factors; all subjects responded to all conditions.

Results and Discussion

Results were treated in the same way as in Experiment 1. Data were analysed by a four-way, within-subjects analysis of variance. This showed the orientation of the adapting stimulus to be significant, $F(1, 6) = 16.92, p < .01$, and whether the adapting stimulus was presented to the same eye as the test stimulus, or the opposite eye (IOT), also to be significant, $F(1, 6) = 20.82, p < .01$. No other main effects or interactions were significant. The results are graphed in Figure 3.

Figure 3 shows that all contrast conditions produced a reliable direct TAE that did not differ among conditions. The results in the left panel confirm the result of Experiment 1, and that of Magnussen and Kurtenbach (1979): OC adaptation conditions lead to about the same amount of direct TAE as SC conditions. The right panel allows us to extend this conclusion to direct TAEs that have been generated interocularly. Despite the deleterious effect of contrast reversal on binocular phenomena such as stereopsis and binocular summation, there seems to be little effect on IOT of TAE.

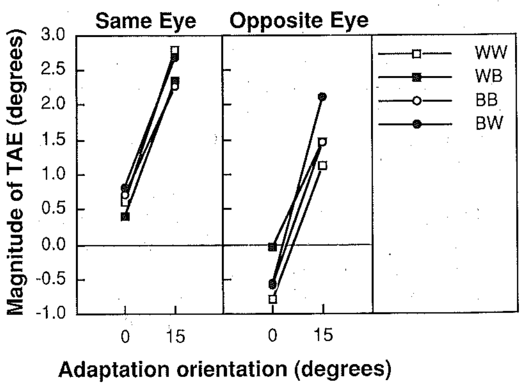

Figure 3. Plot of the magnitude of the TAE against orientation of the adapting stimulus for the four conditions of adaptation and test contrasts (WW, both adapting and test lines were white; WB adapting line white, test line black; BB, both adapting and test lines black; BW, adapting line black, test line white). The left panel shows TAEs when adapting and test stimuli were presented to the same eye; the right panel when the stimuli were presented to opposite eyes.

There are differences in the absolute level of TAE between the same-eye condition and the 15-degree, binocular, adaptation condition of Experiment 1 (same-eye gave more TAE), and between same-eye and opposite-eye conditions of Experiment 2 (again, same-eye gave more TAE). The differences in the TAE between the two experiments are minimized if the "TAEs" to the respective 0-degree adapting condition are subtracted from the TAEs to the 15-degree adapting conditions. It is the same for the same-eye and opposite-eye conditions of Experiment 2 (revealed by the absence of a significant interaction between adapting orientation and adapted eye, $F = 0.26$, from the above analysis).

We should emphasize that in both experiments, TAEs have already had subtracted from them the orientation judged to be vertical following adaptation to a blank field. The differences in apparent vertical that follow adaptation to a vertical stimulus may represent figural aftereffects (e.g., Köhler & Wallach, 1944) arising from slight differences in the alignment of different adapting and test stimuli. The absence of a difference in the amount of TAE following same-eye and opposite-eye adaptation is harder to account for. IOT usually produces less aftereffect than when the adapting and test stimuli are presented to the same eye (e.g., Mohn & van Hof-van Duin, 1983), although at least one study has found 100% IOT (Campbell & Maffei, 1971). We have not discovered the critical procedural differences that account for differences in the amount of IOT of TAE from different studies.

What we can say with confidence from the results of Experiments 1 and 2 is that opposite contrasts do not impair the direct TAE. We can add from Experiment 2 that opposite contrasts do not seem to impair interocular transfer of the direct TAE.

General Discussion

The TAE seems typical of other aftereffects in its independence of contrast polarity. Contrast-polarity-independent adaptation phenomena include size aftereffects (Mayhew, 1973), size-contingent motion aftereffects (Mayhew, 1973), motion-in-depth aftereffects (Regan & Beverley, 1978) and metacontrast (Breitmeyer, 1978).

In the same way as we have set out in the model shown in Figure 1, information from contrast-polarity-specific channels must be combined for a contrast-polarity-independent aftereffect to occur. We assume that opposite contrasts must be rectified at some stage in the visual system, so that a light line becomes perceptually equivalent to a dark line. This stage of contrast rectification must precede the site of the aftereffect. We have diagrammed this in Figure 4.

Some aftereffects do appear to depend on contrast polarity. These include threshold-elevation to gratings (Burton, Nagshineh, & Ruddock, 1977; De Valois, 1977) and edges (Tolhurst, 1972), motion aftereffects (Mayhew, 1973), and temporal masking (Stelmach, Bourassa, & Di Lollo, 1987). Cavanagh, Brussell and Stober (1981),

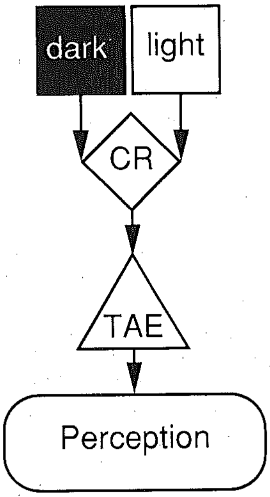

Figure 4. Flow chart illustrating the relationship between opposite-contrast channels (dark and light boxes), the site of the TAE (triangle) and perception. As the TAE is independent of contrast polarity, information from different contrast channels must be combined before the TAE mechanism. Combination takes place at the site of contrast rectification (CR, shaded diamond).

however, have reinterpreted apparently contrast-specific threshold-elevation aftereffects in terms of phase. Whatever the outcome of this debate, any such contrast-polarity-dependent aftereffects must be mediated relatively early in visual processing, serially before contrasts are rectified. We suggest that it would be useful to determine whether such contrast-specific effects transfer interocularly.

Very little other work appears to have been done on IOT of aftereffects as a function of contrast polarity. Our study suggests that IOT of TAE is unaffected by contrast polarity. The only other study we can find was of a motion-in-depth aftereffect; it also shows contrast-polarity-independent IOT (Regan & Beverley, 1978). To explain contrast-polarity-independent IOT, while preventing opposite-contrast information from combining for such tasks as stereopsis and binocular summation, contrast rectification must take place after the site of binocular combination. This is illustrated in Figure 5.

It is possible to achieve the same result, contrast-polarity-independent IOT of TAE, in other models (e.g., separate eye-channel CRs could precede a single BC). However, we believe the version in Figure 5 is the most parsimonious (i.e., in the above example, stereopsis and binocular summation need to be processed in parallel). We should emphasize that we do not intend our model to represent anatomical connections in the visual system (e.g., van Essen, Anderson, & Fellerman, 1992, recently reviewed 305 interconnecting pathways between 32 visual centres in the primate brain). Nevertheless, our model depicts the logical ordering of processing, whether it is accomplished serially, as we have shown it, or in parallel with feedback.

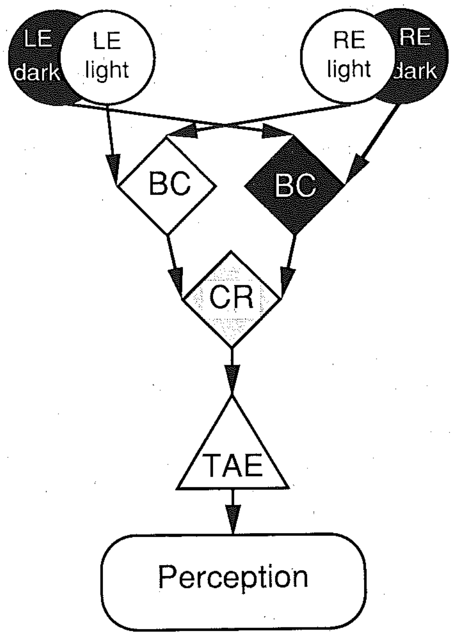

Figure 5. Flow chart illustrating the ordering of sites for contrast-polarity-independent IOT of TAE. Information from same-contrast channels but from opposite eyes must be converged (at separate BCs). After binocular combination, contrast rectification must take place (at CR) before the site of the TAE.

In conclusion, we have found that OC adaptation leads to just as much direct TAE as traditional SC adaptation, that the indirect TAE appears to be immune to the effects of contrast polarity and that IOT of the direct TAE is minimally affected by changes in contrast polarity of adapting and test stimuli. These results suggest the relative ordering in the visual system of binocular combination, contrast rectification and the mechanisms of the direct and indirect TAEs. Study of IOT of other aftereffects, especially those that are contrast-polarity-dependent, should help test this sort of serial model of visual processing.

Footnotes

1 Of course this is a a much simpler model than those proposed to account for all the details of IOT (e.g., Blake, Overton, & Lema-Stern, 1981; Cogan, 1987; Moulden, 1980).

2 As will be seen, we have a potential problem of nomenclature in Experiment 2, in which we study IOT of the direct TAE. In studies of IOT of aftereffects, when adaptation and testing take place in the same eye, this is sometimes referred to as the direct effect. We will avoid this usage to minimize confusion with the direct TAE as we have already defined it.

3 Note that for the usual, direct TAE, an objectively-vertical test stimulus would appear to be tilted anticlockwise after inspection of our clockwise-tilted adaptation stimulus. In order to make it appear vertical, the subject must set its orientation in the opposite direction, that is, clockwise from vertical.

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