Strong influence of test patterns on the perception of motion aftereffect and position

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In a completely linear system, the behavior of a square wave pattern can be predicted by its sinusoidal components. However, we observed a complete breakdown of the linear system prediction in the perception of the motion aftereffect (MAE). The duration of the MAE was measured following a one-minute adaptation to a rotating radial grating. Three different luminance patterns were used for both the adaptation and test stimulus: (1) sine wave, (2) square wave, and (3) complex grating with the same Fourier amplitude spectrum as the square wave, but with randomized phases. The sine wave stimulus generated the highest magnitude MAE, followed by the random-phase complex grating, and lastly the square wave grating. To test whether the square wave grating is a weak adaptor or a weak test for the MAE, we performed a cross adaptation experiment in which the sine wave, square wave, and complex gratings were paired in seven ways. Results show that the strength of the MAE critically depended on the test pattern. Regardless of the adaptor, MAE strength is in a decreasing order with the test pattern as sine wave grating, complex grating, and square wave grating. Further experiments ruled out the possibility that differential MAEs between these conditions are due to different peak contrasts in these patterns. Additionally, the MAE from a square wave grating as the test pattern is not accompanied by a significant concurrent shift in the apparent position. Linear system theory cannot predict the magnitude of the MAE using complex gratings. The spatial features of a test stimulus, such as position reliability or luminance uniformity, strongly influence the magnitude of MAE. Sharp edges and local luminance uniformity can greatly reduce MAE.

Keywords: motion aftereffect, spatial pattern, linear system, adaptation, position

Introduction

The motion aftereffect (MAE) refers to the change in motion perception following prolonged observation of a regularly moving stimulus. Typically, the MAE involves the apparent motion of a stationary stimulus in the opposite direction to a previously observed one, but it can also result in a change in the apparent velocity of a moving stimulus (Mather, Verstraten, & Anstis, 1998).

Sine wave gratings gained their popularity after Blakemore and Campbell (1969) introduced the idea of the visual system as a set of "spatial-frequency channels." These socalled "spatial-frequency channels" were suggested to form the basis of a visual Fourier analysis of the retinal image (Robson, 1975). Sine wave gratings have been widely used in visual detection and discrimination tasks (see Wilson & Wilkinson's review, 1997), and it is a natural extension to use them in studies of MAE. Meanwhile, the square wave grating has also been frequently used in MAE studies for its spatial simplicity. With the Fourier transform, the squarewave can be decomposed into a series of sinusoid harmonic components.

The MAE is a very robust phenomenon in the sense that after motion adaptation, almost any static pattern will be seen as moving. Because any spatial pattern can be decomposed into its Fourier components, the generality of the MAE implies that the motion adaptation occurs on the underlying channels tuned to different spatial frequencies, not on the specific adapting pattern per se.

Some very general underlying assumptions of the MAE (Mather et al., 1998) are that when we "adapt" to a pattern, we assume that some mechanisms, neurons, or synapses in the visual pathways are excited, stimulated, or activated. In addition, it is assumed that the greater the excitation, stimulation, or activation during adaptation, the greater the mechanisms, neurons, or synapses are adapted, fatigued, or habituated, resulting in a stronger MAE (Priebe & Lisberger, 2002). Because the multiple sinusoid components in a square wave grating can stimulate a range of spatialfrequency channels in the visual system simultaneously, one may want to predict that the MAE produced by square wave grating will be stronger than that produced by a sine wave grating, especially given that there is evidence showing that some MAE signals can be linearly combined (Mather & Moulden, 1980; Verstraten, Fredericksen, & van de Grind, 1994). In these studies, subjects adapted to two motions simultaneously. The MAE direction was predicted by the vector sum of the adaptation components. Is it the case that the MAE magnitude produced by square wave grating

can be predicted from those produced by its Fourier components?

However, the advent of "spatial-frequency channels" analysis may be partly responsible for the general neglect of nonlinear interactions in the visual system. Recent work has demonstrated that early visual channels interact through a variety of nonlinear pooling mechanisms. Such nonlinear interactions perform important computations in texture perception, stereopsis, and motion and form vision (Wilson & Wilkinson, 1997). It is possible that nonlinear interactions exist in the generation of MAE, which in turn will lead to a failure of predicting MAE of a complex grating from its sinusoidal components. Actually, some studies have demonstrated the effects of cross-channel interaction on visual aftereffects (Levinson & Sekuler, 1975; Magnussen & Kurtenbach, 1980).

To test whether MAE can be predicted based on a linear model, we measured the strength of MAE to a number of different spatial patterns. In particular, in Experiment 1, we tested whether changing the relative phases of sine wave components in a pattern will alter the perceived MAE. Given that we did find a contribution from spatial phase in Experiment 1, we further tested whether the pattern influence occurs during the adaptation or testing phase in Experiment 2. Nishida and Johnston (1999) showed that motion aftereffect could alter the perceived position of a visual target. In Experiment 3, we also test if spatial pattern can influence the perception of illusory position shift following motion adaptation.

Experiment 1: Does spatial phase matter in MAE?

The purpose of this experiment is to compare the MAE magnitudes generated by sine wave and square wave gratings. We also measured the MAE from a complex grating that shares the same amplitude spectrum with the square wave grating, but with scrambled phases. Because randomizing the phases of sine wave components could make the peak contrast of a complex grating higher than a square wave, and some studies (Keck, Palella, & Pantle, 1976; Nishida, Ashida, & Sato, 1997) have shown that increasing adaptation contrast increases the MAE, it was necessary to do a control experiment to test whether differences in peak contrast are responsible for the different MAE between the complex and square wave gratings observed in Experiment 1.

Method

Apparatus and stimuli

All experiments were conducted on a PC controlling a SONY 19-inch Trinitron high-resolution monitor (1280 \times 1024) set at 100-Hz refresh rate. Stimuli were radial gratings of three types of waveforms: sine wave (SIN),

square-wave components with scrambled phases (SCR), and square wave (SQU). The diameter of each stimulus was 8.2 deg. The fundamental frequency for all three stimuli was 4 cycles per revolution at 50% contrast. The mean luminance of the stimuli is 40 cd/m². SCR was generated by randomly scrambling the phase spectrum of SQU with the constraint that the maximal and minimal luminance values in SCR are within the luminance range of the monitor. The stimuli and their luminance profiles are shown in Figure 1.



Figure 1. Three types of stimuli and their luminance profiles used in Experiment 1.

Observers

Two experienced observers (FF and SH) and two naïve observers (WL and MK) participated in this experiment. All observers in this series of experiments had normal or corrected-to-normal vision.

Procedure

At the viewing distance of 57 cm, observers fixated at the center of the adaptation stimulus, which was rotating at a speed of 150 deg/s. They adapted for 1 min, then the motion stopped, and the static stimulus remained on the screen. All of the observers experienced MAE. They were instructed to press a key when MAE stopped and the duration of MAE was recorded. For every stimulus type, each subject ran 12 trials on four different days (3 trials each day). A minimum 5-min interval was placed between two trials, to dissipate residual MAE.

In this experiment, the peak contrast of SCR could potentially reach 1.0 (Michelson contrast), higher than that of the SQU. In a control experiment, the contrast of SQU was increased to 1.0, ensuring that the contrast of SQU was never lower than that of SCR. The SQU and SCR were presented side by side with a fixation point in between. Their rotating directions were randomized, but always mirror-reversed. Their relative positions were also randomized. After 1-min adaptation, the same four observers were asked to make a forced-choice judgment about which grating's MAE lasted longer. Each observer ran 10 trials, with a minimum 5-min interval between trials.

Results

As shown in Figure 2, for all observers, the most robust result is that the MAE generated by SQU is surprisingly weak (~10 s), and the SIN generated the longest MAE (> 30 s). The duration of MAE from SCR lies between the other two (20-30 s). The difference of MAE duration between any pair of stimuli types reached statistical significance (p < .01).

For the control experiment directly comparing the MAE from SCR and SQU, all four subjects judged the MAE from SCR stronger than that from SQU in all 40 trials. This result shows that when the peak contrast of SQU was increased to exceed that of the SCR, the SCR still generated a stronger MAE.

It should be noted that equating the peak contrast between SIN and SQU did not make the amplitude of the fundamental frequency equal. We found equating the amplitudes of their fundamental frequencies had a negligible effect on our results.

Adapting Experiment 2: versus test stimulus: cross adaptation between different patterns

Experiment 1 demonstrated that the square wave grating produced much weaker MAE than the complex and sine wave gratings. Why was the MAE from the square wave grating so weak? The MAE duration reported in Experiment 1 for square wave grating probably overestimates the actual strength of the square wave MAE. All subjects reported that they could hardly perceive any significant illusory rotation of the square wave grating after adaptation, but saw only weak "vibration" of the borders between bright and dark regions. To further explore whether the lack of strong MAE from square wave grating is because square wave grating is a poor adaptor or a poor test pattern for MAE, we performed a cross adaptation experiment pairing complex (SCR), square wave (SQU), and sine wave (SIN) gratings across each other.

Method

There were seven experimental conditions, depicted in the insets in Figure 3, consisting of adaptation – test pairs as following: (1) sine wave - sine wave, (2) square wave sine wave, (3) complex - complex, (4) square wave - complex, (5) sine wave - square wave, (6) complex - square wave, and (7) square wave - square wave. In the complexcomplex condition, the adapter and test were identical. The experimental procedure was the same as that of Experiment 1. One experienced (FF) and three naïve observers (WL, JZ, and JW) participated in this experiment.

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Figure 2. Average MAE durations for three types of stimuli from four observers (n = 12). Vertical bars denote 1 SD.

Results

The duration of MAE highly depended on the test pattern, but not adaptor (see Figure 3). As the test pattern, the sine wave grating generated the longest MAE (close to 30 s), the complex grating generated shorter MAE (low 20 s), and the square wave grating generated the shortest MAE $(\sim 10 \text{ s})$. The difference of MAE duration among different test patterns was significant (p < .01). Somewhat surprisingly, for each test pattern, there was no significant difference between different adaptors.



Figure 3. The results of Experiment 2. Average MAE durations for four experimental conditions from four observers (n = 12). Vertical bars denote 1 SD.

Control experiment

A possible explanation for weak MAE from SQU as test pattern is that subjects used different criteria for judging when the different patterns are (and are not) in motion. For example, if it were in some sense "harder to see" a particular pattern moving, then that would tend to shorten the measured MAE duration, even though the effect had nothing to do with that pattern's susceptibility to adaptation per se. We did a simple control experiment to measure (unadapted) minimum motion thresholds of two subjects (FF and WL) for the three different patterns. The experimental procedure was very similar to that used by Tadin, Lappin, Gilroy, and Blake (2003). We measured the threshold exposure duration required for human observers to accurately identify the motion direction of a horizontally drifting vertical linear grating (SIN, SQU, and SCR). The stimuli extended 8.2 \times 8.2 deg². The fundamental frequency for all three stimuli was 0.31 c/deg at 50% contrast, which was the average frequency of radial pattern used in Experiments 1 and 2. Other experimental conditions were the same as those used in Experiments 1 and 2. On each trial, a drifting patch was presented foveally and observers indicated the perceived direction (left or right) by a key press. Duration thresholds (82%) were estimated by Quest staircases (Watson & Pelli, 1983), six times for each subject and stimulus type. We found that SIN was harder to detect than SQU and SCR. For observer FF, the motion thresholds (mean±STD) for SIN, SCR, and SQU were 67 ± 5, 47 \pm 5, and 42 \pm 4 ms, respectively. For WL, they were 82 \pm 4, 60 ± 9 , and 43 ± 5 ms, respectively. This result demonstrated that weak MAE from SQU cannot be attributed to the explanation that moving SQU is more difficult to be detected than moving SIN.

Experiment 3: Influence of MAE on spatial position for different patterns

Recently, Snowden (1998), Nishida, and Johnson (1999) and McGraw, Whitaker, Skillen, and Chung (2002) showed convincingly that the MAE can be accompanied by a concurrent shift in that apparent position of the physically stationary test pattern. As we found in the previous experiments, the MAE generated by the square wave grating is very weak. Can we predict that the apparent position shift of the square wave grating is smaller than that of the sine wave grating after motion adaptation?

Method

Stimuli

As depicted in Figure 4, both adaptation and test stimuli were two strips of vertical grating (sine wave or square wave) with the spatial frequency of 0.71 cycles/deg and 50% contrast. Each strip had a height of 3.94 deg and a width of 8.94 deg. Its luminance ranged from 20 to 60 cd/m^2 . The luminance of blank frame (background) was 7.24 cd/m^2 . The two gratings were displaced vertically from the fixation point by 0.28 deg. For the adaptation stimulus, vertical gratings moved in opposite directions (one left and one right) at the speed of 2.8 deg/s. For the stationary test stimulus, the phase of the upper grating was shifted in the adaptor's motion direction in steps of 1 pixel. In other words, the upper and lower gratings were misaligned. One pixel shift equals 0.028 deg at the viewing distance of 57 cm.

Observers

Two experienced observers (FF and SH) and one naïve observers (JM) participated in this experiment.

Procedure

Observers first viewed the adaptation pattern for 30 s, in which the upper and lower gratings moved in opposite directions, as indicated in Figure 4. After a gap of 1-s blank screen, the test stimulus was presented to observers for 0.2 s. Observers made a two-alternative choice as to which direction the upper grating appeared to be relative to the lower grating. For the test stimulus, a standard staircase program was used to search for the size of physical shift between the two gratings so that they appeared aligned. After 60-s rest, the adapt-test cycle was rerun. For each observer, the shift was measured 4 times for sine wave and square wave gratings, respectively.



Figure 4. Illustration of the adaptation and test regime in Experiment 3.

Here we describe the staircase program in more detail. In the first trial, after 30-s adaptation, observers were presented with aligned upper and lower gratings. Observers judged the relative position of upper grating to the lower one (left or right). In the subsequent trials, the relative position of these two gratings was adjusted according to observers' responses in the immediate preceding trial, with the step size of one pixel (0.028 deg). The test was stopped until six response reversals had occurred. The amount of position shift was calculated by averaging six values at reversing points.

Results

As shown in Figure 5, spatial pattern played an important role in the MAE-induced position change. For the sine wave grating, all three subjects needed a significantly larger (about 3 times larger) spatial shift between the two gratings to perceive them as aligned, compared with the square wave grating ($p \le .01$). A potential explanation of this phenomenon is that the square wave grating provides a strong position cue to prevent the illusory position shift.



Figure 5. Physical shifts of the upper gratings (n = 4) required to make the upper and lower gratings look like they are aligned, for sine wave and square wave, respectively. Data are plotted for three subjects. Vertical bars denote 1 *SD*.

Discussion

We found that the square wave grating produced much weaker MAE than the sine wave and complex gratings. Cross adaptation between these patterns showed that the square wave grating was not a weaker adaptor for the motion system. The weak MAE was only observed when square wave grating was used as the test stimulus.

Why does square wave grating as a test pattern generate very weak MAE? We suggest that two properties of the square wave pattern may contribute to this result: position reliability and local luminance uniformity. Intuitively, if a test stimulus provides reliable cues on spatial position, then it will be difficult to generate illusory motion. The square wave grating, with the black and white boundaries sharply localized, presumably provides such reliable position cues. Similarly, the reliable positions cues can prevent the illusory position shift of the test pattern. This point was supported by a parallel study (Fu, Shen, & Dan, 2001). In their experiment, motion-induced perceptual extrapolation of both first- and second-order targets depended critically on spatial blurring of the targets. For example, the perceptual displacement of a sharp-edged target was near zero; however, for a target with Gaussian profile, its displacement was very significant. The influence of visual motion on perceived position has been well acknowledged (see a review by Whitney, 2002). The current study highlights the reverse

influence, that the reliability of position cues strongly affects the strength of perceived illusory motion. It supports the intricate relationship between representations of an object's (or pattern's) location and its motion, possibly supported by the interactions between MT and V1 neurons (Ramachandran & Anstis, 1990; De Valois & De Valois, 1991; Whitney & Cavangh, 2000; Pascual-Leone & Walsh, 2001; Murray, Kersten, Olshausen, Schrater, & Woods, 2002). With this explanation, it is not surprising to find that the MAE from a square wave grating as a test pattern is not accompanied by a concurrent shift in the apparent position.

The second property of a square wave, namely its local luminance uniformity, could also contribute to its weak MAE. A uniform luminance field cannot support motion perception. Not surprisingly, Spitz (1958) found no motion aftereffect when a clear blue sky was used as a test field. For the square-wave grating, the areas within each bar have uniform luminance, only the boundaries between neighboring areas can support illusory motion. This explanation in essence states that what is important for MAE is not only the pattern's amplitude (or power) spectrum, but also the relative phases of the components.

The contrast between a square wave grating and a complex grating consisted of its Fourier components with scrambled phases provides strong support for the two possible explanations stated above. Although the two stimuli have the same component waveforms, the complex grating with scrambled phase provides more local luminance variations as well as weaker position cues than the square wave grating.

Many studies on MAE (Cameron, Baker, & Boulton, 1992; Bex, Verstraten, & Mareschal, 1996) have shown the spatial tuning of the motion aftereffect on static test patterns. Generally speaking, the greatest effects are seen when the test stimulus most closely resembles the adaptation stimulus. The results of our experiment do not support the strict interpretation of this claim. For example, after adapting to a square wave grating, a sine wave test pattern gives a stronger MAE than using the same square wave grating as the test. The effect of square-wave test seemed to prevent them from producing the percept of illusory motion. When the MAE stopped with a square wave, we replaced the square wave with a sine wave, and we can still perceive a weak MAE from the sine wave. In a sense, the square wave grating produced a variant of the so-called storage of MAE.

Conclusion

The strength of MAE cannot be predicted based on the linear system analysis, but it critically depends on the test pattern's luminance profile. Patterns that provide reliable position cues and have minimal local luminance variation, such as a square wave grating, are more difficult to perceive in illusory motion. Such patterns are also more resistant to being misperceived in location.

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