Pergamon

0042-6989(94)00270-3

Vision Res. Vol. 35, No. 13, pp. 1825–1833, 1995

0042-6989/95 $9.50 + 0.00

Motion Aftereffect with Flickering Test Stimuli Depends on Adapting Velocity

HIROSHI ASHIDA,*† NAOYUKI OSAKA*

Received 4 July 1994; in revised form 19 October 1994

Temporal tuning property of motion aftereffect (MAE) with flickering test stimuli (flicker MAE) was examined. Using sinusoidal gratings of several spatial frequencies (SF), MAE strength was measured for various adapting temporal frequencies (TF). Unlike the traditional MAE with static test field, the results indicated that flicker MAE did not depend on TF. Rather, when plotted as a function of velocity, the peaks had approximately the same adapting velocity of 5–8 deg/sec for all SF conditions tested, suggesting velocity dependence. This is further support of the idea that the two kinds of MAE are of different origin and suggests a higher origin of flicker MAE, perhaps in the area MT or MST.

Motion Motion aftereffect Flicker Velocity

INTRODUCTION

Motion aftereffect (MAE) is a kind of negative aftereffect caused by prolonged viewing of image motion: After gazing at a moving stimulus for a while, a stationary scene will appear to move in the opposite direction. MAE has been used in quite a lot of studies of motion perception, and still has considerable importance in modern theories.

It has been pointed out that two types of MAE are distinguishable: traditional MAE observed with a stationary test field which we call 'static MAE', and the one observed with a flickering test field which we refer to as 'flicker MAE'. These two were sometimes confused and just called 'MAE', but recent studies have clarified that they have quite distinct characteristics. First of all, there is considerable evidence showing that flicker MAE is induced by second-order (non-Fourier) motion stimuli‡ (Ledgeway, 1994; McCarthy, 1993; Nishida, Ashida & Sato, 1994; Nishida & Sato, 1993, 1995) while static MAE is not (Anstis, 1980; Derrington & Badcock, 1985; Nishida *et al.*, 1994). Nishida and Sato (1993, 1995) demonstrated that the same adapting stimulus could induce static and flicker MAE in different directions and the second-order property was preferable to flicker MAE. They used a compound grating consisting of second and third harmonic components, without the fundamental one. When such a grating is moved discretely in steps one fourth of the missing fundamental cycle, its Fourier power spectrum implies motion in the opposite direction to that of the whole pattern. It was observed that static MAE reflected the Fourier power and flicker MAE followed the pattern direction, which was the second-order property of the stimulus in that case. It is suggested that two types of MAE reflect different processing levels.

While it is widely accepted that static MAE showed only partial interocular transfer (see Wade, Swanston & de Weert, 1993 for review), Nishida *et al.* (1994) demonstrated that flicker MAE showed complete transfer. In their experiment, drift-balanced motion stimuli (Chubb & Sperling, 1988) which contained no luminance based motion information induced flicker MAE as strongly as luminance gratings, and complete transfer was seen also in that case. Flicker MAE is processed later than the point where the information regarding eye of origin is lost, while static MAE somewhat depends on monocular processes. This is thought to be strong evidence of the different origin of each types of MAE.

Static MAE is known to show spatial frequency selectivity (Cameron, Baker & Boulton, 1992), that is, maximum aftereffect is obtained when the spatial frequency of adapting and test stimuli are the same. And it depends on the temporal frequency of adapting stimuli rather than velocity (Pantle, 1974; Wright & Johnston,

---

*Department of Psychology, Faculty of Letters, Kyoto University, Yoshida Honmachi, Sakyo-ku, Kyoto 606, Japan.

†To whom all correspondence should be addressed at present address: ATR Human Information Processing Research Laboratories, 2-2 Hikaridai, Seika-cho, Soraku-gun, Kyoto 619-02, Japan.

‡Second-order motion is defined by the second- or higher order statistics of the image (Cavanagh & Mather, 1989), while first-order motion is defined by the first-order statistics (i.e. luminance, and possibly colour). Two types of motion are also distinguished based on Fourier analysis (Chubb & Sperling, 1988). Second-order motion defined by Cavanagh and Mather is thought to be a subset of Chubb and Sperling's non-Fourier motion (Mather & West, 1993), but the term *second-order* seems to be used more generally to include a wider range of non-Fourier motion in some cases (e.g. Solomon & Sperling, 1994). In this paper, the distinction between pure *second-order* and non-Fourier motion is not critical, and we use the term *second-order* in the more general sense.

1985), in that maximum aftereffect is seen at constant adapting temporal frequency regardless of spatial frequency. It is suggested that static MAE basically reflects the activity of early spatio-temporal filtering mechanisms. However, Ashida and Osaka (1995) showed that spatial frequency selectivity was not seen in the case of flicker MAE.

All these findings consistently suggest that flicker MAE is processed at a later stage than static MAE. However, one point must still be considered. Temporal frequency tuning of static MAE is widely accepted, but the temporal tuning property of flicker MAE has not yet clarified. Velocity v is described by

$$v = \mathrm{TF}/\mathrm{SF} \tag{1}$$

where TF is temporal frequency and SF is spatial frequency. Therefore, velocity changes with spatial frequency if the temporal frequency is constant. If we admit that our final perception is based on objects rather than pixels, velocity is a more appropriate measure to describe a single object. For the movement of a rigid object is described by a single velocity (at least in the case of translation motion), but it contains many spatial frequency components and therefore many temporal frequency components. McKee, Silverman and Nakayama (1986) showed that precise velocity discrimination could be made even when the temporal frequency was randomized. They suggested that our perception is based on velocity, and velocity is computed from temporal frequency information at the lower level.

It should be noted that Smith and Edgar (1991) showed that it was also possible to discriminate temporal frequency under varying velocity conditions. Their results should be thought to indicate the availability of temporal frequency information, however, they did not deny the superiority of velocity at the perceptual level. Indeed, they admitted that temporal frequency discrimination is more difficult for a naive subject and suggested the primacy of velocity.

Considering these points, it is suggested that flicker MAE might depend on velocity rather than temporal frequency if it reflects later stages of processing. The objective of the present study was to test this assumption. We performed some experiments to examine the temporal property of flicker MAE and the results were compared to those of static MAE. We measured the aftereffect duration to apply the same method for both types of MAE. The procedure was basically the same as that used by Nishida *et al.* (1994).

METHOD

Apparatus and stimuli

The stimuli were generated by a computer (IBM PS/V) and displayed on a colour CRT monitor (SONY GVM1411) with an SVGA card (NANAO HA50). Normal SVGA cards have look-up tables with only 6-bit depth, but with this card an 8-bit depth colour-palette is available in VESA-defined 256 colour modes. The 640 × 480 dot, 256 colour mode was used for the experiment. To obtain better gamma correction through look-up tables, only the green phosphor was used, except for the red fixation cross. The image refresh rate was 60 Hz.

The stimulus configuration is shown in Fig. 1. There were three rectangular windows in the screen, each subtending 14.0 × 3.0 deg and separated by 1.0 deg. The central window was for adapting and testing, and the upper and lower ones were for reference. A red cross was displayed for fixation at the centre of the stimulus grating. The edges were abrupt without windowing, but the vertical edges were quite far from central region and the effect of harmonic components around the edge was not thought very serious. The viewing distance was 63.6 cm, and the mean luminance was 51.3 cd/m^2.

Adapting stimuli were drifting vertical sinusoidal gratings of 40% Michelson contrast presented in the central window. Test stimuli were sinusoidal gratings which were sinusoidally counterphase-flickering at 0.0, 2.5 or 5.0 Hz. They were presented in the central window. The spatial frequency of adapting and test gratings were 0.5, 1.0 and 2.0 c/deg. Test contrast was set as 10%, quite lower than the adapting one. It might be possible that the fixed adapting contrast introduced some artifact due to different sensitivities to each adapting temporal frequency. Such an effect, if any, was the same for both static and flicker conditions, and would not explain the difference of results obtained in both conditions at any rate. However, the effect could be minimized using high adaptation and low test contrast, as it was shown in the experiments by Nishida, Ashida and Sato (in preparation) that the effect of adapting contrast on both types of MAE magnitude showed saturation at quite low contrast provided the adapting contrast was high and the testing one was low. The reference gratings were presented during the adapting and test periods, to help judgement of the perceived direction especially in the static condition. The reference gratings were always stationary and the contrast was fixed at 10%. The spatial frequency

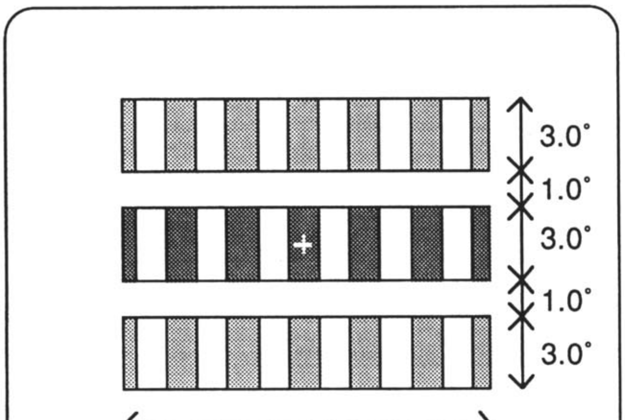


FIGURE 1. The stimulus configuration. Sinusoidal gratings were presented in the three windows. The central window was for adaptation and testing, and the other two were for reference.

of reference gratings was equalized with that of the stimulus grating, while the phase of the test and the reference gratings was randomly set in each trial.

Subjects viewed the screen binocularly using a head and chin rest. The experiments were performed in a dimly lit room.

Procedure

The subjects initiated each trial by pressing mouse buttons. During the 20 sec adaptation period, a grating drifting in one direction was presented in the central window, and the subject continued fixating at the fixation cross. After adaptation, the test grating was immediately presented with a short beep sound. The subject's task was to continuously report the apparent direction of the test stimuli during the 30 sec test period, by pressing either the left or the right mouse button. The subjects were instructed not to press buttons when clear motion was not seen. At least 60 sec of resting was inserted between trials.

The index of MAE strength was obtained as $Dn - Dp$, when Dn and Dp represent the aftereffect duration for negative (i.e. opposite to adapting) and positive (i.e. same as adapting) directions respectively. This index was also used by Nishida *et al.* (1994). It was designed to extract the directional bias in the flicker case, as the perceived direction often flipped over in the flicker condition.

The adapting TF was changed in a systematic manner either increasing or decreasing, and the adapting direction was alternated after each trial. The increase/decrease sequence and the adaptation direction was counterbalanced between sessions. Sessions were divided according to the spatial frequency, and each session contained seven trials. Four sessions were conducted for each condition.

Subjects

HA was the author. NW and TM were undergraduate students in our laboratory, who did not have much experience with psychophysical experiments and were naive to the purpose of the study. All had normal or corrected-to-normal vision.

RESULTS

Experiment 1

The dependence on temporal frequency of the flicker MAE was investigated. Static test condition was also tested for comparison. Spatial frequency was the same for adapting and test stimuli, 0.5, 1.0 or 2.0 c/deg. Test temporal frequencies were 0.0 (static), 2.5 and 5.0 Hz. Adapting temporal frequencies varied from 2.0 to 16.0 Hz. When expressed as velocity, they corresponded to 4.0–32.0 deg/sec for 0.5 c/deg, 2.0–16.0 deg/sec for 1.0 c/deg and 1.0–8.0 deg/sec for 2.0 c/deg.

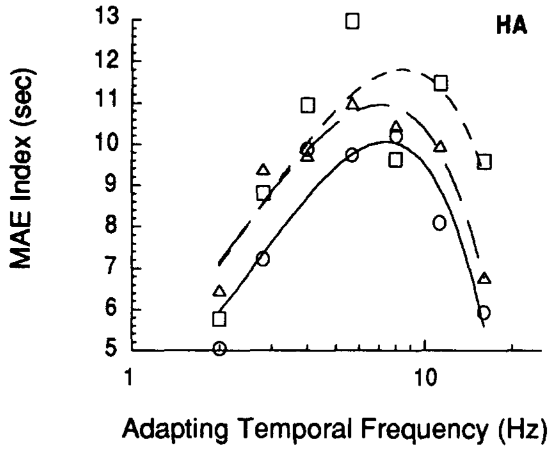


FIGURE 2. Results from static condition (0.0 Hz test) in Expt 1. Mean MAE index was plotted as a function of adapting temporal frequency for three spatial frequency conditions: ○, 0.5 c/deg; △, 1.0 c/deg; □, 2.0 c/deg.

Figure 2 shows the data from the static test condition (test temporal frequency of 0.0 Hz) for subject HA. MAE index was plotted as a function of adapting temporal frequency. Three curves represent data from three spatial frequency conditions. Each point shows the average of four trials. Curves were fitted by the least square method; MAE index f was described by:

$$f(t) = kc/p \ln[t \exp(-t/k)/c + \exp(-t/k)] \qquad (2)$$

where t represents the adapting temporal frequency and k, c and p are the fitting parameters. This equation was devised by Wright and Johnston (1985). In this figure, it is easily seen that maximal aftereffect was obtained almost at the same adapting temporal frequency regardless of spatial frequency, supporting temporal frequency dependence described by Pantle (1974) and Wright and Johnston (1985).

However, the results from the flicker condition were rather different. The data for two subjects in the 2.5 Hz test condition are presented in Fig. 3. In Figs 3(A) and 3(B), the MAE index is plotted as a function of adapting temporal frequency, just as in Fig. 2. In these figures, each curve peaks at a different adapting temporal frequency. Unlike the static condition, temporal frequency dependence was not found in this condition. In Figs 3(C) and 3(D), the data from Figs 3(A) and 3(B), respectively, are re-plotted as a function of adapting velocity. Curve fitting was also performed using equation (2) but t represents velocity in these plots. In Figs 3(C) and 3(D), though the shapes are not always quite similar, all the curves have peaks nearly at a constant adapting velocity. The exact positions of the peaks are quite unclear because of the large variance of the data and the limited range of the adaptation velocity, especially for adapting spatial frequency of 0.5 c/deg. Data fluctuation also made the precise positions unclear especially for subject TM. However, it can nevertheless be said that the curves show much better coincidence in Figs 3(C) and 3(D) than in Figs 3(A) and 3(B). It can be said that flicker MAE depends more on velocity rather than on temporal frequency.

In Fig. 4, the data from the 5.0 Hz test condition are presented. As in Figs 3(A) and 3(B) shows the temporal frequency plots, and Figs 3(C) and 3(D) the velocity plots. The general trend is quite the same as in Fig. 3, showing more dependence on velocity than on temporal frequency. Moreover, the peak adapting velocity is almost the same as that seen in Fig. 3, around 8 deg/sec. Therefore, the relation between adapting and test temporal frequencies is thought irrelevant for the preferred velocity: perhaps the important point is not the flickering frequency, but the fact that it is flickering.

Experiment 2

If flicker MAE is really velocity dependent, it should be so regardless of the adapting spatial frequency. It is quite possible, as Ashida and Osaka (1995) reported that flicker MAE did not show spatial frequency selectivity. In Expt 2, some additional experiments were performed with different adapting and test spatial frequencies. Adapting spatial frequency was either 0.5 or 2.0 c/deg, and the test spatial frequency was 1.0 c/deg. Test flickering frequency was 2.5 or 5.0 Hz. Adapting temporal frequency for the 2.0 c/deg adapting condition was 2.0–16.0 Hz, corresponding to 1.0–8.0 deg/sec in velocity. In Expt 1, the peaks were almost at the left end for the 0.5 c/deg condition, therefore the range of adapting temporal frequency was lowered to 1.0–8.0 Hz for the 0.5 c/deg adapting condition, corresponding to 2.0–16.0 deg/sec. The measuring procedure was the same as in Expt 1.

Figure 5 shows the results. Unlike the previous figures, temporal frequency plots are on the left side and corresponding velocity plots are on the right side. For comparison, the data from adapting spatial frequency of 1.0 c/deg obtained in Expt 1 are also included in the plots. Generally, Fig. 5 shows the same tendency as that seen in Fig. 4: all curves have peaks almost at the same adapting velocity, showing velocity dependence. This time the peaks were found within the adapting stimulus range.

Some fluctuation of peak positions is seen especially in Fig. 5(C). Actually it is quite hard in this figure to judge whether MAE depends on temporal frequency or velocity. This is mainly due to the peak-shift in the 0.5 c/deg condition. We replicated the experiment under this condition for this subject, but the tendency was the same. Another point to be noted is that the peaks of 2.0 c/deg condition shifted slightly toward the lower velocity, that is, toward the direction of temporal frequency dependence. This tendency was also seen in Figs 3 and 4, though it was less clear. Therefore, the dependence on velocity is not very robust, nevertheless the general tendency is clearly seen. We conclude to say that there is general tendency in flicker MAE for greater dependence

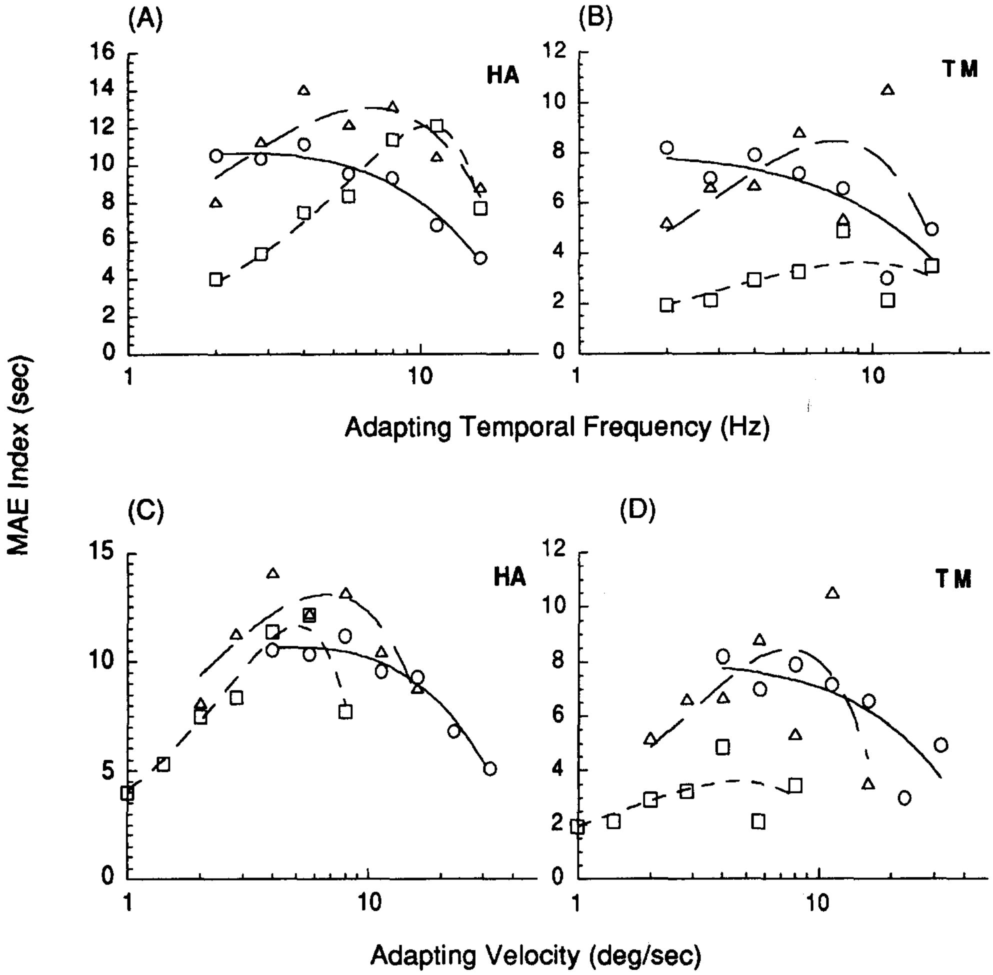


FIGURE 3. Results from flicker condition (2.5 Hz test) in Expt 1 for two subjects. (A) and (B) Mean MAE index was plotted as a function of adapting temporal frequency. (C) and (D) The same data in (A) and (B) were re-plotted as a function of adapting velocity. Data from three spatial frequency conditions are presented: ○, 0.5 c/deg; △, 1.0 c/deg; □, 2.0 c/deg.

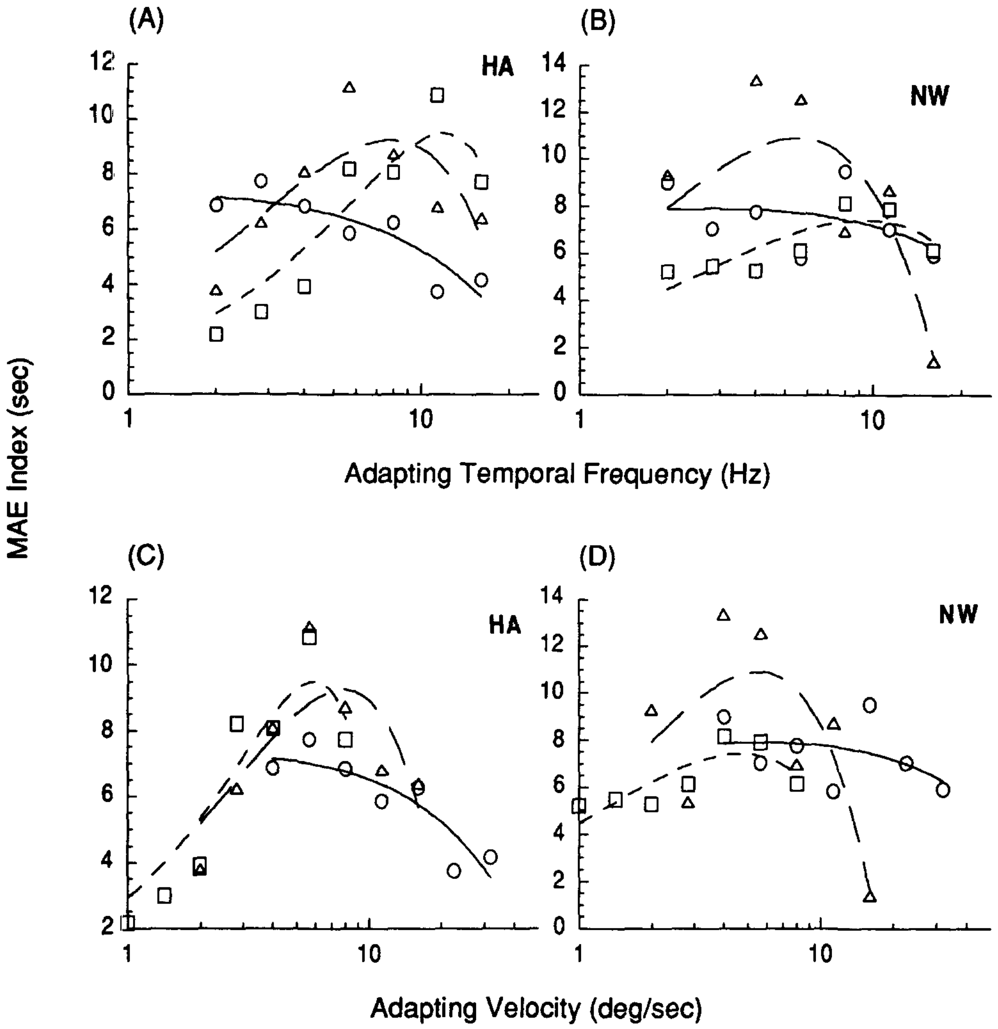


FIGURE 4. Results from flicker condition (5.0 Hz test) in Expt 1 for two subjects. Each plot shows the data from three spatial frequency conditions: ○, 0.5 c/deg; △ 1.0 c/deg; □, 2.0 c/deg. Details are the same as Fig. 3.

on velocity rather than on temporal frequency. This further demonstrates the definite discrepancy between the two types of MAE.

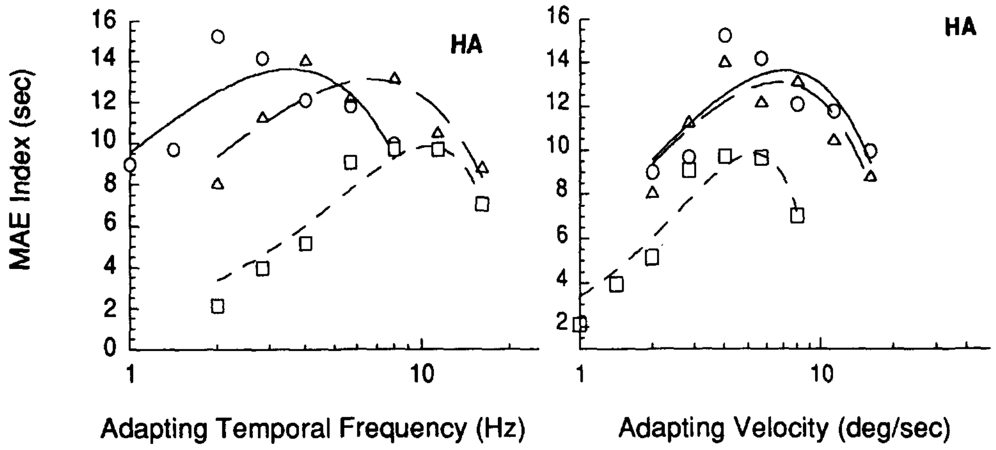
DISCUSSION

It was shown that flicker MAE is more likely to depend on velocity than on temporal frequency. With the same adapting stimuli, static MAE showed temporal frequency dependence as shown in earlier studies (Pantle, 1974; Wright & Johnston, 1985), and it is unlikely to be an artifact due to the adapting stimuli used. This is additional evidence showing the different processing levels underlying static and flicker MAEs, and quite consistent with other results suggesting the higher-level origin of flicker MAE.

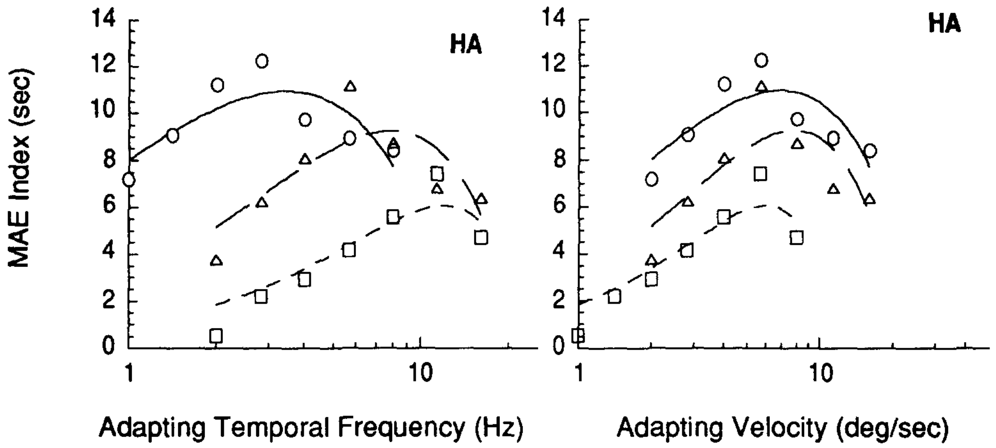
It is also important that the test flickering frequency did not affect the peak velocity. This means that temporal frequency of each component grating is not important for flicker MAE, at least in a certain range, and suggests the relevance of rather qualitative property of the directional ambiguity caused by flickering. The results of Green, Chilcoat and Stromyer (1983) are suggestive on this point: they reported MAE on a uniform flickering field, which showed rather different properties from the present flicker MAE, such as the absence of interocular transfer. The critical difference is that the test stimuli they used were not directionally ambiguous (Nishida & Sato, 1995).

It might seem odd to some people to dissociate two serially ordered processes with a single type of adapting stimuli. In our study, the adapting stimuli were the same first-order luminance gratings in both static and flicker conditions, and the lower level detectors were also subjected to adaptation. The key point is consideration of the relative strength of the activities of the underlying mechanisms. We consider that the aftereffect at the integrating process relatively stronger, thus concealing the aftereffect of low-level detectors when flickering test stimuli were used. A higher process is thought be active especially when the motion contains ambiguity. In the case of static test, there is less ambiguity and the adaptation at the earlier levels would be more decisive for the aftereffect. Our data didn't always show perfect velocity tuning and sometimes peak shift toward temporal frequency tuning was seen. This finding is thought to support our idea in that the effect of lower level mechanisms might not be entirely negligible in some cases.

(A) HA test=2.5Hz



(B) HA test=5.0Hz



(C) NW test=5.0Hz

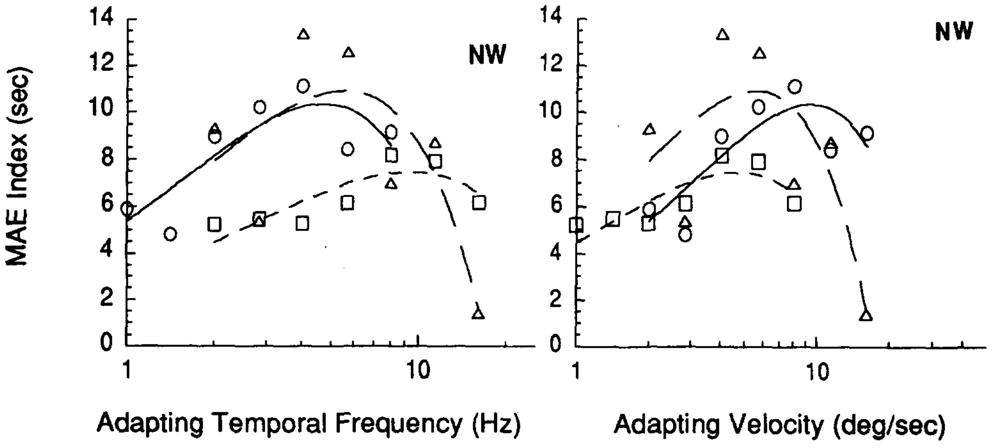


FIGURE 5. Results from Expt 2 for (A) 2.5 Hz and (B) (C) 5.0 Hz test conditions. Plots on the left side show the data as a function of adapting temporal frequency, while the plots on the right side were re-plotted using the same data as a function of velocity. Mean MAE index was plotted for three adapting spatial frequency conditions: ○, 0.5 c/deg; △, 1.0 c/deg; □, 2.0 c/deg. Data for the 1.0 c/deg condition are re-plotted from Figs 3 and 4.

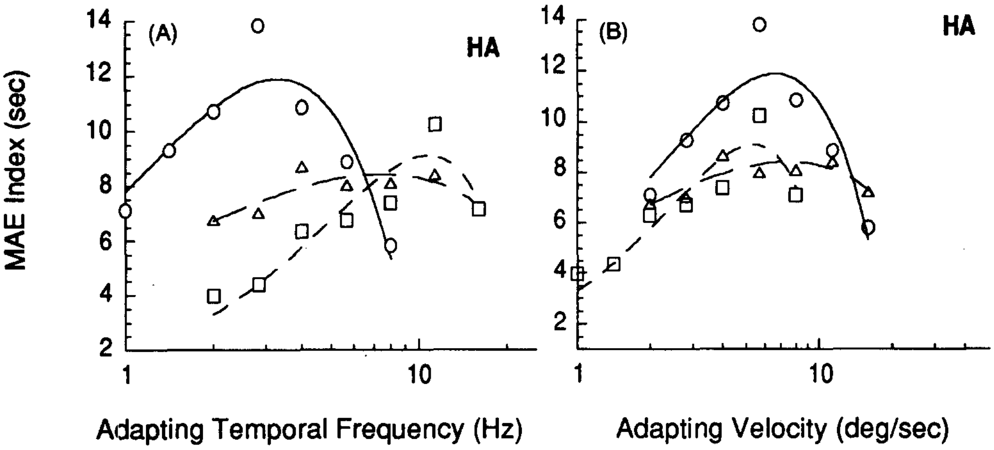


FIGURE 6. Results of the second-order test condition for subject HA. Adapting stimuli were first-order gratings of three spatial frequencies: ○, 0.5 c/deg; △, 1.0 c/deg; □, 2.0 c/deg; and the test stimuli were second-order gratings of 1.0 c/deg flickering in squarewave at 2.5 Hz. (A) Temporal frequency plot, (B) velocity plot.

Possible site of flicker MAE

Our data suggested that the underlying mechanism of flicker MAE is velocity tuned. Considering the present results with earlier ones, we assume that flicker MAE reflects the integrating process of motion signals for the extraction of velocity. An important fact is that flicker MAE is induced by both first- and second-order stimuli. Wilson, Ferrera and Yo (1992) proposed a model of velocity coding to account for plaid motion perception. In a quantitative model to predict the perceived direction of moving plaids, they assumed a stage where Fourier and non-Fourier pathways are summed, and suggested that the integration occurred in area MT (middle temporal). It is especially of interest that they asserted the necessity of input from the non-Fourier pathway for the computation of speed,* to account for the speed perception of plaids reported by Ferrera and Wilson (1991). The properties of flicker MAE are explained if we assume that flicker MAE reflects the activities of such an integrating stage.

Two other possibilities should be considered before we proceed. First, flicker MAE might reflect only the system for second-order motion, as most of the first-order stimuli are thought to activate second-order detectors, too. However, this idea is not plausible, if we consider the results obtained by Nishida *et al.* (1994) in which flicker MAE was observed when adapting to luminance grating whose contrast was as low as twice the detection threshold. The contrast sensitivity of the second-order system is thought to be lower than that of the first-order system (Nishida, 1993), and it is more plausible that flicker MAE is also induced by pure first-order motion.

Secondly, there would be a case that flicker MAE occurs independently in the first- and second-order systems, rather than at the single integration process. This idea is rejected as Ledgeway (1994) showed flicker MAE by cross-adaptation between first- and second-order stimuli. They also showed that the obtained psychometric function for varying modulation depth ratio of two components of the flickering grating was quite similar in shape under every combination of first- and second-order stimuli for adaptation and test. Their results strongly support the idea that flicker MAE occurs at the single integration level of first- and second-order signals.

The stimulus in our experiments were all first-order gratings. To get further support for the site at the integration level, we conducted an additional experiment with second-order test stimuli. As the test stimuli, we used two-dimensional static binary noise whose contrast was modulated by a sinusoidal grating. The dot density was 50%. The mean contrast was 50% and the modulation depth was 20%. The phase of the modulating sinusoidal grating was changed by 180 deg at 2.5 Hz. Other conditions were the same as Expt 2. To confirm that there was little contamination of first-order components, we checked that no static MAE was induced by such a grating when drifted in one direction. The results are shown in Fig. 6, and the same tendency of velocity tuning is seen. However, we should be cautious with the results as we had an experimental problem which we could not fully cope with: as the random noise contained first-order static spatial frequency components, strong static MAE was induced on the field itself in some cases and judging flicker MAE seen on the second-order grating was more difficult in such cases. The flicker MAE almost always lasted longer than the static MAE and the duration measure was not affected when an expert subject was tested, but it was also possible that the magnitude of flicker MAE itself might have been affected. The situation was even worse with dynamic random noise as a test, as stronger MAE was seen on the whole field like the DMAE reported by Blake and Hiris (1993). We also have to be careful regarding the difficulty in assuring that it was really a cross-adaptation effect. To put these points aside, the data supported our assumption that flicker MAE occurs at the

---

*In this case, *speed* corresponds to the absolute value of *velocity*. This distinction is especially important in two-dimensional cases such as plaids. We used only one-dimensional stimuli and we can substitute the term *speed* for *velocity* in most cases throughout this paper, but we used *velocity* considering the fact that MAE depends on the direction of adapting stimuli.

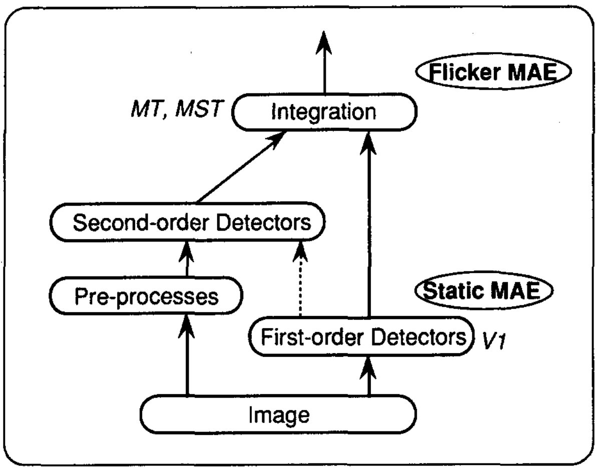


FIGURE 7. A schematic diagram showing our concept of the stream of motion processing. First and second order pathways are integrated at a higher level, and flicker MAE is thought to reflect this stage.

integration level. Further study is necessary to confirm this point.

von Grünau and Dubé (1992) reported that MAE can be seen at a region quite different from the adapted area when a flickering test grating was used and called it a remote MAE, though they did not distinguish two kinds of MAE and used only the flickering test. It is accounted for when we think of larger receptive fields at later processing stages. As for static MAE, aftereffect is seen quite locally. Zaidi and Sachtler (1991) demonstrated that static MAE was observed at the non-adapted region between the two adapting gratings, but this is a rather special case and the test region was much closer to the adapting one than those in von Grünau and Dubé's case. von Grünau and Dubé (1992) also reported that flicker MAE is sensitive to the direction of adapting plaids rather than to that of their component gratings. From these results, they concluded that MAE (flicker MAE) occurs in area MT or higher. Thinking of the fact that cells in V1 are tuned for temporal frequency rather than velocity, their idea is consistent with our results in showing the higher origin of flicker MAE than that of static MAE. It also agrees well with the prediction from the complete interocular transfer, as almost all the cells in MT have binocular inputs (Maunsell & Van Essen, 1983b).

It is noted that some physiological studies suggested that there are velocity tuned cells in MT (Maunsell & Van Essen, 1983; Rodman & Albright, 1987). Wilson *et al.* (1992) also suggested, with their model of velocity coding, that the first- and second-order motion signals are integrated in MT to compute velocity. If we assume that flicker MAE reflects the activity in MT or later, our results are quite consistent with those studies. The velocity coding in MT is not thought to be a well established fact at present, but our results might be considered as part of psychophysical support for velocity processing in MT or later, along with the results of von Grünau and Dubé (1992) and Nishida *et al.* (1994).

Figure 7 shows a schematic diagram of the processing stages according to the present discussion This scheme is quite compatible with the model proposed by Wilson *et al.* (1992).

Second-order motion stimuli are thought to be processed in two separate pathways, one is energy-based and the other is feature-based (Smith, 1993a,b). Smith and Ledgeway (1994) reported that motion through the feature-based pathway did not induce flicker MAE. If it is true, the scheme in Fig. 6 should be modified to include a separate pathway for the feature-tracking system, and a higher stage might be expected where tracking-based motion and energy-based motion are integrated. Culham and Cavanagh (1994) showed that subjects could intentionally track the features with attention to see motion on flickering gratings, and this attentional feature tracking could cause flicker MAE but not static MAE. The effect of attention on motion perception is still not clear, but some modification of the scheme will be needed to include such a top-down effect. Further experimental studies are expected to clarify this point.

REFERENCES

Anstis, S. M. (1980). The perception of apparent motion. *Philosophical Transactions of the Royal Society of London B*, *290*, 153–168.

Ashida, H. & Osaka, N. (1995). Difference of spatial frequency selectivity between static and flicker motion aftereffects. *Perception*, *23*, 1313–1320.

Blake, R. & Hiris, E. (1993). Another means for measuring the motion aftereffect. *Vision Research*, *33*, 1589–1592.

Cameron, E. L., Baker, C. L. & Boulton, J. C. (1992). Spatial frequency selective mechanisms underlying motion aftereffect. *Vision Research*, *32*, 561–568.

Cavanagh, P. & Mather, G. (1989). Motion: The long and short of it. *Spatial Vision*, *4*, 103–129.

Chubb, C. & Sperling, G. (1988). Drift-balanced stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A*, *5*, 1986–2007.

Culham, J. C. & Cavanagh, P. (1994). Attentive tracking of a counterphase grating produces a motion aftereffect. *Investigative Ophthalmology and Visual Science*, *35*, 1622.

Derrington, A. M. & Badcock, D. R. (1985). Separate detectors for simple and complex grating patterns? *Vision Research*, *25*, 1869–1878.

Ferrera, V. P. & Wilson, H. R. (1991). Perceived speed of moving two-dimensional patterns. *Vision Research*, *31*, 877–893.

Green, M., Chilcoat, M. & Stromyer III, C. F. (1983). Rapid motion aftereffect seen within uniform flickering fields. *Nature*, *304*, 61–62.

von Grünau, M. & Dubé, S. (1992). Comparing local and remote motion aftereffects. *Spatial Vision*, *6*, 303–314.

Ledgeway, T. (1994). Adaptation to second-order motion results in a motion aftereffect for directionally-ambiguous test patterns. *Vision Research*, *34*, 2879–2889.

Maunsell, J. H. R. & Van Essen, D. C. (1983a). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed and orientation. *Journal of Neurophysiology*, *49*, 1127–1147.

Maunsell, J. H. R. & Van Essen, D. C. (1983b). Functional properties of neurons in middle temporal visual area of the macaque monkey. II. Binocular interactions and sensitivity to binocular disparity. *Journal of Neurophysiology*, *49*, 1148–1167.

Mather, G. & West, S. (1993). Evidence for second-order motion detectors. *Vision Research*, 33, 1109–1112.

McCarthy, J. E. (1993). Directional adaptation effects with constant modulated stimuli. *Vision Research*, *33*, 2653–2662.

McKee, S. P., Silverman, G. H. & Nakayama, K. (1986). Precise velocity discrimination despite random variations in temporal frequency and contrast. *Vision Research*, *26*, 609–619.

Nishida, S. (1993). Spatiotemporal properties of motion perception for random-check contrast modulations. *Vision Research*, *33*, 633–645.

Nishida, S. & Sato, T. (1993). Two kinds of motion aftereffect reveal two types of motion processing. *Investigative Ophthalmology and Visual Science*, *34*, 1363.

Nishida, S. & Sato, T. (1995). Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Research*, *35*, 477–490.

Nishida, S., Ashida, H. & Sato, T. (1994). Perfect interocular transfer of flicker motion aftereffect. *Investigative Ophthalmology and Visual Science*, *35*, 2157.

Pantle, A. (1974). Motion aftereffect magnitude as a measure of the spatio-temporal response properties of direction sensitive analyzers. *Vision Research*, *14*, 1229–1236.

Rodman, H. R. & Albright, T. D. (1987). Coding of visual stimulus velocity in area MT of the macaque. *Vision Research*, *27*, 2035–2048.

Smith, A. T. (1993a). Two mechanisms for detecting second-order motion. *Investigative Ophthalmology and Visual Science*, *34*, 1363.

Smith, A. T. (1993b). Energy-based and feature-based mechanisms for detecting second-order motion. *Perception (Suppl.)*, *22*, 31.

Smith, A. T. & Edgar, G. K. (1991). The separability of temporal frequency and velocity. *Vision Research*, *31*, 321–326.

Smith, A. T. & Ledgeway, T. (1994). Dissociation of second-order motion and "long-range" motion by adaptation. *Investigative Ophthalmology and Visual Science*, *35*, 1268.

Solomon, J. A. & Sperling, G. (1994). Full-wave and half-wave rectification in second-order motion perception. *Vision Research*, *34*, 2239–2257.

Wade, N. J., Swanston, M. T. & de Weert, C. M. M. (1993). On interocular transfer of motion aftereffects. *Perception*, *22*, 1365–1380.

Wilson, H., R., Ferrera, V. P. & Yo, C. (1992). A psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience*, *9*, 79–97.

Wright, M. J. & Johnston, A. (1985). Invariant tuning of motion aftereffect. *Vision Research*, *25*, 1947–1955.

Zaidi, Q. & Sachtler, W. L. (1991). Motion adaptation from surrounding stimuli. *Perception*, *20*, 703–714.

Acknowledgements—H. Ashida was supported by Fellowships of the Japan Society for the Promotion of Science for Japanese Junior Scientists. Part of this research was supported by Grants 05801013 and 04801012 from the Ministry of Education, to N. Osaka. An earlier version of the data was presented at *2nd IEEE workshop on Robot and Human Communication* (Tokyo, Japan, November 1993). Portions of this work were presented at the annual meeting of the *Association for the Research in Vision and Ophthalmology* (Sarasota, FL, May 1994).