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Displacement limit (*d*max) of sampled directional motion: Direct and indirect estimates

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The maximum displacement at which directional motion can be seen, known as *d*max, has been said to define the spatial limits of the short-range motion system. Turano and Pantle (1985) used duration of motion aftereffect (MAE) to estimate the spatial limit of the short-range system, the assumption that *d*max (a direct measure of motion perception) and MAE (an indirect measure) are equivalent indices of the same underlying perceptual process. In a series of four experiments, we examined this assumption by measuring *d*max and duration of MAE across a range of displacements, stimulus waveforms (sine- or square-wave gratings), and spatial frequencies. We found that *d*max and duration of MAE were affected differently by changes in the same variables. Therefore, we concluded that the two indices cannot be regarded as equivalent measures of the spatial limits of the short-range process. Two novel effects that separated MAE from motion detection are described, and suggestions for exploring them are outlined.

Apparent motion can be produced with a simple display sequence comprising a leading frame (F1) and a trailing frame (F2) identical to F1 except for a small unidirectional displacement of the contents of the image. Under appropriate spatiotemporal conditions, motion is seen in the direction of the displacement. The largest displacement at which directional motion can be seen is known as *d*max, and it has been taken as the spatial limit of a motion system designated as "short-range" (see, e.g., Baker & Braddick, 1985). Random-dot images have been used frequently to study short-range motion (e.g., by Braddick, 1974). However, other stimuli such as sinusoidal gratings (Bischof & Di Lollo, 1990; Nakayama & Silverman, 1985) and band-pass filtered images (Bischof & Di Lollo, 1990; Chang & Julesz, 1985; Cleary & Braddick, 1990a), have been used to define the spectral composition of the stimuli more stringently and hence the spatial characteristics of the short-range motion system.

Estimates of *d*max have been obtained most commonly with direct methods, in which observers are required to detect the direction of motion of the stimuli. Indirect methods, however, have also been used, as was done by Turano and Pantle (1985) with duration of motion aftereffects (MAE). Duration of MAE is presumed to reflect the degree of adaptation of the directionally selective mechanisms that underlie perception of motion. The stimuli used by Turano and Pantle were vertical sine-wave or square-wave gratings shown in a multiple-frame sequence. Successive frames were displaced by the same amount in a given direction to produce the appearance of motion. The moving gratings were displayed for a period sufficient to produce a measurable MAE. The objective of the work was to study the spatiotemporal limits of the short-range process in terms of duration of MAE. Although no quantitative rule was provided, the largest displacement that produced a measurable MAE was regarded as an index of *d*max.

Crucial to this method is the assumption that the spatiotemporal limits inferred indirectly from MAE are based on precisely the same short-range mechanisms as those that are tapped by direct methods such as detection of directional motion. As noted by Turano and Pantle (1985), the simplest way of verifying this assumption is to demonstrate that *d*max and duration of MAE respond in similar ways to changes in a given independent variable.

Overall, the results obtained by Turano and Pantle (1985) justify the conclusion that direct and indirect methods yield homologous estimates of the limits of the short-range motion process. This conclusion is consistent with the inference that the two types of measure reflect the activity of common underlying mechanisms.

One aspect of Turano and Pantle's (1985) findings that is of particular relevance to the present investigation must be considered in some detail. With sine-wave gratings, Turano and Pantle found the displacement limit (indirectly estimated through MAE) to be just short of half the period of the grating. This finding is in accordance with direct estimates of *d*max (Bischof & Di Lollo, 1990; Nakayama & Silverman, 1985). However, an unexpected result was obtained with square-wave gratings: at a displacement of ¼ cycle (a displacement that yielded substantial MAE with sine-wave gratings), MAE was completely absent.

An account of this result was offered in terms of conflicting motion signals produced by the fundamental and the harmonic frequencies of the square-wave grating. That

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is, at a displacement of ¼ cycle, the fundamental frequency (f) and every alternate odd harmonic (5f, 9f, etc.) produce optimal stimulus conditions for perceiving motion in the "correct" direction. At the same time, the third harmonic (3f) and every alternate odd harmonic (7f, 11f, etc.) produce optimal stimulus conditions for perceiving motion in the opposite ("incorrect") direction. Turano and Pantle (1985) made two further observations: first, that the saturation threshold for contrast in the human motion system is very low; and, second, that the energy of a harmonic decreases as its frequency increases, such that harmonics much above 5f would probably not reach threshold. Therefore, the bulk of the contribution toward adaptation of the directional motion sensors is made by the fundamental frequency and the first two or three odd harmonics (i.e., f, 3f, 5f, and 7f). On the assumption that all frequencies that exceed saturation-threshold contribute equally to adaptation, Turano and Pantle concluded that, at a displacement of ¼ cycle with square-wave gratings, adaptation occurs equally in motion sensors tuned to either direction of motion, with consequent nulling of MAE. An argument along similar lines was used to explain why MAE of duration similar to that found with sine-wave gratings was obtained with square-wave gratings at displacements of ⅛ (and, by inference, ⅜) cycles.

In the course of studying detection of directional motion, we came across evidence that seemed inconsistent with the result from Turano and Pantle's (1985) that we have described above. We found direct estimates of *d*max to be quite comparable, whether obtained with sine-wave or with square-wave gratings. This was true even with stimulus parameters (spatial frequency of 2 cpd, displacement of ¼ cycle) that yielded substantial differences between the two waveforms in Turano and Pantle's study. This discrepancy is potentially interesting. If confirmed, it would question the equivalence of direct and indirect measures of the short-range process, and it would broach the possibility that the two measures might tap separate motion mechanisms, affected in different ways by the intensity profile of the stimulus.

To elucidate these issues, two sets of comparisons would be helpful. First, differences in *d*max obtained with sine-wave and square-wave gratings should be examined systematically both with direct and with indirect measures. Second, direct and indirect estimates of the spatial limit of directional motion perception should be compared, preferably with the same observers and with the same display equipment. Turano and Pantle's (1985) experiment did not include direct estimates of *d*max, and, although sine-wave gratings were varied over comprehensive ranges of spatial frequencies and displacements, this was not done with square-wave gratings.

In the present work (Experiment 1), we replicated and extended Turano and Pantle's (1985) experiments by estimating duration of MAE with sine-wave and square-wave gratings over a common range of displacements and spatial frequencies. In addition (Experiment 2), we obtained direct estimates of *d*max with both waveforms through detection of directional motion over the same range of frequencies. Our results confirmed those of Turano and Pantle with sine-wave gratings. However, the results with square-wave gratings could not be explained in terms of conflicting motion signals, as proposed by Turano and Pantle. In further experiments, we found marked differences between direct (*d*max) and indirect (MAE) estimates that clearly implicate nonequivalent underlying mechanisms.

EXPERIMENT 1

The stimuli in Experiment 1 were either sine-wave or square-wave gratings displayed at each of four spatial frequencies and at each of four displacements. With both types of gratings, we obtained estimates of duration of MAE. As far as was practicable, we endeavoured to duplicate the display conditions of Turano and Pantle (1985).

Method

Observers. Seven paid graduate and undergraduate students, naive with respect to the purpose of the study, served as observers. All were practiced psychophysical observers, and all had normal or corrected-to-normal vision.

Stimuli and Procedures. All stimuli were generated by an Innisfree Picasso CRT image synthesizer, and they were displayed on a Hewlett-Packard 1333A oscilloscope equipped with P15 phosphor. The frequency of the image synthesizer was set at 100 Hz; thus, it took 10 msec to display one complete image. The stimuli were displayed within a 7×7 cm area at the center of the screen. From the viewing distance of 1 m, set by a headrest, the display area subtended a visual angle of 4°. The observer sat facing the oscilloscope in a dimly lit testing room. A hand-held box containing five pushbuttons permitted the observer to initiate the displays and to enter the responses. All timing and control functions were performed by a computer.

The stimuli were either sine-wave or square-wave gratings, displayed at one of four spatial frequencies: ½, 1, 2, and 4 cpd. Any one trial consisted of a multiframe display of a grating of given waveform and spatial frequency. To produce the appearance of motion, the grating in each successive frame was displaced in a fixed direction by one of four horizontal displacements: ⅛, ¼, ⅜, or ½ cycles. The direction of the displacement (left or right) was decided randomly on each trial. The exposure duration of a single frame was 30 msec (i.e., the image was refreshed three times). Within a multiframe sequence, each successive frame was displayed immediately upon termination of the preceding frame, without any interframe interval. In every case, the space-average luminance of the screen was 12 cd/m^2. The Michelson contrast was 30% for sine-wave gratings, and 23.5% for square-wave gratings, which made the amplitude of the fundamental component equal to that of the corresponding sine-wave grating.

The experimental design was a 2 (sine- or square-wave gratings) × 4 (spatial frequencies) × 4 (displacements) factorial. In any given session, waveform and spatial frequency were held constant, and three estimates of the duration of MAE were taken at each of the four displacements. Thus, one session contained 12 separate trials, 3 at each displacement. Each observer served in a total of eight sessions, one at each combination of waveform and spatial frequency. To minimize the build-up of adaptation over trials, we followed Turano and Pantle's (1985) procedure of introducing a 90-sec pause between successive trials within a session. Also, the direction of apparent motion of the adapting grating was alternated in successive trials.

Each trial consisted of two parts: the adaptation period, during which the observer fixated a moving grating, and a test period, during which the observer fixated the same, but stationary, grating. In the test period, MAE was seen as an apparent drift of the stationary grating in the direction opposite to the direction of motion during adaptation. At the beginning of a trial, the screen contained a grating of the appropriate waveform and spatial frequency and a central dark fixation dot, approximately 20 arc min in diameter. Upon a buttonpress by the observer, the grating began to move at the appropriate displacement, with the fixation dot remaining stationary. After 48 sec, the grating stopped and the fixation dot disappeared from the screen. This was done because, in preliminary trials, the fixation dot seemed to interfere with the perception of MAE. The observer continued to fixate the stationary grating until all appearance of directional motion (MAE) had stopped; then the observer pressed a button to indicate the cessation of MAE. The observer was instructed to wait for a brief interval (a few seconds) before pressing the button after the cessation of MAE. This was done because, on occasions, the apparent drift of the stationary grating seemed to stop briefly before starting again. No MAE was ever seen with displacements of ½ cycle, but the observer was instructed to delay the buttonpress by the same brief interval that had been allowed to elapse after cessation of MAE with the other displacements. The net duration of MAE for each displacement was calculated by subtracting the mean duration of the interval obtained with the ½-cycle displacement from the mean estimates obtained with each of the other three displacements.

Results

Mean durations of MAE in relation to displacement and spatial frequency are illustrated in Figure 1 for both sine-wave and square-wave gratings. In all statistical analyses, displacement was considered to vary over only three levels. That is, as mentioned above, the score obtained at a displacement of ½ cycle was used as a correction factor to calculate MAE scores for the remaining three displacements. Therefore, the scores for ½-cycle displacements were not included in the analyses.

An analysis of variance showed that all three main effects were significant: spatial frequency [$F(3,6) = 15.19$, $p < .001$], waveform [$F(1,6) = 16.75$, $p < .01$], and displacement [$F(2,6) = 5.44$, $p < .05$]. Also significant were two interaction effects: frequency × waveform [$F(3,18) = 11.32$, $p < .001$], and waveform × displacement [$F(2,12) = 4.69$, $p < .05$].

Discussion

Markedly different patterns of results were obtained with the two stimulus waveforms. Sine-wave gratings produced a close replication of Turano and Pantle's (1985) results (Figure 1, left panel): in both our experiment and theirs, duration of MAE decreased as displacement increased, with spatial frequency having no discernible effect. With square-wave gratings, on the other hand, spatial frequency had a powerful and systematic effect on duration of MAE (Figure 1, right panel).

A discrepancy should be noted between the present results and the corresponding results of Turano and Pantle (1985) with square-wave gratings of 2 cpd at a displacement of ¼ cycle. In contrast to the substantial duration of MAE obtained in the present work (Figure 1, right panel), no MAE was found in Turano and Pantle's study (1985, Figure 2). However, the discrepancy is due entirely to differences in the display phosphors used in the two studies (P15 in ours, P31 in Turano and Pantle's). Turano and Pantle's results were duly replicated when we repeated the experiment with a display oscilloscope equipped with P31 phosphor (see Experiment 4). A sug-

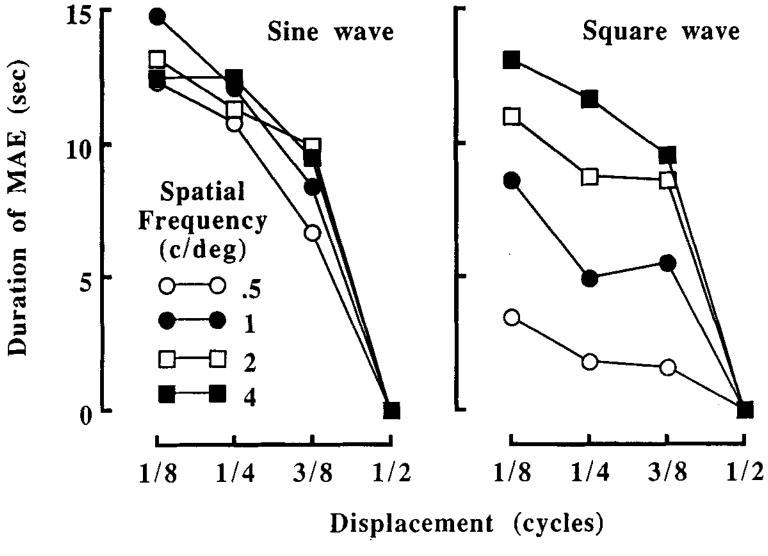

Figure 1. Duration of motion aftereffect (MAE) as a function of displacement and spatial frequency for sine-wave gratings (left panel) and for square-wave gratings (right panel). Each symbol represents the mean of 3 trials for each of 7 observers (21 trials in all). For each observer, the duration of MAE at each of the three shortest displacements consisted of the score for that displacement minus the score for the ½-cycle displacement, at which directional motion was never seen.

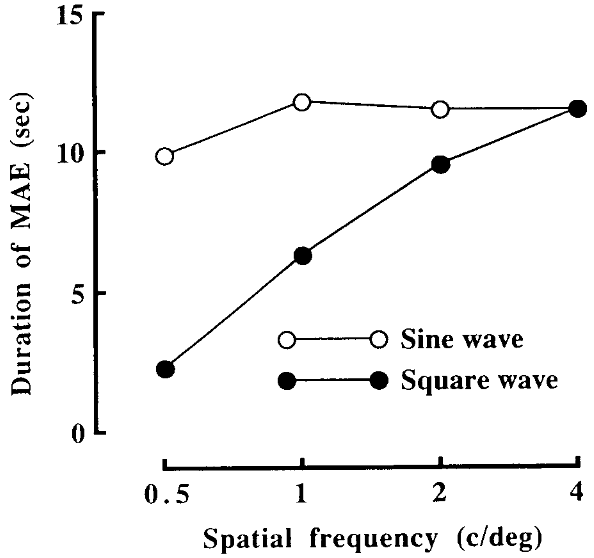

Figure 2. Duration of motion aftereffect (MAE) as a function of waveform and spatial frequency. Each value was derived from the results illustrated in Figure 1, by averaging over the three shortest displacements in the corresponding combination of waveform and spatial frequency.

gested account of the phosphor specificity of this result is presented in Experiment 4.

Figure 2 shows the combined effects of waveform and spatial frequency on duration of MAE. As well as illustrating the highly significant frequency × waveform interaction, the information in Figure 2 serves as the basis for comparing the indirect estimates of Experiment 1 with the direct estimates of Experiment 2.

An account of the differences illustrated in Figure 2 is best postponed to Experiment 3. However, it should be stressed that the results obtained with square-wave gratings (Figure 1, right panel, and Figure 2) are beyond what can be explained in terms of conflicting motion signals alone (Turano & Pantle, 1985). Turano and Pantle's hypothesis has been described above and need not be repeated. Suffice it to say that, at a displacement of ¼ cycle, no MAE should be expected at any spatial frequency, yet duration of MAE is seen to vary substantially with spatial frequency (Figure 1, right panel). Other factors are clearly responsible for these differences. The influence of one such factor is examined in Experiment 3.

A potential ambiguity in interpreting the significant effect of displacement should be noted. Of necessity, changing the extent of displacement produced concomitant changes in the temporal frequency of the display. In practice, the gratings appeared to move faster as displacement was increased. Therefore, the decrement in duration of MAE illustrated in Figure 1 (left panel) could conceivably be attributed to temporal rather than—or as well as—spatial factors (e.g., Pantle, 1974). However, the outcomes of two investigations, specifically designed for this purpose, all but discount the temporal option. Under display conditions similar to ours, Baker, Baydala, and Zeitouni (1989) and Turano and Pantle (1985) varied temporal frequency while holding displacement constant and found that, within the salient range, temporal frequency had a negligible effect on duration of MAE.

Differences in the phenomenal appearance of the moving displays during the adaptation period should be noted. When in motion, sine-wave gratings did not change noticeably in overall appearance: they were seen simply as drifting sine-wave gratings. By contrast, the appearance of square-wave gratings changed quite dramatically. Instead of the alternating light and dark vertical bands seen in stationary gratings, observers saw narrower bands of different gray levels, all moving together in the same direction. In addition, a much dimmer, higher frequency grating was seen sporadically as drifting in the opposite direction when the displacement was ¼ cycle. The latter was noted by Turano and Pantle (1985), who regarded it as corroborative of their account of the absence of MAE with ¼-cycle displacements. The former is a far more stable and compelling effect. It was seen throughout the adaptation period, at all displacements, and it was particularly strong at the lower spatial frequencies. As was done in Experiment 3, this effect can be used as a source of conjectures for studying the effect of stimulus waveform on duration of MAE.

Before following this line of inquiry, however, we proceeded to check whether direct estimates of *d*max would yield results comparable to those obtained with duration of MAE in Experiment 1. This was done in Experiment 2.

EXPERIMENT 2

The main objective of Experiment 2 was to obtain estimates of *d*max for directional motion with stimuli and conditions that duplicated closely those of Experiment 1.

Method

Data were collected from the same 7 observers who had served in Experiment 1. The stimuli and procedures were the same as in Experiment 1, with the following exceptions. On any one trial, the display consisted of a motion sequence of eight successive frames containing a grating of given waveform and spatial frequency, with direction of motion (left or right) chosen randomly on each trial. The observer pressed a button to initiate a display, and then responded with one of two buttons to indicate the direction of motion. It should be noted that the display sequence commonly used to study sampled motion consists of only two frames (e.g., see Baker & Braddick, 1985; Bischof & Di Lollo, 1990; Chang & Julesz, 1985). In the present work, we opted for a sequence of eight frames to obviate possible effects of temporal aliasing (cf. Cleary, 1990; Derrington & Goddard, 1989).

As in Experiment 1, the design was a 2 (sine- or square-wave gratings) × 4 (spatial frequencies) × 4 (displacements) factorial. The displacements used in Experiment 2 were $^{12}/_{32}$, $^{13}/_{32}$, $^{14}/_{32}$, and $^{15}/_{32}$ cycles. Preliminary trials had shown that the displacements used in Experiment 1 (⅛, ¼, and ⅜ cycles) yielded virtually errorless detection of directional motion at all spatial frequencies and waveforms. The larger displacements and smaller steps employed in Experiment 2 permitted *d*max to be estimated with finer resolution. One session comprised 200 trials, 50 at each displacement, in random sequence. Each observer served in a total of 8 sessions, one at each combination of waveform and spatial frequency.

Results

In this experiment, *d*max was defined as the displacement that produced 80% correct detections of directional motion. Eight values of *d*max were computed for each observer, one for each combination of waveform and spatial frequency. Unless a given displacement yielded precisely 80% correct responses, values of *d*max were computed by interpolation. Performance was never lower than 80% at the smallest displacement. In a few cases, performance at the largest displacement ($^{15}/_{32}$ cycles) exceeded 80%. In those cases, *d*max was obtained by interpolation between that score and the theoretically expected score of 50% at a displacement of ½ cycle (i.e., the displacement at which the grating reaches counterphase and at which the directional motion signal becomes entirely ambiguous). It should be noted that expressing the scores in terms of *d*max effectively eliminated displacement as a factor and reduced the experimental design to a 2 (waveforms) × 4 (spatial frequencies) factorial.

Mean values of *d*max for each combination of waveform and spatial frequency are shown in Figure 3. An analysis of variance performed on the individual scores revealed a significant effect of spatial frequency [$F(3,6) = 7.31, p < .01$]. Neither the effect of waveform [$F(1,6) = 0.18, p > .1$] nor the interaction effect [$F(3,18) = 0.97, p > .1$] approached significance.

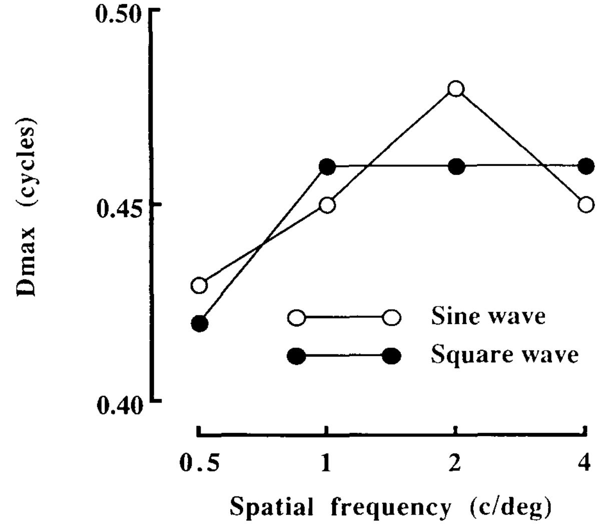

Figure 3. Values of *d*max as a function of waveform and spatial frequency. Each symbol represents the mean of the *d*max values of 6 observers.

Discussion

With the exception of the lowest spatial frequency, the *d*max values in Figure 3 are essentially the same for all frequencies and waveforms. Very similar results have been reported by Bischof and Di Lollo (1990). The lower values obtained at a spatial frequency of ½ cpd is likely due not to low spatial frequency but to the fact that the images contained only two cycles of the gratings. It is known that perception of both directional motion and contrast sensitivity is adversely affected if the grating contains less than about three cycles per image (Bischof & Di Lollo, 1990; Hoekstra, van der Goot, van den Brink, & Bilsen, 1974). At any rate, it is clear from Figure 3 and from the statistical analysis that detection of directional motion was the same with sine- and square-wave gratings at all spatial frequencies.

For the purpose of the present work, the comparison of principal interest is that between Figures 2 and 3. Substantial differences between the two patterns of results are immediately obvious. Notably, the marked differences between the curves for sine- and square-wave gratings for MAE (Figure 2) are totally unmatched in the corresponding curves for motion detection (Figure 3). On the basis of this comparison, it must be concluded that stimulus waveform has a pronounced effect on duration of MAE but not on detection of directional motion.

On the face of it, this conclusion has potentially weighty implications. As noted in the introduction, it is generally agreed (e.g., by Turano & Pantle, 1985) that if duration of MAE is to be regarded as a metric equivalent to *d*max for studying the limits of the short-range motion process, it must be shown that estimates obtained in terms of MAE behave in the same way—and respond similarly to the same variables—as estimates obtained with direct methods, notably detection of directional motion. This is clearly not the case when the indirect estimates in Figure 2 are compared with the direct estimates in Figure 3.

It must be stressed that the two sets of data were obtained with the same observers and under viewing conditions that were as similar as we could make them. Indeed, for the first 240 msec of each trial, the displays for MAE and for motion detection were identical not only on the screen but also in phenomenal appearance. That is, the peculiar appearance of moving square-wave gratings noted in the MAE displays of Experiment 1 (narrow vertical bands of different gray levels, moving in a uniform direction) was maintained in the motion-detection displays of Experiment 2. Yet, similarities notwithstanding, stimulus waveform affected duration of MAE and detection of directional motion in substantially different ways.

A possible source of confounding in comparing the outcomes of Experiments 1 and 2 (Figures 2 and 3) should be considered. The range of displacements of the stimuli differed between the two experiments: the MAE values obtained in Experiment 1 (Figure 2) were based on displacements ranging from ⅛ to ⅜ cycles. By contrast, the *d*max values obtained in Experiment 2 (Figure 3) were based on displacements ranging from ⅜ to $^{15}/_{32}$ cycles. Smaller steps were used in Experiment 2 to increase the resolution of the estimates of *d*max. Nevertheless, the option must be considered that the different outcomes of the two experiments might have been due, at least in part, to differences in the ranges of displacements. This option can be examined by comparing duration of MAE and values of *d*max based exclusively on the displacement that was common to both experiments, namely ⅜ cycles.

We recomputed mean durations of MAE, using only the data for displacements of ⅜ cycles in Experiment 1. As might be surmised from Figure 1, the absolute level of the two curves was slightly lower than in Figure 2, but the relation between them (notably the interaction between spatial frequency and waveform) remained the same. We also recomputed mean values of *d*max, using only the data for displacements of ⅜ cycles in Experiment 2. As was the case for MAE, the values of *d*max were uniformly lower than those seen in Figure 3. However, the two curves (sine- and square-wave) remained parallel throughout the domain, confirming the absence of an interaction effect between spatial frequency and waveform. Thus, the same patterns of results are obtained when differences in range of displacements are eliminated. On this basis, we can be confident that range of displacements was not a major determinant of the results illustrated in Figures 2 and 3.

Unquestionably, this pattern of results offers prima facie evidence for the option that MAE and detection of directional motion are mediated by nonidentical underlying processes. This line of reasoning is pursued further in the general discussion, after some empirical hunches are examined in Experiment 3, as to why square-wave and sine-wave gratings produce different durations of MAE.

EXPERIMENT 3

Why do square-wave gratings of low spatial frequency yield shorter durations of MAE than do corresponding sine-wave gratings? We noted earlier (and we elaborate in Experiment 4) that Turano and Pantle's (1985) account in terms of conflicting motion signals is not sufficient.

We believe that development of a tenable theoretical account would be facilitated if more information were available regarding the phenomenal appearance of the displays. As noted above, moving low-frequency square-wave gratings took the appearance of a series of vertical bars of considerably higher spatial frequency than the fundamental frequency of the grating, all moving in the same direction. Intensity appeared to be uniform within each bar, but varied between adjacent bars. Whether this appearance was due to energy summation on the screen, or to temporal summation within the visual system, is an issue that is considered later.

Perhaps the most prominent feature of such displays was the presence of sharp and distinct edges that separated adjoining vertical bars. The distinctiveness of the edges was greatest at the lowest spatial frequency of the grating; it diminished as spatial frequency increased. At the highest frequency (4 cpd), the edges were virtually invisible, and moving square-wave gratings had essentially the same appearance as moving sine-wave gratings. Reduced visibility of the edges at the higher spatial frequencies is in accordance with the contrast sensitivity function, which shows markedly reduced sensitivity to the corresponding spatial frequencies (cf. Bischof & Di Lollo, 1990). Although directional motion was clearly seen in the whole display, the edges between adjoining bars were seen as stationary. The display could best be described as consisting of a grid of stationary vertical lines, with bars of different gray levels moving between them.

The present experiment was an attempt to examine the role of these edges in reducing the duration of MAE. As a first approximation, we asked whether the mere presence of a grid of stationary vertical lines placed on the screen would reduce the duration of MAE obtained with sine-wave gratings. In accordance with the overall objectives of the present work, we also asked whether the same grid would affect detection of directional motion. The answer was as decisive as it was unexpected: detection of directional motion was somewhat facilitated by the grid lines, but MAE was totally eliminated.

Method

Data were collected from 6 of the 7 observers who served in Experiments 1 and 2. The stimuli consisted exclusively of sine-wave gratings with spatial frequency of ½ cpd. The gratings were viewed as in the previous experiments, except that a grid of thin vertical lines had been placed on the screen. The lines, drawn in black ink on a transparent film, were approximately 2 arc min thick and were spaced at intervals of ½°. Both duration of MAE and detection of directional motion were estimated in Experiment 3, as follows.

Duration of MAE. Duration of MAE was estimated under two viewing conditions. One was a direct replication of the corresponding condition in Experiment 1, but with the addition of the grid lines during both adaptation and testing periods. In the other condition, the grid was presented during the adaptation period but not during the testing period. In this condition, the transparent film containing the grid lines was swiftly removed from the screen by the experimenter at the instant the grating stopped moving and the fixation dot disappeared.

Detection of directional motion. There were two conditions. The first was a direct replication of the corresponding condition in Experiment 2 (sine-wave grating of ½ cpd, no grid lines). The second condition was the same as the first, except that viewing took place with the grid lines in place on the screen. In every other respect, the relevant procedures in Experiments 1 and 2 were followed in Experiment 3.

Results

Mean durations of MAE are shown in Figure 4 for the two MAE conditions of Experiment 3. Also shown in Figure 4 are the corresponding mean durations of MAE obtained in Experiment 1 by the same 6 observers; these provide a direct basis for comparison. As in Experiment 1, only three levels of displacement, ⅛, ¼, and ⅜ cycles, were included in the statistical analyses.

An analysis of variance revealed a significant effect of grid (grid during adaptation and testing, grid during adaptation only, no grid) [$F(2, 10) = 13.51, p < .01$], a significant effect of displacement [$F(2,10) = 7.58, p < .01$], and a significant interaction [$F(4,20) = 8.95, p < .001$].

Mean percentages of correct responses in identifying directional motion are shown in Figure 5. An analysis of variance performed on the individual scores revealed a significant effect of the grid [$F(1,5) = 16.55, p < .01$], a significant effect of displacement [$F(3,15) = 78.55, p < .001$], and a significant interaction effect [$F(3,15) = 3.99, p < .05$]. Individual values of *d*max were calculated for both conditions as in Experiment 2. The mean values of *d*max were: .46 cycles (with grid) and .43 cycles (without grid). An analysis of variance performed on the individual values showed that *d*max was significantly greater when the gratings were viewed through the grid lines [$F(1,5) = 17.24, p < .01$].

Discussion

Addition of the grid lines produced unambiguous—if unexpected—results. Perhaps the most striking outcome was the diametrically opposite effect of the grid on duration of MAE and on detection of directional motion. This is another instance (see the discussion of Experiment 2) of a variable that affects direct and indirect estimates of motion perception in different ways. To the extent that duration of MAE and detection of directional motion are affected differently by the same variable (i.e., presence of the grid), they must be regarded as being based on separable underlying processes. The implications of this conclusion are pursued in the general discussion.

Why was MAE drastically reduced or totally eliminated by the presence of the grid? And, just as importantly, can the reduction in MAE seen in Experiments 1 (with square-wave gratings) and 3 (with grid-lines) be regarded as instances of the same class of events? At this stage, even tentative answers to these questions are likely to be inconclusive. At present, we need systematic investigations to identify just what attributes of the grid lines are effective in reducing the duration of MAE.

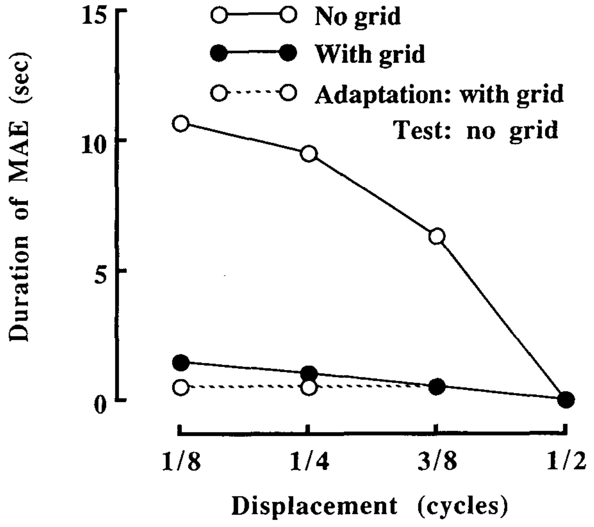

Figure 4. Duration of motion aftereffect (MAE) in relation to displacement and grid condition, as indicated in the legend. The stimuli were sine-wave gratings of spatial frequency equal to ½ cpd. Each point represents the mean of three trials for each of 6 observers (18 trials in all). The results illustrated in the no-grid condition (open symbols, continuous lines) were obtained in Experiment 1 by the same observers.

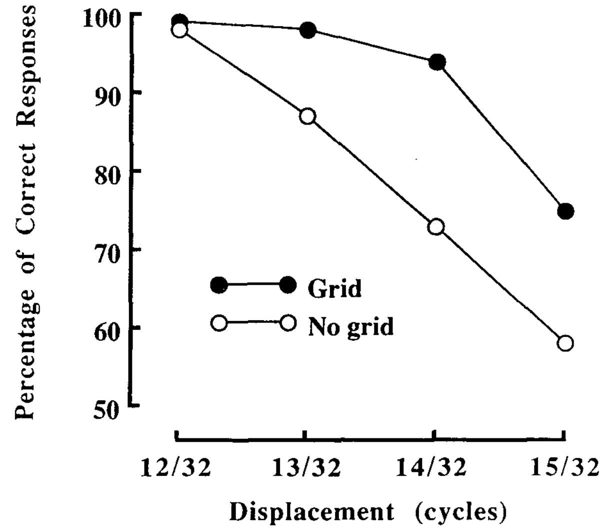

Figure 5. Percentage of correct responses in detection of directional motion in relation to displacement and grid condition. The stimuli were sine-wave gratings of spatial frequency equal to ½ cpd. Each point is based on 50 observations by each of 6 observers.

One example of such investigations is provided by the condition in which the grid lines were presented only during the adaptation period. The outcome shows that absence of MAE was due not to any spatial reference provided by the grid lines during the testing period, but to (as yet unknown) perceptual events taking place during adaptation. In the same vein, we ran informal trials with grid lines oriented horizontally on the screen, and we found duration of MAE to be substantially longer than with no grid lines. Clearly, orientation of the grid lines relative to the orientation of the grating is an important variable, but the systematic work remains to be done. The same can be said for the relation between spatial frequency of the grid and that of the grating.

In contrast to duration of MAE, detection of directional motion was enhanced by the grating. This effect could be related to the finding that threshold velocity is lowered if stationary grid lines are superimposed on a moving display (Leibowitz, 1955). It must be noted, however, that this finding relates to *d*min (the minimum displacement required for detection of motion) rather than to *d*max. Just as was the case with MAE, little can be said about this effect without further investigation.

Although a systematic examination of the effects of the grid on MAE and on motion detection was clearly indicated, it was beyond the scope of the present work. However, there was one issue that came within the ambit of the present work and that required investigation. It regarded the specific discrepancy, noted above, between our results with square-wave gratings (Experiment 1) and the corresponding results of Turano and Pantle (1985). This discrepancy was examined in Experiment 4.

EXPERIMENT 4

Duration of MAE with square-wave gratings was studied by Turano and Pantle (1985) only at a spatial frequency of 2 cpd and at displacements of ⅛ and ¼ cycles. Their results and ours agree remarkably well at a displacement of ⅛ but not of ¼ cycles (see Turano & Pantle's Figure 2, as well as our Figure 1, right panel). That is, while a displacement of ⅛ cycle yielded a substantial MAE in both studies, a displacement of ¼ cycle yielded substantial—albeit slightly reduced—MAE in our study but no MAE at all in Turano and Pantle's. It has already been noted that this pattern of results cannot be explained in terms of conflicting motion signals generated by the fundamental and harmonic frequencies of square-wave gratings.

An alternative account, capable of accounting for both sets of results, can be couched in terms of the detrimental effect of sharp edges on MAE, as seen in Experiment 3. We make the plausible assumption that the effect becomes stronger as the edges become more visible. In turn, we suggest that the edges were more visible in Turano and Pantle's study than in ours, because of longer phosphor persistence; Turano and Pantle (1985) used P31 phosphor, whose persistence is longer than the persistence of P15 phosphor by a factor of about 15 (Bell, 1970). Because of the longer persistence of P31 phosphor, it is possible that the edges of a square-wave grating in a given screen location may not have faded completely before being repainted in succeeding frames of the motion sequence. This would produce a set of stationary edges similar to those used in Experiment 3. As is explained below, this effect would occur with greater strength at a displacement of ¼ cycle than at ⅛ or ⅜ cycles. The upshot would be that the greater visibility of the edges would reduce the duration of MAE obtained at a displacement of ¼ cycle with P31 phosphor. A similar effect would not occur with P15 phosphor, because of its very short persistence.

To test this hypothesis, in Experiment 4, we replicated the relevant conditions of Experiment 1 and of Turano and Pantle (1985). However, instead of using P15 phosphor as in Experiment 1, we used an oscilloscope equipped with P31 phosphor, as used by Turano and Pantle.

Method

Data were collected from the same 6 observers who served in Experiment 3. The stimuli and procedures were the same as in Experiment 1, with the exception that only one spatial frequency, 2 cpd, was used with both sine-wave and square-wave gratings. All stimuli were displayed on a Kikusui COS-1711 oscilloscope equipped with P31 phosphor.

Results

Mean durations of MAE are shown in Figure 6 (left panel). Shown in the right panel of Figure 6 are the corresponding mean durations of MAE obtained in Experiment 1 by the same 6 observers: these provided a basis for comparing the results obtained with P15 and with P31

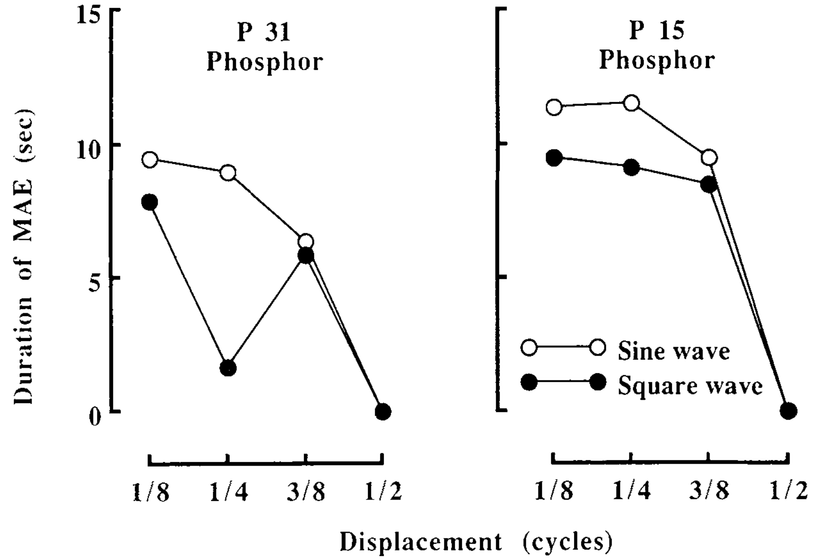

Figure 6. Duration of motion aftereffect (MAE) in relation to displacement, waveform, and type of phosphor. The spatial frequency of the sine-wave grating (open symbols) and the fundamental frequency of the square-wave grating (filled symbols) was 2 cpd. Each point represents the mean of three trials for each of 6 observers (18 trials in all). The results illustrated in the right panel (P15 phosphor) were obtained in Experiment 1 by the same observers whose results in Experiment 4 are illustrated in the left panel (P31 phosphor). The rate of decay is approximately 15 times faster for P15 than for P31.

phosphor. As in Experiments 1 and 3, only three levels of displacement—⅛, ¼, and ⅜ cycles—were included in the statistical analysis.

An analysis of variance on the scores obtained with P31 phosphor (Figure 6, left panel) revealed a significant effect of waveform [$F(1,5) = 16.48, p < .01$] and a significant interaction between waveform and displacement [$F(2,10) = 4.13, p < .05$]. The same analysis performed on the scores obtained with P15 phosphor (Figure 6, right panel) yielded no significant effects.

Discussion

A sharp decrement in duration of MAE at a displacement of ¼ cycle is clearly evident in the left panel of Figure 6, and it is confirmed by the significant interaction between waveform and displacement. No such effect is evident in the right panel of Figure 1. Thus, the large decrement in duration of MAE reported by Turano and Pantle (1985) was replicated in the present work with P31 but not with P15 phosphor. This pattern of results is precisely what might be expected on the basis of the hypothesis outlined above: sharp edges in the display have a detrimental effect on MAE, and the visibility of the edges is enhanced by the long persistence of P31 phosphor.

A second aspect of the results is also in keeping with this hypothesis. Namely, the large decrement in duration of MAE with P31 phosphor occurred at displacements of ¼ but not of ⅛ or ⅜ cycles. This can be understood in terms of Turano and Pantle's (1985) suggestions (see above), but also in terms of the rate at which the edges were refreshed on the screen. Bearing in mind that the duration of a single frame was 30 msec, it can be easily shown that the edges were refreshed every other frame (i.e., every 60 msec) when the displacement was ¼ cycle, but only every four frames (i.e., every 120 msec) when the displacement was ⅛ or ⅜ cycles. Being refreshed at twice the rate, the edges corresponding to displacements of ¼ cycle were more visible and thus had a greater detrimental effect on MAE. Incidentally, these considerations strongly suggest that the critical features in reduction of MAE are the edges themselves rather than the specific gray levels of the bars.

As discussed in the section on Experiment 3, it is probably premature to formulate a theoretical account of the detrimental effect of the edges on MAE. However, it can be asked whether the edges that are seen in the moving displays are actually on the screen, or whether they are perceptual effects whose locus is in the visual system. We did not have ready access to equipment capable of monitoring rapid luminance changes on the screen with the required accuracy. However, it does seem unlikely that, with P15 phosphor, the edges were due solely—or even principally—to energy summation of successive frames on the screen. The persistence of P15 phosphor is too brief to permit useful summation of successive frames whose duration is 30 msec. It is more likely that temporal integration occurred within the visual system, whose constant is known to be in the tens of milliseconds even in photopic viewing (e.g., Di Lollo, 1980; Di Lollo & Hogben, 1985, 1987). Of course, this does not preclude that the edges might also be integrated on the screen if the phosphor persistence is sufficiently long, as was probably the case with P31.

It must be stressed that the different results obtained with P15 and P31 phosphors must be ascribed to the phosphors themselves rather than to other characteristics of the oscilloscopes. For example, the two oscilloscopes had the same bandwidth, capacitance coupling, and slew rates. In addition, great care had been taken to ensure that image luminance varied linearly with input voltage in both oscilloscope (this was part of the procedure for calibrating the Picasso image synthesizer). In a similar vein, it might be asked whether temporal factors other than phosphor persistence could have had an effect. In this respect, it must be remembered that the image refresh rate (100 Hz) and the image update rate (33.3 Hz) were the same for both types of phosphor and waveform. Thus, if such temporal factors played a part, it must have been in the form of an interaction among phosphor persistence, image refresh rate, image update rate, and waveform. In a sense, our account in terms of the relative visibility of the edges with square-wave gratings in the two types of phosphor is based on just such an interaction. Although no plausible alternative comes readily to mind, other models of this interaction may well be possible. However, the development and verification of such models would be beyond the scope of the present paper.

It should also be stressed that the above considerations do not necessarily invalidate Turano and Pantle's (1985) account in terms of conflicting motion signals. As already noted, all observers reported seeing—at least occasionally—a grating whose characteristics were compatible with those of the third harmonic. By the same token, such a grating would be difficult to distinguish from a grating whose characteristics corresponded to the fourth harmonic—namely, the harmonic produced by the temporal integration of successive frames.

GENERAL DISCUSSION

Direct and Indirect Measures

Substantial differences between direct and indirect estimates of directional motion perception have been found in the present experiments. Stimulus waveform can have a powerful effect on indirect (MAE) but not on direct (*d*max) estimates (Figures 2 and 3). In addition, direct and indirect estimates are affected in opposite ways by the superimposition of a stationary grid on the adapting display (Experiment 3). The precise causes of these differences are unclear and remain to be investigated. However, at a purely empirical level, there is little doubt that *d*max and duration of MAE are affected in different ways by changes in the same independent variables.

In turn, this evidence has clear implications for the equivalence of MAE and *d*max as indices of the short-range motion process. Although Turano and Pantle (1985) did not provide a rule for deriving specific values of *d*max from duration of MAE, they explicitly regarded them as equivalent ways of defining the attributes and limits of the short-range motion system. This option is disconfirmed by the outcome of the present work. Because MAE and detection of motion respond differently to changes in the same variables, they cannot be regarded as equivalent measures of the spatial limits of the short-range process.

Short- and Long-Range Motion Systems

Also questioned by the present outcome is the role of MAE as a criterion for separating the short-range from the long-range motion systems (see also von Grünau, 1986). It has been said (e.g., by Anstis, 1986) that the short-range process is uniquely defined by a set of criteria that include a small and fixed value of *d*max and a brief and fixed value of *t*max (the maximum interframe interval at which directional motion can be seen reliably), as well as the presence of MAE. Recent findings, however, have questioned the validity of the defining criteria. Baker and Braddick (1985), Bischof and Di Lollo (1990), and Burr, Ross, and Morrone (1986), among others, have shown that *d*max can vary over a wide range of values; Dawson and Di Lollo (1990) have shown the same for *t*max. In general, although it seems likely that perception of motion is based on more than one system (cf. Chubb & Sperling, 1988), there appears to be little support for a classification based on range of displacement. This is essentially the same conclusion as that reached by Cavanagh and Mather (1989) in a recent evaluation of the experimental evidence.

Although unsupportive of a range-based distinction, the outcome of the present work strongly suggests that direct and indirect measures reflect the activities of separable motion systems. Separation of the processes on both psychophysical and neurophysiological grounds requires further experimentation. However, on the strength of current knowledge (see, e.g., von Grünau, 1986), it can no longer be assumed that the locus of MAE must be confined to the primary visual area (V1), as might have been inferred from early results reported by Anstis and Gregory (1965). Psychophysical evidence compatible with extrastriate involvement in both the tilt and the motion aftereffects has been reported by Wenderoth and Johnstone (1988) and by Wenderoth and van der Zwan (1989). Involvement of extrastriate mechanisms in tuning aftereffects has also been suggested by Saul and Cynader (1989a, 1989b), who measured the aftereffects of adaptation to gratings on the spatiotemporal frequency tuning of single units in the visual cortex. Finally, a compelling case that motion is based on neural activity at more than one level has been made recently by Hess, Baker, and Zihl (1989), who studied a patient with bilateral lesions involving area V5 (MT). While perception of moving stimuli was unimpaired, perception of the more complex attributes of motion, such as direction and relative velocity, were severely impaired, suggesting the activities of separate mechanisms.

Effects of the Grid

The present thesis that MAE and *d*max cannot be regarded as equivalent indices of a single underlying process is based on two sources of evidence: the results obtained with square-wave gratings in Experiments 1 and 2, and the differential effects of the grid in Experiment 3. The effects appear to be novel, in that no immediate counterpart can be readily found in the experimental literature. On the basis of the similarity in phenomenal appearance, it is conceivable that the two effects may be related. However, within the ambit of the present work, they remain essentially unexplained.

Some potentially promising approaches to investigating the effects of the grid on MAE and on motion detection have been noted in the discussion of Experiment 3. A less immediate—though no less promising—approach could be based on changes in the spectral composition of the sine-wave displays brought about by the superimposition of the grid. It is known that the superimposition of a stationary sine-wave grating has no significant effect on the perception of a moving sine-wave grating (van Santen & Sperling, 1985). However, it is not known what effect this procedure would have on duration of MAE. The present need is for a systematic investigation of how MAE and direct measures of motion (e.g., *d*max) are affected by the superimposition of a stationary grating whose intensity profile varied systematically between sine wave and square wave, with intermediate levels consisting of appropriate compound gratings. Were such a study to show that static higher frequency components enhance motion detection, the result would be particularly intriguing. This is so, because in recent studies (Bischof & Di Lollo, in press; Cleary & Braddick, 1990b), it has been found that the addition of dynamic higher frequency components (i.e., moving at the same rate as the rest of the display) produces an impairment in detection of directional motion.

Regardless of outcome, the effects of the grid on both MAE and detection of directional motion are potentially important, and clearly invite further investigation.

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