

Fatigue and Structural Change: Two Consequences of Visual Pattern Adaptation

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In a tilt aftereffect (TAE) paradigm, 2 min of adaptation produced an aftereffect that decayed almost completely within 4 min. Four minutes of adaptation produced a TAE that lasted more than 2 wk. Two modes of adaptation contribute to the TAE and account for other aftereffects: (1) short-term fatigue, produced very quickly and (2) long-term structural change, requiring more extended adaptation. Invest Ophthalmol Vis Sci 27:538-543, 1986

Two classes of visual aftereffects can be produced by adaptation to a visual stimulus: (1) The threshold for detecting that stimulus and similar stimuli may be raised,¹ and (2) The suprathreshold appearance of related stimuli may be altered (eg, orientation, motion, spatial frequency, and color).²⁻⁵ Threshold elevation aftereffects are explained as temporary reductions in the sensitivity of the mechanisms detecting the stimulus. Adaptation fatigues the mechanism, and some period of time is required for recovery. Fatigue has been proposed as an explanation of aftereffects of the second kind.⁵⁻⁷ However, several of these, notably the McCollough effect⁵ and the motion aftereffect⁸ can last for hours, days, or even weeks. Faced with these long durations and other attributes of these aftereffects, some have proposed that these effects represent a form of classical conditioning or a related, simple form of learning.^{9,10} Efforts to tie aftereffects closely to the classical condition paradigm have not always been experimentally successful.¹¹⁻¹³

This report presents tilt aftereffect (TAE) data supporting a model with two qualitatively different stages of adaptation. Initial presentation of an adapting stimulus produces a TAE due to fatigue. This TAE appears very rapidly and decays rapidly, following rules similar to those governing, for example, photopigment bleaching in simple light adaptation. More extensive adaptation yields a TAE that does not decay completely when the adapting stimulus is removed. The residual

TAE can be measured at least 2 wk later. This extreme persistence probably reflects structural change in the visual nervous system.

Materials and Methods

The basic TAE paradigm is shown in Figure 1. If the reader fixates Figure 1a and then shifts gaze to 1b, it will be seen that 1b comes to look like 1c. These stimuli and the data presented below demonstrate that the TAE develops rapidly. With just these stimuli, however, the reader will have more difficulty producing the week-long TAEs that are the main topic of this paper.

A tracking-staircase procedure was used to monitor the TAE continuously. A stimulus like 1b was flashed for 50 msec. Subjects stated that it appeared to point either to the right or left (1a 'points right'). If the subject said "right," the next stimulus was 0.5 deg more to the left and vice versa. This staircase will converge on the point that appears to point neither right nor left, a state of subjective colinearity. The deviation of that point from true colinearity is an estimate of the TAE. As the TAE changed over time, the staircase tracked those changes.

Measuring the obtuse angle, test stimuli ranged from 170 deg pointing to the left to 170 deg pointing right. Stimuli were standard, black and white 2 × 2 slides presented in a Scientific Prototype tachistoscope. They were high contrast (>90%) with a spatial frequency of 7.7 cpd and a mean luminance of 2.5 log cd/m-sq. The circular field was 1.6 deg in diameter. All stimuli were presented to the right eye of naive subjects who had or were corrected to at least 20/20 acuity in that eye. All subjects gave their informed consent after the nature of the experiment was explained to them.

Initially, the staircase was run until the subject reversed direction ten times. This established a pre-adaptation baseline against which subsequent aftereffects

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Research was supported by grants from the N.I.H. (#EY05087, #RR07047), Whitaker Health Sciences Fund, and Sloan Foundation support of the Center for Cognitive Science.

Submitted for publication: June 6, 1985.

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could be measured. The baseline was almost always within 1 deg of physical colinearity. (Data presented in experiment 4 show the variability of baseline settings between and within subjects.) After the baseline was established, adaptation was started by presenting the adapting stimulus for 3 sec between each trial. Two hundred msec after the adapting pattern was extinguished, test patterns were flashed for 50 msec. The adapting pattern reappeared as soon as the subject responded. Total trial length was about 4 sec. The hemifields in the adapting stimulus formed a 150 deg angle pointing to the right. Since the TAE develops at an initial rate greater than 0.5 deg per 4 sec, the staircase was started 4–6 deg from the baseline during adaptation. Starting position was based on previous studies in which the TAE was seen to rise to this level within the first 5 adapting trials.^{14,15}

Experiment 1

There were five conditions in experiment 1. Each observer was a subject for just one condition. The TAE was tracked during exposure to 10, 20, 40, 60, or 80 adapting trials, corresponding to 30, 60, 120, 180, or 240 sec of total exposure to the adapting stimulus. Following adaptation, 80 further trials were run without the adapting stimulus in order to track the decay of the TAE. Five subjects were tested in each condition.

Experiment 2

In experiment 2, adaptation was always for 240 sec (80 trials). No test trials followed the end of adaptation. Instead, subjects were asked to return at 1 hr, 2 hr, 1 day, 2 days, 1 wk, or 2 wk after adaptation. Each subject returned only once. When they returned, residual TAEs were measured by repeating the initial baseline measurement procedure and comparing the measure to the subject's initial baseline. The method is similar to that used by Jones and Holding¹⁶ to test long-term McCollough effects. They found that the McCollough effect lasted longer if the subject was not tested during the interval following adaptation and before the final test. All adapting and testing was done with the right eye. Five subjects were tested in each of the six conditions.

Experiment 3

Stimuli were identical to those in experiments 1 and 2. Subjects were adapted for either 90 or 240 sec. Following adaptation, 80 test trials were run (as in experiment 1). Residual, long-term TAEs were assessed by testing each subject four more times on 4 different days over the course of the next week. The final test was 7 days after the first. Due to difficulties with forgetful

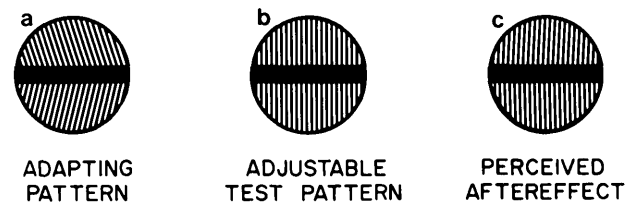


Fig. 1. The basic tilt aftereffect paradigm. Following exposure to 1a, a truly colinear pattern (1b) will appear to tilt in the opposite direction (1c).

subjects and intervening weekends, all subjects were not tested on the same days (eg, days 1, 3, 5, and 7).

In this experiment, the TAE was measured in each eye to assess the binocularity of any long-term, residual aftereffects. The right eye always viewed the adapting stimulus. Ten naive subjects were tested in the 90 and nine in the 240 second conditions. In each group, five subjects tracked the aftereffect in the right eye during the first session. The others tracked the effect in the left eye. The non-tracking eye was tested at the beginning, the middle, and the end of the first session. On subsequent days, the TAE was assessed in each eye. Order of testing was random across subjects.

Experiment 4

To measure the stability of baseline measures over time, experiment 4 was run as a control. Five naive subjects were tested in the same manner as those in experiment 3 but without any adaptation. They simply had their baselines measured five times over the course of 1 wk. All methods and stimuli were identical to those used in the previous experiments.

Results

Experiment 1

The average results for each duration of adaptation (30, 60, 120, 180, and 240 sec) are shown in Figure 2. Each data point is the average of five subjects. Within a condition, all subjects show similar results. Error bars are omitted to avoid clutter. Standard deviations of individual points average 0.7 deg. The vast majority lie between 0.4 and 1.0 deg. The range is 0.2 to 2 deg. To facilitate comparison with other TAE data, magnitudes are given as deviations of each half of the pattern from true vertical. Thus, a TAE of 3 deg means that a pattern with an obtuse angle of 174 deg looked colinear. In all cases, the TAE develops rapidly. Within five trials (15 sec of adaptation), the TAE is at more than 50% of its final strength. The decelerating functions resemble those obtained, for example, when measuring the bleaching of photopigment¹⁷ or that might be expected in any system where one is using

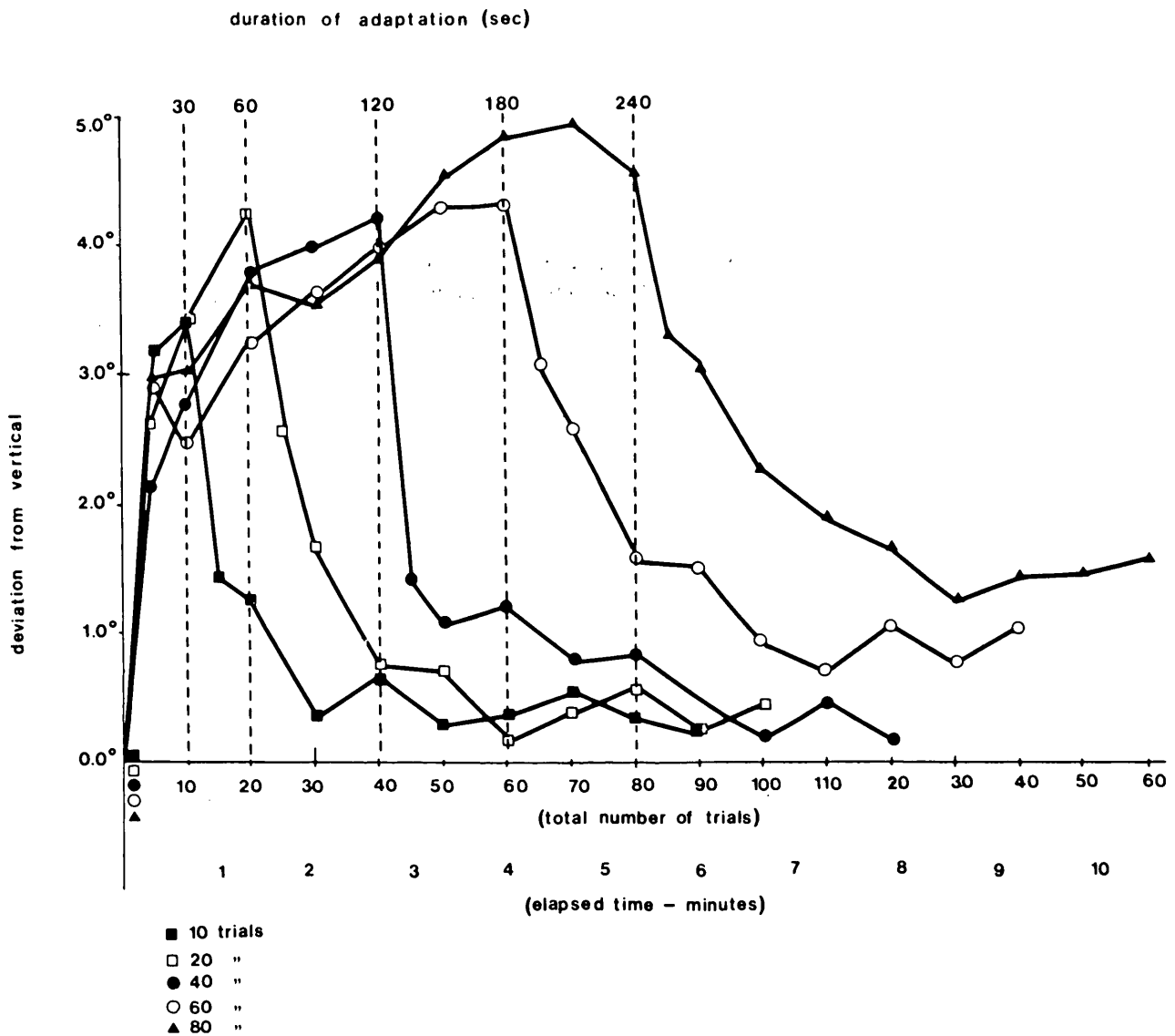


Fig. 2. Tilt aftereffect tracked over time. Five adaptation times are used ranging from ten adapting trials (30 sec total exposure) to 80 (4 min). Each vertical line marks end of adaptation for one condition. Adaptation rises very rapidly, then plateaus after 1-2 min. Decay is nearly total for adaptation times less than 3 min. For 3- and 4-min conditions, the TAE does not return to baseline. Each function is the average of five subjects.

up a fixed percentage of some limited resource as a function of time. Such functions are exponential with a negative exponent. After 60 sec of adaptation, TAE magnitude reaches a plateau with little further increase seen.

Looking at the decay of the aftereffect, it is clear that there is a qualitative difference between the results for 30, 60, or 120 sec of adaptation and those for 180 or 240 sec. Following 30, 60, or 120 seconds of adaptation, there may be some residual aftereffect after the 5-min test period, but it is small. The final position of the staircase is just statistically different from the baseline for 60 sec ($t = 3.1, P < 0.05$). There is no statistical difference between the initial baseline and the final position for 30 or 120 sec (30 sec $t = 0.9$; 120 sec t

$= 0.7$). The approximately exponential decay resembles that found in regeneration of some limited resource (again, compare this to photopigment regeneration).¹⁶ Following 180 or 240 sec of adaptation, the TAE declines exponentially but does not return to baseline levels. There is a statistically significant residual TAE that never disappeared in this experiment (180 sec $t = 4.3, P < 0.01$; 240 sec $t = 7.9, P < 0.005$).

Experiment 2

In experiment 2, the durability of the residual TAE was assessed by measuring perceived colinearity up to 2 wk after an initial 4-min adaptation period.

The differences between pre- and post-adaptation

baselines are shown in Table 1. The residual TAEs are, of course, smaller than the large initial TAEs measured in experiment 1. However, they are significant for all but the 1-hr condition. The failure to find a significant effect at 1 hr is the result of statistical noise introduced by a single subject who failed to show an aftereffect in the expected direction. With the exception of that subject, all subjects in all delay conditions show a residual TAE. The TAEs have a magnitude of about 0.5 deg, meaning that a pattern with an angle of 179 deg appeared to be colinear. Although it is probably the case that the TAE will eventually disappear, there is no measurable decrease during this 2-wk period. A regression produces a slope of 0.001. (There is no guarantee that the effect will vanish. Anecdotal reports by after-effect researchers, in particular those who study the McCollough effect, speak of effects that can last for years.) Caution must be used in interpreting the apparent lack of decay of the TAE. Since the step size in the staircase is 0.5 deg, it might be difficult to detect any change over the 2-wk period in a residual TAE that measures 0.5 deg.

Experiment 3

Experiments 1 and 2 leave several questions unanswered. (1) In preserving a long-term aftereffect, is it important, as Jones and Holding¹⁶ report, not to expose the subject to test stimuli prior to the final test? (2) Would the long-term TAE be seen following less initial adaptation? Results from experiment 1 suggest that little or no long-term effect should follow less than 180 sec of adaptation. (3) Does the long-term TAE show interocular transfer? That is, if the right eye is adapted, can the long-term TAE be measured when the left eye is tested? (4) Given the small size of the residual effect and the failure to reach statistical significance at 1 hr, are the results of experiment 2 a statistical fluke or can the long-term aftereffect be replicated?

Experiment 3 is a modified replication of experiment 2. Instead of a single test after adaptation, each subject was tested four times over the course of a week. After-effects were measured in each eye. Finally, one group adapted for a total of 240 sec (80 trials) as in experiment 2. A second group adapted for just 90 sec (30 trials). On the basis of the results of experiment 1, the shorter duration should produce little or no long-term TAE.

Average results are shown in Figure 3 for each eye in both 90- and 240-sec conditions. Error bars are plus and minus one standard error. Statistical significance is shown on the figure. TAEs are plotted for those days when seven or more subjects were tested. As noted above, each subject was tested four times after the initial setting. The third session was held on days 3, 4, 5, or

Table 1. TAE as a function of time after four minutes of adaptation

	Test condition					
	1 hr	2 hr	1 day	2 days	1 wk	2 wk
avg TAE	0.5 deg	0.6	0.7	0.5	0.7	0.6
s.d.	0.6 deg	0.5	0.2	0.2	0.3	0.6
t (df = 4)	1.46	2.22	6.60	6.26	5.16	2.30
P <	n.s.	0.05	0.01	0.01	0.01	0.05

Long-term TAE as a function of time since adaptation. Data are from 30 subjects (5 per condition).

6 for different subjects. The small number of subjects renders the average TAE less reliable for those days.

Several points can be made. For the 240-sec condition, significant TAEs are measured at 0, 1, 2, and 7 days for each eye. Interocular transfer of the long-term TAE seems to be about 100%. This is significantly higher than the 50–70% transfer of the short-term TAE measured with the same stimuli.¹⁸ The magnitude of the long-term TAE is comparable to that seen in experiment 2, suggesting that repeated testing does not weaken the long-term effect.

For the 90-sec condition, the TAE in the adapted right eye is statistically significant at the end of the first session. As was suggested by the marginal significance of the 60-sec TAE in experiment 1, adaptation of less than 180 sec may produce a weak TAE lasting beyond 5 min. The TAE is not statistically significant at either 1 or 2 days but regains a very marginal significance at

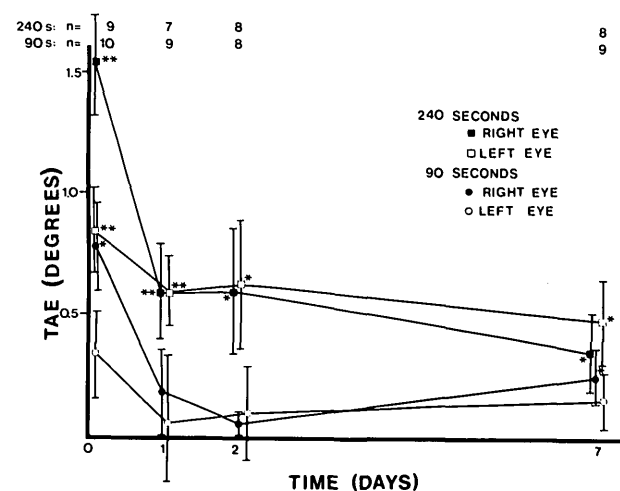


Fig. 3. Residual TAEs measured up to 1 week after the end of adaptation. Two hundred forty seconds of adaptation produces reliable long-term TAEs even with repeated tests. TAE magnitude is the same in the right (adapted) and left (unadapted) eyes. Ninety seconds of adaptation does not consistently produce reliable long-term effects in either eye. Error bars are 1 standard error. T-test significance values: “***” denotes $P < 0.01$, “**” denotes $P < 0.05$.

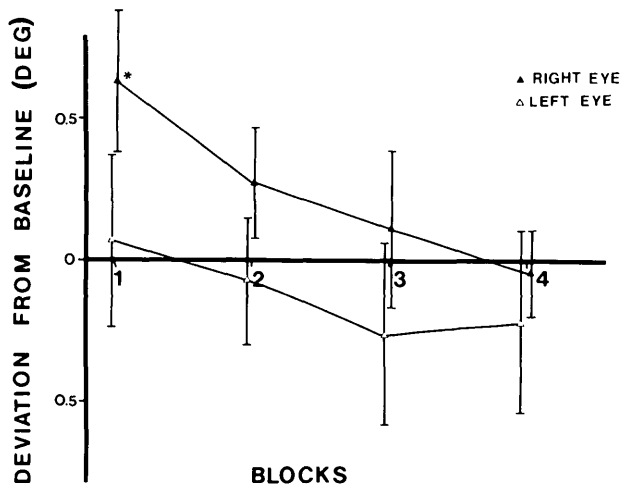


Fig. 4. Measures of apparent colinearity (baselines) show variability over time even when there is no adaptation. Error bars are one standard error. "*" denotes $P < 0.05$.

7 days. As in experiment 1, convincing demonstration of the reality of this long-term aftereffect would require many more subjects. The TAE was never statistically significant in the unadapted left eye.

Experiment 4

In order to determine the variability in baseline measures of apparent colinearity, baselines were taken five times over the course of a week without any adaptation for a group of five subjects. To make the data comparable to those in Figure 3, the results for the four sessions following the initial session are expressed as deviations from the baselines established in the first session. Average results are shown in Figure 4.

Error bars are plus and minus one standard error. As if to accent the fragility of the evidence for long-term TAEs after 60 or 90 sec of adaptation, there is a statistically significant deviation from the initial baseline for the right eye on the first day after the initial session. Obviously, this has nothing to do with adaptation as there was no adaptation. No other data points are statistically different from the initial baselines. The results of this control experiment give a feeling for the range of variability in subject's assessments of colinearity.

Discussion

Using aftereffects other than the TAE, long duration aftereffects have been previously reported.^{4,5} In this experiment, we can produce both a short and a long duration aftereffect in the same session with a single paradigm. The results show that it is highly unlikely that

long- and short-term TAEs are manifestations of a single type of fatigue. In these experiments, all durations of adaptation produce a large TAE very rapidly. When the adapting stimulus is removed, the large TAE dissipates very rapidly. The rapid rise and fall resemble the effects of light and dark adaptation and are of the general form that would be expected from fatigue resulting from the depletion and regeneration of a limited resource such as a neurotransmitter. Longer durations of adaptation produce a reliable long-term aftereffect. It is measurable 1 or 2 wk after the end of adaptation. The long-term TAE cannot be plausibly explained as the result of neural fatigue.

The two types of adaptation may occur at different points in visual processing. Identification of a stimulus can be broken down into two steps. Stimuli are detected by broadly tuned "channels."¹⁹ Stimuli are specifically identified when "labelled lines" find specific ratios between the outputs of the broadly tuned channels in an opponent process fashion. A highly speculative account of adaptation might say that the fast component of adaptation is due to fatigue of the broadly tuned channels. Perhaps repeated stimulation depletes a neurotransmitter rendering a neuron less active until the transmitter can be regenerated. The second, slower but long-term component of adaptation could be due to a change in the specific output patterns of labelled lines. Here, perhaps, more prolonged adaptation causes a strengthening of existing synapses or the creation of new ones. There is neuroanatomical evidence in favor of changes of this sort in response to visual stimulation.²⁰ This model would predict that there would be no long-term threshold elevation effects. This is supported by the observation that threshold elevation effects produced in a McCollough effect paradigm vanish long before the chromatic aftereffect.²¹ It suggests that threshold elevation aftereffects take place earlier in the visual pathways than suprathreshold effects, as reported by Parker.²²

Why would the system want to undergo this sort of structural change? The long-term aftereffects involve changes in the perception of properties such as vertical, straight, stationary, and white. Given a moving eye, a curved retina, the changing shape of the eye, and the changing status of the eye's optics, vertical, straight, stationary, and white are not given in the retinal image and must be computed. Those computations must change if any of factors governing the retinal image change. The visual system receives its information about those changes from visual input. Thus, adaptation to systematic changes in the retinal image grows out of the system's need for continuous recalibration.²³

Key words: vision, adaptation, plasticity

Acknowledgments

Thanks go to Dan Turner and Jeanny Liu for help in conducting the experiments, Julie Sandell and Mary Kelsey for drawing figures, and Andrew Parker and Olga Favreau for helpful comments.

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