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Temporal and Spatial Frequency Tuning of the Flicker Motion Aftereffect

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The motion aftereffect (MAE) was used to study the temporal and spatial frequency selectivity of the visual system at supra-threshold contrasts. Observers adapted to drifting sine-wave gratings of a range of spatial and temporal frequencies. The magnitude of the MAE induced by the adaptation was measured with counterphasing test gratings of a variety of spatial and temporal frequencies. Independently of the spatial or temporal frequency of the adapting grating, the largest MAE was found with slowly counterphasing test gratings (at approximately 0.125–0.25 Hz). The largest MAEs were also found when the test grating was of similar spatial frequency to that of the adapting grating, even at very low spatial frequencies (0.125 c/deg). These data suggest that MAEs are dominated by a single, low-pass temporal frequency mechanism and by a series of band-pass spatial frequency mechanisms. The band-pass spatial frequency tuning even at low spatial frequencies suggests that the "lowest adaptable channel" concept [Cameron *et al.* (1992). *Vision Research, 32,* 561–568) may be an artifact of disadvantaged low spatial frequencies using static test patterns. Copyright © 1996 Elsevier Science Ltd.

Adaptation Motion aftereffects Temporal tuning Spatial tuning

INTRODUCTION

It has been suggested that the early stages of human visual processing involve analysis by a parallel set of "channels" that may be defined in terms of their spatial and temporal tuning characteristics [see Graham (1989) for an overview]. Spatial frequency selectivity is well established and has been demonstrated both physiologically (e.g. Enroth-Cugell & Robson, 1966) and psychophysically (e.g. Campbell & Robson, 1968). The results indicate that spatial processing involves a range of band-pass spatial frequency-selective filters each with a band width of approximately one octave (e.g., Maffei & Fiorentini, 1973). Temporal frequency selectivity has received less attention, but existing data suggest that there may be two or three temporal channels, one low-pass and one or two band-pass filters (Mandler & Makous, 1984; Hess & Plant, 1985; see also Fredericksen & Hess, 1996a,b). Physiological data from the macaque (Foster *et al.*, 1985) show that neurons in V1 and V2 are broadly tuned for temporal frequency and may be either low-pass or band-pass.

Motion aftereffects and channel theories

One interesting demonstration of the existence of spatial frequency tuned mechanisms in the human visual system has been established using a well documented visual illusion known as the Waterfall Illusion or the motion aftereffect [MAE: see Wade (1994) for a selective overview]. When a stationary image is examined after prolonged viewing of a moving image, the stationary image appears to move in the opposite direction to that of the inducing image: the MAE. MAEs are particularly interesting because they can be used for selective adaptation [see Sekuler & Pantle (1967) for the rationale of this procedure].

Spatial frequency tuning. The contribution of spatial frequency selective mechanisms to motion detection has been established by comparing MAE characteristics for gratings of differing spatial frequencies. In this paradigm, observers view a drifting grating (the adapting pattern) of a given spatial frequency, then the magnitude of the MAE is measured for static gratings (the test pattern) of differing spatial frequencies. Using this procedure, several researchers have demonstrated that the strongest MAE is elicited when the test and adapting gratings are of similar spatial frequency (Over *et al.*, 1973; Cameron *et al.*, 1992). However, Cameron *et al.* showed that when the adapting grating is lower in spatial frequency than about 0.5 c/deg, this relationship breaks down and a peak

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MAE is always found at around 0.5 c/deg. This relationship suggests that motion detection involves mechanisms narrowly tuned for spatial frequency (at least for spatial frequencies above 0.5 c/deg).

Temporal frequency tuning. Support for the existence of temporal frequency-selective mechanisms using MAEs is more scarce. Most research has examined the temporal parameters which result in the largest MAEs (e.g., Pantle, 1974; Wright & Johnston, 1985). Specifically, Pantle (1974) studied whether a constant velocity or temporal frequency resulted in maximal MAEs for a range of spatial frequencies. The optimal parameters were a product of spatial frequency and adapting velocity (i.e., temporal frequency), not velocity *per se*. No experiments have been reported which describe the relationship between the temporal frequency of adapting patterns and the temporal modulation frequency of the test pattern. This relationship is explored in experiment 1.

In the research described above, the magnitude of MAEs was measured using static test patterns. However, a recent distinction has emerged between MAEs which are measured using static test patterns and those measured with dynamic "flickering" test patterns (e.g., Hiris & Blake, 1992). For example, in general no MAE is induced by non-Fourier motion stimuli if tested with static patterns (Anstis, 1980; Derrington & Badcock, 1985; Nishida *et al.*, 1994), but a flickering test pattern reliably reveals a MAE (McCarthy, 1993; Ledgeway, 1994; Nishida *et al.*, 1994). These differences in the psychophysical data have led to the speculative suggestion that the two different types of MAE originate at different sites along the path of visual motion processing. Nishida & Sato (1995) suggested V1 as a possible candidate for the static MAE and area MT or MST for the flicker MAE (see also Ashida & Osaka, 1995).

Using flickering test patterns, Ashida & Osaka (1995) found that the optimal temporal frequency for inducing a MAE is found to be partially velocity tuned, not temporal frequency tuned, as is the case for static MAE. These results support the proposal of two different sites of MAE. Furthermore, Ashida & Osaka (1994) confirmed that the magnitude of static MAEs was greatest if test and match gratings were of similar spatial frequency, but this relationship was not found if the test grating was flickering. In this case no spatial frequency selectivity was observed. This finding appears to contradict a previous finding in which spatial frequency tuning was shown using flicker MAE (von Grünau & Dubé, 1992). The different results were attributed to experimental differences (Ashida & Osaka, 1994).

In the present experiments, we were interested in the spatial and temporal frequency tuning of flicker MAE. In the same way that spatial frequency tuning of the (static) MAE reveals spatial frequency-selective motion detection mechanisms, we hypothesized that any temporal frequency selectivity of motion detection mechanisms would be exhibited by temporal frequency tuning of the flickering MAE. We measured the magnitude of MAEs elicited after adaptation to drifting sine gratings whose spatial and temporal frequencies were manipulated. Following Ashida & Osaka (1994), the magnitude of the MAE was estimated by recording the duration of the MAE. The test grating in each case was a sine grating of the same spatial frequency and peak contrast as the adapting grating, but whose contrast was counterphased sinusoidally at between 0.125 to 16 Hz. A comparison condition was recorded using stationary gratings (0 Hz). Using this protocol, we found no evidence for narrow temporal frequency tuning of the flickering MAE. For any spatial and temporal adapting frequencies, the peak flicker MAE was found at low counterphase frequencies.

In a second experiment, we measured the spatial frequency tuning of flicker MAE for low spatial frequency adapting gratings (0.125–2 c/deg). The results showed clear spatial frequency tuning at all spatial scales, in good agreement with von Grünau & Dubé (1992) and suggest that the absence of such tuning reported by Ashida & Osaka (1994) may be related to their stimulus parameters. The spatial frequency tuning at low spatial frequencies shows that the lowest adaptable channel (Cameron *et al.*, 1992) revealed using static MAE does not exist using flicker MAE.

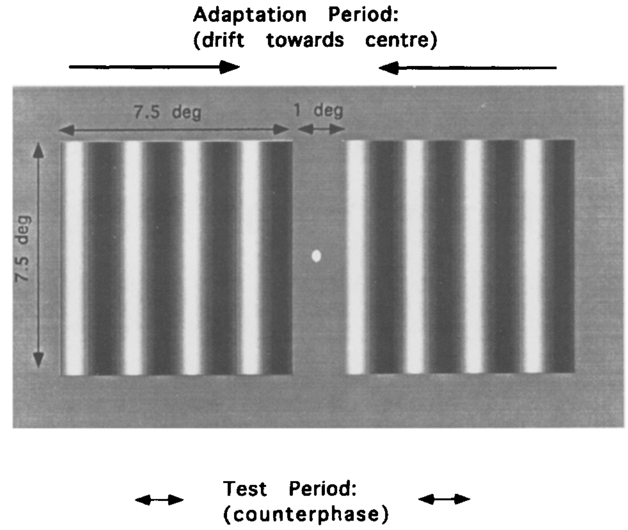

FIGURE 1. Schematic diagram illustrating the geometry of the display. Sinusoidal grating were presented in two horizontal regions (7.5 by 7.5 deg), separated by a horizontal strip of 1 deg width with a central fixation point. The sine gratings were all 50% peak contrast, the remainder of the display was at mean luminance (32 cd/m^2). During a 20 sec adaptation period, the sine gratings drifted towards the fixation point to aid steady fixation. During the test phase, the gratings were sinusoidally counterphased in each window until the observer reported the end of the MAE.

EXPERIMENT 1: TEMPORAL FREQUENCY TUNING OF FLICKER MAE

Methods

Apparatus and stimuli. Stimuli were generated using a VSG 2/1 graphics card (Cambridge Research Systems) in a host PC microcomputer (DELL 333D) and were presented on a Nanao Flexscan 6500 monitor with P4

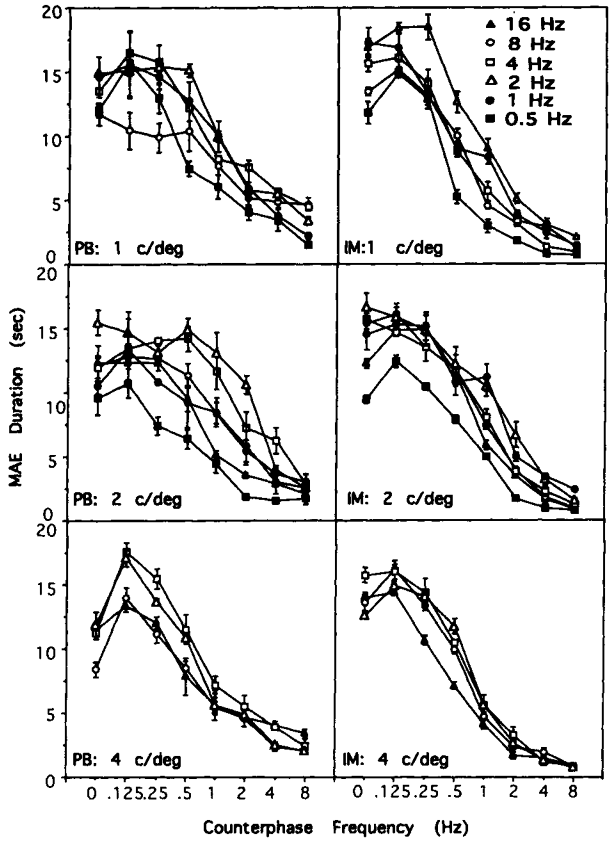

FIGURE 2. Magnitude of MAE as a function of the temporal frequency of the counterphasing test grating. The data for the two observers are shown in separate columns and the data for the three adapting spatial frequencies (as well as test spatial frequencies) are shown in separate rows. The temporal frequency of the adapting grating is shown in the caption and the temporal frequency of the adapting grating is shown in the legend. The spatial frequency of the test grating was the same as that of the adapting grating in each case. The temporal frequency of the test grating is shown on the x-axis with semi-log coordinates (to permit the inclusion of the 0 Hz data, where the test grating was static). The duration of the MAE is shown on the y-axis. Each data point is the mean of at least four observations. Error bars show ± S.E.

phosphor and with a frame rate of 118 Hz. The mean luminance of the display was 32 cd/m^2. The luminance of the display was linearized using an ISR attenuator (Pelli & Zhang, 1991) and calibrated using a UDT Photometer. The image was 16 deg horizontally (512 pixels) by 13.4 deg vertically (428 pixels) and was viewed from a distance of 118 cm. Subjects viewed the screen binocularly in a dim room. The spatial layout of the display is shown schematically in Fig. 1. There were two square windows on the screen, each subtending 7.5 deg by 7.5 deg. The windows were separated horizontally by a 1 deg strip of mean luminance, in the center of which was a prominent fixation point. The remainder of the display was blank and at the mean luminance.

Adapting and test stimuli were vertical sinusoidal gratings of 50% Michelson contrast, which were presented in the square windows. The adapting gratings drifted towards the fixation point. The test gratings were sinusoidally counterphase flickering. The spatial frequency of the adapting gratings was either 1, 2 or 4 c/deg. The temporal frequency of the adapting gratings was varied between 0.125 and 16 Hz, in steps of one octave. The spatial frequency of the test pattern was also 1, 2 or 4 c/deg and in experiment 1 was always the same spatial frequency as the adapting grating which had preceded it. The test gratings were counterphased at a temporal frequency between 0.125 and 16 Hz, in steps of one octave. An additional condition was measured in which the test grating was static (0 Hz counterphase frequency). The starting phase of all gratings was randomized before each presentation.

Procedure

The subject was instructed to maintain steady fixation during adaptation and testing and initiated each trial by pressing a mouse button. This was followed by a 20 sec adaptation period during which the adapting sine grating was presented. The adapting grating was always drifting towards the center of the screen to facilitate steady fixation. The adaptation period was immediately followed by a brief tone and the test period. During the test period, the counterphasing test grating was presented in both windows. The subject was required to press a mouse button when the MAE had finished. If the subject experienced no MAE, the duration was recorded as zero sec. Subjects practiced the task many times before formal data collection. The direction of the MAE was always seen in the opposite direction to that of the adapting grating (in this case it always appeared to move away from the fixation point) and it was not necessary to record the perceived direction of MAE. Several studies (e.g. Georgeson & Harris, 1978) have found that counterphasing gratings viewed parafoveally appear to drift away from the center even without adaptation: the foveofugal drift effect (FFDE). However, the FFDE would result in motion away from fixation which never terminated whereas the MAE measured in the present study reliably halted. Furthermore, on some trials, observers reported that they experienced no MAE even after adaptation, again inconsistent with the intrusion of FFDE into our results. Subjects had normal or corrected-to-normal vision.

Each trial was followed by a inter-trial recovery interval of not less than 1 min. The whole procedure was repeated for each of the combinations of spatial and temporal frequencies measured. The presentation sequence for the various spatial and temporal frequencies was randomized and the data were collected over a period of several weeks. The mean and standard deviation of at least four estimates of MAE duration for each condition were recorded.

Results

Estimates of the MAE duration as a function of test temporal frequency are shown for the two observers in Fig. 2. The top panels represent the results where the adapting and test spatial frequencies were 1 c/deg. For the middle panels the spatial frequencies were 2 c/deg and in

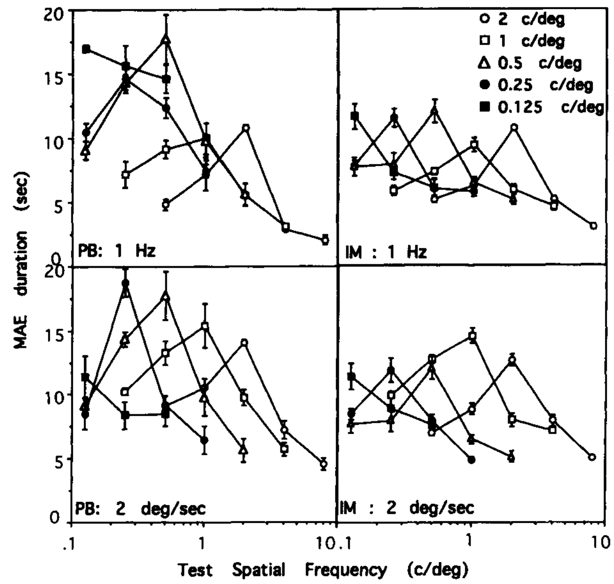

FIGURE 3. Magnitude of MAE as a function of the spatial frequency of the counterphasing test grating. The data for the two observers are shown in separate columns and the data for the separate temporal frequencies are shown in separate rows. The spatial frequency of the adapting grating is shown in the caption. In the top row, the temporal frequency of the adapting grating was 1 Hz (its speed varied), in the bottom row, the speed of the adapting grating was 2 deg/sec (its temporal frequency varied). The spatial frequency of the adapting grating is shown on the x-axis with semi-log coordinates. The temporal frequency of the test grating was 0.25 Hz in each case. The duration of the MAE is shown on the y-axis. Each data point is the mean of at least four observations. Error bars show $\pm$ 1 S.E.

the bottom panels they were 4 c/deg. In all cases, it can be seen that the longest MAE was found when the test grating was counterphasing at a low temporal frequency. Three combinations of adapting spatial and temporal frequency resulted in no or negligible MAE (1 c/deg adapting temporal frequency 16 Hz, 4 c/deg adapting temporal frequency 1 or 0.5 Hz).

The results of the temporal frequency tuning of the flicker MAE clearly show that the most pronounced MAEs are found when the test grating is slowly counterphasing. This effect is found for both observers and for all conditions measured. The effects of the adapting frequency are not as clear. The data show weak band-pass tuning of the MAE, but there is no clear support that the MAE is tuned to either the temporal frequency or the speed of the adapting grating. Together with different observations of temporal frequency and drift speed determinants of MAE (Pantle, 1974; Ashida & Osaka, 1995), these data suggest that both may contribute to MAE magnitude in the same way that both contribute to the perceived speed of moving images (Smith & Edgar, 1994).

EXPERIMENT 2: SPATIAL FREQUENCY TUNING OF FLICKER MAE

In experiment 2, the spatial frequency tuning of flicker MAE was measured. The procedure was the same as for experiment 1 except that the spatial frequency of the adapting gratings was between 0.125 and 2 c/deg in steps of one octave. We included these low spatial frequencies because Cameron *et al.* (1992) presented evidence that the spatial frequency tuning breaks down for spatial frequencies below 0.5 c/deg. Although the results of Ashida & Osaka (1994) argue against spatial frequency selectivity for flicker test stimuli, to our knowledge nobody has reported whether the flicker MAE at low spatial scales is spatial frequency tuned. Moreover, the difference in results between Ashida & Osaka (1994) and those reported by von Grünau and Dubé (1992: experiment 4) requires investigation. The latter found spatial frequency selectivity with flickering test stimuli, whereas Ashida & Osaka (1994) did not. Differing techniques have been suggested as the source of the discrepancies in the results (Ashida & Osaka, 1994).

The temporal frequency of the adapting patterns was either 1 Hz or was varied with spatial frequency such that drift speed was 2 deg/sec. For each adapting spatial frequency, MAEs were measured using five test spatial frequencies, one of the same spatial frequency, two of higher and two of lower spatial frequency, in steps of one octave. This range was employed except at the lowest spatial frequencies measured, which would have resulted in too few visible cycles of the grating. In these cases the lowest frequency measured was 0.125 c/deg. The results of experiment 1 showed that a maximal MAE occurs with a counterphase frequency of around 0.125–0.25 Hz, independently of spatial frequency. Test gratings were counterphased at a temporal frequency of 0.25 Hz because this was near or at the peak of the temporal frequency tuning curve. The starting phase of all gratings was randomized before each presentation.

Results

Estimates of the MAE duration as a function of test spatial frequency are shown for the two observers in Fig. 3. In the top panels, the temporal frequency of the adapting grating was 1 Hz, which means that the speed varied. In the bottom panels the speed of the adapting grating was 2 deg/sec, so temporal frequency varied. The spatial frequency of the adapting grating is shown along the x-axis.

The results are unambiguous: in all cases, it can be seen that the longest MAE is found when the adapting grating and test grating are of the same spatial frequency. The data show clear evidence for spatial frequency tuning even at the lowest spatial frequencies measured.

GENERAL DISCUSSION

In this paper we have investigated both spatial and temporal frequency tuning of the flicker motion aftereffect. We found no evidence for band-pass temporal frequency tuning of the flicker MAE, but clear evidence for band-pass spatial frequency tuning was revealed by measuring MAE duration. The data from experiment 1 show that maximum MAEs were found using flickering test patterns, counterphasing at low temporal frequencies.

The tuning was independent of the spatial or temporal frequency of the adapting grating.

The low-pass temporal tuning of flicker MAE suggests that flicker MAE may be dominated by a single low-pass temporal mechanism. The low-pass mechanism must be broadly tuned because test patterns of high temporal frequency can produce robust MAEs, but the peak tuning of the MAE is always at a low counterphase temporal frequency. It should be emphasized that the results do not preclude the existence of additional temporal mechanisms which are band-pass and tuned to higher temporal frequencies. Instead, the results suggest the contribution of such mechanisms to flicker MAE may be substantially less than that of a single, low-pass temporal mechanism.

A comparison of the MAE for the static and counterphasing test patterns shows no clear distinction between the two. Instead, there is a steady transition of MAE magnitude from high temporal frequency counterphasing gratings to gratings counterphasing at zero Hz (static). This is supported by the subjective impressions of the MAEs which were approximately the same under the various conditions, although of differing duration. The data provide no evidence to suggest that the two types of MAE may be mediated by separate mechanisms. This does not imply that there are no such mechanisms. For example, it is known that the MAE direction of orthogonally directed transparent motion (see Verstraten *et al.*, 1994a) can change drastically depending on whether the test pattern is dynamic or static (Verstraten *et al.*, 1994b). Moreover, differences found in recovery from adaptation with static and dynamic stimuli favor a two mechanism interpretation (Verstraten *et al.*, 1996). Also, Culham & Cavanagh (1994) have shown that after attentive tracking of a radial grating, a MAE is perceived for a counterphasing test grating, not for a stationary grating. MAE studies using inter-ocular transfer techniques (IOT) also show great differences between static and dynamic test patterns (Raymond, 1993; Nishida *et al.*, 1994; Steiner *et al.*, 1994). In sum, there is plenty of evidence for different gain controls along the path of motion processing. However, the temporal tuning characteristics we report here do not justify the conclusion as drawn by Ashida & Osaka (1994).

In experiment 2, we tested a range of spatial frequencies for spatial frequency tuning of flicker MAE. The results show that the maximum MAE was found using flickering test patterns of similar spatial frequency to that of the adapting pattern. This result is in good agreement with von Grünau & Dubé (1992), notwithstanding the fact that they used a different technique. However, the results are not consistent with those of Ashida & Osaka (1994), even though they also used MAE duration as the dependent variable. This inconsistency contributes to a growing body of evidence showing that MAE varies with a number of experimental parameters, including the stimulus geometry and the method of MAE magnitude estimation (Wade, 1994). One key parameter which may contribute to these differences is the use of sub-optimal temporal conditions for the flicker frequency of the test pattern. In our experiments, we used the optimal temporal frequency determined in experiment 1, which should reveal tuning differences more clearly.

More interesting, perhaps, is the comparison between the results of experiment 2 and those of Cameron *et al.* (1992). Using static test patterns, these researchers presented evidence for a "lowest adaptable channel" of 0.5 c/deg. This hypothesis was based on the observation that the peak MAE for a 0.25 c/deg grating was found when tested with a static 0.5 c/deg grating (Fig. 2, p. 516). This is apparently not the case for dynamic "flicker" test patterns, even at lower spatial frequencies than those measured by Cameron *et al.* Part of this difference may arise from the particular method of MAE magnitude estimation. Cameron *et al.* used a tracking procedure, where a subject manually matched the speed and direction of the MAE over a fixed period, using a potentiometer. These data were later combined to give a mean velocity estimation. Using this procedure, these authors found "no measurable MAE at spatial frequencies lower than 0.25 c/deg" (p. 561). Using our method of MAE duration estimation, we found robust MAEs at very low spatial frequencies (we measured as low as 0.125 c/deg), even using static test gratings. We have also verified that MAEs can be measured using the duration method with the same stimulus geometry used by Cameron *et al.* (two horizontal adapting fields, one above and one below fixation). This shows that stimulus geometry alone cannot account for these differences. It is tempting to conclude that it might not be possible to record MAEs using the tracking methodology for low spatial frequency gratings. Consequently, with this procedure it is not possible to record a MAE for low spatial frequencies or to measure any spatial frequency tuning.

This finding is redolent of early observations that the lowest spatial frequency channel was originally believed to be around 1–3 c/deg (Blakemore & Campbell, 1969; Campbell *et al.*, 1981). However, when larger field sizes and higher temporal frequencies were used, separately adaptable and maskable mechanisms were found to exist down to 0.2 c/deg (Stromeyer & Julesz, 1972; Tolhurst, 1973; Kranda & Kulikowski, 1976; Stromeyer *et al.*, 1982). This suggests that an absence of temporal modulation, combined with a MAE magnitude estimation technique which does not detect MAEs for very low spatial frequencies, may have contributed to the different results of Cameron *et al.* (1992) and our experiment 2.

Our results and the suggestions by Ashida & Osaka (1994) may appear to complicate the understanding of the spatial and temporal tuning of MAEs. Ashida and Osaka suggest that since spatial frequency selectivity is a property of mechanisms (channels) at a relatively early stage of the visual system, the absence of spatial frequency tuning is evidence for higher level MAEs. However, the narrow spatial frequency tuning reported in this paper and by von Grünau & Dubé (1992) make this argument disputable. We show that selecting optimal conditions for maximizing MAEs can avoid confounding variables and reveal the tuning characteristics of the motion mechanisms in human vision.

CONCLUSION

We used the flicker MAE to study the temporal and spatial frequency tuning of the visual system at supra-threshold contrasts. The results show that the magnitude of the flicker MAE is dependent on the temporal frequency of the counterphasing test grating, such that lowest temporal modulation frequencies give the largest MAEs. The relationship is independent of the spatial and temporal frequency of the adapting grating. This suggests that the flicker MAE is dominated by a single, low-pass temporal mechanism. The data show that the magnitude of flicker MAE is also dependent on the spatial frequency of the test grating, such that the largest MAE is found when the adapting and test patterns are of similar spatial frequency, even at very low spatial frequencies. This relationship suggests that the flicker MAE involves a series of band-pass spatial frequency-selective mechanisms. The differences between our data and some previous data may be based on the use of sub-optimal conditions, resulting in weak or non-measurable MAEs, the tuning of which are consequently difficult to determine.

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