



Enhanced motion aftereffect for complex motions

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Abstract

We measured the magnitude of the motion aftereffect (MAE) elicited by gratings viewed through four spatial apertures symmetrically positioned around fixation. The gratings were identical except for their orientations, which were varied to form patterns of global motion corresponding to radiation, rotation or translation. MAE magnitude was estimated by three methods: the duration of the MAE; the contrast required to null the MAE and the threshold elevation for detecting an abrupt jump. All three techniques showed that MAEs for radiation and rotation were greater than those for translation. The greater adaptability of radiation and rotation over translation also was observed in areas of the display where no adapting stimulus had been presented. We also found that adaptation to motion in one direction had equal effects on sensitivity to motion in the same and opposite directions. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Contemporary models of motion perception typically postulate local mechanisms that are selective for the direction of motion and spatio-temporal frequency of moving patterns (e.g. Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). Little is known about how such motion signals combine to provide information about the movement of more complex objects, but the authors of several recent studies have proposed that large receptive fields selective for meaningful configurations of movement (such as rotation and radiation) are assembled from smaller, uni-directional receptive fields that might be encoded by such local motion models (Freeman & Harris, 1992; Zhang, Sereno & Sereno, 1993; Lappe & Rauschecker, 1994; Morrone, Burr & Vaina, 1995; Gurney & Wright, 1996; Snowden & Milne, 1996; Bex & Makous, 1997; Bex, Metha & Makous, 1998).

The existence of such a hierarchical motion processing system is supported by many adaptation studies that have revealed mechanisms specialized for the de-

tection of complex patterns of motion. The first evidence was reported by Regan and Beverly (1978), who measured detection thresholds following adaptation to the motion of the edges of square patterns. Out-of-phase oscillation of the edges resulted in looming motion about a central point, but in-phase oscillation resulted in diagonal translation of the square, with no change in size. Out-of-phase adaptation raised thresholds for detecting looming motion much more than equivalent in-phase adaptation, despite the fact that the only difference in motion was the relative phase of motion at opposite sides. The results were taken as evidence of separate pathways for the detection of looming and translational motion, but can easily be incorporated into a hierarchical framework. In this case, while both adapting patterns fatigue local detectors, only the out-of-phase oscillations adapt looming detectors at a higher level. Similarly, Regan and Beverly (1985) measured thresholds for detecting rotational movement formed by four patches of drifting noise. The directions of the noise patches for the adapting patterns were arranged to form either a global pattern of rotation or else the patterns were jumbled, giving no coherent global motion. Once again, sensitivity was higher when the local directions of the noise

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patches formed global rotation, even though the local motion signals were the same in all cases, but in different combinations.

Studies of a different adaptation phenomenon, the motion aftereffect (MAE), also provide evidence of higher-order motion analyzers. After prolonged adaptation to a moving image, a static image appears to move in the opposite direction: this is the motion aftereffect (for review see Wade, 1994). Most studies of the MAE have concentrated on simple translational motion of gratings or random dot patterns in the fronto-parallel plane, but several researchers have studied the MAEs elicited by complex patterns of motion, and the results provide additional evidence for specialized detectors. For example, Cavanagh and Favreau (1980) measured MAE duration after adapting to spiral motion. One test pattern was a mirror image of the adapting spiral, with all its contours at 90° to those of the adapting spiral. Local motion detectors tuned to the directions of the mirror image spiral should fail to respond, and therefore not adapt, to the adapting spiral. Nevertheless, MAEs were present when tested with the mirror image spiral and lasted one-third as long as the MAEs measured with a test figure that was the same as the adapting spiral. Several researchers have studied adaptation to large patterns of motion that have been presented through small apertures (Bonnet & Pouthas, 1972; Hershenson, 1984; Snowden & Milne, 1997). As well as concrete MAEs in the areas of the display in which the adapting pattern was presented, phantom MAEs were also recorded where no adapting pattern had been presented. Such phantom MAEs are thought to reflect adaptation of higher level mechanisms with large receptive fields.

Recently, Snowden and Milne (1996) studied the motion aftereffects elicited by adaptation to noise patterns undergoing radial, rotational or spiral motions. Following adaptation to a large patch of motion, a smaller test patch was placed in a region of the display where the local motion during adaptation was exclusively translational. Some observers reported a MAE in this sub-region that had the characteristics of the MAE expected for the global pattern; e.g. during adaptation to expansion, adapting dots in the region to the left of fixation translated to the left, but a test patch placed at this location sometimes appeared to contract. Also, adaptation to a large field of expansion selectively raised thresholds for detecting expansion on the local field where the dots underwent only translational motion. The same was true for contraction, spiral and rotational motions, indicating adaptation of specialized mechanisms beyond the stage where local motion vectors are encoded. The results suggest that not only are there higher level mechanisms selective for complex configurations of motion, but these specialized detectors are relatively insensitive to the location of the

center of radiation or rotation—an insensitivity termed position invariance. Note however that Regan and Beverly (1978) also examined the MAE following adaptation to expansion in this manner yet observed no such position invariance: the aftereffect disappeared when fixation shifted by approximately half the length of the square edge.

Steiner, Blake and Rose (1994) hypothesized that as neurones selective for complex motion are found only at higher stages of visual processing where neurones are mostly binocular, there should be high inter-ocular transfer of MAE for expansion and rotation. Neurones selective for simple translation are found at many levels of visual processing, including early monocular areas, and so less inter-ocular transfer of MAE was expected. Following adaptation to radiating, rotating or translating dot patterns, the signal: noise ratio of a patch of test moving dots was manipulated to null the resultant MAE. The inter-ocular transfer of the MAE for translation (76%) was less than for expansion (91%) or rotation (86%), consistent with their expectations. It should be noted that Regan and Beverly (1978) found much less inter-ocular transfer (about 40%) following adaptation to a looming square.

Steiner, Blake and Rose's (1994) results also showed evidence that a higher signal: noise ratio was needed to null rotation and expansion MAEs than that required to null translation MAEs, suggesting that the MAE following rotation and expansion is qualitatively stronger than that following simple translational movement. However, Hershenson (1993) found that the durations of the MAEs for rotating and translating patterns were approximately the same. He used magnitude estimation to compare the MAEs elicited by rotational and translational gratings. Observers generated decay curves by rating the strength of the MAE at varying intervals after adaptation. The decays of the MAEs for rotational and translational patterns were of similar shape and duration.

Here we sought to establish whether rotational and radial motions elicit stronger MAEs than translational motion when the local components of motion are identical. We used both subjective and objective techniques to measure the MAE elicited by equivalent adaptation to rotation (clockwise, anti-clockwise), radiation (expansion, contraction) and translation (left, right). The stimuli were four isolated gratings, identical except for local orientation. The transfer of the MAE to unadapted areas within the display was also measured to infer the spatial extent of the higher level mechanisms.

2. Methods

Two of the authors (PB and AM) and two naive subjects (XQ and SH) served as observers. All had

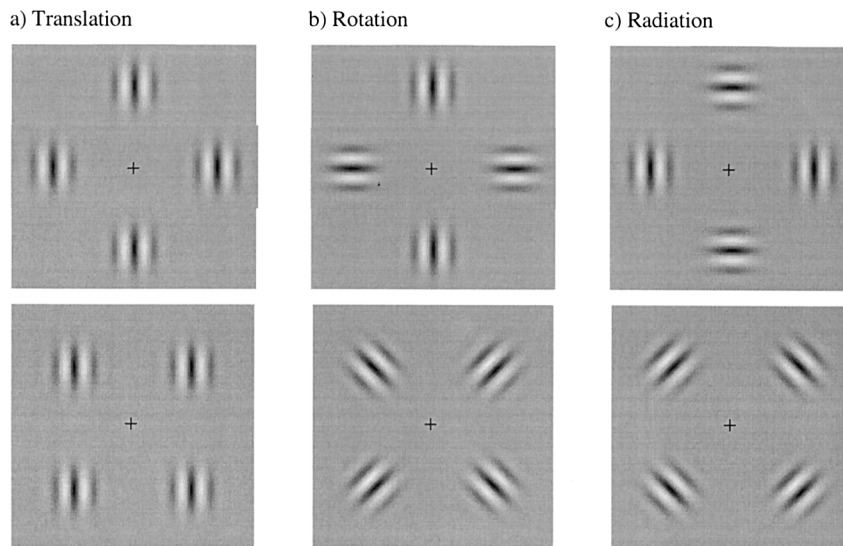


Fig. 1. Example of the stimuli. Six stimulus configurations were presented, each consisting of four Gaussian windows containing a moving grating with a 2 cycle/degree sinusoidal luminance profile. The locations of the windows were either in a + (top row) or an x (bottom row) arrangement around fixation. The orientation of the gratings varied to form three compound patterns forming: (a) rotation; (b) radiation; and (c) translation. The cross is for fixation.

normal or corrected visual acuity. Stimuli were generated on Macintosh computers (7600/120 or 8600/200) using software adapted from the VideoToolbox routines (Pelli, 1997), and were displayed on a Nanao Flexscan 6500 or 6600 gray-scale monitor at a frame rate of 75 Hz and mean luminance of 55 cd/m². The luminance of the display was linearized with pseudo-12 bit resolution (Pelli & Zhang, 1991) and calibrated with a Minolta Chromameter. Pseudo-12 bit resolution in this case allowed presentation of 2⁸ gray levels from a possible range of 2¹² levels. The display measured 36.0 cm horizontally (1152 pixels), 27.2 cm vertically (870 pixels), and was 115 cm from the observer, in a dark room.

Stimuli: Six stimulus configurations were presented, each consisting of four windows, 2° from fixation, containing a grating with a 2 c/deg sinusoidal luminance profile, as illustrated in Fig. 1. Each grating was multiplied by a stationary Gaussian envelope with a radially symmetrical space constant, $\sigma_s = 0.4^\circ$, and had a peak contrast of 40%. The Gaussian windows were arranged about fixation, and the orientation of the gratings was varied to form three global patterns of motion: (i) radiation; (ii) rotation or (iii) translation (see Fig. 1). In all experiments, the sinusoidal carrier of the adapting pattern was 2 c/deg and was drifting at 4 c/sec. In Experiment 1, we measured the simple duration of the MAE following 30 s of adaptation to each of the adapting patterns. At the end of the adaptation period, the patterns were stationary, but appeared to move in the opposite direction to adaptation—the MAE. Observers were instructed to press a button when the MAE had finished and the test pattern ap-

peared stationary. The mean and standard deviation of four such estimates were recorded for each condition.

2.1. Experiment 1: MAE duration

Fig. 2 shows the mean and standard errors of at least four estimates of MAE duration for one of the authors (PB) and a naive observer (SH) for each class of pattern. MAE durations for each direction of movement were approximately equal and have been combined for clarity. The durations of the MAEs for rotating and radiating patterns were approximately equal, but were considerably longer than those for translating patterns.

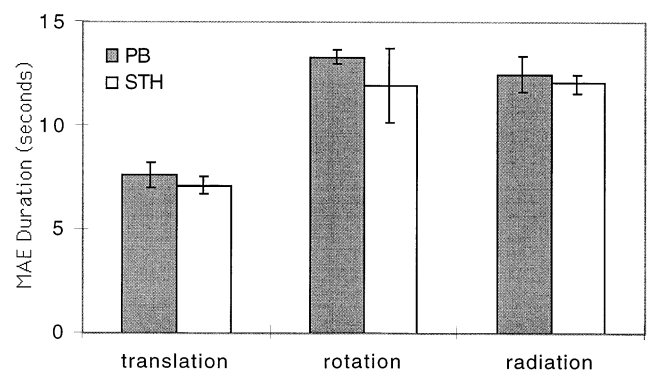


Fig. 2. Duration of the MAE for the author (PB) and a naive observer (SH) for translation, rotation and radiation. Data for the two directions of each class of motion have been combined. Error bars show ± 1 S.E.

2.2. Experiment 2: MAE nulling

In Experiment 2, the adapting stimuli were the same as those in Experiment 1, but the test stimuli were positioned in either + or x positions (see Fig. 1). The test stimuli were once again Gaussian windowed, sinusoidal gratings with orientations that varied to form global patterns of radiation, rotation or translation. Adapting stimuli were in the + positions in all conditions, and the sinusoidal carrier of 2 c/deg was moving at 4 c/sec. The test gratings were formed by the addition of two gratings of the same orientation, but moving in opposite directions at 2 c/sec. These temporal frequencies were selected because they produce robust MAEs (Bex, Verstraten & Mareschal, 1996). The relative contrast of the test component gratings varied from trial to trial according to an adaptive procedure (QUEST; Watson & Pelli, 1983) that controlled the directional signal as follows: when the contrast of each grating was equal, the test gratings flickered in counterphase with no net direction of motion (see Section 3). Changing the relative contrasts of the two gratings introduces a net direction of motion for the composite pattern, the magnitude of which depends on the relative contrast. The relative contrast of the component gratings was varied, while holding the peak contrast of the composite pattern constant at 40%, to null the illusory movement of the MAE. For example, after adaptation to an expanding pattern, a counterphase flickering test pattern (one in which the contrast of each component grating was equal) appeared to contract. The contrast of expanding components in each of the four windows increased from trial to trial until the observer reported that the test pattern expanded, and then it was decreased until it appeared to contract again, and so on. In practice, the initial relative contrasts of the components were randomly determined about a contrast estimated from pilot studies, and the test pattern in the first trial could appear to move in either direction. Each run contained 64 trials consisting of 10 s of adaptation, followed by a 1 s test, except that the first trial had 30 s of adaptation. Observers fixated the central cross and pressed one of two buttons to indicate the apparent direction of the test pattern. The test patterns were presented in the + and x configurations, at random between trials. Direction of adaptation varied randomly in separate runs.

The plots in Fig. 3 are typical psychometric functions for one observer, showing the apparent direction of motion following adaptation to a range of relative contrasts of the component test gratings for translation (squares), rotation (triangles) expansion (open circles) and contraction (filled circles). A psychometric function (Weibull, 1951) has been fitted to the data by a least χ^2 fit (continuous lines for translation and rotation, broken lines for expansion and contraction). Error bars

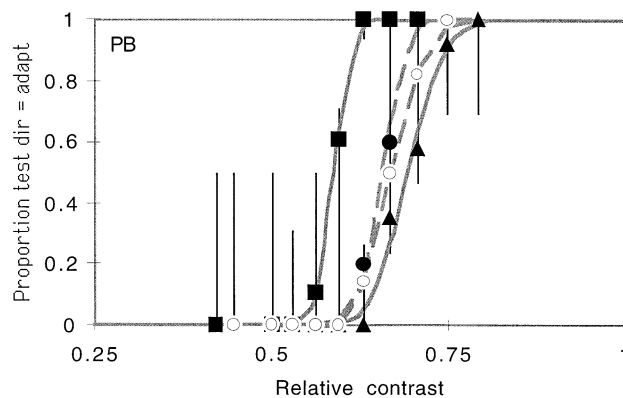


Fig. 3. Typical psychometric functions for one observer (PB), showing the proportion of trials on which the reported direction of the MAE was the same as that of the adapting pattern. The relative contrast of the two components of the test pattern is shown on the x-axis; 0.5 indicates equal contrast where the test pattern flickered in counterphase and thus did not move in either direction. The data for the two directions have been pooled for translation (squares) and rotation (triangles), but are shown separately for expansion (open circles) and contraction (filled circles). The data are fitted by Weibull functions with a least χ^2 algorithm. Error bars represent the standard deviation of each point according to the binomial distribution.

show the binomial standard deviation at each point. Psychometric functions for the two possible directions of motion were collected separately, but as can be seen from the psychometric functions for expansion and contraction, the results were essentially the same for opposite directions and were added together for clarity, as they were for rotation and translation. We define the contrasts of the component gratings that observers reported moving in one direction on 50% of trials as the *nulling contrast*. This value, along with 95% confidence intervals, was estimated from the best fitting psychometric function.

The nulling contrasts for the combined directions of translation, rotation and radiation are shown for two observers in Fig. 4; error bars show 95% confidence intervals. Filled bars show the nulling contrasts where the adapting and test patterns were both in the + locations, open bars show the nulling contrasts where the test patterns were in the x locations (see Fig. 1). It can be seen that the nulling contrast was greater for rotation and radiation than for translation, and the effect is greater for the + locations than for the x locations. In no case did the absolute direction of motion affect the results, whether translation (left or right), rotation (clockwise or anti-clockwise) or radiation (contraction or expansion).

2.3. Experiment 3: threshold elevation following adaptation

The measurement of MAE magnitude is inherently problematic and typically involves subjective estimation

techniques such as those employed in Experiments 1 and 2. Recently however, Simpson, Newman and Aasland (1997) developed an objective technique for measuring MAE duration. They exploited the finding that the size of a sudden jump needed to detect the jump increased with the speed of periodic patterns that actually moved, or else *appeared* to move because of a MAE. Detection thresholds for the jump were measured at multiple intervals after adaptation and steadily fell with time (except for occasional increases in threshold at durations beyond around 10–20 s, consistent with brief recovery of MAE that observers occasionally report). The thresholds were used to deduce the apparent speed of the MAE by cross-referencing with jump detection thresholds for gratings that actually were moving. The steady decline in jump detection thresholds with time after adaptation suggested a gradual decay of the MAE, followed by occasional periods where the MAE seemed to recover briefly.

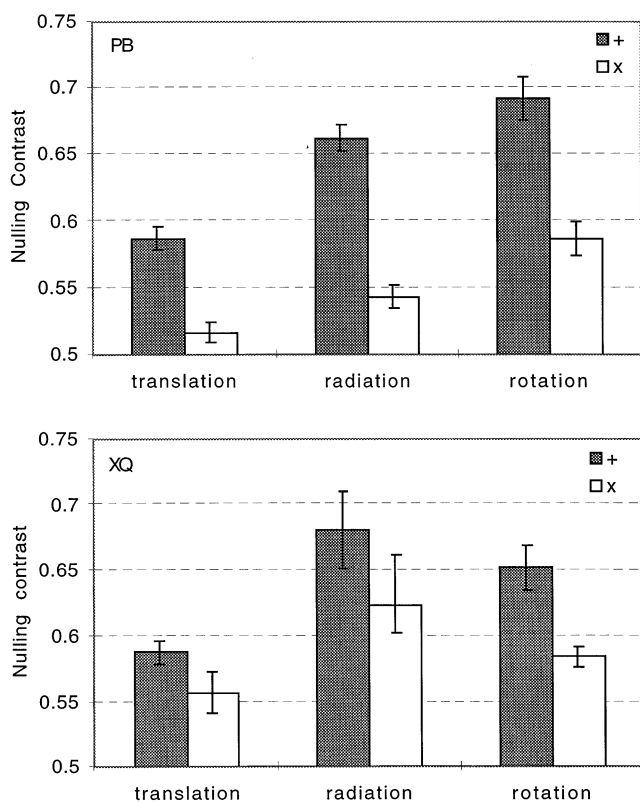


Fig. 4. Relative contrast of the component gratings of the test at which the test pattern had no apparent direction after adaptation. We define this as the *nulling contrast*. Data are shown for two observers: one of the authors (PB) and the naive observer (XQ). Filled bars show the data for the conditions in which adaptation and test patterns were in the + locations (Fig. 1 top row); open bars show data for the conditions in which test patterns were presented in the x locations (Fig. 1 bottom row). A value of 0.5 indicates equal contrast; values above 0.5 indicate that real movement was required to null the illusory movement of the MAE. Error bars show 95% confidence limits.

We adapted this technique to derive an objective estimate of MAE magnitude for our three classes of motion. The procedure was as in Experiment 2 except that the test period contained a static, Gaussian-windowed grating (2 cpd, 40% contrast, as before). The test period was divided into two intervals of 500 ms each, separated by a tone. At a random point within one of the 500 ms intervals, the phase of the grating was abruptly shifted by an amount defined by a QUEST staircase, and the observer's task was to detect the interval containing the shift. There was feedback for incorrect responses. Increment and decrement detection thresholds were measured separately. In the increment detection task, observers were asked to detect an abrupt jump in the same direction as that of the MAE—e.g. when the adapting pattern was expanding, the static test pattern appeared to contract, and observers were asked to detect an abrupt jump towards fixation by all four components. Decrement detection required the detection of a jump in the opposite direction to that of the MAE—e.g. in the above case, observers experienced a contracting MAE and were required to detect an abrupt jump away from fixation: expansion.

Fig. 5 shows the relative changes in detection thresholds (adapted/unadapted thresholds) for both increments and decrements following adaptation to each class of motion; error bars show $\pm 95\%$ confidence intervals. Filled bars show the conditions where the adapting and test patterns were both in the + locations; open bars show the conditions where adapting patterns were in the + locations, but test patterns were in the x locations. It can be seen that detection thresholds for radiation and rotation are higher than for translation for both + and x locations of the test pattern, although the effect is considerably weaker for the x locations. The results also compare increment and decrement detection thresholds. It can be seen that there were no consistent differences between increment and decrement detection thresholds across observers and conditions.

3. Discussion

These results show that adaptation to radial and rotational patterns produced stronger motion aftereffects than translating patterns. Moreover, the results are the same whether measured by either subjective techniques (duration or motion nulling) that correspond to what the observers report seeing, or by a threshold elevation technique that is objective and free of many of the defects of subjective techniques. All patterns comprised local motion signals that were identical except for orientation, so the differences in MAE magnitude suggest that at least two stages of processing are involved in encoding motion: a mechanism to code

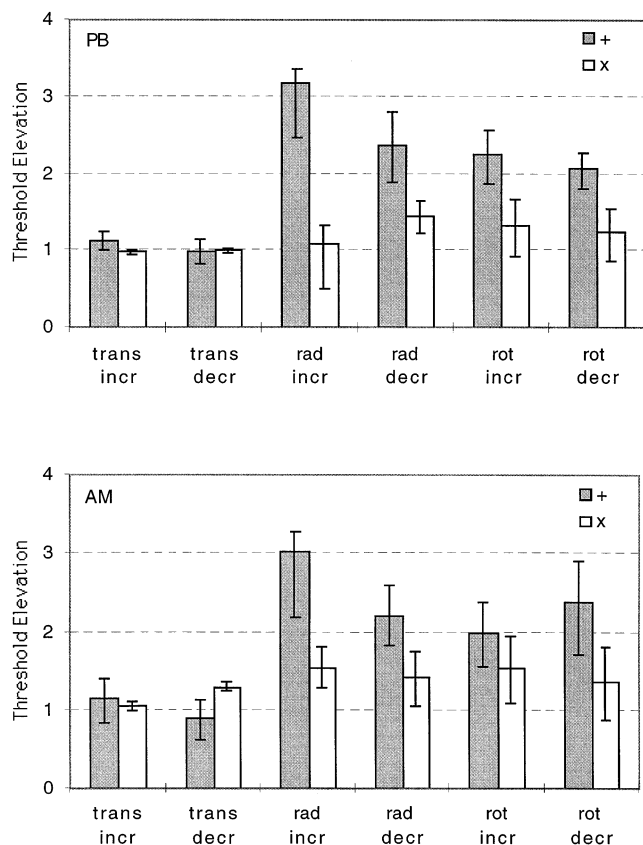


Fig. 5. Threshold elevation (adapted thresholds/unadapted thresholds) for the detection of an abrupt jump. Data are shown for two observers, both authors (PB and AM). Filled bars show the data for the conditions in which adaptation and test patterns were in the + locations (Fig. 1 top row); open bars, data for the conditions in which test patterns were presented in the x locations (Fig. 1 bottom row). A value greater than 1.0 indicates that adapted thresholds were greater than unadapted thresholds. Increment and decrement detection thresholds are plotted side by side to facilitate comparison. Increment jumps were in the same direction as the apparent direction of the MAE; decrement jumps were in the opposite direction. Error bars show 95% confidence limits.

the local direction and speed of motion, followed by a global mechanism that integrates such signals to represent meaningful patterns of movement.

There is now a large body of evidence, both psychophysical and physiological, supporting the existence of multiple stages of motion processing, and the present results add further behavioral evidence to support this view. Much of the support for such hierarchical organization comes from studies of motion adaptation. The present results show that MAE magnitude is greater for radial and rotational motion, consistent with the results of Steiner, Blake and Rose (1994) and the speculations of Regan and Beverly (1978), summarized in Section 1. The present study extends these findings to include periodic patterns and rotating and radiating patterns. Hershenson (1993) used a magnitude estimation scale to measure MAE, and we have taken from his results

the time at which estimates approached 0 as an indication of MAE duration. This value is approximately the same for translation and rotation. However, Hershenson's data are presented as proportions of the initial MAE strength (given an arbitrary value of unity), and it would be interesting to compare the absolute ratings for rotating patterns, for our results suggest that rotating MAE magnitude estimates might have been greater than those for translating patterns.

We also confirmed that a weak MAE can be elicited in areas of the display that were unadapted—so called phantom MAEs (Bonnet & Pouthas, 1972; Weisstein, Maguire & Berbaum, 1977; Snowden & Milne, 1997). The magnitudes of phantom MAEs were greater for rotating and radiating configurations, like the concrete MAEs in adapted locations.

3.1. Perceptual bias favouring centrifugal/foveofugal motion

Several researchers have shown a perceptual bias favouring centripetal motion (motion towards the fovea or contraction) over centrifugal motion (away from the fovea, expansion). These results include reports of a MAE of longer duration following adaptation to contracting spirals (expanding aftereffect) than expanding spirals (contracting aftereffect) (e.g. Bakan & Mizusawa, 1963; Scott, Lavender, McWhirt & Powell, 1966; Reinhardt-Rutland, 1994). The absence of a directional bias in rotating patterns (Taylor, 1963) suggests that the bias is carried by the contracting component of these patterns. Studies of the sensitivity to motion without adaptation are conflicting: while Georgeson and Harris (1978) reported that counter-phase flickering patterns appeared to expand, Edwards and Badcock (1993) reported that sensitivity to contracting dot fields was lower for contracting patterns than for expanding patterns. Similarly, reaction time and latency studies are conflicting: Mateeff and Hohnsbein (1988) and Mateeff, Yakimoff, Hohnsbein, Ehrenstein, Bohdanecky and Radil (1991) report perceptual latencies and reaction times that are shorter for motion towards the fovea, whereas Ball and Sekuler (1980) report the opposite result: motion away from fixation evoked faster reaction times, but only for horizontal motion in which case there was no difference. In many of these studies there are large differences between observers, some of whom show no effect at all, and further evidence suggests that some effects may be lost following practice (Scott et al., 1966).

In the present experiments, we found that the direction of adaptation did not noticeably affect the MAE magnitude for expanding or contracting patterns, for any of the three tasks employed. Nevertheless, it is possible that sensitivities to the different classes of motion could be different, and that this could account

for the reduced MAE magnitude for translating patterns. However, we have reported that contrast detection thresholds for the three patterns are not significantly different and that supra-threshold contrast matches among the patterns are equal (Bex et al., 1998), and so this explanation seems unlikely.

3.2. *Role of eye movements*

A potential problem in comparing the MAEs among the three classes of motion is that a translating pattern could elicit a greater tendency for an observer to make pursuit eye movements, the result being a reduction in the retinal velocity of translating patterns. No such tendency for pursuit eye movements in response to radiating patterns or rotating patterns is likely. Therefore it is possible that radial and rotational MAEs were greater than translational MAEs because the retinal motion of translational patterns was interrupted and slowed by pursuit eye movements. Consistent with this proposal is the observation that radial patterns appear to move faster than translational patterns (Geesaman & Qian, 1996; Bex & Makous, 1997); however, the same would be expected for rotational motion, but the apparent speed of translation and rotation is equal (Bex et al., 1998), and in some conditions rotation may appear slower than translation (Geesaman & Qian, 1998). All subjects were experienced psychophysical observers and were explicitly instructed to fixate a central cross, and there was no motion at the point of fixation (the center of the display was uniform); nevertheless, it is inherently more difficult to maintain steady fixation of translating patterns than the other motion patterns. We therefore attempted to test objectively whether observers did make pursuit eye movements when adapting to translation. The eye movements of a naive observer and one of the authors (PB) were recorded by an ASL eye-tracker during two 30 s adaptation periods for each pattern, as in the main experiment. Analysis of video tape recordings of the eye movements revealed that fixation was equally steady (or equally unsteady) for each class of adapting pattern. Furthermore, an independent judge was not able to indicate at greater than chance levels which pattern the observer was fixating from the pattern of eye movements alone. We conclude that observers maintained steady fixation for all conditions, and therefore our results are not an artifact of a reduction in the retinal velocity accompanying pursuit eye movements during adaptation to translation.

3.3. *Similarity of increment and decrement detection thresholds*

One persuasive explanation of the basis of MAEs concerns the relative activity of a population of directionally selective units (Barlow & Hill, 1963; Levinson

& Sekuler, 1976; Mather, 1980; Grunewald & Lankheet, 1996). In such models, it is proposed that during adaptation units selective for the direction of motion are strongly activated, supporting the percept of motion in that direction. After prolonged adaptation, these units become adapted, fatigued or habituated, while detectors tuned to different directions of motion are relatively unaffected. Immediately following adaptation, the relative activity of the adapted units falls below that of the units that were unaffected by the adaptation, and this pattern of activity is similar to that in response to real motion in the direction of the MAE. The results in Fig. 5 complicate this theory, for they show that the changes in sensitivity associated with any such changes in activity are the same in the adapted direction as those in the opposite direction.

3.4. *Jump detection thresholds to estimate MAE magnitude*

Relating thresholds to supra-threshold measures has been problematical. Typically, supra-threshold measures of MAE magnitude are subjective (e.g. duration estimation, nulling or motion matching) whereas psychophysicists strive for objective measures of perceptual events (e.g. elevation of detection thresholds). Threshold elevation aftereffects offer an objective measure of the effects of adaptation, but the decay of adaptation differs according to the technique employed to measure it (Rose, 1992). In the present study, we employed both subjective and an objective measures of MAE magnitude and, in this case, both gave the same basic result (enhanced MAEs for radiation and rotation relative to translation). However, Fig. 5 shows that translation increment and decrement thresholds were not significantly greater than thresholds without adaptation. These results suggest that there was no measurable MAE. However, in all cases a conventional MAE was clearly visible, suggesting that the jump detection task might be inappropriate for general use in estimating MAE magnitude. Nakayama (1981) has shown that (real) image motion can increase thresholds, but for slow movement, there is little change, and in some cases it can enhance the detection of motion (Hadani, Gur, Meiri & Fender, 1980; Hadani, Gur & Meiri, 1981), analogous to the classic dipper function for contrast discrimination. Indeed studies of MAE magnitude that have employed threshold elevation have typically used complex configurations of motion for adapting and test patterns (e.g. Regan & Beverly, 1978; Simpson, Newman & Aasland, 1997; Snowden & Milne, 1997). Perhaps the insensitivity to adaptation shown by the jump thresholds for translation shown here explains why these techniques have not been more widely adopted for estimating MAE magnitude.

3.5. Comparison with related psychophysical literature

Psychophysical evidence for the existence of complex motion detectors in humans requires the measurement of an effect that cannot be based on local signals alone, and the present results add to a growing body of evidence for such effects. Freeman and Harris (1992) found that direction discrimination thresholds for coherently expanding and rotating groups of dots were lower than for coherently translating groups or incoherent groups containing the same distribution of local motions, suggesting pooling of local motion signals by higher-level mechanisms sensitive to expansion and rotation. Freeman and Harris also found that the detection of rotation was unaffected by the presence of expansion and vice versa, suggesting separate mechanisms may exist for each class of global motion. However, Sekuler (1992) showed that speed discrimination thresholds for looming, rotating and translating dot patterns were the same and argued that the results required simple pooling of local motion signals without any need to invoke higher level mechanisms selective for particular configurations of motion in depth. Why speed discrimination should differ in this respect from direction discrimination and, especially, jump detection, is an outstanding question.

Morrone et al. (1995) and Burr, Morrone and Vaina (1998) have studied the perception of optic flow (radiation, rotation and translation) in random dot kinematograms that were masked into sectors of varying size. While there was little summation for contrast sensitivity across segments, signal to noise sensitivity for direction discrimination increased in a predictable way with stimulus area, up to 30–70°. The results suggest that motion in opposing directions is integrated by specialised neural mechanisms with huge receptive fields. It was argued that the difference in the spatial summation for contrast sensitivity and direction discrimination could reflect integration limitations at different stages of cortical processing—small receptive fields in V1 limit contrast sensitivity, while large receptive fields in area MSTd limiting motion integration. Similarly, Verghese and Stone (1995, 1996) have proposed that changes in speed discrimination thresholds with changes in pattern configuration implicate high-level image segmentation processes in speed encoding. Gurney and Wright (1996) used stimuli similar to ours to compare detection and direction identification thresholds for radiation and rotation. Equivalence of these thresholds implies the existence of labeled detectors (Watson & Robson, 1981). Their results showed that detection and identification thresholds were approximately equal and were taken as evidence for labeled detectors for radiation and rotation. Recently, it has been shown that the apparent speed of translating patterns is approximately equal to that of rotating

patterns (Bex et al., 1998), but is slower than that of radial patterns of noise (Geesaman & Qian, 1996) or gratings (Bex & Makous, 1997) even though the *local* speed signals for all patterns were the same. The results have been interpreted as evidence that higher level mechanisms, such as cells in area MSTd, work with input from local unidirectional motion signals, but the rules for combining the local motion inputs depend on the configuration of the local motions. It has been speculated that the increased apparent speed of radial patterns could be a consequence of the greater number of cells in area MSTd that respond to expansion (Geesaman & Qian, 1996), or alternatively the bias could be the manifestation of some low level encoding of the speed of motion in depth (Bex & Makous, 1997; Bex et al., 1998).

Other studies of interactions among local motion detectors include studies of global motion perception in random dot kinematograms. Smith, Snowden and Milne (1994) argued that, in principle, global motion perception in random walk kinematograms could be mediated by co-operative interactions among local motion detectors with small receptive fields, or by single motion detectors with large receptive fields. However, they were able to rule out the latter hypothesis by showing that the perception of global motion was unimpaired when the patterns were high-pass filtered. This finding confirms that global motion must be mediated by co-operative interactions among local motion detectors selective for high spatial frequencies.

3.6. Relation to electrophysiological studies of primate visual cortex

Neurophysiological observations in primates suggest that local motion analyzers lie at the bottom of a hierarchical arrangement of motion sensitive mechanisms (Van Essen, Anderson & Felleman, 1992). Simple translational motion is encoded in the first stage of cortical processing (V1), where many cells respond selectively to direction of motion. Such uncomplicated directional selectivity is maintained in neurons throughout the next four levels in the hierarchy (up to area MT), with a concomitant sharpening of speed tuning and large increase in receptive field area (Maunsell & Van Essen, 1983; Saito, Yuki Tanaka, Hikosaka, Fukada & Iwai, 1986; Pasternak, Maunsell, Polashenki & Merigan, 1991). At the next level (MSTd), cells become selective for more complex forms of pattern movement, such as the radial or rotational motion associated with optic flow (Tanaka & Saito, 1989; Duffy & Wurtz, 1991; Graziano, Andersen & Snowden, 1994; Orban, Lagae, Raiguel, Xiao & Maes, 1995). Specialization of response selectivity at later stages of visual processing is not unique to primate visual systems; selectivity for complex patterns of motion has

also been reported for cells in the lateral suprasylvian area of the cat (Kim, Mulligan & Sherk, 1997; Mulligan, Kim & Sherk, 1997) and for inter-neurons in the third visual neuropile of the blowfly (Krapp & Hengstenberg, 1996), where cells with large receptive fields respond selectively to optic flow components. In the present study, we recorded MAEs in unadapted retinal locations, and the magnitude of the MAE was greater for rotating and radiating patterns than for translating patterns. Our finding is consistent with such neurophysiological evidence that receptive field size and pattern specialization increase at higher levels of visual processing. The increasing selectivity for particular configurations of motion at larger spatial scales implies a functional hierarchy that integrates local motion signals into a representation of optic flow and the movement of real objects.

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