
The role of intervening patterns in the storage of the movement aftereffect

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Abstract. Wohlgenuth, having measured the duration of the motion aftereffect (MAE), instructed subjects to close their eyes immediately after adaptation for a period of time longer than the MAE. Upon opening their eyes the subjects reported a residual effect, albeit somewhat shorter than the original effect. Thus the decay of the aftereffect appeared to have been retarded by the period of darkness. This effect is known as ‘storage’ and poses a problem for any model of the MAE based on the fatiguing of direction-selective units in the visual pathway. A reexamination is made of storage of the MAE, again concentrating on the intervening stimulation between movement adaptation and aftereffect test. The results suggest that the nature of the intervening pattern between adaptation and test conditions is remarkably unimportant. A total of 11 different storage patterns were examined after adaptation to high-contrast drifting horizontal sinewave gratings. For 10 of these patterns large and robust storage effects were found. The exception occurred when the spatial pattern of the storage stimulus was identical to the adaptation and test stimuli. It is proposed that storage cannot be understood in terms of a simple fatigue model of the MAE and that one component of the effect may share similarities with contingent aftereffects.

1 Introduction

Storage of the movement aftereffect (MAE) was first reported by Wohlgenuth (1911). In the first experiment in his remarkable monograph he first measured the duration of the MAE after an adaptation period of 30 s. He then instructed subjects to close their eyes, immediately after adaptation, for a period longer than the normal duration of the aftereffect. Upon opening their eyes the subjects reported a residual effect lasting approximately half the length of time of the original effect. Thus the decay of the effect appeared to have been retarded in some way by the period of darkness. This effect was studied further by Spigel (1960, 1962a, 1962b, 1964), who termed the phenomenon ‘storage’, and, though his studies did not constitute a set of thorough parametric measurements, he did demonstrate that darkness was not necessary to effect storage. Recently Verstraten et al (1993) have shown, in elegant experiments, that a textured and moving pattern shown between the adaptation and test phases can result in storage-like behaviour.

Thompson and Movshon (1978) determined that storage could also be exhibited in the contrast-threshold-elevation paradigm demonstrated by Blakemore and Campbell (1969). Similar results were reported by Heggelund and Hohmann (1976). In their paper, Thompson and Movshon refer to work on the storage of movement aftereffect by “Thompson (1976, in preparation)” (Thompson and Movshon, 1978, page 71). This paper represents an update on that work.

There are few convincing explanations of the MAE. The most widely accepted model appeals to the selective adaptation of direction-selective units that are grouped in pairs with opposite preferred directions of motion. This has become known as the ‘ratio model’, first described by Exner and later popularised by Sutherland (1961). Barlow and Hill (1963) provided physiological plausibility to the model when they demonstrated that direction-selective ganglion cells in the rabbit exhibited adaptation

after extended stimulation, which was manifest both by a reduction in firing rate over time in response to prolonged stimulation and by the abolition of all firing in the cells after the stimulation ceased. Adaptation effects of this sort have also been demonstrated in cat cortex by, amongst others, Maffei et al (1973), Vautin and Berkley (1977), Hammond et al (1985), Ohzawa et al (1982), and by Movshon and Lennie (1979) who reported adaptation effects both in simple and in complex cells of cat cortex, though not of the lateral geniculate nucleus. There can be little doubt that this physiological support for the plausibility of a fatigue model of the MAE has been influential.

However, there are strong reasons for questioning such a solution. Clearly, storage itself represents a challenge to the simple adaptation model of aftereffects. Adaptation seen simply as some form of fatigue would be expected to dissipate after the adaptation period in a manner largely independent of subsequent stimulation. But there have been other challenges to this model too, for example the McCollough effect (McCollough 1965) and other 'contingent' aftereffects can be elicited many months after one adaptation period (Jones and Holding 1976), and Chaudhuri (1990) has shown that the duration of the MAE can be significantly shortened if the subject must attend to a seemingly irrelevant discrimination task during adaptation. As a final example, consider the findings of Harris et al (1981) who demonstrated that the presence or absence of self motion influences the magnitude of the MAE—the laboratory confirmation of the well-known fact that we do not experience strong MAEs after driving a car.

One explanation of contingent aftereffects, that is somewhat different from the traditional fatigue theory, proposes that the contingent dimensions of the adaptation patterns are associated by 'simple' conditioning (Skowbo 1984). Thus, suppose we accept that there does exist a simple MAE that owes its existence to a fatigue-like adaptation, then we could regard this aftereffect as an unconditioned response to the adaptation movement in the same way that salivation is the unconditioned response to the presentation of food to a dog. We can also propose a contingent MAE as well—the conditioned stimulus in the MAE would be the spatial pattern of the moving stimulus. It could be argued that, in the adaptation phase of the MAE, an association is built up between the pattern of the adaptation stimulus and the direction of its motion in the same way that a bell may be paired with food by a dog. Eventually, just as the bell alone elicits the salivation in the dog, the adaptation pattern elicits the aftereffect. This association of pattern with aftereffect motion will persist until extinguished, ie the presentation of the adaptation pattern without the adaptation movement will elicit the aftereffect but the strength of the association will weaken over presentations. Storage now becomes less mysterious: testing the aftereffect with a stationary version of the adaptation pattern extinguishes the MAE but there is little reason why an intervening different pattern should affect the MAE.

Recently, Barlow (Barlow and Földiák 1989, Barlow 1990) has proposed that adaptation serves a real function in acquiring, storing, and accessing knowledge and is not just fatigue following stimulation. He draws an analogy between the adaptation that produces aftereffects and that which produces light adaptation. The latter is an example of an automatic gain-control system which changes the mean value of a single variable and allows ganglion cells to signal information effectively over an enormous dynamic range. The adaptation seen in aftereffects seems to modify the relationships between input variables (eg colour and orientation in the case of the McCollough effect). The crux of this approach is the insight which it yields, that a high correlation in the firing of two neurones is inefficient. Barlow proposes that two highly correlated neurones will benefit from a mutual repulsion such that if a stimulus excites one cell it will inhibit the other. Such a network may lack anatomical plausibility at present but it does focus the attention on the possibility of a functional role for aftereffects.

In view of the fact that we see that storage may have a useful role to play in determining a model of aftereffects that goes beyond simple fatigue, we have examined in some detail the conditions necessary for MAE storage.

2 Methods

In both the experiments reported here subjects adapted for 90 s to a pattern comprising two horizontal high contrast (0.80) sine-wave gratings—one to the left and one to the right of a fixation point (see figure 1a). The spatial frequency of all gratings reported in this study was $0.5 \text{ cycles deg}^{-1}$. The left grating moved upwards at a velocity of 1.0 deg s^{-1} while the right grating moved downwards at the same speed. At the end of the adaptation period either the gratings stopped moving and the aftereffect was observed—and measured by a method of cross-modal matching—or a storage stimulus was fixated for a period of time and then the residual aftereffect was observed and measured. In all cases the adaptation pattern was the same and all the MAEs were measured with a test pattern that was a stationary version of that adaptation pattern.

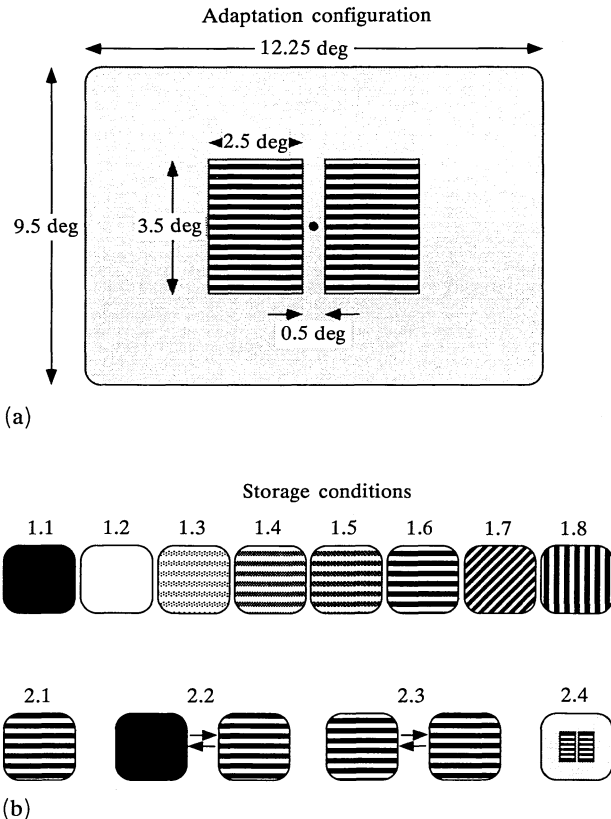


Figure 1. (a) The stimulus configuration. The adaptation pattern comprised two patches of grating, the left one moving upwards and the right one moving downwards at equal speeds. Subjects fixated throughout the experiment upon the point between the gratings. The remainder of the screen was maintained throughout at the mean luminance of 50 cd m^{-2} . The test pattern was a stationary version of the adaptation pattern. Although shown here as a square wave, the luminance profile of the gratings in these experiments was always sinusoidal. (b) The storage conditions. The storage patterns covered the whole screen except in the case of condition 2.4 which was precisely a copy of the test pattern. See text for a full description of the storage conditions.

For all subjects, the first condition to be completed was the baseline, which provided the duration of the MAE when tested immediately after adaptation. In experiment 1 there was a replication of this baseline determination at the end of the experiment. There was no significant difference between these baseline values and the replication was therefore omitted from experiment 2. Each condition was carried out on a different day, and the order of the storage conditions was randomised between subjects. The mean duration of each individual subject's MAE in the first baseline condition was used as the storage interval in the subsequent conditions, which all interposed some stimulus between the adaptation and test presentations.

The cross-modal matching was achieved by the subject being instructed to move a pen at the apparent rate of the now-upward motion of the right-hand adaptation grating. This pen, mounted on an $X-t$ chart recorder provided information about the velocity and duration of the MAE observed. Unfortunately, the velocity measures proved very unsatisfactory and are not reported upon further here.

3 Experiment 1

In experiment 1, eight naive subjects carried out 10 conditions: the 2 baseline and 8 storage conditions. Each condition was repeated three times, the mean figure of the three being reported here. These 8 storage conditions (see figure 1b for schematic representation) were:

Condition 1.1 A period of darkness, screen luminance 0 cd m^{-2} .

Condition 1.2 A period of unpatterned illumination, screen luminance 50 cd m^{-2} .

Condition 1.3 A stationary very low-contrast (0.07) horizontal sinusoidal grating identical in spatial frequency to the adaptation pattern. The grating filled the whole screen, an area of $12.25 \text{ deg} \times 9.5 \text{ deg}$.

Condition 1.4 As 1.3 above but of contrast 0.24.

Condition 1.5 As 1.3 above but of contrast 0.48.

Condition 1.6 As 1.3 above but of contrast 0.80.

Condition 1.7 A stationary high-contrast (0.80) grating oriented at 45° . Other details as 1.3 above.

Condition 1.8 A stationary high-contrast (0.80) vertical grating. Other details as 1.3 above.

In condition 1.1 the MAE was measured with the most commonly reported storage stimulus: a period of darkness. Condition 1.2 allowed us to determine whether darkness or merely the absence of contour is important to establish storage. In conditions 1.3–1.6 we investigated the effects of patterns of increasing contrast, whereas in conditions 1.7 and 1.8 we looked at the orientation specificity of the effect. For all conditions in which a pattern was present the mean luminance of the screen was 25 cd m^{-2} .

3.1 Results

The mean MAE durations in each condition are displayed in figure 2. The first baseline measures of the MAE were compared with those collected after the storage conditions; there was no significant difference in the durations of the MAE, suggesting that subjects were maintaining a consistent criterion in their judgments and that there was no appreciable buildup in adaptation throughout the course of the experiment. The mean of the first baseline durations was 13.2 s, the mean of the second baseline MAE durations was 12.2 s. These durations are not significantly different ($T = 17, p = 0.94$). The first measurements are used in all subsequent considerations.

The results demonstrate that the configuration of the pattern presented in the storage interval is remarkably unimportant. After a log transform to reduce skew in

the data, a within-subjects ANOVA showed no significant difference between any of the storage conditions ($F = 0.63$, $p = 0.73$).

One particular result here demands further comment: a storage field which is nearly identical to the test pattern (condition 1.6) is just as effective as is any other pattern in 'inhibiting' decay of the MAE. This suggests that either the MAE decays rapidly only if the test pattern is spatially exactly the same as the adaptation pattern, or that the structure of the storage pattern is unimportant but that the temporal transition from one pattern to another can rejuvenate the aftereffect. This was investigated in experiment 2.

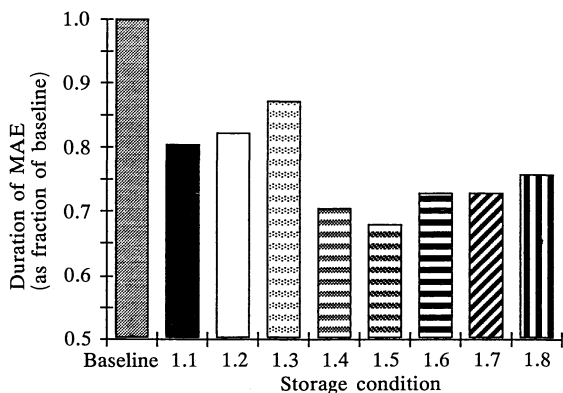


Figure 2. The results of experiment 1. The data, mean of eight subjects, for each storage condition, are plotted as a fraction of each subject's respective baseline measurement to reduce the effect of between-subject variance.

4 Experiment 2

Eight subjects undertook an experiment identical to experiment 1 except that different storage conditions were investigated (see figure 1b for schematic representation) and only one set of baseline measures was taken, before the subjects were exposed to storage conditions:

Condition 2.1 A stationary high-contrast horizontal grating identical in spatial frequency and contrast to the adaptation pattern. The grating filled the whole screen, an area of $12.25 \text{ deg} \times 9.5 \text{ deg}$ —a replication of storage condition 1.6 in experiment 1.

Condition 2.2 A pattern that alternated between a horizontal grating (condition 2.1 above) and darkness every 5 s.

Condition 2.3 A horizontal grating, as in 2.1 above, but counterphase modulated at $0.4 \text{ cycles s}^{-1}$.

Condition 2.4 The stationary adaptation pattern, with a 0.5 s period of darkness interposed between the adaptation and storage periods and between the storage and test periods.

Condition 2.1 provided a replication of the surprising result obtained in experiment 1 with condition 1.6. Condition 2.2 had a storage period during which two patterns, which had been found to be equally effective for storage in experiment 1, are alternated. This tested the possibility that transitions between stimuli might encourage dissipation of the aftereffect. Condition 2.3 provided a storage stimulus against which it is hard to perceive any MAE. This allowed us to investigate whether the phenomenal appearance of the aftereffect is necessary to dissipate the MAE. The use of conditions 2.2 and 2.3 was prompted by our observations that a fading MAE can be revived by an eye movement or blink. Condition 2.4 had, as its storage pattern, precisely the MAE test pattern. This should have ensured that we had a condition in which there was no storage.

4.1 Results

The mean MAE durations in each condition are displayed in figure 3, again as proportions of the baseline MAE measures. An ANOVA on the log-transformed storage durations proved significant ($F = 6.44$; $p = 0.003$) and submission of the data on Tukey's HSD revealed that conditions 2.1, 2.2, and 2.3 are not significantly different from one another but that each is different from condition 2.4 ($p < 0.05$; $p < 0.01$; $p < 0.05$, respectively).

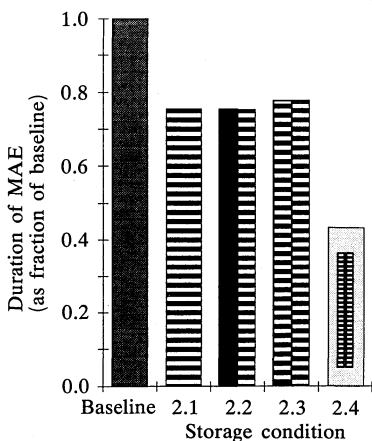


Figure 3. The results of experiment 2. The data, mean of eight subjects, for each storage condition, are plotted as a fraction of each subject's respective baseline measurement to reduce the effect of between-subject variance.

5 Discussion

The main finding of this study is that the nature of the intervening pattern (or lack of it) between adaptation and test conditions is remarkably unimportant. We have examined a total of 11 different storage patterns (8 in experiment 1 with 3 different ones in experiment 2); it would appear that storage is comparable with 10 of the 11 patterns.

The exception is condition 2.4 with which the MAE was reduced but still present after storage on the precise pattern to which the subject adapted. Thus it would appear that the aftereffect should not be regarded as having been fully dissipated simply because upon its first testing it has disappeared. It would appear that the initiation of another test trial will revive the effect. This shows a pattern which is familiar in the contingent-aftereffect literature. Mayhew and Anstis (1972) reported in their paper on contingent MAEs that at each transition between the test patterns the aftereffect motion became visible momentarily, but quickly disappeared until the next transition. They stated that this is a very different behaviour from 'the simple' aftereffect that "is always strongest immediately after adaptation and decays away monotonically never to return". The present results might call into question whether there are any such effects as 'simple aftereffects'. We would prefer to suggest that there may be 'simple' aftereffects but that they may be accompanied by contingent aftereffects rather more commonly than is usually supposed. This position is not very different from that proposed by Favreau (1976) and Cavanagh and Favreau (1980).

We are aware that Strelow and Day (1971) have reported some results that are similar in certain respects to ours. They adapted subjects to a moving grating that was surrounded by a stationary pattern. A subsequently shown test pattern (the stationary adaptation pattern) with no surround elicited a poor MAE but the reintroduction of the surround grating restored a vigorous aftereffect. Strelow and Day

interpreted these results as a demonstration of the importance of a patterned surround for the movement aftereffect. Further, they suggested that the reason storage occurs is because the MAE is inhibited by the storage pattern.

Strelow and Day's results, if not their interpretation of them, fit well with ours. We adapted subjects simultaneously to opposite directions of movement so that each grating in our display acted as a surround for the other. The storage which Strelow and Day found when their test pattern was not quite identical to the adaptation pattern (the surround was missing) is similar to that which we found in our conditions 1.6 and 2.1. Indeed, these conditions provided a control condition that perhaps Strelow and Day themselves should have included. We could argue that it is not the presence or absence of a surround that is important, but merely whether the test patterns differ from the adaptation patterns.

We believe that we now have to regard MAE duration in a somewhat different light. To illustrate this, consider the ingenious experiment on MAE storage reported by Wiesenfelder and Blake (1992). They demonstrated the standard storage phenomenon with a dark period interposed between adaptation to a moving grating (presented to one eye alone) and the test with the stationary adaptation pattern (presented to the same eye). Next they showed that storage was also achieved if the stationary adaptation pattern was presented to the adapted eye but was not seen because of a strongly rivalrous and salient pattern (randomly moving high-contrast dots) presented to the other eye. The authors claim that this storage indicates that test patterns must be experienced phenomenally in order to expedite the decay of the effect and that this is a very different result from that reported by Lehmkuhle and Fox (1975), who found that adaptation to movement which was not experienced, because of the presence of a strongly rivalrous stimulus, did not prevent a subsequent aftereffect. Unfortunately, these results, taken by Wiesenfelder and Blake as evidence of at least two sites for the MAE, must be cast into doubt by the results obtained with our storage condition 2.4: it would appear that even if the grating in their experiment were not suppressed by rivalry, subjects would still experience 'storage'. Just because the test pattern has stopped moving we should not assume that the aftereffect has been fully dissipated.

6 Conclusion

For many years it has been convenient and respectable to regard the MAE as the reflection of some adaptation-induced imbalance in the activity of direction-selective neurones. The existence of neurones within the cortex of several species (most notably cat) that show precisely the type of adaptation required by this model strengthens its plausibility. However, we believe that this cannot be the whole story. Several aspects of the MAE do not sit comfortably with the notion that low-level adaptation alone is responsible. We have shown, in this paper, that storage is the rule rather than the exception and that we may have to regard even the simplest movement adaptation as promoting both simple and contingent aftereffects—the latter being capable of being elicited time and time again.

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