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SHORT TEST FLASHES PRODUCE LARGE TILT AFTEREFFECTS

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Abstract—Using a staircase method, the tilt aftereffect (TAE) was measured with test flashes of durations ranging from 10 to 600 msec. The TAE is largest with brief duration test stimuli and reaches an asymptotic value at a test flash duration of 200–300 msec. A series of control experiments rule out a variety of explanations for this finding. The decline in TAE magnitude with increasing test duration is not due to decay, nor can the large TAEs produced by brief stimuli be explained in terms of their lower effective luminance or contrast. The results suggest that brief stimuli are processed by a different subset of processes or channels than are longer stimuli.

A few seconds or minutes exposure to the leftward pointing pattern of Fig. 1(a) will cause the co-linear halves of Fig. 1(b) to apparently point to the right [Fig. 1(c)]. This "Tilt Aftereffect" (TAE) represents a change in one of the basic features of a visual stimulus, its perceived orientation. Many other basic features can be similarly altered: Motion (Wohlgemuth, 1911), spatial frequency (Blakemore and Sutton, 1969), color (e.g. McCollough, 1965), size (Frome and Danielson, 1974) and spacing (e.g. Kohler and Wallach, 1944).

By manipulating the perception of different features, we may be able to determine how the visual system extracts these features from the retinal image. The purpose of this study was to use the TAE to uncover some temporal factors in the analysis of orientation. To this end, we have examined the effects of varying the duration of the test stimuli on the magnitude of the TAE. Considerable evidence exists that brief stimuli are processed differently by the visual system than are stimuli of longer duration. Brief or intermittent stimuli tend to appear brighter than equivalent sustained stimuli (Brucke, 1864; McDougall, 1904; Bartley, 1939). Briefly presented grating patterns tend to have altered, usually higher, apparent spatial frequencies (Tynan and Sekular, 1974; Kulikowski, 1975; Gelb and Wilson; 1983). They also have altered, usually lower, "effective contrast" (Kitterle and Corwin, 1979). Further, different stimuli presented to each eye do not produce normal binocular rivalry if the stimuli are presented briefly (e.g. Hering, 1920; Kaufman, 1963; Wolfe, 1982). Finally, and of most relevance to the study of the TAE, orientation can be systematically misjudged if short lines are briefly presented (Andrews, 1967).

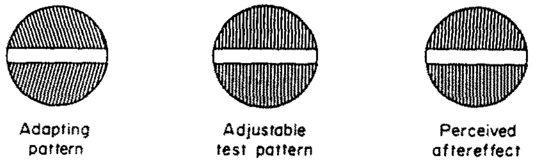

Fig. 1. Adapting and test stimuli for a tilt aftereffect. If one scans the midline of (a) for 30–60 sec, the physically co-linear halves of (b) will appear tilted as illustrated in (c).

Is the processing of orientation, as studied with the TAE, different for brief stimuli? One way to approach this question is to measure the TAE with brief stimuli rather than with the longer duration stimuli that have been used previously. As the title suggests and as the results of the main experiment will show, the TAE changes under these conditions. Brief test stimuli produce large TAEs. Subsequent experiments rule out luminance, contrast and recovery from adaptation as causes for these large TAEs suggesting that brief and longer duration stimuli are processed differently.

MAIN EXPERIMENT: EFFECTS OF TEST FLASH DURATION

Method

The TAE was measured with stimuli similar to those shown in Fig. 1, by use of a staircase procedure. The overall orientation of the adapting and test patterns is not important. In this experiment, a set of stimuli was created ranging from a chevron with a 170 deg obtuse angle pointing up to a 170 deg chevron pointing down in 0.5 deg steps. Chevrons pointing left and right as in Fig. 1 produce the same effects. To aid comparison with other TAE results, TAE magnitude will be expressed as the deviation from horizontal of one arm of the chevron. This is equivalent to:

$$(180\ \text{deg} - \text{the obtuse angle})*0.5.$$

Thus, the stimuli ranged from 5 deg pointing up to 5 deg pointing down with the 0 deg stimulus having physically co-linear halves. The TAE was produced by having subjects view a chevron pattern as shown in Fig. 1(a) for 4 min. In these experiments, the adapting pattern was a 15 deg chevron, pointing up.

Chevron stimuli were 7.7 cpd, high contrast (>90%) square wave gratings with a mean luminance of 2.5 log cd m^{2}. The circular stimuli had a diameter of 1.6 deg. Stimuli were presented in a Scientific Prototype 6-Channel binocular tachistoscope whose lamps have rise and decay times of less than 1 msec.

To initiate the staircase, a chevron that physically pointed down was presented to the subject as the first trial. If it appeared to the subject to point down, the subject was instructed to press a switch that caused the next stimulus to point up by a 0.25 deg. If it appeared to point up, the subject pressed another switch causing the next stimulus to point 0.25 deg further down. Obviously, this staircase converges to the point that appears neither up nor down but co-linear. Staircases were always started with a stimulus that apparently pointed down and continued for 10 trials after the first reversal. The last ten trials were averaged to produce and estimate of the point of colinearity (Dixon and Massey, 1969).

In all sessions, staircases were run prior to adaptation. These baseline measures were almost always within a degree of physical co-linearity. The TAE, therefore, was defined as the difference between physical co-linearity and the post-adaptation measures made by the S. This eliminated the need for baseline measures at all test flash durations.

In these experiments the TAE, we sought to produce and maintain a full-strength TAE and to measure it under a variety of test conditions. The 4 min, initial adaptation period generates a strong TAE that does not grow stronger with continuing exposure to the adapting pattern. After the initial 4 min adaptation period, a series of test trials were run. Each test trial was preceded by 5 sec of re-exposure to the adapting stimulus in order to keep the TAE at full strength. Next came a 500 msec, dark ISI with a warning tone, followed by a presentation of the test pattern. The subject responded and that response started the next 5 sec re-adaptation period.

Two groups of subjects were tested using this paradigm. The first group of 8 subjects were tested at a variety of different test flash durations ranging from 10 to 2000 msec. The results of these sessions were used to pick seven durations between 10 and 600 msec. Five subjects were tested with these seven durations. One staircase was run for each duration. All subjects had normal or corrected to normal acuity and stereopsis as assessed by their ability to see depth in random-dot stereograms. All were naive about the purposes of this experiment with the exception of the authors. Some were experienced in other TAE experiments. In the second group of 5 subjects, each subject was tested twice, once with each eye.

Results

The general form of the results was similar for all subjects in both groups. Results from a single subject who was tested at a large number of different durations are shown in Fig. 2. Figure 3 shows averaged data for the 5 subjects in the second group. Both Figs 2 and 3 show that the magnitude of the TAE changes dramatically with changes in the test flash duration. Brief test produce very large TAEs; larger, in fact, than any we have found in comparable experiment using these stimuli (e.g. Wolfe and Held, 1983). The curve relating TAE magnitude to flash durations falls rapidly as duration increases to 150 msec and then declines more slowly. Four of 5 subjects produced TAEs in excess of 5 deg for the shortest test durations exhausting the available test stimuli. TAEs that were too large to measure were set, somewhat arbitrarily, to 5.5 deg for purposes of averaging. The probable result is an underestimation of the magnitude of the TAE at the shortest test durations.

The reduction of aftereffect size with increasing test flash duration has been previously noted by Krauskopf (1954; cf. Parducci and Brookshire, 1958) using figural aftereffects and substantially longer test periods (300–1500 msec). I will argue that there are two processes revealed by this finding. One contributes

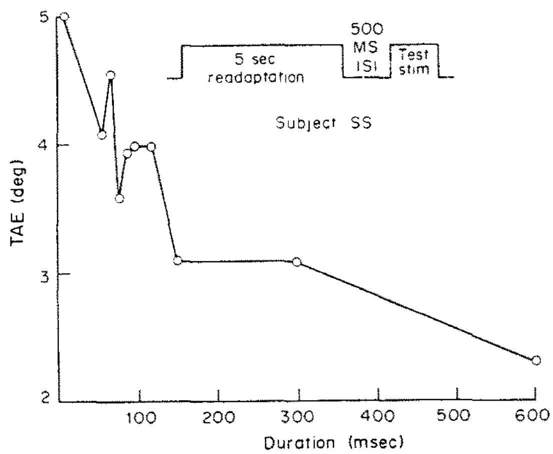

Fig. 2. Magnitude of the TAE as a function of test flash duration for 1 subject. The TAE is larger for shorter durations and the decline levels off after 150–200 msec.

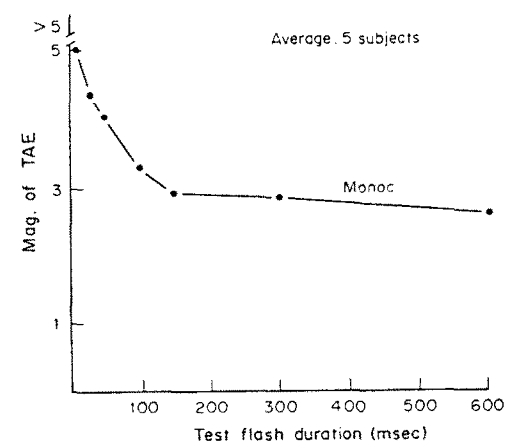

Fig. 3. Magnitude of the TAE as a function of test flash duration: averaged data from 5 visually normal subjects. The results are similar in form to those in Fig. 2.

most heavily to the perception of brief stimuli and is strongly adapted. The other contributes to the perception of longer stimuli and is less susceptible to adaptation.

This two-process explanation was arrived at by the elimination of other more parsimonious explanations on the basis of the results of a series of control experiments presented below. Aftereffects begin to decay after the adapting stimulus is removed. Decay is a possible cause for the decline in TAE magnitude with increasing test duration. Since aftereffects begin to decay after the removal of the adapting stimulus, the TAE would have more opportunity to decay during longer test periods. Krauskopf (1954) proposes just such an interpretation of his results. Other factors such as changes in the apparent contrast or the luminance of the test patterns with changes in test flash duration could also contribute. A series of control experiments suggest that none of these explanations is adequate.

CONTROL EXPERIMENTS

Passive Decay: Varying Test Stimulus Offset

In the initial experiment, the ISI that followed the 5 sec of readaptation was always 500 msec. Since the test flash duration varied from 10 to 600 msec, the duration of the test trial varied from 510 to 1100 msec. If the TAE decayed substantially during this period, trials with longer total durations would be expected to produce smaller TAEs. To test this hypothesis, the length of the ISI was varied while test flash duration was held constant.

Method

ISIs of 100, 300 and 1000 msec were used with a test flash duration of 10 msec. ISIs of 10, 100, 300 and 1000 were used with a test flash duration of 300 msec. Two normally-sighted subjects were tested. All other aspects of this experiment were identical to that of the previous experiment.

Results

Average results are presented in the table below:

Test duration	10	10	10	300	300	300	300
ISI	100	300	1000	10	100	300	1000
Avg. TAE (deg)	>5	4.9	4.6	4.2	4.0	4.2	4.0

The 10 msec flash produces larger TAEs regardless of the length of the ISI. When total trial duration is 310 msec, the 10 msec flash produces a 4.9 deg TAE while the 300 msec flash produces a 4.2 deg TAE.

This experiment is evidence against a decay model that explains the effect of test flash duration by maintaining that the TAE decays rapidly when the adapting stimulus is turned off. Apparently, the effect does not decay rapidly enough. It is known, however, that the rate of decay is not a simple function of time after the removal of the adapting stimulus. Testing causes aftereffects to decay more rapidly (e.g. Jones and Holding, 1975; Keck and Pentz, 1977). Thus, it could be that the longer test flashes produce smaller TAEs because they actively reduce the magnitude of the TAE more than the short test flashes. The next experiment addresses that possibility.

Active Decay: The Two-Flash Experiment

Methods

Methods were identical to those of the main experiment with the addition of a second test flash. Following the 4 min of initial adaptation, the following sequence of stimuli constituted a trial:

5 sec readaptation → 500 msec dark ISI → 300 msec test flash → 400 msec dark ISI → 10 msec test flash.

For each staircase, subjects were asked to judge the appearance of either the first or the second test flash; a task that is quite easy to do. The results of the main experiment showed that the first, 300 msec flash produced about a 3 deg TAE. What will be the magnitude of the second, 10 msec flash? If the 300 msec flash depresses the TAE to about 3 deg, then, in the absence of any re-adaptation, the second flash must produce a TAE less than or equal to that produced by the first flash. The results for 9 subjects are shown in Fig. 4.

Results

Contrary to the active decay hypothesis the TAE was significantly larger in the 10 msec test condition for all subjects. The average TAE was 3.6 deg for the 10 msec flash and 2.8 deg for the 300 msec flash, a statistically significantly difference ($t = 4.15$, d.f. $= 7$,

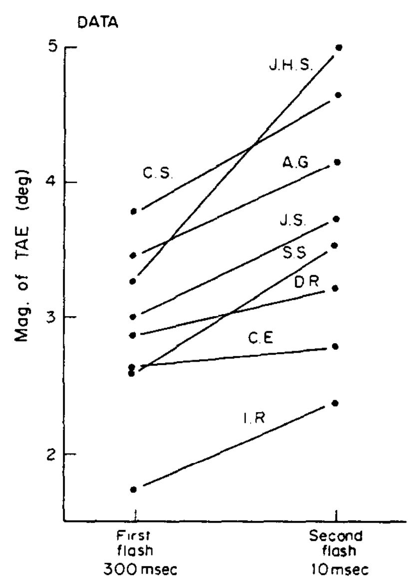

Fig. 4. Magnitude of the TAE as assessed with two sequential test flashes. The second, 10 msec, yields a larger TAE than the first, 300 msec, flash even though there is no re-exposure to the adapting stimulus between the first and second flashes. This rules out a simple decay explanation of the effect.

$P < 0.01$). It is, in fact, possible to arrange situations where the first, longer test stimulus appears to point in one direction while the second, shorter flash points in the other direction even though the same physical stimulus is presented in both flashes. These results are incompatible with an active decay hypothesis. If the TAE decayed during the first, longer flash, it could not recover and produce a larger TAE for the second, briefer flash without re-adaptation. The results are consistent with the hypothesis that different processes contribute to the TAE measured with short and longer flashes.

Certainly, some decay does occur after the offset of the adapting pattern. This can be seen by comparing the magnitude of the TAE obtained with a 10 msec flash in the two flash experiment to the TAE obtained with a 10 msec flash in the initial experiment. In the two flash experiment, the 10 sec flash occurs 1200 msec after the offset of the adapting pattern. In the initial experiment the ISI was only 500 msec. Further, in the two flash experiment, the 10 msec test occurs after 300 msec exposure to the test pattern. Not surprisingly, the 10 msec TAE is smaller in the two flash experiment than in the initial experiment. The conclusion of the two flash experiment is that decay, though it does occur, is not sufficient to explain the main effect of test flash duration.

Counter-Adaptation

Given that exposure to test stimuli can weaken aftereffects, another explanation of the effect of test flash duration is possible. Suppose that the test stimuli act as "counter-adapting" stimuli. That is, following 4 min of exposure to the adapting chevron, the adapted state becomes the new baseline state. Test stimuli cause adaptation back towards the pre-adapted, baseline state. The magnitude of this adaptation would increase as test flash duration increases. Thus, a 300 msec test flash would counter-adapt more than a 10 msec test flash and would produce a smaller TAE relative to baselines measured before any adaptation.

The counter-adaptation hypothesis can also explain the results of the two-flash experiment. Brief exposure to the test stimuli might be expected to produce only a brief counter-adaptation. During the ISI, after removal of the first test stimulus, the counter-adaptation would rapidly decay and the visual system would return to the fully adapted state produced by longer duration exposure to the adapting chevron. If this is the case, then the magnitude of the TAE measured with the second test flash should become larger as the ISI between the first and the second test flash grow larger and the counter-adapting effects of the first flash decay.

This hypothesis relies on a couple of assumptions. First, a brief exposure to the test pattern must produce significant counter-adaptation. Secondly, that adaptation must last for a few hundred msec. Either assumption could be invalid. If so, the counter-adaptation explanation would not explain the results of the main experiment. The assumptions are not particularly implausible, however, so the hypothesis was tested in order to eliminate a final version of a single-process, decay explanation for the results of the first experiment.

To test the hypothesis, the two-flash experiment was repeated with a variety of ISIs between the first and second test flashes. If the first flash is causing counter-adaptation, then shorter ISIs should produce smaller TAEs while longer ISIs should allow the counter-adaptation to decay and produce larger TAEs.

Methods

Methods were similar to those in the two-flash experiment. Two test flashes were presented on each trial. The first test flash was 300 msec long and the second, 10 msec. The ISI between the flashes was either 200, 400 or 600 msec. ISIs shorter than 200 msec could not be used because it became impossible to assess the orientation of the second flash. One staircase was run for each ISI. Readaptation was reduced to a minimum of 2 sec per trial because this proved to work as well as the 5 sec periods used in preceding experiments. Eight subjects with normal acuity and stereopsis were tested.

Results

The average results are shown below:

TAE MAGNITUDES

ISI	300 msec flash	10 msec flash
200	2.0	2.7
400	2.0	2.9
600	2.0	2.8

For each ISI the TAE was significantly larger when measured with the second flash than with the first. There was no significant effect of ISI on TAE magnitude for either flash. The TAE for the second flash does not appear to grow as a function of ISI. No support can be obtained from these results for the notion that the initial test stimulus resulted in significant counter-adaptation.

Effects of Test Flash Light Level

None of the variants of a decay hypothesis seem to explain the large TAEs that are found when the test flash is brief. Other possible interpretations still exist. Brief stimuli can behave both like dim stimuli and like low contrast stimuli. Both light level and contrast are variables that are thought to have effects on aftereffect magnitude. Nevertheless, the following two control experiments show that neither variable can account for the size of the TAE at brief test durations.

Dimmer stimuli could produce larger TAEs. Again, this is the case with simple negative afterimages. Afterimages appear more saturated if viewed against a dim gray field. Further, there are many anecdotal reports and, at least, one published report that various aftereffects are larger when tested with dim stimuli (McCollough Effect—White, 1976). Assuming some form of temporal integration, brief stimuli in these experiments would be, in effect, dim stimuli. That is, a 10 msec test flash would be the equivalent of a 100 msec flash of 1/10th the brightness. Control Experiment Four rules out the possibility that the results of the main experiment are due to light level.

Methods

The methods were almost identical to those in the initial experiment with the following changes. Only two test flash durations were used: 30 and 300 msec. Even assuming complete temporal summation (an unlikely assumption), the 300 msec flash would be effectively 10 times as bright as the 30 msec flash. If the change in TAE magnitude with duration is due to change in light level, then reducing the light level by a factor of 10 should boost the 300 msec TAE to the level obtained with a bright 30 msec flash. In this experiment, a light level was reduced by a factor of 100 by introducing a 2.0 log unit neutral density filter in front of the test stimuli. Bright stimuli had a mean luminance of 2.5 log cd/m^2. The dim stimuli were 0.5 log cd/m^2. If brief stimuli produce large TAEs because brief stimuli are effectively dimmer, then the dim 300 msec flash should produce a larger TAE than the bright 30 msec flash. After 4 min of adaptation to a bright adapting stimulus, bright and dim measures were taken for 30 and 300 msec test durations. For the 5 subjects tested, two staircases were run at each of the four conditions.

Results

Results show that decreasing the light level does increase the magnitude of the TAE but the increase is not large enough to explain the results of the initial experiment. Average results for all four conditions are given below.

Conditions	Avg TAE (deg)
30 msec dim	4.4
30 msec bright	4.1
300 msec dim	3.0
300 bright	2.6

The 300 msec dim condition produces a TAE that is significantly smaller than the 30 msec bright condition ($t = 3.5$, d.f. $= 4$, $P < 0.025$) ruling out the possibility that the short durations are the equivalent of dim stimuli in TAE experiments.

Effects of Contrast

Kitterle and Corwin (1979) have shown that the "effective contrast" of a sinusoidal grating is lower for very brief presentations than for longer presentations. (Effective contrast is enhanced for a middle range of durations.) Thus, the brief test flash durations could be the equivalent of low contrast stimuli. Parker (1972) has found that low contrast stimuli produce larger TAEs. The final control experiment was undertaken to determine if low contrast stimuli would produce the large TAEs seen here with brief test durations.

Method

Methods were similar to previous experiments. Low contrast test stimuli were created by flickering the high contrast (90%) stimuli in alternation with a blank field of the same average luminance. Flicker was at 100 Hz and was imperceptible. Contrast was varied by changing the duty-cycle of the flicker. Test flash duration was held constant at 1000 msec. Six test contrasts were used: 13, 20, 35, 55, 77 and 90%. The contrast of the adapting stimulus was always 90%. Four subjects were tested, once with each contrast.

Results

No systematic effect of contrast was found. Average results for the four subjects are presented below:

Contrast	13	20	35	55	77	90
TAE magnitude	2.6	2.8	2.7	2.4	3.0	3.2

It is clearly not the case that low contrast stimuli produce larger TAEs. This is a somewhat puzzling finding in light of the results of Parker (1972) where dimmer stimuli did produce larger TAEs. Keck and Pentz (1977) have found similar results for the motion aftereffect. The reason for the difference is probably methodological. Parker (1972) and Keck and Pentz (1977) used the method of adjustment. Each setting would take several seconds. Though decay or counter-adaptation do not effect the results reported here, it is clear that prolonged viewing of the test stimulus does reduce the strength of an aftereffect. It is also clear that high contrast stimuli are more potent in this regard than low contrast stimuli. Thus, when using the method of adjustment, high contrast stimuli will weaken the TAE more than low. The brief stimuli used in the staircase method employed here do not significantly reduce the TAE so no effect of contrast is seen. For the purposes of this paper, the important conclusion is that contrast effects cannot explain the large TAEs seen with brief test durations.

DISCUSSION

The results of the main experiment are not an artifact of the effective contrast or luminance of the test stimuli. They do not reflect a decay in TAE magnitude with increasing test duration or counter-adaptation by longer test stimuli. These hypotheses are eliminated by the control experiments. Each experiment used a different set of subjects and, thus, TAE magnitudes obtained in different experiments cannot be compared to each other. Figure 4 gives a fair impression of the range of TAE magnitudes across subjects. In general, as can be seen in Fig. 4, all subjects produced similar patterns of results but the absolute magnitude of the TAE could vary substantially from subject to subject. When experimental conditions are similar from experiment to experiment, similar results are obtained. For example, in both the main experiment and the control for the effects of light level, TAEs were measured with 30 and 300 msec test flashes. In both cases, 30 msec yields a TAE about 1.5 deg larger than does 300 msec. Similar comparisons cannot be done across all the experiments. For example, in the "two flash" experiment a 10 msec test flash follows a 300 msec test flash. The results for that 10 msec condition are not comparable to those obtained with an isolated 10 msec test flash in the main experiment.

Having eliminated light level, contrast and aftereffect decay, an explanation is needed for the results of the main result of this paper; that large TAEs are seen with brief test stimuli. It appears that different processes are involved in the perception of brief and longer duration stimuli. Within this broad hypothesis lie more specific proposals that cannot be evaluated on the basis of the preceding results. Two main versions emerge. It could be that there exist separate processes for brief and longer duration stimuli. The brief process would be highly effected by the adapting stimulus; the long process, less so. The brief process would be the only active process during very brief test flashes. The other process would be the only active process during long flashes. For flashes of intermediate length, both processes would contribute to the TAE.

Another possibility is that there exist two processes with different latencies. One, highly adapted, would have a very short latency. It is active from the onset of the test stimulus. The second process would be less adapted (perhaps, not at all) and would make its contribution to the assessment of orientation more slowly. It would take about 150 msec to reach full strength. Both processes could contribute to the assessment of orientation at longer test durations or, perhaps, the first process could become inactive after responding for 100–200 msec. The differences between these two classes of proposal are not merely semantic. The first proposal suggests that the duration of stimuli may be important. The second proposes that stimulus duration serves as a psychophysical tool that distinguishes between processes that may not, themselves, be concerned with stimulus duration. The effects of duration, in the second proposal, would arise only as a by-product of the longer latency of one or more processes.

A version of the second proposal would propose that brief exposure to a test pattern activates only a subset of the orientationally tuned channels that are activated by long exposure. Andrews (1967) invokes a model of this sort to explain his finding of systematic errors in the assessment of the orientation briefly flashed lines. Further experiments are needed to choose between these various hypotheses.

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