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Integration after adaptation to transparent motion: static and dynamic test patterns result in different aftereffect directions

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Abstract

One of the many interesting questions in motion aftereffect (MAE) research is concerned with the location(s) along the pathway of visual processing at which certain perceptual manifestations of this illusory motion originate. One such manifestation is the unidirectionality of the MAE after adaptation to moving plaids or transparent motion. This unidirectionality has led to the suggestion that the origin of this MAE might be a single source (gain control) located at, or beyond areas that are believed to be responsible for the integration of motion signals. In this report we present evidence against this suggestion using a simple experiment. For the same adaptation pattern, which consisted of two orthogonally moving transparent patterns with different speeds, we show that the direction of the resulting unidirectional MAE depends on the nature of the test stimulus. We used two kinds of test patterns: static and dynamic. For exactly the same adaptation conditions, the difference in MAE direction between testing with static and dynamic patterns can be as large as 50°. This finding suggests that this MAE is not just a perceptual manifestation of a passive recovery of adapted motion sensors but an active integrative process using the output of different gain controls. A process which takes place after adaptation. These findings are in line with the idea that there are several sites of adaptation along the pathway of visual motion processing and that the nature of the test pattern determines the fate of our perceptual experience of the MAE.

Keywords: Aftereffect; Adaptation; Transparent motion; Motion; Illusion

1. Introduction

In the year 1887, Exner, and somewhat later, Borschke and Hescheles (1902), reported that the perceived direction of a horizontal and a vertical grating, moving superimposed and linearly behind a circular aperture, is in between the two physical directions of the moving patterns. In essence, this was an early version of the well known plaid stimulus of Adelson and Movshon (1982).

Both Exner (1887), and Borschke and Hescheles (1902) also looked at the motion aftereffect (MAE) of their stimuli. The MAE, also known as the 'waterfall illusion' (Thompson, 1880), does not require an elaborate introduction. It has a history that goes back at least as far as the time of Aristotle (Wade & Verstraten, 1998; Verstraten, 1996). The phenomenon refers to an illusory movement of a stationary scene that follows prolonged observation of a moving pattern. The direction of this aftereffect is generally opposite to the adaptation direction. Exner (1887) reported that after adaptation to two superimposed gratings, the MAE appears to move opposite to the previously *perceived* direction.

It is believed that area MT/V5 is involved in the perceptual coherence of superimposed patterns like those mentioned above (Stoner & Albright, 1994). It has therefore been suggested that the MAE of these kind of patterns arises from that level as well (e.g Wenderoth, Bray & Johnstone, 1988; see also Alais, van der Smagt, Verstraten & van de Grind, 1996).

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Similar ideas have been suggested for the MAE of a related but different stimulus, the so-called transparent motion of random dots. For a transparent motion stimulus multiple random dot patterns are presented in the same part of the visual field, moving in different directions and/or at different speeds. Although there is generally no perceptual coherence for these patterns during adaptation—the direction of the individual patterns is clearly perceived—the MAE has only one direction. The MAE direction of two equal speed patterns moving in, say, orthogonal directions is the opposite to the vector sum of the two velocities (Verstraten, Fredericksen & van der Grind, 1994). Verstraten et al. suggested that the adaptation that gives rise to the MAE takes place at a level at or beyond that of motion integration (see also von Grünau & Dubé, 1992).

It is generally acknowledged that gain controls that are responsible for MAEs can be found at different sites along the pathway of visual motion processing, depending on adaptation and test conditions (Anstis, 1986). However, it is still a matter of debate whether a *single* mechanism is responsible for the MAE of transparent motion. For their orthogonal transparent motion stimulus, where both patterns had different speeds, Verstraten et al. (1994) argued that the absence of a change in direction of the MAE during the recovery from adaptation process was strong evidence for a single gain control explanation. If the MAE of transparent motion consisting of two *different* speeds is a product of adaptation of individual direction specific channels (that is, two sources or gain controls), the MAE should change its direction during the time the channels recover from adaptation. The idea being that for two adaptation patterns with different speeds and sensitivities, the MAE direction should always end up opposite to the direction of the most sensitive pattern, simply because it has the longest MAE-duration (see also Verstraten, 1994).

On the other hand, it appears that a bi-directional MAE can be observed after adaptation to oppositely directed transparent motion, which seems to indicate the presence of two gain controls (Grunewald & Lankheet, 1997). The MAE-direction, however, is orthogonal to the adaptation directions and only occurs under specific adaptation and test conditions. Their psychophysical result was obtained with a dynamic test pattern.

It is now known that the type of test pattern is important for several MAE-characteristics. Some dramatic differences between MAEs obtained with static test patterns and dynamic test patterns have been obtained (von Grünau, 1986; Green, Chilcoat & Stromeyer, 1983; Hiris & Blake, 1992; Raymond, 1993; Culham & Cavanagh, 1994; Ledgeway, 1994; Nishida, Ashida & Sato, 1994; Nishida & Sato, 1995; Verstraten, Fredericksen, van Wezel, Lankheet & van de Grind, 1996).

Since there are many reports on MAEs behaving differently under dynamic test conditions we became interested in whether the MAE of transparent motion is also affected by the nature of the test pattern. In Verstraten et al. (1994) static test pattern was used. If the idea that the MAE stems from a single gain control were correct, there is no reason to expect any difference between the MAE tested with a dynamic or a static test pattern, at least as far as the direction of the MAE is concerned. However, the result turned out to be quite different. The MAE direction differences were very large with a clear dependence on the type of test pattern.

2. The experiment

2.1. Methods

2.1.1. Stimulus generation

A random-pixel array was generated by a specially designed hardware noise pattern generator controlled by a Macintosh computer. Patterns were presented on a CRT display (ElectroHome model EM-1200, P4 phosphor) at a display rate of 90 Hz (for a more detailed description, see Fredericksen, Verstraten & van de Grind, 1993).

2.1.2. Procedure

Observers adapted for 45 s to two simultaneously presented random pixel arrays (RPAs) moving transparently in orthogonal directions (Fig. 1). The speeds of the inducing patterns V_1 and V_2 were 8 deg s^{-1} (2 pixels displaced every frame) and 2 deg s^{-1} (1 pixel displaced every two frames). These speeds were randomly assigned to the inducing patterns, which means that the possible combinations for V_1–V_2 were 2 and 8 deg s^{-1}, respectively, 8 and 2 deg s^{-1}. After adaptation, a test pattern was shown for 2 s[2]. This test pattern could either be static visual noise (SVN, a stationary 256*256 RPA) or dynamic visual noise (DVN). In the case DVN was presented, its cut off temporal frequency was 90 Hz (which means that all the pixels are refreshed every 11 ms). After the test pattern was shown, a horizontal black line of one pixel width was presented on an always static RPA. The observers were asked to adjust the orientation of the line such that it was parallel to the direction of the MAE as they experienced it immediately after the test pattern was pre-

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[2] A length of 2 s might seem long, but it is about the time an average observer needs to get an indication in which direction the MAE is drifting. Especially static MAEs take some time to show up. Dynamic MAEs on the other hand are almost immediately present. This is an interesting observation as such but discussion goes beyond the scope of this research note.

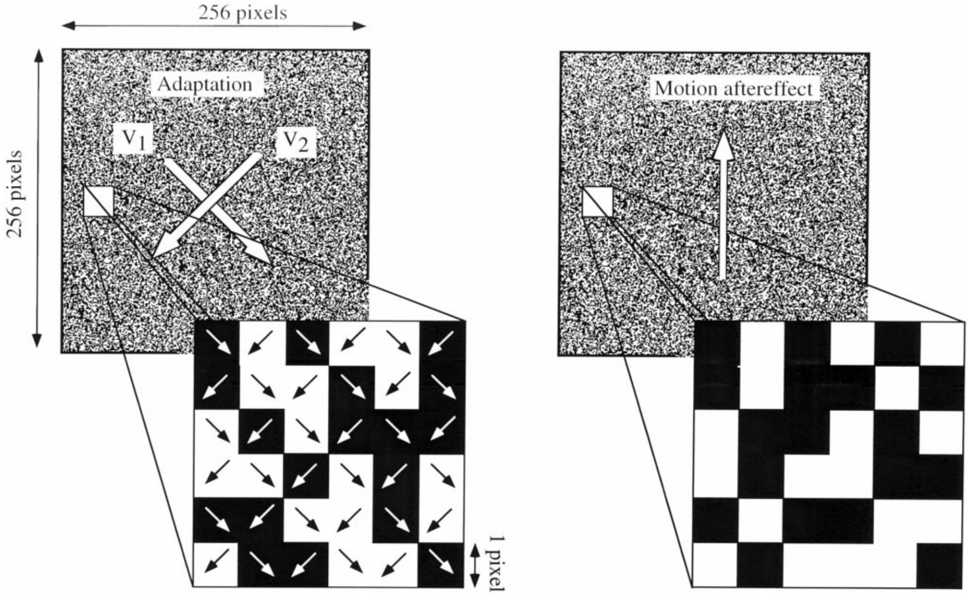

Fig. 1. Transparent motion for equal speeds is illustrated on the left and its MAE (the opposite of the vector sum of the inducing patterns) on the right side of the figure. In the experiment in this paper we used the same adapting directions but unequal speeds (2 and 8 deg s^{-1}) and the MAE direction was measured for two different test patterns: a static pattern as represented on the right side of the figure, and a dynamic pattern where all pixels were refreshed every frame at 90 Hz. The inset in the left figure shows the way we generate transparent motion: a checkerboard pattern of contiguous windows (1*1 pixels).

sented. If no MAE was experienced the observers were asked not to adjust the line or bring it back to the initial horizontal position. The direction was automatically registered by the computer. After the observer indicated the direction a 45-s pause was given. The static and the dynamic test conditions were presented in a random order. The experiment was carried out at 1 m viewing distance, resulting in a display area of 8 deg of arc, in a room with dimmed lighting conditions. Viewing was binocular and a fixation dot was present in the center of the display. A chin rest and forehead support was provided. The four conditions—$V_1 = 2$ deg s^{-1} and $V_2 = 8$ deg s^{-1} or vice versa, tested with either SVN or DVN—were presented three times each.

2.1.3. Observers

Initially, seven observers participated in the experiment. All were naive as to the purpose of this study, two observers were experienced psychophysical observers (ML and MS). The others were one graduate and four undergraduate students in the Biology department of Utrecht University and had no or little experience with psychophysical experiments and none with MAE experiments. One observer was not able to see MAE directions in a consistent way (if at all) and her data were discarded.

3. Results

The results for each observer individually are displayed in Fig. 2a and the average over all observers in Fig. 2b. Since our only interest was the MAE direction, we collapsed the data for the two conditions (V_1 and $V_2 = 8$ and 2 deg s^{-1} vs 2 and 8 deg s^{-1}) and treated the data as the 2 and 8 condition (see inset of Fig. 2b). This implies that the MAE direction of the 8 and 2 adaptation condition had to be mirrored about the y-axis. We statistically tested whether there was an effect of the adaptation direction for each combination of speeds for each observer. Using a t-test, this was found not to be significant for $p = 0.05$.

Our basic finding is that the direction of the MAE differs drastically depending on the type of test stimulus. As is shown in Fig. 2a and Fig. 2b, a static MAE tends to move vertically and for some observers even anticlockwise from the vertical (average over all observers is 97.7°, see Fig. 2b). For dynamic test stimuli the MAE is much more oblique (average over all observers = 47.5°, see Fig. 2b) which means that the faster pattern contributed much more to the MAE. The difference between MAE directions obtained with a static and a dynamic test was statistically significant for all our observers individually, as revealed by a t-test where $p < 0.005$ or smaller). The finding that the MAE direction for dynamic testing is almost opposite to direction of the fast pattern seems to imply that there is nearly no influence of the other pattern. Note that the MAE direction concerns an average value, though we can only speculate on the question of why some observers also tend to see the MAE direction more horizontal than 45° once in a while (the result of integration should fall between 45° and 135°).

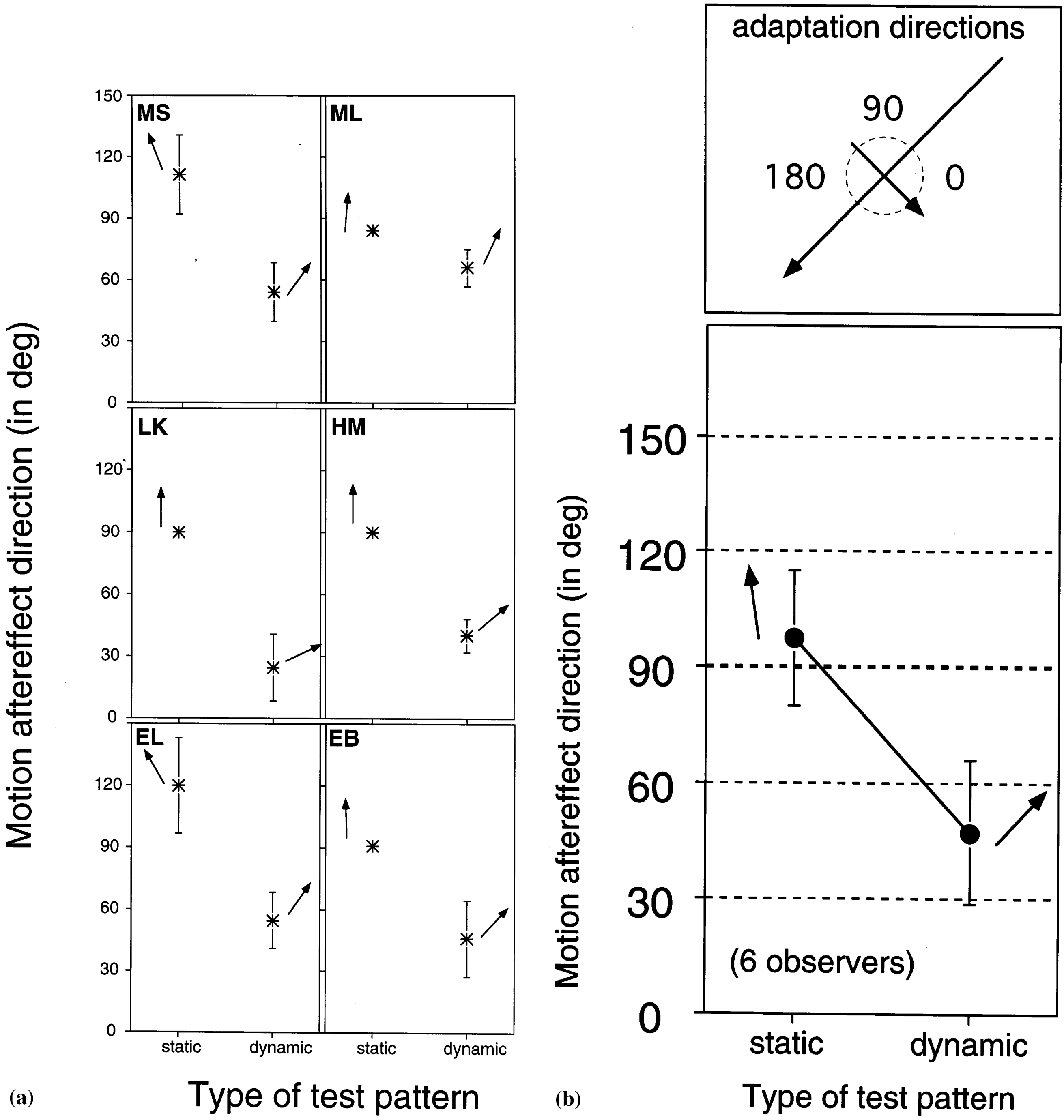

Fig. 2. (a) Results for six observers. Perceived direction is shown on the ordinate and the type of the test pattern on the abscissa. In general, for a static test pattern the MAE is more in the direction of the slower speed (2 deg s^{-1}) and for the dynamic pattern the direction is mostly determined by the fastest speed (8 deg s^{-1}). The arrows indicate the average perceived direction for each observer. Vertical bars represent ± S.D. (b) Results averaged over six observers. Perceived direction is shown on the ordinate and the nature of the test pattern on the abscissa. The average direction of the static MAE is in a different quadrant than the direction of the dynamic MAE. The average difference is about 50 degrees (97.7 vs 47.5°). The inset on top of the figure shows an iconic representation of the adaptation vectors (2 and 8 deg s^{-1}).

Some observers reported that the MAE, as perceived with a dynamic test pattern, shows up very fast, faster than the static MAE. But, in contradistinction to the static MAE, the dynamic MAE seems to change its direction towards the vertical as time progresses.

In retrospect, it would have been better to use a non-textured average luminance pattern while setting the MAE direction. As a control we repeated several points for comparison on an average luminance non-textured display for one expert and two naive observ-

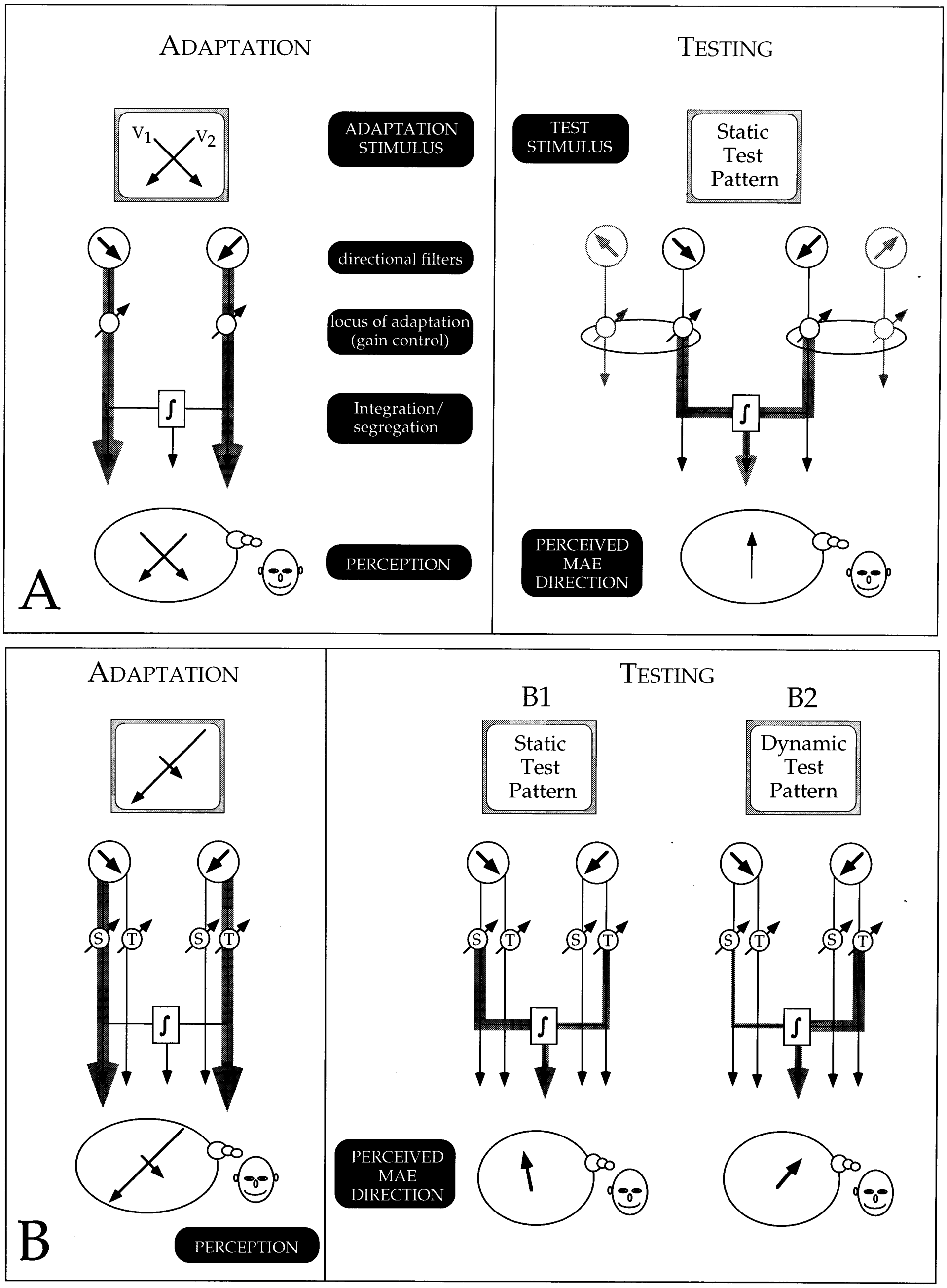

Fig. 3. (A) The MAE of transparent motion. Left panel, a simplified description/model for transparent motion in orthogonal directions moving at the same speed. The activity in two direction selective channels results in a transparent motion percept for the observer. Along the pathway of visual motion processing, adaptation occurs (see locus of adaptation). Right panel, if after adaptation a stationary test pattern is presented, the recovery from adaptation starts and a MAE is perceived. This MAE is unidirectional and must be a result of an integration (see text for details). (B) Left panel, the stimulus as used in the present experiments: transparent motion with different speeds for both vectors. The two motion directions of the stimulus we used in this paper and their direction specific channels are shown. Each channel has slow and fast motion sensors in their population of motion detectors, here represented as 'S and T-units', respectively. During adaptation no coherence but transparent motion is perceived and therefore these channels are drawn as maintaining their independence (see gray arrows). Right panel, in the right-hand panel the test conditions of our experiment are shown. We assume that the contribution of 'S-units' to the MAE is dominant when a static test pattern is presented (B1), and that the contribution of 'T-units' is more prevalent when a dynamic test pattern is shown (B2). The dominant contributors for both directions are for illustrative purposes represented by the thickness of the gray lines.

ers. No significant differences in MAE directions for different background displays were found.

In sum, although the adapting pattern is always the same for a given combination of pattern speeds, the average MAE direction for the two types of test stimulus can differ as much as 50 deg immediately after adaptation. It is clear that the fact that the same adaptation stimulus can result in two different MAE directions cannot easily be explained in terms of a single source or gain control. We will elaborate on this finding in Section 4.

4. Discussion

This simple experiment shows that the direction of the MAE of transparent motion depends on the type of test pattern. For the same adaptation stimulus, testing with static and dynamic patterns results in MAE directions that differ on average as much as 50 deg.

What do these results mean? It is hard to defend the idea that the MAE of transparent motion is the result of a recovery from adaptation of a single source. A single source would result in the same MAE-direction irrespective of the test stimulus. For our stimulus configuration, the simplest assumption seems to be that two sources (pools of neurons) contribute to the MAE direction and, depending on the nature of the test stimulus, one source contributes more than the other.

For illustrative purposes, consider Fig. 3A (left panel). V_1 and V_2 represent transparent motion in orthogonal directions. Both patterns are moving at the same speed. Two pools of direction selective motion sensors are active during adaptation and transparent motion is perceived as represented by the gray shaded arrows and the percept of the observer. Since the subsequent MAE is unidirectional (see the right panel), an integration of activity must take place. Since both adaptation speeds are the same, the 'directions' contribute equally to the 'integration stage'. Here, we have to emphasize that the 'model' as represented in Fig. 3 is a simplification. It is difficult to imagine how a mechanism like this can give rise to a MAE, simply because adapted sensors alone cannot drive other neurons. They require interactions with other direction selective pools to compare their (relative) activities. We represented this by a connection to oppositely tuned sensors in the right hand panel of Fig. 3A. The question whether this is implemented as a strict ratio-model (Barlow & Hill, 1963), a distribution-shift model (Mather, 1980), or a release of inhibition (Cornsweet, 1970) is interesting but beyond the scope of this paper.

The output of the integrative stage is responsible for the perceptual experience of the MAE. This is the classical case and, as mentioned, a unidirectional vertical MAE direction is expected and normally perceived. We also know for static test conditions that, in case the inducing patterns have different characteristics like different speeds, the most sensitive pool of neurons contributes more than the other. As a result, the MAE will be more directed towards the opposite direction of the most sensitive contributor to this MAE (Verstraten et al., 1994). The problem is that in the current experiments we found different directions for the same adaptation conditions, with a dependency on the type of test pattern. Therefore, the 'model' in Fig. 3A is only part of the explanation.

A starting point for a possible explanation is a paper by van de Grind, Koenderink and van Doorn (1986). They proposed that motion detectors that code for high velocities have short delays (which may correlate with transient characteristics (T)) and detectors for slower velocities have longer delays (which may correlate with sustained characteristics (S)). Although it is rather speculative to state that these different neural substrates are actually responsible for the different direction of the MAE, it is a useful distinction for illustrative purposes: the S- and T-pools might contribute differently to the MAE depending on the nature of the test pattern.

The stimulus and test condition as used in this study are represented in Fig. 3B. We now also make a distinction between pools that are tuned to different speeds, as represented by the S- and T-pools for each direction. Adaptation to transparent motion of different speeds will result in a bi-directional percept during adaptation. However, it is assumed that the low speed is processed dominantly by the S-pool and the fast pattern dominantly by the T-pool as represented by the gray lines.

The static test condition is represented in the right-hand panel of Fig. 3B as B1 and the dynamic test condition as B2. In the lower part of the panels the perceived MAE direction as found in this study is displayed. We know that the adapting stimulus for both test conditions is exactly the same and therefore the difference in the MAE direction must be due to the type of the test pattern. In the case of a dynamic test pattern, presuming the adaptation stimulus results in the same gain settings in activated sensors, the T-channel dominates during testing, resulting in a MAE-direction predominantly opposite to the faster of the inducing patterns. The S-channels are more dominant in the static test condition, hence the MAE is more in the direction opposite of the slow pattern. However, given that the MAE direction is moving close to the 90 deg direction the T-pool must contribute to the MAE as well, even under static test conditions. We have represented this idea by the thickness of the gray lines.

An interesting implication is that the MAE apparently is not just a manifestation of a passive recovery from adaptation process. It is an active construction that happens after adaptation and is dependent on the type of test pattern. Imbalances in gain and/or response occur at several sites along the visual pathway and we think that percepts are based on active integrative processes which take these activities into account. Which gain controls contribute and how much is, again, dependent on the test pattern.

Sometimes this integration does not take place. For example, manipulating monocular and binocular presentation of the adaptation stimulus can result in different MAEs, the main difference being that depending on the way of testing, different sites of adaptation are 'tapped' and these sites are responsible for the perceived MAE, often resulting in so called contingent aftereffects (see Howard & Rogers, 1995; Moulden, Patterson & Swanston, 1998 for reviews). The same is true for adapting to first-and second order motion (Nishida & Sato, 1995). At first sight Nishida and Sato's results appear to be rather similar to ours. They adapted their observers to simultaneously presented first and second order motion. When observers were presented with a static test pattern the MAE was mainly opposite to the first order motion direction, whereas it was opposite to the second order motion direction in case of a dynamic test pattern. These different kind of motions, however, are assumed to be processed at different levels of visual motion processing and by different pathways. Nishida and Sato (1995) suggest that these pathways, although not strictly divided and functionally overlapping, are either specialized in processing first-order or second-order motion (Cavanagh & Mather, 1989). Moreover, they present convincing evidence that the MAE as found with a dynamic test pattern originates at a higher level of visual motion processing. Their idea of a higher level origin is in line with a report by Culham and Cavanagh (1994), who found that attentive tracking of a counterphasing radial grating results in a MAE but only for a dynamic test pattern. In case a static pattern was shown no MAE was perceived. For our stimulus, which is mainly luminance based first-order motion[3], the directional filters or channels are parallel and at the same level of visual motion processing. The output of these channels is integrated at a later stage resulting in the perceptual manifestation of the MAE.

This idea that two gain controls at the same level along the pathway of visual motion processing are responsible for the MAE of transparent motion seems also closely related to the model of Grunewald (1996) (see also Grunewald & Lankheet, 1996). However, this model has yet to be formalized in greater detail. As mentioned before, their psychophysical results were obtained using a dynamic test pattern. Grunewald's current model also predicts a transparent MAE for static tests after adaptation to oppositely directed transparent motion, something that clearly does not happen perceptually. The perceptual appearance of Grunewald and Lankheet's (1996) MAE is also rather different from the more conventional MAEs, it is short and seems to be highly dependent on the stimulus configuration. In our case we clearly get two different MAEs, a static and dynamic MAE, for the same adapting stimulus. It would also be interesting to see what other models predict as far as the MAE is concerned (Qian, Anderson & Adelson, 1994) (see also Murakami, 1997).

To conclude, yet another phenomenon in MAE research can be added to the bulk of reports suggesting that there are several sites for adaptation along the pathway of visual motion processing. And yet again it emphasizes the importance of the nature of the test pattern in determining the fate of our perceptual experience of the MAE. Our present results do not necessarily rule out that there are gain controls beyond the integrative level, as we have previously suggested (Verstraten et al., 1994). However, it would be far from parsimonious to defend that idea in the context of the present results, which can be explained more simply as sketched above.

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[3] Note that there are always second order components in these stimuli.

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