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Linking Lower and Higher Stages of Motion Processing?

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The spatial frequency selectivity of motion detection mechanisms can be measured by comparing the magnitude of motion aftereffects (MAEs) as a function of the spatial frequency of the adapting and test gratings. For static test gratings, narrow spatial frequency tuning has been reported in a number of studies. However, for dynamic test patterns, reports have been conflicting. Ashida & Osaka [(1994). *Perception, 23,* 1313–1320] found no tuning whereas Bex *et al.* [(1996) *Vision Research, 36,* 2721–2727] reported a narrow tuning. The main difference between the two studies was the temporal frequency of the test pattern. In this study we measured the spatial frequency tuning of the MAE using test patterns for a range of temporal frequencies. The results confirmed that there was narrow spatial frequency tuning when the test pattern was counterphasing at a low temporal frequency. However, the spatial frequency selectivity broadened as the temporal frequency of the test pattern was increased. © 1997 Elsevier Science Ltd.

Motion aftereffects Static Dynamic Flicker Tuning

INTRODUCTION

The role of spatial frequency selective mechanisms in motion detection has been confirmed in studies of the tuning characteristics of the motion aftereffect (MAE, see Wade, 1994). Typically, the strongest MAEs were elicited when drifting adapting and static test patterns were of similar spatial frequency (e.g. Over *et al.*, 1973; Cameron *et al.*, 1992; Bex *et al.*, 1996).

Hiris & Blake (1992), recently compared the MAEs recorded using static and dynamic random dot test patterns. They found that the MAE measured using static test patterns did not look like apparent motion, whereas the MAE measured using dynamic test patterns was not discriminable from a real apparent motion stimulus. Using adaptation displays of random dots moving within a directional bandwidth of approximately 10 deg from vertical, they found that the dynamic MAE was dependent on the bandwidth of motion directions, whereas the static MAE was not. Subsequently, Nishida & Sato (1995) and Nishida *et al.* (1994) showed that the visual system reveals several different characteristics depending on whether a static or flickering test pattern is used. Nishida and his colleagues argued that the static MAE involved low-level mechanisms, whereas the dynamic MAE involved higher levels of visual motion processing.

This idea of a distinction between lower and higher levels of visual motion processing was the central motive for the work by Ashida & Osaka (1994). They reported differences between the spatial frequency tuning of the MAE measured using flickering and static sine wave gratings. It was found that static test gratings showed narrow spatial frequency tuning, whereas no tuning was found using counterphase flickering test gratings. This was regarded as evidence for the idea that the MAEs are mediated by different levels of visual motion processing.

In a recent report, however, Bex *et al.* (1996) found conflicting results. Bex *et al.* reported a clear spatial frequency tuning for the dynamic MAE. The main difference between their study and that of Ashida & Osaka (1994) was the temporal frequency of the test pattern. Ashida and Osaka used 5 Hz, whereas Bex *et al.* (1996) used 0.5 Hz as the testing frequency.

Using random dot pixel arrays, Verstraten *et al.* (1994) found that the direction of the MAE induced for transparent motion changes as a function of the temporal frequency of the test pattern. Although the spatial and temporal bandwidth differs for drifting noise and drifting

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gratings, this study illustrates that the temporal frequency of the test patterns can influence the properties of the MAE. We sought to determine whether differences in the temporal frequency of the test pattern selected by Ashida & Osaka (1994) and by Bex *et al.* (1996) may have contributed to their different results.

To reconcile the differences between the results of the two studies, we measured the effect of the test temporal frequency on the spatial frequency tuning of the dynamic MAE. Spatial frequency tuning has been shown elsewhere (see above), here we examined the spatial frequency tuning of the dynamic MAE for a single adapting grating (2 c/deg) using counterphasing test sine gratings of a range of spatial and temporal frequencies. We found that at low test temporal frequencies, the MAE showed clear spatial frequency tuning, but the tuning was lost as the temporal frequency of the test grating increased. The results suggest that the differences found between the two studies can be accounted for by the temporal properties of the test stimulus.

METHODS

Apparatus and stimuli

Stimuli were generated using a Macintosh 7100/66 Power PC using software based on VideoToolbox routines (Pelli & Zhang, 1991) and were presented on a 17″ Apple Multiscan monitor at a refresh rate of 75 Hz. The mean luminance of the display was 43 cd/m^2. The luminance of the display was linearized and calibrated using a UDT Photometer. The image was 13 deg horizontally (832 pixels) by 9.75 deg vertically (624 pixels) and was viewed from a distance of 140 cm. Subjects viewed the screen binocularly in a dim room. Stimuli filled both halves of the screen, separated horizontally by a 0.33 deg strip of mean luminance, in the center of which was a prominent fixation point.

Adapting and test stimuli were vertical sinusoidal gratings of 50% Michelson contrast. The adapting gratings drifted towards the fixation point. The test gratings were sinusoidally counterphase flickering. The spatio-temporal parameters of the adapting grating were selected to give robust MAEs of optimal duration (Bex *et al.*, 1996). The adapting spatial frequency was 2 c/deg and the adapting temporal frequency was 2 or 4 Hz. The spatial frequency of the test pattern was varied from 0.5 to 8 c/deg in steps of one octave. The test gratings were counterphased at a temporal frequency between 0.125 and 8 Hz, in steps of one octave. An additional condition was measured in which the test grating was static (0 Hz). The starting phase of all gratings was randomized before each presentation.

Procedure

Two of the authors (PB and IM) and a naïve subject (CF) served as observers, all had normal or corrected-to-normal vision. Each run consisted of five trials. The spatial and temporal frequency of the adapting grating was constant on each run. The temporal frequency of the test grating was constant, but its spatial frequency was varied from trial to trial in random order. Observers were instructed to maintain steady fixation during adaptation and testing and initiated each trial with the press of a keyboard 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. The observer was required to press a keyboard button when the MAE had finished. If no MAE was experienced, the trial was noted and the MAE duration was recorded as 0 sec, however, in practice this never happened. Observers practised 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.

Each run was followed by a 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. The mean and standard deviation of at least four estimates of MAE duration for each condition were recorded.

RESULTS

Estimates of the MAE duration are shown for the three observers in Fig. 1 as a function of the test temporal frequency. The left panels represent the results for a 2 c/deg adapting grating, which was drifting at 2 Hz. In the right panels the adapting grating was also 2 c/deg, but was drifting at 4 Hz. For low test temporal frequencies, it can be seen that the largest MAEs were recorded when the adapting grating and the test grating were of the same spatial frequency. However, for higher temporal frequency test gratings, this relationship was lost and the MAE duration was approximately independent of the test spatial frequency. In addition, as the temporal frequency of the test pattern increased the duration of the MAE decreased. All three observers perceived a brief MAE, even at the highest temporal frequencies. Therefore, the reduction of the MAE duration at these temporal frequencies is not simply a floor effect. This issue is addressed below in the control experiment. A two-way analysis of variance was carried out to test the main effects of the temporal and spatial frequencies, as well as their interaction. For the three observers, these main effects were significant ($P < 0.0001$). We also examined the simple effect of the temporal frequency at each level of spatial frequency. For two observers, temporal frequency had a significant effect on spatial frequency up to 1 Hz. For the third observer (PB) the effect of temporal frequency was significant up to 2 Hz.

In this experiment, the observer's task was to detect

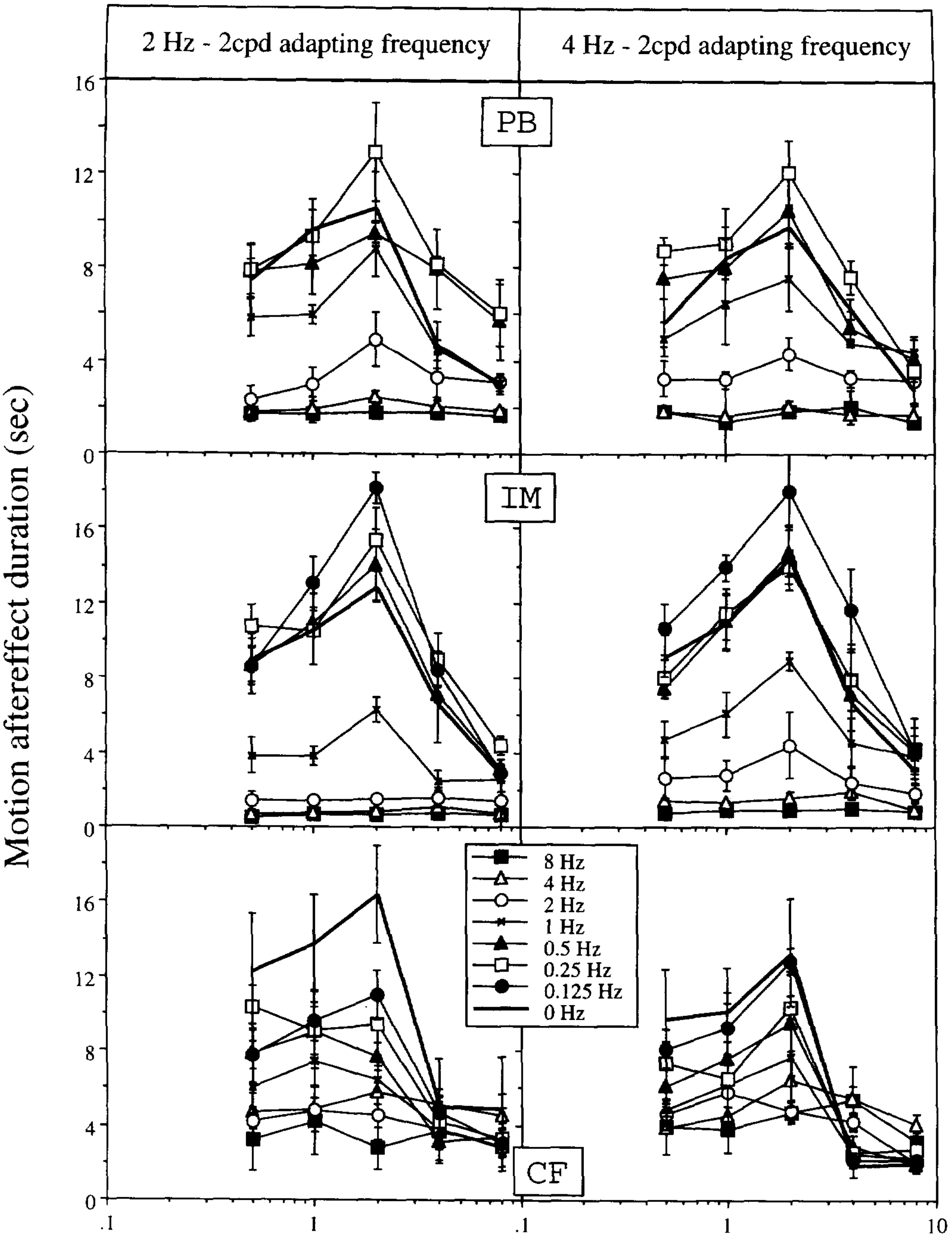

FIGURE 1. Magnitude of the MAE as a function of the spatial frequency of the counterphasing test grating. The temporal frequency of the test grating is shown in the legend, and the temporal frequency of the adapting grating is shown in the caption. The spatial frequency of the adapting grating was always 2 c/deg. The spatial frequency of the test grating is shown on the x-axis with semi-log coordinates. 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 + or − 1 SD.

illusory motion in the presence of counterphase flicker. This method relies on the assumption that the detection of motion (real or illusory) is independent of the temporal frequency of the counterphase flickering test grating. In a control experiment, we tested this assumption by measuring contrast thresholds for detecting a drifting grating in the presence of a counterphasing grating. The observer was required to detect the direction of real target motion (a drifting sine wave grating) in the presence of a counterphasing grating of the same spatial and temporal frequency. Stimuli were presented in an 8 deg circular aperture for 1 sec with abrupt onset and offset. The contrast (50%) and the spatial frequency (2 c/deg) of the counterphase grating were the same as for the main experiment. The temporal frequency of the counterphasing grating also covered the same range as for the main experiment (0–8 Hz) and was varied from run to run. The target grating was a drifting sine wave grating of

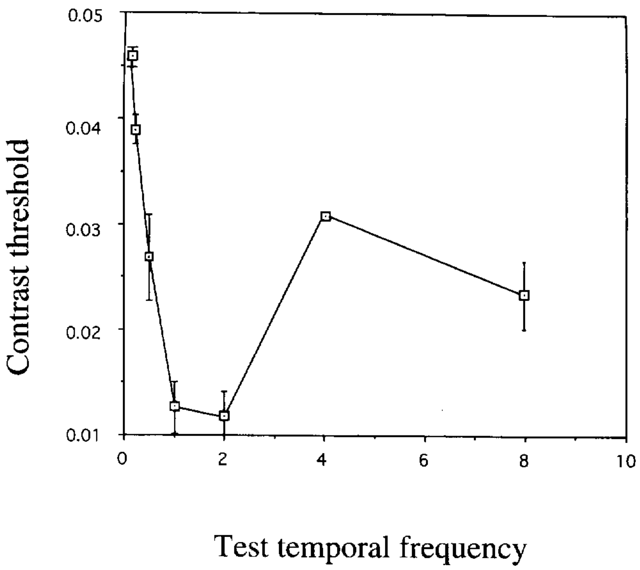

FIGURE 2. Detection thresholds of a drifting grating in the presence of a counterphasing grating. The temporal frequency of the counterphasing grating is plotted along the x-axis in Hz. The spatial frequency of the counterphasing grating was 2 c/deg and its contrast was 50%. The drifting grating was set to the same spatial and temporal frequency as the counterphasing grating.

the same spatial and temporal frequency as the counterphasing grating, but its contrast was varied over 32 trials according to a QUEST procedure (Watson & Pelli, 1983). The direction discrimination threshold for the target grating was the contrast at which the observer identified the correct direction of motion on 75% of trials. Direction discrimination thresholds are plotted as a function of the temporal frequency in Fig. 2. The results show that direction discrimination thresholds increased at both high and low temporal frequencies. This shows that any reduction in the detectability of motion (real or illusory) would affect both high and low temporal frequencies. In the main experiment, it was found that MAE duration and spatial frequency tuning were reduced only at high temporal frequencies. This shows that the reduction in MAE duration and spatial frequency tuning is not simply caused by an increase in motion detection thresholds at high test temporal frequencies.

DISCUSSION

In this study we examined the effect of the spatial and temporal parameters of the test stimulus on the duration of the MAE. We found that the MAE recorded using both static and dynamic test patterns showed narrow spatial frequency tuning under some conditions and broad or no spatial frequency tuning under other conditions, reconciling differences between previous reports (Bex *et al.*, 1996; Ashida & Osaka, 1994). When the test grating was static or its counterphase frequency was low, there was narrow spatial frequency tuning, i.e., the longest MAE was measured when the test and adapting gratings were of similar spatial frequency. However, when the temporal frequency of the test grating was increased, the spatial frequency selectivity of the MAE disappeared, in line with the findings by Ashida & Osaka (1994).

The absence of spatial frequency tuning of the dynamic MAE was cited as evidence to support the hypothesis that static and dynamic MAEs were processed in two separate streams (Nishida & Sato, 1995). According to this view, the static MAE is generated at a low level of visual processing which confers certainty of its characteristics (e.g. spatial frequency selectivity), whereas the dynamic MAE is generated at a higher level (Nishida *et al.*, 1994). The present findings indicate that the spatial frequency tuning differences are the result of the spatial and temporal properties of the test stimulus.

The results suggest that the absence of narrow spatial frequency tuning for the dynamic MAE may not necessarily provide evidence for separate streams for static and dynamic MAEs. However, evidence from other sources does support the two–stream model. For example, differences have been demonstrated between the static and dynamic MAE based on other characteristics, such as their adaptability to first- and second-order stimuli (Nishida & Sato, 1995), their relative interocular transfer (Raymond, 1993; Nishida *et al.*, 1994), and differences in recovery from adaptation (Verstraten *et al.*, 1996).

Given the support for the two-stream model derived from other experimental paradigms, the present results suggest that the distinction between the two types of MAE may be too strict. Instead of an abrupt segregation between mechanisms, there could be a gradual transition between the two mechanisms: one selective for lower temporal frequency test patterns (including static patterns) and a separate mechanism selective for higher temporal frequency patterns. However, Bex *et al.* (1996) found that the temporal frequency tuning of the MAE for a wide range of combinations of adapting and test spatial and temporal frequencies was low-pass. There was no evidence for a separate high temporal frequency mechanism. In this report we demonstrate that spatial frequency tuning is not specific to the static MAE. It is also present for the dynamic MAE, but only at low test temporal frequencies.

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