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# Context and the motion aftereffect: Occlusion cues in the test pattern alter perceived direction

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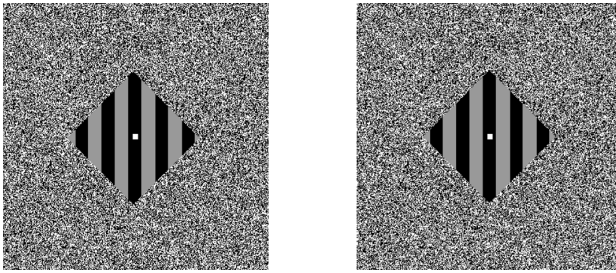
**Abstract.** A horizontally moving vertical grating viewed through a diamond-shaped aperture can be made to appear to move either upwards or downwards by introduction of appropriate depth-ordering cues at the boundaries of the aperture (Duncan et al, 2000 *Journal of Neuroscience* **20** 5885–5897). The grating is perceived to move towards (and sliding under) occluding ‘near’ surfaces, and parallel to ‘far’ surfaces. Here we show that these depth-ordering cues affect the perceptual interpretation of the motion aftereffect (MAE) as well. After adaptation to unambiguous horizontal motion, the MAE direction deviates from horizontal towards near surfaces. However, the influence of depth-ordering cues on the illusory motion of the MAE is generally less than that seen for ‘real’ motion. Implications for theories of depth–motion and depth–MAE interactions are discussed.

## 1 Introduction

The barber-pole illusion (Wallach 1935) results when an obliquely oriented grating is viewed through a rectangular aperture. The percept is usually of motion in the direction of the long axis of the rectangle and is commonly attributed to motion signals arising in response to the grating terminators, which are more numerous along that axis. Placing the aperture stereoscopically in front of the grating, however, markedly reduces the barber-pole illusion (Shimojo et al 1989). It has been proposed that this release from the illusion results from the terminators being classified as ‘extrinsic’ to the grating and their corresponding motion signals being suppressed. Though depth–motion interactions of this type have been much studied psychophysically (eg Anderson 1999; Lidén and Mingolla 1998; Shimojo et al 1989; Vallortigara and Bressan 1991) and neuronal correlates recently identified (Duncan et al 2000), this particular mechanism has yet to be validated.

### 1.1 The ‘barber-diamond’ stimulus

Duncan et al (2000) devised a variation of the original barber-pole illusion to investigate the neuronal mechanisms underlying the influence of depth ordering on visual motion interpretation. Rather than using depth cues to render all of a grating’s terminators either intrinsic or extrinsic as Shimojo et al (1989) had done, they simulated partial occlusion so that half of the grating terminators would be seen as intrinsic and half as extrinsic. In their ‘barber-diamond’ stimuli (see figure 1) a vertical square-wave grating moved horizontally within a diamond-shaped aperture. While the grating itself had zero disparity, two of the four panels defining the aperture were placed in front of the grating (crossed disparity), while the remaining two were situated behind (uncrossed disparity). As a result of these manipulations, the grating terminators at the ‘far’ panels were perceived as intrinsic to the grating, whereas those at the ‘near’ (occluding) panels were perceived as extrinsic. Duncan et al showed that the motion of the grating under these conditions was generally perceived as following the oblique



**Figure 1.** Barber-diamond stereogram. A stereo pair for one of the depth-ordering conditions used as a test pattern in our experiments. Cross-fusing the two images promotes an illusion of depth ordering between the square-wave grating and the surrounding textured regions. Two diagonally opposite regions should be perceived as foreground surfaces, the other two as background surfaces. The zero-disparity grating should be perceived to lie in the middle depth plane.

path of the intrinsic terminators, thus ‘sliding under’ the occluding panels.<sup>(1)</sup> Moreover, they established that a subset of neurons in the middle temporal area (area MT/V5) of the primate visual cortex, exhibited directional selectivity consistent with the perceived motion rather than with the motion of the image features present in their receptive field.

### 1.2 Occlusion and the motion aftereffect

The motion aftereffect (MAE) occurs after an observer has watched a moving stimulus for some time (adaptation) and then looks at a stationary stimulus (the test stimulus—see Anstis et al 1998 for a review). The observer perceives an illusory movement, usually in the direction opposite to that of the adapting stimulus.

Different test stimuli, however, have been shown to yield different MAEs (eg Nishida and Sato 1995; Verstraten et al 1998; Wade and Salvano-Pardieu 1998). Furthermore, MAEs tested with static patterns are never mistaken for real motion (Hiris and Blake 1992). While both real motion and the MAE produce a perception of motion, static test patterns, after adaptation, do not appear to change position commensurate with their perceived motion. This suggests that either a positional signal arising from the static test stimulus counteracts the effects of adaptation, or that the neural substrate underlying the perception of the classic MAE is somewhat different than that of real motion.

Given this presumed difference between real motion and the (static) MAE, we wondered whether the ability of depth cues to affect motion interpretation extended to the illusory motion of the MAE. Specifically, we asked whether a static barber-diamond grating, presented after adaptation to horizontal motion, would be seen to move obliquely underneath the near surfaces just as if it were possessed of physical rather than illusory motion.

In our main experiment we show that depth ordering in the test pattern does indeed influence MAE direction. The magnitude of this effect, interestingly, was found to depend strongly upon the observer. In a second experiment we show that this deviation from horizontal does not appear to involve the suppression of motion signals arising from the grating terminators. We discuss the implications of these results as they apply to the neuronal mechanisms underlying depth–MAE and depth–motion interactions.

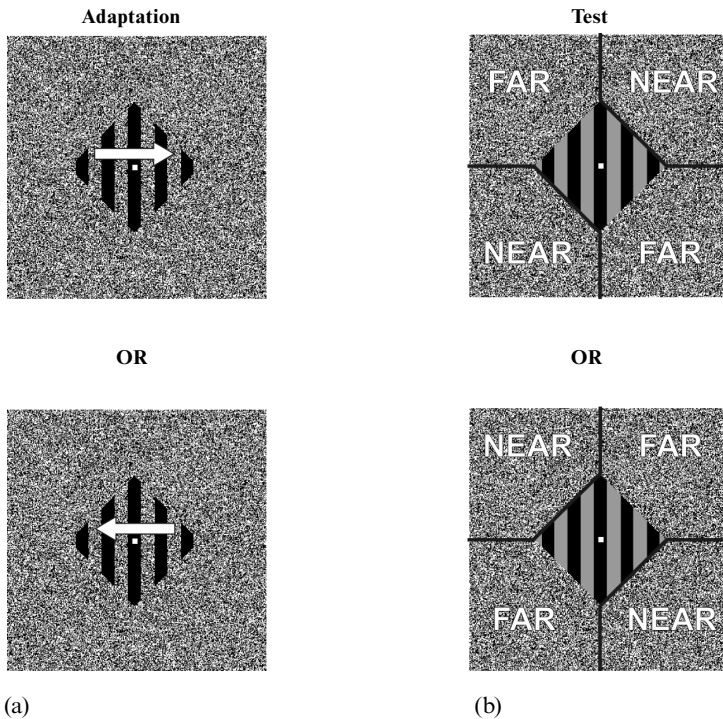
## 2 Main experiment

In this experiment we used the basic barber-diamond design developed by Duncan et al (2000, see figure 1). Red–green anaglyph glasses were used to create the different binocular disparities that define the three depth planes. Pilot experiments confirmed the psychophysical results of Duncan et al with this paradigm.

<sup>(1)</sup> A demonstration of these stimuli can be found at <http://www.sn1.salk.edu/~gene/demos.htm>.

## 2.1 Stimuli

Figure 2 shows schematically the stimuli used in this experiment. The adaptation stimulus (left panels) consisted of a vertically oriented square-wave grating (0.8 cycle  $\text{deg}^{-1}$ , duty-cycle 50%), which moved either leftward or rightward (velocity  $2.5 \text{ deg s}^{-1}$ ), and was viewed through a diamond-shaped aperture. The aperture subtended 6 deg visual angle (as measured horizontally or vertically from corner to corner), the aperture plus surround (see below) subtended 12 deg.



**Figure 2.** Example of the stimuli used in the main experiment. (a) Both the grating and the surround of the adaptation stimulus were at zero disparity. Texture with the same statistical properties as that of the surround replaced the bright regions of the grating. The grating plus texture moved either leftward or rightward. (b) The two depth-ordering configurations of the test pattern used. The top-right and bottom-left regions of the surround were foreground surfaces, while the top-left and bottom-right were background surfaces, or vice versa. The binocular disparities of the foreground and background surfaces were obtained by using red–green anaglyph glasses.

Both the grating and the textured surround had zero binocular disparity. To disambiguate the perceived motion direction during adaptation, random texture with statistical properties identical to the surround was added to the bright regions of the grating. Observers always perceived this stimulus as moving horizontally (see Duncan et al 2000).

The test stimuli consisted of two mirror-symmetric ‘depth-ordering’ conditions (figure 2b). Two diagonally opposed textured regions flanking the aperture had 0.12 deg crossed disparity (situating them in front of the grating), while the two complementary regions had 0.12 deg uncrossed disparity (placing them behind the grating).<sup>(2)</sup> The zero-disparity *stationary* grating was untextured, but otherwise identical to the adapting grating.

## 2.2 Procedure

Eight paid, naïve observers participated in the experiment. All had normal or corrected-to-normal acuity and were able to distinguish the different depth planes in the test patterns.

<sup>(2)</sup>These depth manipulations also introduced monocular half-occlusions (see Anderson 1999; Castet et al 1999).

None of them had previously been exposed to either barber-pole or barber-diamond stimuli. Upon fixating a small yellow annulus (0.4 deg outer diameter) in the center of the screen, observers initiated movement of the adaptation stimulus (lasting 30 s). Subsequently, the test stimulus was presented for 3 s, after which a randomly oriented small line appeared in the center of the screen. The observer's task was to rotate this line parallel to the MAE direction by using the keyboard's arrow keys, or to indicate the absence of an MAE by pressing the 'space' key. The observer's report was followed by a 20 s recovery period, during which the stationary test stimulus remained on the screen and observers were allowed to move their eyes.

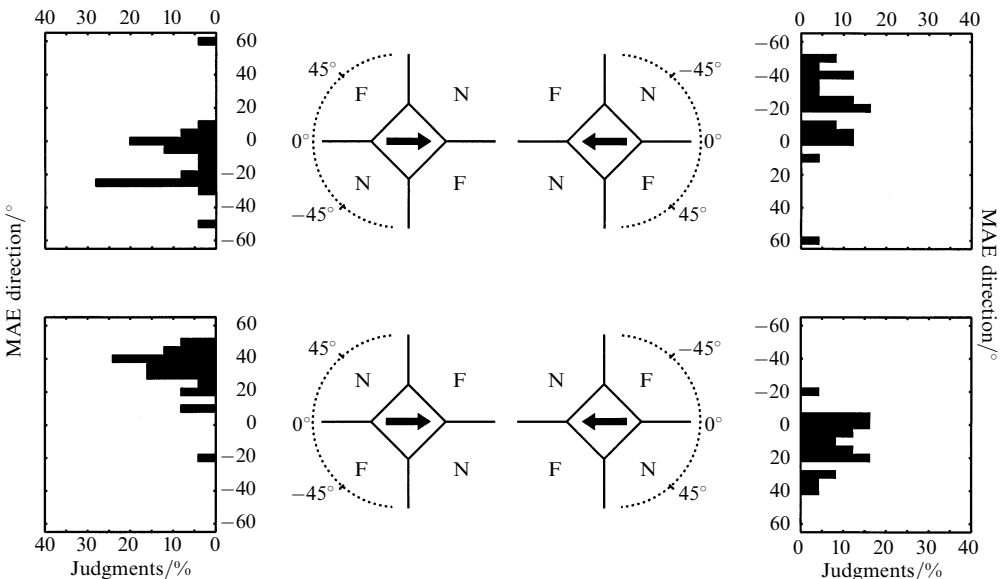
The 2 test conditions combined with the 2 adaptation directions (leftward and rightward) resulted in 4 experimental conditions, which were randomly presented to the observers. Each block of trials consisted of 20 trials and lasted about 25 min. Each observer completed 6 blocks of trials, but the first block was regarded as a training session and its data discarded. No feedback was given during any session. The 5 non-training blocks yielded 25 trials per condition.

### 2.3 Prediction

The adaptation stimulus was always seen to move horizontally. Hence, if not influenced by depth ordering, MAEs should presumably be mainly horizontal (the direction opposite to the adapting motion). However, on the assumption that depth ordering affects the MAE and real motion alike, we predicted oblique MAEs in the direction of one of the near surfaces.

### 2.4 Results

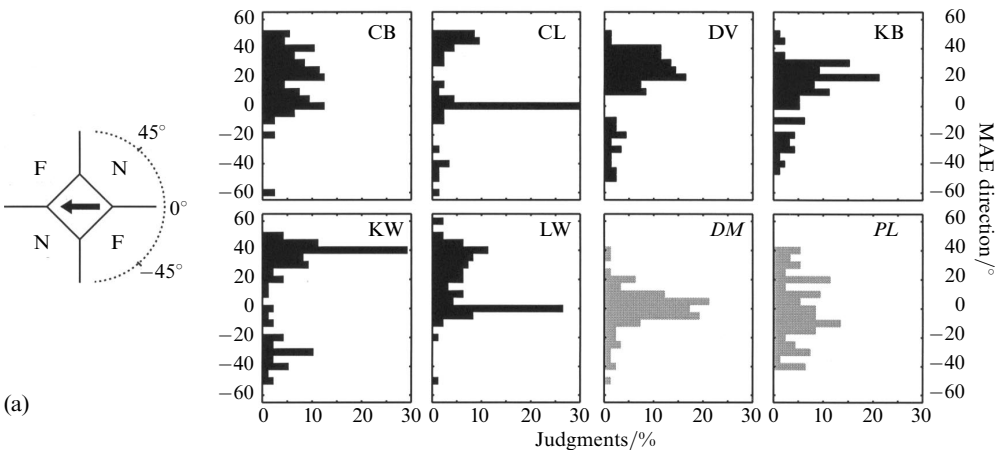
The observers reported seeing MAEs on over 99% of the trials. The remaining trials were excluded from the analysis. Figure 3 shows data from one observer (CB). The histograms (5° bins) show MAE-direction reports for each of the four conditions.



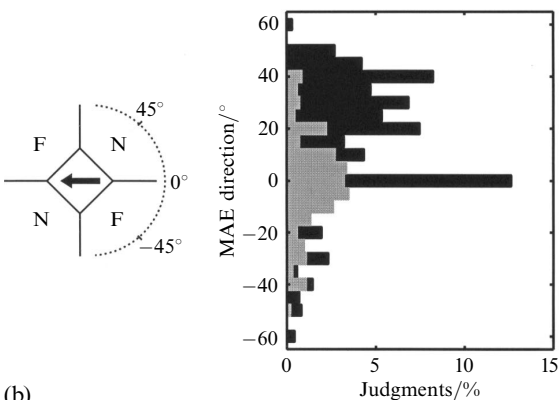
**Figure 3.** Perceived MAE direction for observer CB in the main experiment. The central icons schematically depict the adaptation/test combinations. N = near panel, F = far panel. The central arrow indicates the motion direction of the (textured) grating during adaptation. The corresponding histograms show the perceived MAE direction collapsed into 5° bins. The abscissa shows the percentage of judgments per bin. The ordinate shows the MAE direction. Negative values are counterclockwise from zero, which is opposite the adaptation direction. Positive values are clockwise from zero.

The icons next to the histograms depict both the direction of motion of the adapting grating and the depth ordering of the test stimulus. For example, the top-left histogram shows data for rightward adaptation (indicated by arrow in central diamond) and a test pattern with ‘near’ (crossed disparity) bottom-left and top-right panels, and ‘far’ (uncrossed disparity) top-left and bottom-right panels. For this condition, CB reported a number of horizontal MAEs and an occasional MAE towards the far panel. The majority of CB’s reports, however, were oblique and downward, as if the grating were sliding under the near panel. The top-right panel shows the results for the same test pattern depth ordering after adaptation to leftward motion. The majority of MAEs were oblique and upward, again towards the near panel. The other two conditions yielded the same pattern of results (figure 3, lower panels). Thus, for observer CB, depth ordering in the test pattern clearly biases the direction of the MAE towards the near panels for all four conditions.

To simplify presentation of the data from the other observers, we pooled data from all four depth-ordering conditions to create a composite histogram in which positive and negative angles reflect reports in the direction of ‘near’ and ‘far’ panels respectively. These pooled histograms are shown for each observer in figure 4a. The icon shows the adaptation – test combination onto which the data from the four conditions are mapped.



(a)



(b)

**Figure 4.** Results of the main experiments for all observers, pooled across conditions. (a) The icon shows the depth-ordering condition onto which all the data are mapped. Observers with black histograms report the MAE significantly more often in the direction of the near panel ( $p < 0.01$ ). Those with gray histograms do not show a significant deviation in MAE direction ( $p > 0.05$ ). (b) The same as in (a), but pooled across observers. Black and gray histograms as in (a).

To statistically test the prediction that MAEs would be seen in the direction of one of the near surfaces, we first classified MAE reports as either “near” or “far” (all but pure horizontal reports were so-classified).<sup>(3)</sup> Using the binomial-cumulative-distribution function we then tested the null hypothesis that the number of near reports did not exceed that of far reports.

Six of the eight observers consistently ( $p < 0.01$ ) reported more near than far MAEs (black histograms). The near-reports/far-reports ratio (N/F ratio) varied between observers from  $\sim 1.9$  (CL) to  $\sim 6.8$  (CB). For two other observers (gray histograms) the null-hypothesis could not be rejected ( $p > 0.05$ , N/F ratio  $\sim 1$  and  $\sim 0.8$ ). Figure 4b shows the data of figure 4a, pooled separately for observers that show an effect of the test pattern and those that do not.

### 2.5 Comparing depth – MAE and depth – motion interactions

As mentioned above, none of our observers had previously been exposed to the barber-diamond stimuli of Duncan et al (2000). It is conceivable that the failure of two of our observers (DM and PL) to show an effect in our MAE experiments would be mirrored by a lack of an effect in the original paradigm. To test this, we had those observers and one other (CL, who had shown a significant but relatively weak depth-ordering effect on the MAE), make directional judgments while viewing barber-diamonds with physically moving gratings. Moving, untextured gratings were viewed through the diamond-shaped aperture for 2 s, while the flanking panels were arranged as in our two test patterns. In contrast to their reports in the MAE experiment, all three observers usually reported the moving grating as moving obliquely in the direction of one of the near panels.

The same three observers (DM, PL, and CL) were subsequently retested in our main experiment to determine whether experiencing depth-ordering effects on real visual motion might influence their performance in the MAE paradigm. Observer CL, who in the main experiment exhibited a small but significant bias in favor of near reports, exhibited an enhanced bias when tested again. In addition, CL’s number of horizontal reports decreased significantly. Conversely, observer DM persisted in reporting the MAE mainly along the horizontal axis, and PL reported the MAE slightly deviated towards the *far* direction. We concluded that while experience might be a factor in depth–MAE effects, lack of experience cannot be blamed for the absence of such effects.

### 2.6 Spatial-frequency content

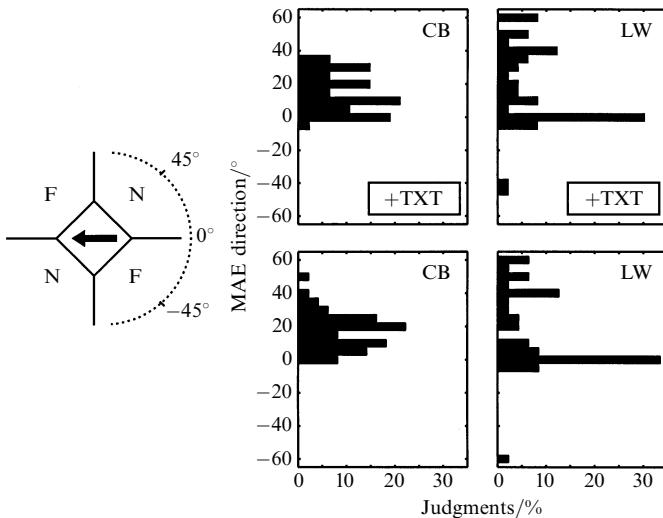
Duncan et al (2000) employed a barber-diamond control condition in which texture was added to the bright regions of the moving grating. They showed that the unambiguously (horizontally) moving texture completely eliminated the influence of depth ordering on the perceived motion direction.

Although our adapting stimulus did not contain any depth ordering, we ensured a percept of purely horizontal motion by, as in Duncan et al’s control, adding texture to the bright region of the moving grating. This manipulation, however, unavoidably caused adapting and test patterns to differ in spatial-frequency content, and MAEs are known to be sensitive to spatial frequency (Cameron et al 1992). To determine whether these spatial-frequency differences were a factor in our results, two observers (CB and LW) participated in an additional experiment. In this experiment, stationary texture was also added to the bright regions of the test grating. Conditions where this texture was omitted from the test grating (same conditions as in the main experiment) were randomly interleaved for comparison.

<sup>(3)</sup>Note that the  $0^\circ$  bin in figures 3, 4, 5, and 7 does not mean that all reports in this bin were exactly  $0^\circ$ . The resolution of the observers’ responses was  $1^\circ$ . The majority of the responses in the  $0^\circ$  bin were classified as either “near” or “far” responses for the statistical analysis.

Figure 5 shows that the results for this control were not distinguishable from those of the main experiment, implying that spatial-frequency content was not a critical factor in the depth–MAE interactions presented here.

These experimental results raise another issue, however. One would expect that, after adaptation to horizontal motion, the test pattern texture would be seen to move horizontally. While the test pattern grating is one-dimensional and hence subject to the aperture problem, the texture is not: its horizontal motion (even if illusory) should presumably be unambiguous. Yet, texture applied to the test grating does not override the influence of depth-ordering, while identical texture applied to the physically moving grating of a standard barber-diamond stimulus does. This discrepancy hints at a potential difference between the mechanisms underlying depth–MAE and depth–motion interactions.

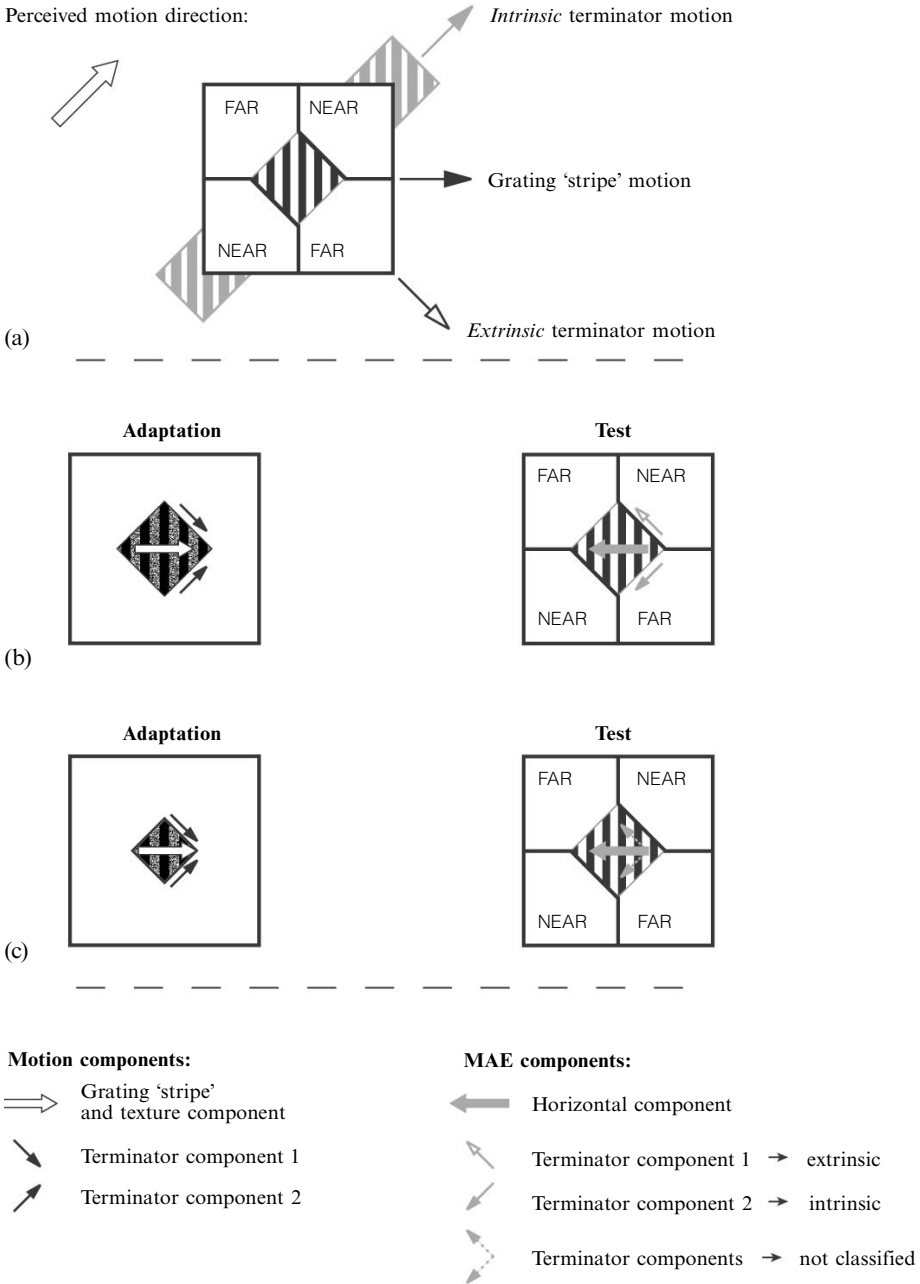


**Figure 5.** Results for two observers when stationary texture was added to the bright regions of the test grating (top), compared to when the texture was omitted (as in the main experiment; bottom). See figures 3 and 4 for methodological details.

### 3 Depth-ordering and MAE interpretation: a role for terminators?

As discussed above, a common explanation of depth–motion interactions of the type seen in barber-diamond stimuli is that motion signals arising from extrinsic terminators are selectively suppressed (eg Lidén and Pack 1999). In the Duncan et al study, the moving grating of the barber-diamond can be considered to have three distinct sets of moving features: terminators that move oblique-upwards, terminators that move oblique-downwards, and the horizontally moving grating stripes. Selective suppression of the motion signals arising from the extrinsic terminators would, consistent with Duncan et al’s findings, lead to a shift in the distribution of motion signals in favor of the intrinsic terminator direction (see figure 6a). This hypothesis, if it is to be judged parsimonious, should extend to our results as well.

Although the horizontally moving texture ensures that the adapting grating is perceived to move horizontally, the grating terminators nevertheless have oblique motion components that presumably activate and adapt neurons selective for those motions. Thus the distribution of motion signals during the test period should resemble that of Duncan et al’s original study: oblique-upward and oblique-downward signals at the margins of the aperture and horizontal signals in the interior. If the above hypothesis accounts for our MAE results, depth ordering at the aperture edges of the test pattern serves to identify extrinsic terminators and this leads to suppression of their motion signals.



**Figure 6.** Physical-motion and illusory-motion components in the main and 'small-aperture' experiment. (a) The stimulus from Duncan et al (2000). Three main motion components are apparent in the stimulus: horizontal (stripe) motion, terminator motion classified by the depth ordering as being *intrinsic* to the grating (right-up), and *extrinsic* terminator motion (right-down). This stimulus is perceived as moving in the direction of the intrinsic terminators. (b) Adaptation and test conditions from our main experiment. During adaptation, three main motion components are apparent (arrows), which can result in three illusory motion components during the test phase. Because the illusory 'terminator components' spatially coincide with the occluding borders of the test stimulus, these illusory components can again be classified as intrinsic and extrinsic. (c) This is not the case when a small aperture is used during adaptation. The illusory terminator components do not coincide with the far and near borders of the test stimulus. Therefore the MAE is expected to be reported mainly horizontal in the small-aperture experiment.

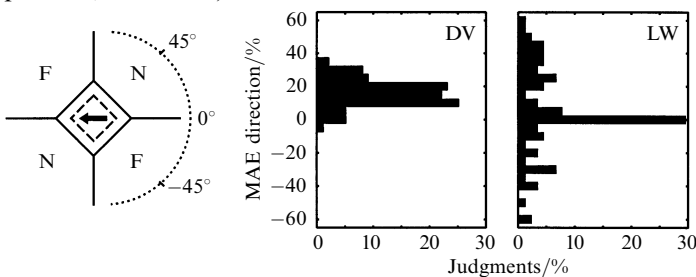


In the original barber-diamond paradigm, as well as in natural dynamic scenes, terminators and depth-ordering cues necessarily spatially coincide (figure 6b). In our MAE paradigm, however, the spatial distribution of motion signals and the spatial positioning of the depth cues are introduced at different points in time, which enables us to differentially position the oblique terminator motion of the adaptation phase and the depth-ordering cues of the test period (figure 6c). By doing so we can investigate the hypothesis of selective suppression of extrinsic motion signals as outlined above.

Therefore, we repeated the main experiment with one critical modification; The diamond-shaped aperture through which the moving textured grating was viewed during adaptation subtended only 4 deg. The aperture in the test phase, as in the main experiment, subtended 6 deg.

Under these conditions, the terminators of the adapting phase do not spatially coincide with the depth-ordered boundaries of the test period and hence selective suppression of oblique motion signals should not occur. The MAE should therefore be predominantly horizontal if the extrinsic-terminator-suppression hypothesis holds. Two participants from the main experiment (DV and LW) also participated in this experiment.

The results, pooled as for the main experiment, are shown in figure 7. Contrary to the prediction presented above, both observers still perceive the MAE direction predominantly as deviated towards the near panels (DV,  $p < 0.01$ ; LW,  $p < 0.05$ ). The results argue against selective suppression of extrinsic motion signals being critical to the depth-MAE interactions documented above (although other interpretations are possible; see below).



**Figure 7.** Results for two observers of the small-aperture experiment. See figures 3 and 4 for methodological details. Contrary to the prediction, depth-MAE interactions are still observed (see text for details).

#### 4 General discussion

The results from our main experiment reveal that depth-ordering cues can alter the interpretation of both real motion and the illusory motion of the MAE. At the same time, we also found significant differences between depth-MAE and depth-motion interactions. This partial congruence between the two phenomena suggests a corresponding partial commonality in their neuronal substrates. In a secondary experiment we took advantage of the MAE paradigm to test the hypothesis that depth-ordering effects depend upon suppression of motion signals elicited by extrinsic terminators. Our findings did not support that hypothesis.

We briefly discuss how our results relate to other studies on the MAE and depth-MAE interactions. Then we consider the mechanisms that might underlie depth-MAE and depth-motion interactions, with special attention given to the role of moving terminators. Finally, we consider the possibly different neuronal substrates of depth-MAE and depth-motion interactions.

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#### 4.1 *MAE, test patterns, and depth ordering*

The importance of the test pattern in modulating MAE characteristics has been demonstrated convincingly (eg Nishida and Sato 1995; van der Smagt et al 1999; Verstraten et al 1998). Similarly, disparity-contingent MAEs (see Moulden et al 1998) have been demonstrated, in which MAE direction depends on the relative binocular disparity of the adaptation and test patterns (Anstis and Harris 1974; Verstraten et al 1994).

In these studies, transparent motion is the adapting stimulus. Their results can be accounted for by assuming that distinct channels are adapted simultaneously, after which appropriate test patterns selectively recall the adaptation state of those channels. Our results do not fall in that category—the disparity of the adapting *and* the test grating is identical. Rather, in our experiments the differential depth ordering of the *surrounding areas* affects MAE direction.

Areas surrounding the adapting/adapted area have previously been shown to significantly impact the MAE (eg Day and Strelow 1971; Wade and Salvano-Pardieu 1998; Wade et al 1996). Our demonstration of the influence of depth ordering in the test pattern demonstrates a qualitatively new type of MAE surround effect. In our experiments the 3-D structure of the surround modulates perceived MAE direction, while the 2-D spatial structure remains the same.

#### 4.2 *Selective suppression of motion signals from line terminators?*

It has been well documented that motion signals arising from line terminators influence motion interpretation (eg Lorenceau and Shiffrar 1992; Shiffrar et al 1995; Shiffrar and Lorenceau 1996; see also Chey et al 1998). Depth ordering has been proposed to modulate the directional distribution of motion signals, by classifying them into signals originating either from intrinsic or extrinsic features. Subsequent suppression of motion signals arising from extrinsic features (Lidén and Pack 1999) might then determine the final distribution of motion signals and hence the perceived direction of motion.

That selective suppression of extrinsic terminator motion signals actually takes place has, however, yet to be confirmed. Indeed, the result of one of our experiments argues against this mechanism. In this experiment we decoupled the spatial positions of the oblique motion signals from the positions of the depth-ordered aperture edges. Under these conditions, depth-ordering cues were seemingly in no position (literally) to classify the spatially distant oblique motions. Yet this manipulation had little impact, suggesting that suppression of extrinsic signals was not responsible for our result.

It might be argued that the spatial precision of the terminator motion signals (generated by the MAE) or the depth-ordering information is less than the 2 deg that separate the moving terminators of the small adapting pattern from the depth-ordered edges of our test pattern. If true, the depth-ordered edges might have been able to remotely influence the interpretation of the MAE despite the lack of spatial registration. While we cannot rule out this possibility, we do not think it likely.

Other types of depth–motion mechanisms have been put forward as well (for a review see Stoner and Albright 1994). One such mechanism is based on ‘amodal’ completion of occluded surfaces (Alais et al 1998; Duncan et al 2000; Lorenceau and Alais 2001; Shimojo et al 1989). Amodal representations could introduce additional motion signals that, when pooled with motion signals arising from the visible part of the surface, might alter motion interpretation. Experiments to test this and other hypotheses are currently underway.

#### 4.3 *Depth–motion versus depth–MAE interactions*

As discussed above, we found significant differences between depth–motion and depth–MAE interactions. First, we found that while all of our observers show depth–motion interactions, not all observers exhibit depth–MAE interactions. Second, even

when present, the magnitude of the depth–MAE effect tended to be less than that seen for physical motion. Finally, application of texture to the MAE test grating had no effect on the influence of depth-ordering cues (see section 2.6; figure 5), whereas texture removes that influence *both psychophysically and neuronally* for physically moving gratings (Duncan et al 2000).

These differences between the ability of depth cues to alter the MAE and real-motion interpretation might reflect differences in their respective neuronal substrates. Several lines of evidence are consistent with this suggestion. First, the MAE when probed with a static test pattern is not confused with real motion: static MAE test patterns appear to move with only a much smaller corresponding change in position (Nishida and Johnston 1999; Snowden 1998).

Interestingly, MAEs tested with dynamic patterns seem to mimic real motion well (Hiris and Blake 1992). In addition, MAEs on static test patterns have been shown to reveal the adaptation of a slow motion channel, while those on dynamic patterns reveal adaptation of a fast motion channel (van der Smagt et al 1999; Verstraten et al 1998). The latter contains a much broader speed range, reminiscent of the range of speed selectivity found in area MT. This leads to the speculation that the difference between depth–motion and our depth–MAE interactions may be due to the latter being restricted to the slow-motion channel. If true, while our data suggest that depth interactions with the slow-motion channel do not depend upon the suppression of terminator motion signals, our findings do not rule out such suppression in the fast-motion channel. It would be interesting to see whether depth–motion interactions are better mimicked with dynamic test patterns.

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