



## Research Note

# Recovery from Adaptation for Dynamic and Static Motion Aftereffects: Evidence for Two Mechanisms

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Received 14 April 1994; revised 14 November 1994; in final form 31 March 1995

**The motion aftereffect (MAE) is an illusory drift of a physically stationary pattern induced by prolonged viewing of a moving pattern. Depending on the nature of the test pattern the MAE can be phenomenally different. This difference in appearance has led to the suggestion that different underlying mechanisms may be responsible and several reports show that this might be the case. Here, we tested whether differences in MAE duration obtained with stationary test patterns and dynamic test patterns can be explained by a single underlying mechanism. We find the results support the existence of (at least) two mechanisms. The two mechanisms show different characteristics: the static MAE (i.e. the MAE tested with a static test pattern) is almost completely stored when the static test is preceded by a dynamic test; in contradistinction, the dynamic MAE is not stored when dynamic testing is preceded by a static test pattern.**

Motion aftereffects   Adaptation   Static visual noise   Dynamic visual noise   Storage

### INTRODUCTION

Prolonged viewing of a pattern moving in a certain direction results in an illusory drift of subsequently viewed stationary elements. This phenomenon is known as the motion aftereffect (MAE) and is normally directed opposite to the adapting pattern direction [e.g. Wade (1994), for an overview]. It is generally assumed that this illusion is a result of adaptation of motion-sensitive components of the visual system. Although some proposals have been made about the possible function of MAEs (e.g. Harris, Morgan & Still, 1981; Wiesenfelder & Blake, 1992; Verstraten, Fredericksen, Grüsser & van de Grind, 1994a) they are mostly used as a tool to explore the organization of the visual system.

Much of the current interest in MAEs is concerned with the nature of the test pattern because it is generally thought to reveal different sites of adaptation along the path of visual motion processing. Due to the limitations of stimulus-presentation technology, "classic" MAE adapting stimuli were presented mechanically (e.g. a

rotating spiral or some periodic pattern on a conveyer belt). The test stimuli were produced using the same patterns presented statically. With the introduction of computers the CRT-display became a popular stimulus presentation device, enabling the use of test stimuli that can differ drastically from the adaptation stimuli. For example *dynamic* test stimuli became much easier to generate. Some examples of dynamic test stimuli are randomly moving dots (e.g. Blake & Hiris, 1993), dynamic random pixel arrays (RPAs) which are random dot patterns with maximal dot density where all pixels are refreshed in a spatially random fashion (this study), uniform patternless sinusoidal flicker (Green, Chilcoat & Stromeyer, 1983) or counterphasing luminance gratings (e.g. Nishida, Ashida & Sato, 1994).

There can be differences between MAEs obtained with dynamic test patterns (dMAEs) and static test patterns (sMAEs). For example, the MAE tested with dynamic visual noise can hardly be distinguished from real motion, whereas an sMAE is immediately recognized as such and never looks like real physical motion (Hiris & Blake, 1992). Evidence is accumulating that static and dynamic MAEs are mediated by different mechanisms (Hiris & Blake, 1992; Raymond, 1993; Nishida *et al.*, 1994; Ashida & Osaka, 1994; Culham & Cavanagh, 1994; Verstraten, van Wezel, Fredericksen & van de Grind, 1994b; Nishida & Sato, 1995). In this study our aim is to further investigate the differences between MAEs obtained with dMAEs and those obtained

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with sMAEs. Static and dynamic random pixel arrays (RPAs) are used and we follow the terminology that is also used by Hiris and Blake (1992): namely dynamic visual noise (DVN) and static visual noise (SVN). The MAE characteristic of interest in this study is the MAE duration.

There are a few previous reports suggesting that the MAE duration is different for dynamic and static test conditions. For example, Green *et al.* (1983), using a patternless flicker test mentioned that the "classic" MAE (i.e. sMAE) lasted longer than the MAE obtained with a dynamic test. In previous experiments we confirmed that a dMAE is shorter in duration than a sMAE, even though a dMAE is perceptually more salient (Verstraten, 1994).

The question addressed here is whether differences in MAE duration need to be explained by a two-mechanism theory or if a one-mechanism explanation is sufficient. The reasoning is as follows: assume that the MAE comes from the same site of adaptation and that the duration of the MAE reflects part of the process of recovery from adaptation. The MAE is still visible if the signal that gives rise to the perceptual appearance of the aftereffect is above a certain noise level. It is reasonable to assume that dynamic noise patterns increase this internal noise level. If one thinks in terms of bi-local motion detectors, receptive fields will be stimulated in a random sequence and detectors tuned to all directions and all displacement sizes will raise their activity (van Doorn, Koenderink & van de Grind, 1985). Because of this random stimulation no global motion direction is perceived but the noise level in the system will increase. As a result, the signal responsible for the MAE reaches a point where it sinks away in the noise faster than in the case when the test pattern consists of SVN. Note that the decrease in MAE duration is not because the process of recovery is faster but because the noise level is higher.

A testable prediction can be made if the underlying MAE comes from a single mechanism: when a DVN test pattern is presented after adaptation and replaced with a SVN pattern as soon as the MAE is no longer perceived, the MAE should reappear because the source of the externally induced noise in the system is taken away. If the single mechanism model holds, the total MAE duration (dMAE + sMAE) should be as long as the MAE duration when tested exclusively with a SVN pattern.

The results indicate that a single-mechanism explanation cannot account for differences between sMAEs and dMAEs. It is found that a sMAE is *stored* [which means that the process of recovery from adaptation is either delayed or started later (e.g. Spigel, 1960; Wiesenfelder & Blake, 1992)] when an SVN test pattern is preceded by a DVN test pattern. Dynamic MAEs, on the other hand, do not show *storage*-effects, since a dMAE is lost if a DVN is preceded by SVN, in which case the underlying system seems to recover from adaptation regardless of what is present in the visual field. As a consequence (at least) two mechanisms are required to explain the results.

## METHODS

The adaptation stimulus was a moving random pixel array (RPA; pixel density 50% black and 50% white). This RPA was generated by a specially designed noise generator controlled by a Macintosh [for a more detailed description see Fredericksen, Verstraten and van de Grind (1993)]. It was presented on a CRT-display with a P4-phosphor (ElectroHome model EVM-1200). The refresh rate of the display was 90 Hz. The display contained  $256 \times 256$  pixels and was 14 cm square (1 pixel  $\approx 0.55$  mm). The viewing distance was 2 m. The display area subtended 4 deg arc. Each pixel subtended an angle of 0.94 min arc. Mean luminance of the CRT-display was  $50 \text{ cd m}^{-2}$  and the contrast was set at 70%.

Three subjects participated (FV, MS and RW). Subject MS was naive as to the hypothesis of the experiment. All had normal or corrected to normal vision. A chin-rest and forehead support were used. A black fixation dot was present in the centre of the display area. The experiments were performed in a dark room with ambient lighting provided by the display screen.

The adapting pattern was either moving horizontally to the right or left. The velocity of the adapting pattern was  $2.8 \text{ deg sec}^{-1}$  (step size 2 pixels every frame). The inducing directions were alternated between trials. After adaptation the subjects were presented with either SVN or DVN. The SVN test pattern was a  $256 \times 256$  RPA with randomly placed black and white dots which held their position during the whole test phase. DVN were generated by refreshing all pixels in a spatially random fashion every  $n$ th frame (temporal frequency = refresh rate of the display/ $n$ ). The noise patterns had a temporal refresh frequency of either 10, 30 or 90 Hz.

As soon as the subject indicated (by pressing a key) that the MAE was no longer visible, the pattern was replaced by either DVN or SVN (see Fig. 1) depending on the nature of the pattern that was shown first. Again the subject had to indicate when the MAE had stopped (if present). Both durations were recorded automatically by the computer. If no MAE was perceived a "zero" button was to be pushed.

## RESULTS

In Fig. 2 the results are shown for all subjects. The left panel for each subject shows the results for test condition A (see Fig. 1; dynamic testing followed by static testing) and the right panel for test condition B. The three pairs of bars show the dMAE duration (shaded bar) and the sMAE duration (open bars). The left bar of each pair represents the test pattern that was presented first after adaptation (DVN—left panel or SVN—right panel).

It follows from the figure that the total MAE duration (dMAE + residual sMAE) in the DVN–SVN test condition is significantly longer than is expected from a single-mechanism explanation. More importantly, the sMAE is almost completely stored while the DVN test pattern is present. In other words, the sMAE duration

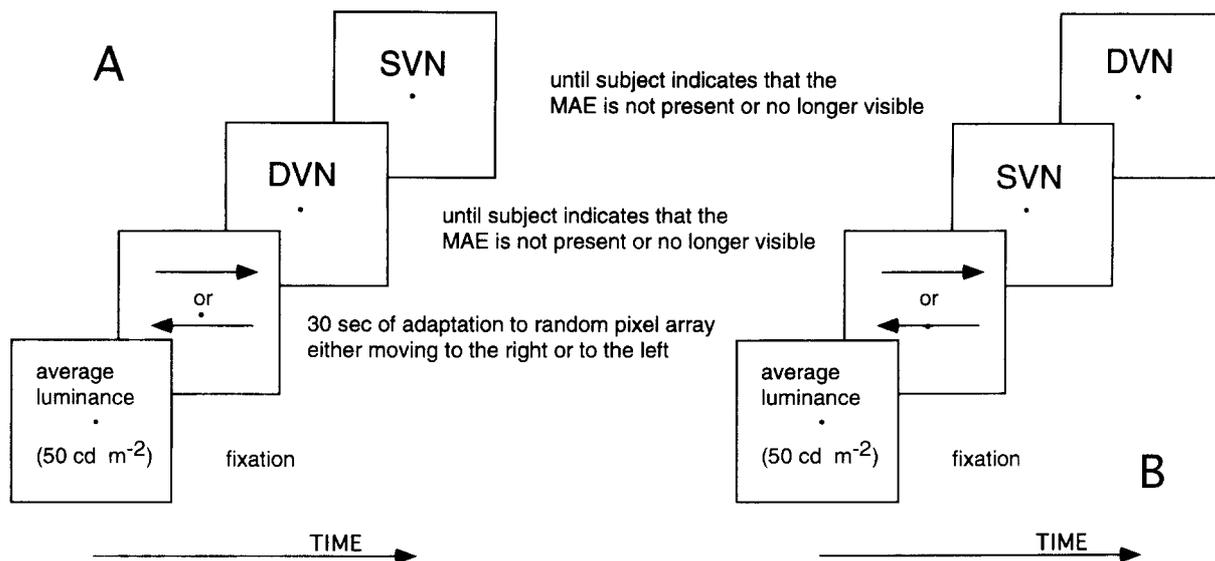


FIGURE 1. The temporal sequence of events on a trial. (A) Adaptation followed by dynamic visual noise. As soon as the subject indicates that the dMAE is not visible anymore the DVN is replaced by a static pattern and the remaining sMAE duration is recorded. (B) The alternate test patterns sequence.

does not recover from adaptation while a DVN pattern is presented to the visual system. As a result of the storage a single mechanism explanation cannot be defended. For test condition B the dMAE is significantly shorter if at all present. This indicates, in contradistinction to the sMAE, that the dMAE is not stored, at least not to any appreciable extent (subject FV). Statistically significant differences (averages of each condition compared with the average sMAE) are shown by asterisks (*t*-tests, two-tailed at the 0.05 level of significance).

## DISCUSSION

In this study we tested the idea that a single-mechanism model can account for differences in the MAE duration for sMAEs and dMAEs. The fact that the sMAEs are all almost completely stored if a DVN test pattern precedes the SVN test pattern indicates that the explanation in terms of a single underlying mechanism does not hold. This makes it tempting to suggest that we are dealing with (at least) two mechanisms and (at least) two gain controls at different loci.

This result is in line with the idea that the human visual system has several sites for MAE generation. von Grünau and Dubé (1993) showed that selective adaptation to gratings that either combined to a coherent plaid or slid transparently interfered with the subsequent perception of ambiguous plaids. For example, adaptation to a coherent plaid favours a transparent sliding interpretation of an subsequently presented ambiguous plaid. This indicates that the percept is mediated by different underlying mechanisms that can be adapted independently. In other work, Nishida and Sato (1995) had their subjects adapt to a stimulus with both first- and second-order structures. These structures were present simultaneously and moving in opposite directions. When tested with a static grating the MAE was directed opposite

to the first-order motion. On the other hand, if the test consisted of a counterphase grating (flicker) the MAE was directed opposite to the second-order motion direction. Their conclusion is that the static MAE shows the adaptation of a low-level motion-mechanism responsible for the processing of first-order motion and the flicker MAE reflects a motion processing at a higher level.

Other evidence for different underlying sites comes from interocular transfer (IOT) studies [adaptation in one eye and testing in the non-adapted eye; see Blake, Overton and Lema-Stern (1981) for the logic of the IOT procedure]. With a SVN test pattern the MAE only transfers partly (e.g. Wade, Swanston & de Weert, 1993). However, with dynamic stimuli an almost complete IOT is found. This is true for DVN (Raymond, 1993) as well as for a counterphase luminance grating (Nishida *et al.*, 1994). It should be noted that for dynamic stimuli differences in IOT are found. Blake and Hiris (1993) reported a partial IOT (79%) and Green *et al.* (1983) found no IOT at all using a patternless flicker test. Using the IOT paradigm and stimuli that are assumed to activate higher visual areas (e.g. expansion, rotation) Steiner, Blake and Rose (1994) showed that there must be different sites of adaptation as well.

As stated above, it has been suggested that dynamic test stimuli show higher stages of motion processing and static test stimuli have their origin at lower levels (Nishida & Sato, 1995). We think that the evidence is compelling, but that the issue is not solved yet. The alternative hypothesis, that dMAEs for DVN (as we have used) stem from front-end mechanisms, can also be defended. The sampling of motion information at the detector level is extremely fine. This implies that front-end mechanisms can be stimulated by DVN. At a higher level along the motion pathway, coarser sampling or integration takes place and since there is no coherent motion in DVN these levels may not be activated. Our results would then suggest that active front-end mechanisms prevent the

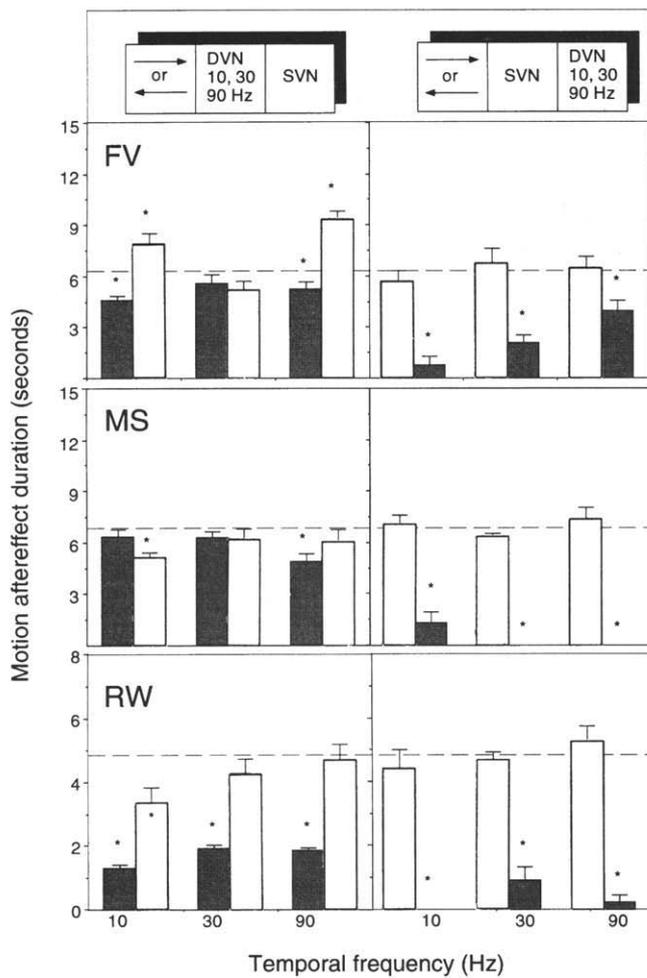


FIGURE 2. Results for all subjects. In the left panel the results are presented for the condition in which the DVN test pattern precedes the SVN test pattern (see inset above the left panel). The right panel shows the results for the reversed testing sequence. dMAE duration is represented by the shaded bars and sMAE duration by the open bars. Results are shown as a function of temporal frequency of the DVN test. The dashed line indicates the average sMAE duration recorded directly after adaptation. Statistically significant differences (compared with the average sMAE) are shown by asterisks. See the text for a discussion of the results.

recovery from adaptation of sMAE that may originate at a higher level with lower spatial and temporal resolution.

The extreme differences resulting from various dynamic stimuli in IOT studies (Nishida *et al.*, 1994; Raymond, 1993 vs Green *et al.*, 1983) suggest that there is insufficient evidence to defend a rigid dichotomy between the mechanisms responsible for dMAEs and sMAEs. Moreover, the direction of the MAE of bi-vectorial transparent motion (see Verstraten, Fredericksen & van de Grind, 1994c) can be changed drastically if the temporal frequency of the DVN test pattern is varied (Verstraten *et al.*, 1994b).

As has been suggested before, in the end there might turn out to be several sites of adaptation along the path of visual motion processing (e.g. Anstis, 1986; Wade, 1994). Which of these sites contribute to the MAE as a perceptual manifestation depends on the test stimulus. Therefore a deeper investigation into the nature of the test stimulus is required. Clearly a distinction between static and dynamic tests will not suffice.

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*Acknowledgements*—Supported by a NWO/NATO-Science fellowship and the Niels Stensen Foundation. We thank Michael Morgan, Maarten van der Smagt, Peter Bex, David Keeble and Jody Culham for constructive comments.