Motion mechanisms with different spatiotemporal characteristics identified by an MAE technique with superimposed gratings

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We investigated spatiotemporal characteristics of motion mechanisms using a new type of motion aftereffect (MAE) we found. Our stimulus comprised two superimposed sinusoidal gratings with different spatial frequencies. After exposure to the moving stimulus, observers perceived the MAE in the static test in the direction opposite to that of the high spatial frequency grating even when low spatial frequency motion was perceived during adaptation. In contrast, in the flicker test, the MAE was perceived in the direction opposite to that of the low spatial frequency grating. These MAEs indicate that two different motion systems contribute to motion perception and can be isolated by using different test stimuli. Using a psychophysical technique based on the MAE, we investigated the differences between the two motion mechanisms. The results showed that the static MAE is the aftereffect of the motion system with a high spatial and low temporal frequency tuning (slow motion detector) and the flicker MAE is the aftereffect of the motion system with a low spatial and high temporal frequency tuning (fast motion detector). We also revealed that the two motion detectors differ in orientation tuning, temporal frequency tuning, and sensitivity to relative motion.

Keywords: motion, MAE, spatiotemporal

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Introduction

Psychophysical and physiological studies have revealed that the visual system analyzes motion signals in several different processes. The process operating at the first stage is believed to detect local motion energies (Adelson & Bergen, 1985; Watson & Ahumada, 1985), independently of actual displacements (Adelson & Bergen, 1985; Anstis & Rogers, 1986; Shioiri & Cavanagh, 1990). As in the detection process of luminance contrast (Blakemore & Sutton, 1969) or disparity changes (Shioiri, Hatori, Yaguchi, & Kubo, 1994; Yang & Blake, 1991), the motion detectors at the first stage are suggested to have several channels with differences in spatial frequency tuning (Anderson & Burr, 1985; Ashida & Osaka, 1994; Bex, Verstraten, & Mareschal, 1996; Cameron, Baker, & Boulton, 1992; Thompson, 1998). In contrast, qualitative differences have also been suggested in motion analyses in different pathways or different stages: short/long range motion (Braddick, 1974), passive/active motion (Cavanagh, 1992), local/global motion (Bex, Metha, & Makous, 1999; Cavanagh & Favreau, 1980; Morrone, Burr, & Vaina, 1995; Snowden & Milne, 1997), component/pattern motion (Adelson & Movshon, 1982; Nishida, 1993), first/second order motion (Cavanagh & Mather, 1989; Nishida & Sato, 1995) and so on.

The motion sensitive mechanism in early vision is often considered to have a temporal frequency tuning with a peak at around 5 Hz (Livingstone & Hubel, 1988; Pantle, 1974). However, several studies have suggested that the visual system has fast and slow motion detectors (Alais, Verstraten, & Burr, 2005; Anstis, 2009; Gegenfurtner & Hawken, 1996b; Hawken & Gegenfurtner, 2001; Hawken, Gegenfurtner, & Tang, 1994; Hirahara, 2006; Mareschal, Ashida, Bex, Nishida, & Verstraten, 1997; Shioiri, Ito, Sakurai, & Yaguchi, 2002; van der Smagt, Verstraten, & van de Grind, 1999; Verstraten, van der Smagt, & van de Grind, 1998). This indicates that there is an additional motion mechanism that is sensitive to slow motion (or low temporal frequency) stimuli. In addition, relatively long temporal integration characteristics of motion processes have been reported (Regan, 1989; Shioiri & Cavanagh, 1992; Shioiri et al., 2002). Among these, the research of Verstraten and his colleagues has shown that a motion aftereffect (MAE) depends on the temporal condition of the test stimulus (Alais et al., 2005; Mareschal et al., 1997; van der Smagt et al., 1999; Verstraten et al., 1998), which strongly suggests the existence of both slow and fast motion detectors. MAE is a phenomenon wherein

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motion is perceived in a static stimulus after the visual system is exposed to a moving stimulus. Despite these studies, the knowledge of these detectors is as yet limited.

In this paper, we report that the slow and fast motion detectors differ in spatiotemporal frequency selectivity. We developed a novel MAE technique that is based on a newly found phenomenon. Using this technique, we investigated the difference in spatial and temporal frequency characteristics between the fast and slow motion detectors. We measured the direction and the duration of the MAE after the adaptation to combined gratings with different spatial frequencies, where the gratings moved in opposite directions. This technique enabled us to isolate the fast and slow motion detectors. This rationale stems from a phenomenon that the first author and his colleagues uncovered when they attempted, but failed, to show the spatial frequency selectivity of an MAE[i].

The stimuli used were two superimposed luminance gratings with different spatial frequencies, moving in opposite directions: left and right. After a prolonged exposure to the stimulus, the observer saw either a static version of the same superimposed gratings, a high spatial frequency grating or a low spatial frequency grating. According to the multiple channel theory, the MAE would be observed in the direction opposite to that of the low spatial frequency motion when the low spatial frequency grating was used as the test stimulus, and in the direction opposite to that of the high spatial frequency motion when the high spatial frequency grating was used as the test stimulus. However, observation revealed that the MAE was always in the direction opposite to that of the motion of the high spatial frequency irrespective of the test stimuli. That is, an MAE selective to spatial frequency was not obtained. We call this the high spatial frequency (SF) superiority or dominance of the MAE[ii]. More surprisingly, the direction of the MAE was the same as that of the dominant motion of the adaptation stimulus (Figure 1). This is unusual since the MAE is a negative aftereffect. When two gratings of the same contrast with different spatial frequencies move in opposite directions, the motion impression as a whole is usually in the direction of the low spatial frequency grating. This is so because the spatial frequency tuning is low-pass when measured with high temporal frequency stimulations (or high speed motion) (Nachmias, Sachs, & Robson, 1969; van der Smagt, Verstraten, Vaessen, van Londen, & van de Grind, 1999).

This is puzzling at first glance. However, this can be explained by assuming two motion detectors with different spatiotemporal frequency tunings. The adaptation effect, including the MAE, is influenced by the sensitivity of the underlying mechanisms to the test stimulus as well as to the adaptation stimulus. Our initial surprise arose from the implicit assumption that the motion detectors had the same spatial frequency sensitivity irrespective of the temporal condition (either moving as in the case of the adaptation stimulus or static as in the case of the test stimulus). However, this is usually not the case. The temporal frequency of the adaptation stimulus (we used 5 Hz) was very different from that of the test stimulus (0 Hz). Figure 2 provides a possible interpretation of this phenomenon. The red and green areas indicate the sensitivity profiles for two motion systems with different spatiotemporal frequency tunings. One motion detector is sensitive to high spatial and low temporal frequencies; the other is sensitive to low spatial and high temporal frequencies. We call the detectors in these systems the slow and fast motion detectors, emphasizing the difference in temporal properties. When the low and high spatial frequency gratings move in opposite directions at a certain temporal frequency as an adaptation stimulus, the fast motion detector responds more than the slow motion detector, providing dominant motion in the direction of the low spatial frequency motion. Such superimposed gratings cause the adaptation effect not only on the fast motion detector but also on the slow motion detector in the opposite direction. The slow motion detector dominates the fast motion detector in terms of the MAE because of its higher sensitivity to the static test stimulus.

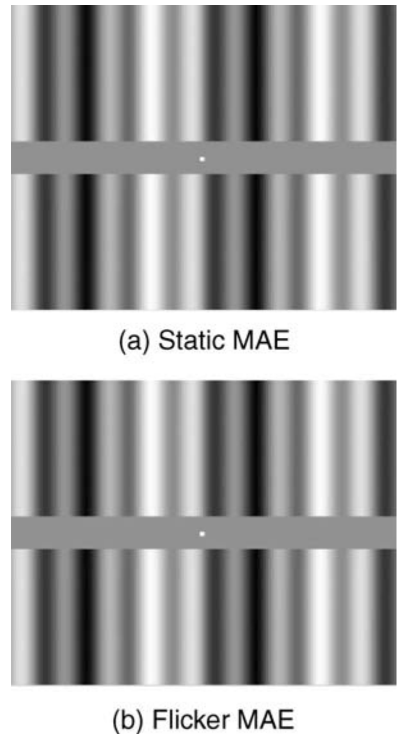

Figure 1. (a) High spatial frequency dominance of the static MAE. Adaptation stimulus comprised two superimposed sinusoidal gratings with different spatial frequencies. After exposure to the moving stimulus, observers perceived the static MAE in the direction opposite to that of the high spatial frequency grating even when low spatial frequency motion was perceived during adaptation. (b) Low spatial frequency dominance of the flicker MAE. In contrast to the static MAE, the MAE in the flicker test was perceived in the direction opposite to that of the low spatial frequency grating.

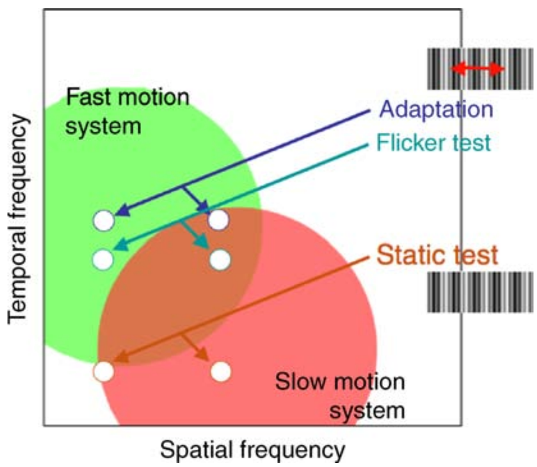

Figure 2. Interpretation of high spatial frequency dominance of the MAE. When the superimposed high and low spatial frequency gratings move in opposite directions, two motion detectors with different spatiotemporal frequency tunings (green: fast motion detector, red: slow motion detector) are adapted in different directions. Since the sensitivity to the static test stimulus is higher in the case of the slow motion detector, the MAE of the high spatial frequency grating is observed even when the motion perception during adaptation is in the direction of the motion of the low spatial frequency grating. The opposite MAE is expected for the flicker test with a temporal frequency similar to that of the adaptation stimulus.

Note that Figure 2 depicts the general concept of the two motion systems. Actual spatiotemporal tunings of the motion systems can be very different from those shown in the figure (see temporal frequency tunings in Figures 8 and 9).

Experiment 1: Fast and slow motion detectors

Experiment 1 investigated the effect of the temporal condition of the test stimulus on the MAE. This was to confirm high SF dominance of static MAE and low SF dominance of flicker MAE. The test stimulus was either static or counter-phase flickering gratings. The assumption of the fast and slow motion detectors as shown in Figure 2 predicts that the MAEs in the static and flicker test stimuli will be in opposite directions. The slow motion detector is sensitive to the static test to a greater extent than the fast motion detector, whereas the fast motion detector is sensitive to the flicker test to a greater extent than the slow motion detector. If the sensitivity is reduced in opposite directions between the fast and slow motion detectors, the MAE in the static and flicker tests will be in opposite directions.

Further, we manipulated the relative motion components in this experiment to examine whether there are differences in the effect of relative motion. This was the second purpose of Experiment 1. When two stimuli that are located spatially adjacent to each other move in opposite directions, sensitivity to detecting the motion is usually higher than when the same two stimuli move in the same direction. For example, if the effect of relative motion is larger with slow motion stimulation (Shioiri et al., 2002), we expect larger differences in the static test than in the flicker test when the results obtained in the conditions with and without the relative motion components are compared.

Method

Apparatus

The stimuli were presented on a display (G520, Sony) controlled by a video card (ViSaGe, Cambridge Research) and a computer with a 1024 × 768 pixel resolution (80 Hz non-interlaced). The distance between the observer and the display was 38 cm. The observer's head was fixed with a chin rest.

Stimulus

The adaptation stimulus consisted of a pair of sinusoidal gratings with different spatial frequencies (Figure 3), drifting in opposite directions (left and right) at 5 Hz. The contrast of each grating was adjusted to a value of 30 times higher than the threshold for detecting the drifting gratings at 5 Hz for all spatial frequencies. The same contrasts were used in both the adaptation and the test phases. The average luminance of the gratings was 68.2 cd/m^2 and the background luminance was also the same. The stimulus color was yellow with CIE xy color coordinates of (0.413, 0.506). The stimulus size was 17.3° × 30°. The spatial frequency of one of the gratings was always 0.53 c/°, and the spatial frequency of the other was either 0.13, 0.26, 1.1 or 2.1 c/°. These spatial frequencies were chosen so that the required contrast of 30 times higher than the threshold could be realized on the display (i.e., spatial frequencies with a contrast threshold lower than 0.033) in the experimental condition.

Procedure

A trial comprised adaptation and test phases. The observers were asked to fixate the central fixation spot and were exposed to adaptation gratings for 30 s in the adaptation phase. The test stimulus was presented after a 0.5 s presentation of a 68.2 cd/m^2 yellow uniform field following the adaptation stimulus. At the moment when the observer judged that the MAE had disappeared, he responded the direction of the MAE by pressing one of

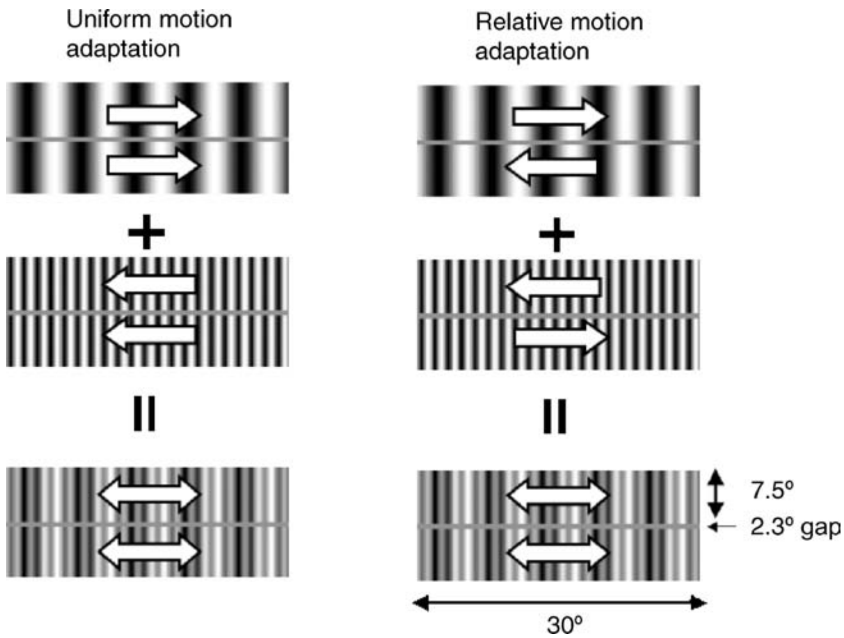

Figure 3. Stimulus configuration of the relative and uniform motion adaptations. Two superimposed gratings with different spatial frequencies (comparison and standard) moved in opposite directions. The upper and lower gratings of the same spatial frequency moved in the same direction in the uniform motion condition and in the opposite directions in the relative motion conditions. The direction and duration of the MAE were measured in a static or a 4 Hz flickering version of the same superimposed gratings.

two keys, which were assigned to left and right. The observer was instructed to press a third key when no MAE was observed: the MAE duration was considered to be 0 s in this case.

A grating of 0.53 c/° was used as the standard and the one of the other grating was used for a comparison. Each observer ran four sessions of twelve trials (4 spatial frequencies × 3 repeats) in each of the two (relative and uniform) motion conditions for both the static and the flicker tests. Each session used a fixed adaptation direction and each observer ran two sessions for each of the two motion directions. The second author and four naive observers participated in Experiment 1. All the observers had normal or corrected-to-normal vision.

Results and discussion

Figure 4 shows the MAE duration as a function of the comparison spatial frequency for static and flicker tests after the relative and uniform motion adaptations. The positive values on the vertical axis indicate the durations of the MAE in the direction opposite to that of the standard stimulus motion and the negative values indicate the durations of the MAE in the direction opposite to that of the comparison stimulus. In the static test, the observer always reported the MAE direction to be opposite to the direction of the higher spatial frequency grating motion, regardless of whether the standard or the comparison gratings had higher spatial frequency. The aftereffect of the grating with a higher spatial frequency dominated the MAE perception (high SF dominance of the static MAE).

The figure also shows clear differences in the MAE durations between the relative and the uniform conditions

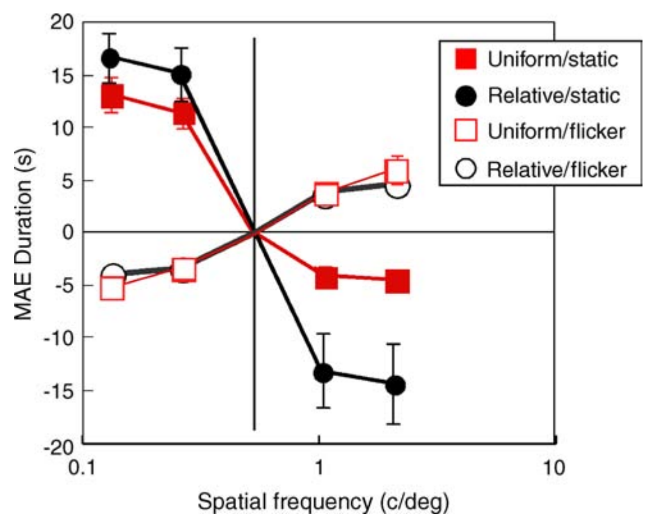

Figure 4. The duration of the MAE averaged over five observers as a function of test spatial frequency. The positive values indicate the MAE in the direction opposite to that of the standard grating and the negative values indicate the MAE in the direction opposite to that of the comparison stimulus. The squares represent uniform motion adaptation and the circles represent relative motion adaptation. The filled symbols represent the static test and the open symbols represent the flicker test. Error bars show the standard error of the mean across the observers.

in the static test. The MAE duration was shorter in the uniform motion condition than in the relative motion condition in all the comparison spatial frequencies. A two-way repeated ANOVA (spatial frequencies x motion type with individual data for repetition) shows the statistical significance between the relative and the uniform conditions for the static MAE ($F(3, 1) = 8.03$, $p < 0.01$). In the flicker test, the observers always reported the MAE direction to be in the direction opposite to that of the lower spatial frequency grating motion, regardless of whether the standard or comparison gratings had higher in spatial frequency. The aftereffect of the lower spatial frequency grating always dominated the perception of the MAE (low SF dominance of the flicker MAE). Slight differences between the relative and the uniform motion were also observed in the opposite of that for the static test (longer MAEs after relative motion for the static test while longer MAEs after uniform motion for the flicker test). The same statistical test shows that the difference between the results obtained in the relative motion condition and those obtained in the uniform motion condition in the case of the flicker MAE is not significant ($F(3, 1) = 2.57$, $p > 0.1$). Although the present results do not necessary indicate that there is no difference in the effect of the relative motion components in the case of the flicker MAE, they indicate that the difference is stronger in the case of the static MAE.

The high SF dominance of the static MAE and the low SF dominance of the flicker MAE confirmed the difference in the spatial frequency property of the two motion detectors. The motion detector sensitive to slow speed (or low temporal frequency) was more sensitive to the higher spatial frequencies. The motion detector sensitive to fast speed (or high temporal frequency) was more sensitive to the lower spatial frequencies. These findings are consistent with the prediction of the model with the fast and slow motion detector with different spatiotemporal frequency tunings (Figure 1). The results also indicate that this MAE technique can be used to isolate each of the slow and fast motion detectors.

Further, this experiment suggests the difference in the effect of relative motion on the fast and the slow motion detectors. A longer MAE was found in the relative motion condition than in the uniform motion condition in the static test, but not in the flicker test, suggesting that the slow motion detector was sensitive to relative motion.

Since MAE directions differ depending on the temporal property of the test stimuli, it is very likely that there are at least two motion detectors. It is hard to imagine a single motion system that produces the MAE in one direction in a static test and in the opposite direction in a flicker test. Under the assumption that there are fast and slow motion detectors, either of the motion detectors can be isolated using the MAE technique. After adapting to the composite gratings with different spatial frequencies moving in opposite directions, the two motion detectors exhibit sensitivity loss in opposite directions. The MAE of the slow motion detector can be obtained with a static test, while the MAE of the fast motion detector can be obtained with a flicker test, provided that the directional interaction (right and left) is only within the same group (either slow or fast) of motion detectors (Figure 5).

It is worth noting that the individual variation in the MAE duration was larger in the static MAE than in the flicker MAE. Observers reported that detecting the disappearance of the MAE was easier in the flicker test than in the static test. Indeed, a clear change in motion appearance is observed at the time when the MAE disappears in the flicker MAE. In the relative motion condition, the observers can easily detect the time when the top and bottom gratings start moving in the same direction. In the uniform motion condition, the observers can easily detect the time when the motion of the gratings changed from one direction to the other. They contrast

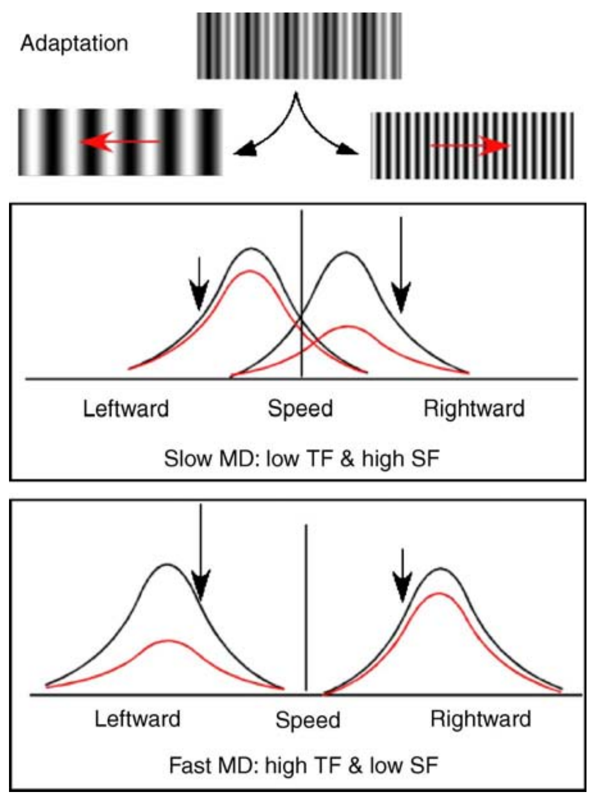

Figure 5. MAE technique to isolate either the slow or the fast motion detectors. These figures depict sensitivity reduction (red lines) of the slow and fast motion detectors after the exposure to the superimposed gratings with two different spatial frequencies drifting in opposite directions. The MAE of the slow motion system is in the direction opposite to that of the high spatial frequency motion (left in the figure) while the MAE of the fast motion system is in the direction opposite to the low spatial frequency motion (right). The static test reflects the MAE of the slow motion detector and the flicker test reflects the MAE of the fast motion detector. The MAE of either motion detector can be assessed without any influence of the MAE of the other, since the MAEs are in opposite directions.

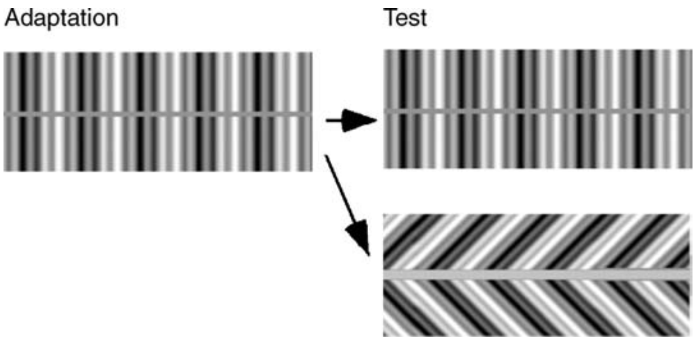

Figure 6. Stimulus of Experiment 2. Test stimulus was either vertical (0°) or tilted at 45° to left or right as shown. Adaptation stimulus was the same as that in Experiment 1, but only one combination of spatial frequencies (0.53 and 2.1 c/°) was used.

with the case of the static MAE, where motion impression becomes weaker with time and the observer has to decide the time at which the weak motion becomes no motion.

Experiment 2: Orientation tuning

Experiment 2 investigated the orientation selectivity of static and flicker MAEs in order to examine whether there is difference in orientation tuning between the motion detectors related to these MAEs. Since the motion mechanisms sensitive to high spatial frequencies are known to have narrower orientation tunings (Georgeson & Scott-Samuel, 2000; Scott-Samuel & Hess, 2002; Snowden, 1992), the slow motion detector might have a narrow orientation tuning while the fast motion detectors might have a broad tuning. In Experiment 2, the test stimulus was a grating with an orientation that was different from that of the adaptation stimulus. If the orientation tuning of a motion detector is too narrow to be sensitive to both the adaptation and the test stimuli, no MAE is expected in the test gratings with an orientation that is different from that of the adaptation gratings.

Method

The experimental method is similar to that of Experiment 1 with some exceptions. The test stimulus was either vertical or tilted at 45° with respect to the vertical axis (top and bottom gratings were tilted in the opposite directions), while the adaptation grating was always vertical (Figure 6). The two test orientations were mixed in a session. The static and flicker tests were used in different sessions. Only relative motion adaptation with one spatial frequency combination of 0.53 and 2.1 c/° was used. Direction judgments in tilted gratings were slightly difficult to make because of the arrow like shape of the grating arrangements. One of the observers from Experiment 1 reported that he always perceived the motion of the flicker test in one direction even without adaptation, perhaps because of the pointed shape of the test pattern. In order to replace him we recruited a new observer and total of five observers participated in Experiment 2.

Results and discussion

Figure 7 shows the MAE duration as a function of test orientation for the static test (a) and the flicker test (b). Positive values indicate that the MAE was in the direction opposite to that of the 2.1 c/° grating motion and negative values indicate that the MAE was in the direction opposite to that of the 0.53 c/° grating motion. In the static test, the MAE was observed in the opposite direction of 2.1 c/° stimulus motion when the test grating was vertical, however, the MAE duration was close to zero on average when the test grating was tilted. While there are only two orientations, they are sufficient to show the difference in orientation tuning between the two conditions. A *t*-test with the data variation across five observers showed that the MAE duration was significantly different between the two orientations in the case of the static MAE ($t(4) = 3.86$. $p < 0.02$) while it was not significantly different in the case of the flicker MAE ($t(4) = 0.20$. $p > 0.8$).

The result indicates that the relative strength of the MAE between the high and low spatial frequency motions

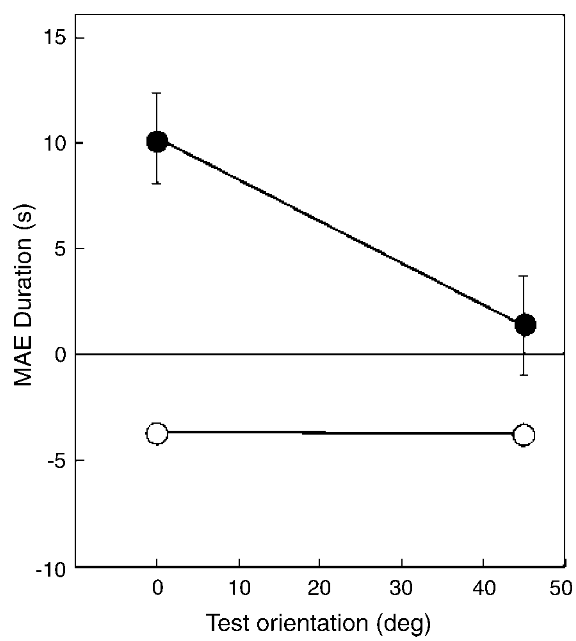

Figure 7. Duration of MAE averaged over five observers as a function of test orientation. Positive and negative values on the vertical axis indicate the MAE durations in the direction opposite to that of the 2.1 and 0.53 c/° grating motion. Filled symbols represent static test and open symbols represent flicker test. Error bars show standard error of the mean across observers.

differed when the test orientation was changed from vertical to oblique. If the orientation tunings of the fast and slow motion detectors are the same, we expect the same relative strength of the MAE in both vertical and oblique tests. The reduction in the MAE duration in the 45° test of the static condition indicates a larger sensitivity reduction in the motion detector sensitive to a high spatial frequency. Therefore, this result suggests that the slow motion detector has a narrower orientation tuning than the fast motion detector. This may explain the covariation of orientation tuning with spatial frequency. A further experiment is necessary to obtain the exact spatial and orientation tuning for each condition.

It is worth noting that these results suggest that the slow motion detector contributes little to the flicker MAE. Less sensitivity of the slow motion detector to the oblique test should enhance the MAE in the opposite direction. Hence, we expect that the flicker MAE would be longer if the slow motion detector contributed to the flicker MAE.

Experiment 3: Temporal frequency tuning

We assumed that there are two motion detectors, a slow motion detector that is sensitive to low temporal frequencies and a fast motion detector that is sensitive to high temporal frequencies. Experiment 3 investigated the differences in the temporal characteristics of these detectors. Using the superimposed grating MAE technique, we estimated the temporal frequency tuning of each detector.

Method

The temporal frequency of one of the gratings (2.1 c/° or the 0.53 c/°) was varied among 0.63, 1.3, 2.5, 5, 10, or 20 Hz while that of the other was fixed (5 Hz). In order to determine the temporal frequency tuning of the slow motion detector, we measured the static MAE by varying the temporal frequency of the 2.1 c/° grating in the adaptation stimulus. We measured the flicker MAE by varying the temporal frequency of 0.53 c/° grating in order to determine the temporal frequency tuning of the fast motion detector. For all the temporal frequency conditions, the stimulus contrast was kept constant at a value of 30 times higher than the threshold at 5 Hz for each grating. Physical contrast was kept constant across different conditions so that MAE duration reflects the sensitivity dependence on temporal frequency. One of the authors and a naive observer from Experiment 1 participated in this experiment. Each observer ran four sessions of three trials (3 repeats) for each combination of temporal frequencies.

Results and discussion

Figure 8 shows the temporal frequency dependence of the MAE duration in the static and flicker tests. We plot the MAE durations as positive in both the static and the flicker tests in this figure in order to compare the difference between the frequency tuning curves although the MAE directions in the static and flicker tests were always opposite except in the 0.21 c/° condition of HN, where the MAE direction was unstable. The MAE duration was found to be long between 1 and 10 Hz in both static and flicker tests, whereas the sensitivity function differed clearly. The sensitivity reduced steeply at temporal frequencies higher than 10 Hz in the static test. In contrast, the sensitivity reduced steeply at temporal frequencies lower than a peak at around 3 Hz in the flicker test. These results suggest that the slow motion detector is sensitive to relatively lower temporal frequencies and that the fast motion detector is sensitive to relatively higher temporal frequencies.

For quantitative comparison, we used a bootstrap procedure for estimating the distribution of the peak data

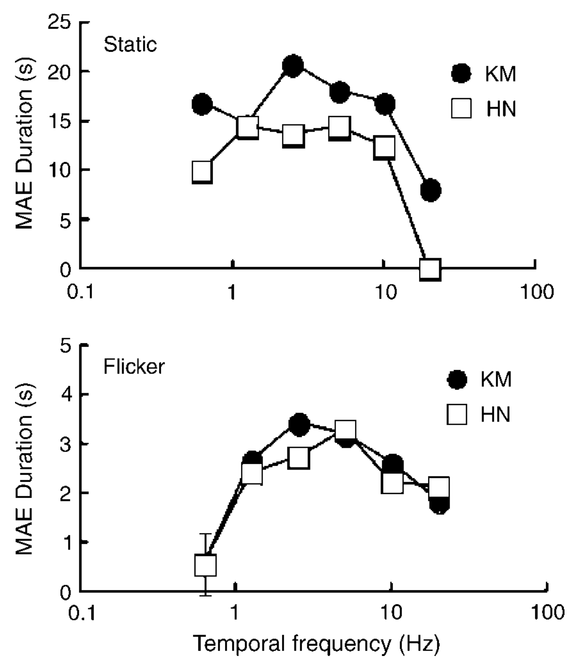

Figure 8. MAE duration as a function of temporal frequency of adaptation grating. The horizontal axis indicates the temporal frequency of 0.21 c/° or 0.53 c/° grating in the static or flicker test. Different symbols represent different observers. The results of the static and the flicker test are shown in separate panels. We have plotted the MAE durations as positive in both in the static and flicker tests in order to compare the frequency tunings easily although the MAE directions were opposite in the static and flicker tests as observed in the previous experiments. Error bars show standard errors across trials; and these bars are smaller than the symbol size except in the case of 0.21 c/° of HN, where the MAE direction was unstable.

of the temporal tuning functions. We fitted a hyperbolic function in a log-log plot to each set of data and tested the statistical significance of the difference in the peaks between the static and the flicker MAEs. Then, we performed a statistical test on the basis of the distribution function of the peak temporal frequency obtained from repeated re-sampling (2000 times) for each condition (a bootstrap method). The test showed that the difference between the peaks in different MAEs was statistically significant (<0.05) for both observers.

Experiment 4: Effect of attention

Experiment 4 investigated the effect of attention on the static and flicker MAEs to examine whether the difference in temporal frequency tuning between the static and flicker MAEs found in Experiment 3 can or cannot be attributed to the contribution of attention to either MAE. We assume that the difference between the static and flicker MAEs stems from the difference in the temporal property of underlying motion detectors. However, flicker (or dynamic in general) MAE has been used to investigate motion analysis at higher stages, which are influenced by attention and/or are sensitive to second order motion (Cavanagh, 1992; Culham, Verstraten, Ashida, & Cavanagh, 2000; Nishida & Ashida, 2000). When the first and second order motion components in a stimulus move in opposite directions, MAE is observed in the direction opposite to that of the first order motion in a static test while it is observed in the direction opposite to that of the second order motion in a flicker test (Nishida & Sato, 1992). The MAE of the second order motion may be explained in part by a higher-order, attention-based motion mechanism, which can be accessed by flicker (or dynamic) MAE (but see General discussion), although, as far as we know, there is no explanation of why the attention-based motion mechanism can be accessed only by a flicker test. A question that arises here is whether the high SF and low SF dominances of the static and flicker MAEs are additional pieces of evidence for the higher and lower stage motion analyses. According to this presumption, the two types of motion detectors that we identified are the low-level motion detector accessed by static MAE and the high-level motion detector accessed by flicker MAE, rather than the slow and fast motion detectors. No previous study has considered this issue seriously.

In order to examine the effect of the attention-based motion system, we repeated measurements of the temporal frequency tuning with a central visual task. The central task was a RSVP (rapid sequential visual presentation) task, where the observer was asked to detect digits in a rapidly presented letter-and-digit sequence. Attentive tracking is not usually possible when the observer focuses on such an attention task at the fixation. Indeed, the observers reported that they could hardly identify any feature of the adaptation gratings while doing the central task in Experiment 4. The characteristics of the low-level motion detectors can be measured in the above-mentioned condition without influence of the attention-based motion system.

Method

In the RSVP task, either a letter or a digit ($1° \times 2°$ in visual angle, 153 cd/m^2) was presented sequentially every 100 ms at the center of the display. The observers were instructed to count the number of digit presented (the number of digits was between 0 and 14) and reported whether it was odd or even after responding the MAE direction and duration. Other conditions were the same as in Experiment 3. One of the authors and a new naive observer participated in the experiment. The performance of the RSVP task was between 75% and 80% for the both observers.

Results and discussion

Figure 9 shows MAE duration as a function of temporal frequency with and without the central attention task. The effect of the central task is clear. Attending to the center of the display reduced the MAE duration in general. However, the shape of the temporal frequency tuning function in the two adaptation conditions is similar for the static and the flicker MAE of both observers. We estimated the peak temporal frequency by fitting the same function as in Experiment 3. The peak temporal frequency of the flicker MAE is higher than that of the static MAE regardless of whether the observer performed the central task or not (No task: static 2.8 Hz and flicker 5.1 Hz; Task: static 3.4 Hz and flicker 6.2 Hz for KM; No task: static 3.1 Hz and flicker 3.7 Hz; Task: static 3.6 Hz and flicker 4.5 Hz for HT). This suggests that the difference in temporal frequency tuning between the static and the flicker MAEs found in Experiment 3 cannot be attributed to the contribution of attention to either MAEs.

For a quantitative comparison of the peaks of the temporal tuning functions, we performed a statistical test on the basis of the distribution function of the peak temporal frequency obtained from repeated re-sampling (2000 times). Peak temporal frequency was estimated from the data set from each sampling process (the same bootstrap method as in Experiment 3). Then, the difference between the peaks of the static and flicker tests was calculated. In order to compare the peak differences between the conditions with and without the central task, the difference of the peak differences was calculated. The distribution of that value was a bell-shaped function with a mean of -0.48 or -0.38 and a standard deviation of

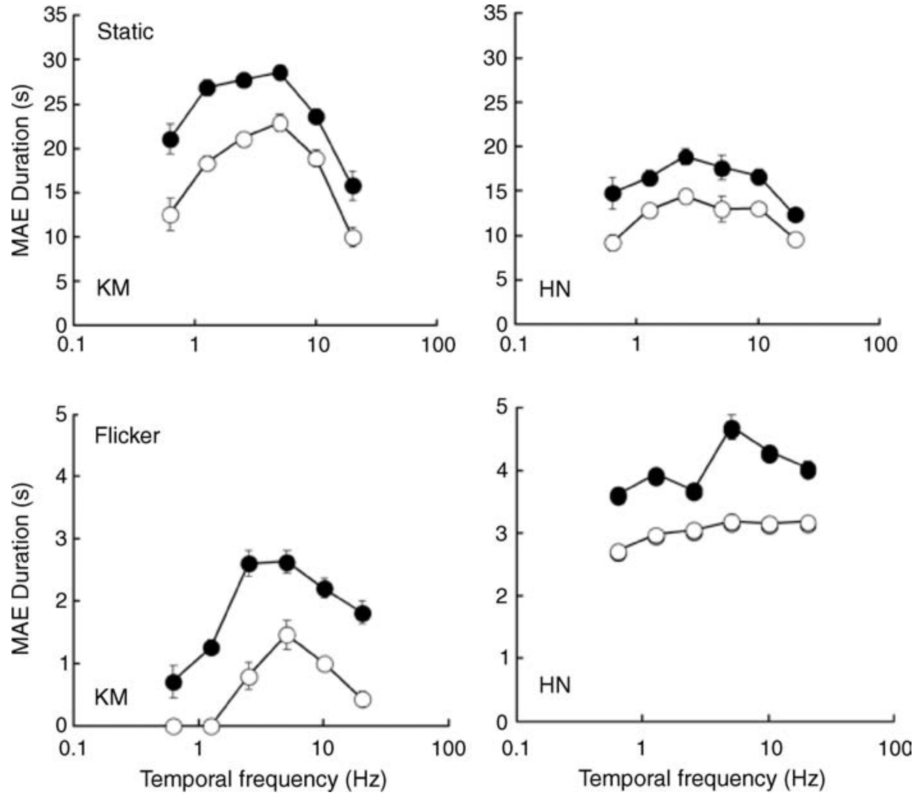

Figure 9. MAE duration as a function of temporal frequency of adaptation grating with and without the central attention task. Open symbols represent the MAE with the task and filled symbols represent the MAE without it. Error bars show standard errors across trials.

0.96 or 1.00 (the difference decreased for both observers). The significant level of the difference in peak difference between the two conditions was very high ($p > 0.36$ for KM and $p > 0.7$ for HT). These results suggest that the difference in temporal frequency tuning of the static and the flicker MAE is not related to the attention-based motion mechanism.

Removing attention from the adaptation stimulus shortened the MAE duration as expected from previous report (Chaudhuri, 1990; Nishida & Ashida, 2000). The reduction rate was not systematically different between the static and the flicker MAEs: 29% and 25% on average for KM and HT in the static MAE and 74% and 24% in the flicker MAE. The large reduction rate of KM in the flicker MAE may be attributed to the short MAE durations. The MAE with the central task of KM may be too weak to compare with other conditions.

Experiment 5: Effect of speed

We controlled the temporal frequencies of the adaptation gratings in the previous experiments and interpreted the difference between the static and flicker MAEs in terms of the spatiotemporal characteristics of the underlying mechanisms. However, the gratings with different spatial frequencies drifting with the same temporal frequency move at different speeds. The higher spatial frequency gratings move slower than the lower spatial frequency grating. It is possible that the difference in the MAEs found in the previous experiment was due to different speed tunings, instead of spatiotemporal frequency tunings. In order to examine whether the speed or the spatiotemporal frequency was crucial, we used adaptation conditions, where two gratings with different spatial frequencies moved at the same speed, manipulating the temporal frequency of the adaptation gratings. Since the motion sensitive cells with speed tuning were suggested to be at stages higher than those for cells with spatiotemporal frequency selectivity, this experiment would provide a clue of the level of motion detector in question.

Method

This experiment used different temporal frequencies of the two adaptation gratings so that the gratings moved with the same speed in the opposite direction. The temporal frequency pairs used were 1.25 and 5 Hz for 0.53 and 2.1 c/° (2.4°/s for both), 5 Hz for both (9.4°/s and 2.4°/s), 5 and 20 Hz (9.4°/s for both), and 1.25 Hz and

20 Hz for 2.4°/s and 9.4°/s. The contrast of the adaptation gratings was 30 times higher than the threshold for each temporal frequency. The contrast of the test gratings was also adjusted to be 30 times higher than the threshold for each of the static and flicker condition. One of the authors and a naive observer from Experiment 1 participated in this experiment.

Results and discussion

The MAE durations for the four different conditions are shown separately in Figure 10. The critical conditions are those with the same speed for the two gratings: the L1.25&H5 (2.4°/s) and L5&H20 (9.4°/s) conditions (L and H stand for 0.53 and 2.1 c/° gratings and the number indicates the temporal frequency). In both of the conditions, the static and the flicker MAEs were in opposites as in the L5&H5 condition (where the 0.53 c/° grating moved faster) and the L1.25&H20 condition (where the 2.1 c/° grating moved faster). The change in relative speed between the two adaptation gratings did not change the MAE direction while it changed the MAE duration slightly: the MAE duration in some conditions significantly differed statistically from the original L5&H5 condition (indicated by asterisks). These results rule out the possibility that the high or the low spatial frequency dominance of the static or the flicker MAE is caused by differences in speed tuning. Equating the speed between the low and high spatial frequency contents did not change the difference in the MAE direction between the static and flicker MAEs. These results suggest that the

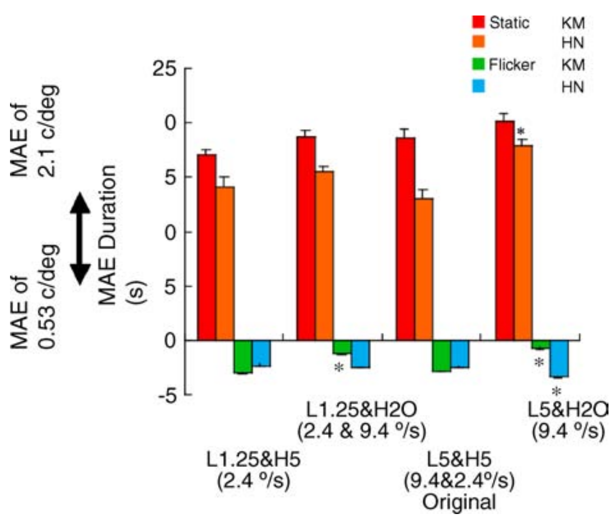

Figure 10. MAE durations for adaptations with different temporal conditions. Red and orange bars represent static MAEs and green and blue bars represent flicker MAEs. L stands for low SF and H stands for high SF in the notation; the numbers after them indicate the temporal frequency of the grating in the adaptation condition. Speeds of gratings are shown in parenthesis. Error bars show standard errors across trials.

stage of the motion detectors in question is relatively early, where motion sensitive units are selective to spatiotemporal frequency rather than to speed.

General discussion

The present results revealed that the visual system has two motion detectors with different spatiotemporal frequency tunings: the fast motion detector is tuned to higher temporal frequencies than those the slow motion detector is tuned to. They also differ in orientation tuning and in sensitivity to relative motion. We showed that the difference in temporal frequency tuning is not influenced by the presence/absence of attention on the motion stimulus. This suggests that the slow and fast motion detectors exist at a stage prior to the attention-based motion analysis. We also showed that the difference is not in speed tuning. The slow and the fast motion detectors are very likely at an early stage of motion analysis.

The present results appeared to be inconsistent with the results of previous studies that suggested the spatial frequency selectivity of the MAE (Anderson & Burr, 1985; Ashida & Osaka, 1994; Bex et al., 1996; Cameron et al., 1992; Thompson, 1998). If there are several motion detectors with different spatial frequency tunings, the MAE is expected to be spatial frequency selective so that little MAE in a test with spatial frequency different from the adaptation stimulus. However, the high SF dominance of the static MAE and the low SF dominance of the flicker MAE pointed out the importance of temporal factors and possible interaction of the different spatial frequencies. To explain these phenomena, two motion systems with a broad tuning at different spatial frequency ranges, instead of many channels, are sufficient (Figure 2). These facts do not have to rule out the possibility of multiple channels with a narrow spatial frequency tuning. The sensitivity regions of the slow and the fast motion systems depicted in Figure 2 can be regarded as regions covered by multiple channels. This issue can be investigated by measuring spatiotemporal frequency tunings using our MAE technique.

There is also an apparent inconsistency between a previous study and ours with respect to temporal frequency tuning. Bex et al showed similar low-pass tuning for motion detectors, irrespective of adaptation temporal frequencies and this is true for three spatial frequencies they used (Bex et al., 1996). In contrast, our results indicated differences between the two test conditions. However, the results of these two experiments are not necessarily inconsistent. Our results suggested that both the fast and the slow motion detectors have sensitivity at relatively low temporal frequencies and that there is a large overlap between the two. Perhaps, in the MAE measurement with a single grating, it would be difficult to isolate each tuning curve. However, note that one observer in Bex et al.'s study showed small but clear differences in temporal frequency tuning among different adaptation conditions (i.e., data of PB with 2 c/° in their Figure 2). Our experiment was designed to isolate each mechanism using two gratings moving in opposite directions. This method is appropriate to measure the tuning curve of one detector in isolation from the other even when the motion detectors had a large overlap in temporal frequency tuning.

Experiment 4 revealed that attention does not change the temporal frequency tuning of the underlying mechanisms of the static and flicker MAEs. This does not indicate there is no effect of attention on the MAEs observed in our study. Performing the central task reduced the duration of both static and flicker MAEs as in previous studies (Chaudhuri, 1990; Nishida & Ashida, 2000). Interestingly, we did not find any systematic attention effect on the reduction in MAE duration between the static and flicker conditions. Nishida & Ashida showed the attention modulation differences in the interocular MAE between the static and the flicker MAEs and suggested that the high-level mechanism is considerably more susceptible to attentional modulation, compared with the low-level mechanism (Nishida & Ashida, 2000). One possible prediction from their model is that the effect of attention is larger on the flicker MAE than on the static MAE. Our results did not show such a difference in the effect of attention between the static and flicker MAEs. However, we do not know whether our results are inconsistent with the model of Nishida and Ashida because their model does not provide any specific prediction for the binocular MAE, and our results are all binocular MAEs. The relationship between the attentional modulation and interocular transfer is an important issue to reveal the stage of motion detectors in question, but it should be remained for a feature study.

Here, we summarize the relationship between motion dichotomies in the cited literature and ours in order to suggest that the difference between the fast and the slow motion mechanisms reflect the differences at an early motion stage. Dichotomies related to the slow and the fast motion detectors may be classified into three groups: the attention-based system and the low level motion energy system, first and second order motion systems, and ones with differences in spatiotemporal properties such as the short/long range motion and the fast/slow motion detectors. Experiment 4 showed that the temporal frequency dependencies of the static flicker MAEs are independent from attention manipulation during the adaptation. The results indicate that the slow and fast motion detectors exist independently of the attention-based higher-level motion mechanism.

The second order motion may be detected by the attention-based motion mechanism because both the second motion and the attention-based motion are accessed only by flicker MAEs (Culham et al., 2000; Nishida & Sato, 1992). However, physiological studies suggested that second order motion is processed at a relatively early motion stages (Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Zhou & Baker, 1993). We should, therefore, consider the relationship between the second order motion analysis and the fast motion detector assumed in this study. First, there is a similarity between them. The second order stimuli have first order carriers (textures or gratings) to build second order features. The carriers have to have a higher spatial frequency of the first order components than the second order feature itself. The spatial resolution of the second order stimuli has to be lower than that of the first order stimuli. Second order stimuli are low spatial frequency stimuli in general. The fact that the MAE of the second order stimuli can be seen with flicker (or dynamic) tests is consistent with the presumption that the motion detectors sensitive to low spatial frequency (i.e., the fast motion detector in our case) are sensitive to flicker tests. Even when the first and second order gratings with the same spatial frequency are compared, the first order components in the second order stimulus could interfere with the motion perception because they do not move in the same way as the second order feature (usually stationary or moving in random directions). Therefore, the second order motion stimuli tend to selectively stimulate the motion detectors sensitive to low spatial frequencies. This contrasts with the first order stimuli, which stimulate motion detectors with sensitivity to relatively high spatial frequencies as long as the detectors are sensitive to the stimulus frequency.

However, the perceived speed of the second order stimulus has been shown to be slower (Smith & Ledgeway, 1998). This is inconsistent with the fact that the motion detectors sensitive to low spatial frequencies are sensitive to high temporal frequencies (Experiment 3). In addition, low spatial frequency gratings usually appear to be faster than high spatial frequency gratings (Smith & Edgar, 1990). Therefore, we should conclude that the dichotomy of the first and second order motion and that of the slow and fast motion are different.

We believe that the fast and slow motion detectors identified with random dot patterns show a clear dependence of the MAE on speed (Alais et al., 2005; van der Smagt et al., 1999; Verstraten et al., 1998). These studies manipulated the stimulus spatiotemporal frequencies as we did in the present experiments and found independent MAEs for the static and the flicker (or dynamic) tests. These and our results can be explained by assuming two motion detectors with different spatiotemporal frequency tunings (Figure 2). Our interpretation differs from the interpretations given in the abovementioned studies with respect to the effect of spatial frequency, which is perhaps related to the size of stimulus displacements in random dot pattern (Anstis, 2009; Hirahara, 2006). Although using random dot patterns has benefit to minimize the possible influence of structures of stimuli, it is difficult to control the spatial and temporal frequency contents of the stimulus. This could be one of the reasons that Alise et al.

needed to a model in order to estimate the speed or temporal frequency tunings of the two motion systems that they identified. We were able to estimate the temporal frequency tuning rather directly in Experiment 3 because we used gratings.

There is no particular reason to determine whether or not our slow motion detector is the same as the slow motion detector with sensitivity to color signals (Gegenfurtner & Hawken, 1996a; Hawken & Gegenfurtner, 2001; Hawken et al., 1994). Further studies with isoluminant color stimuli are required to answer this question.

Next, we discuss whether the slow and fast motion detectors are in separate systems or are two of many detectors in populations with different spatiotemporal frequency characteristics in a single motion system. Although further investigation is required to reveal whether our slow and fast motion detectors are qualitatively different, there are several reasons for why we think they are. First, the difference in sensitivity to relative motion may be related to motion analysis with different roles (Born, Groh, Zhao, & Lukasewycz, 2000; Born & Tootell, 1992; Orban et al., 1995; Shioiri et al., 2002; Shioiri, Ono, & Sato, 2002). Second, we have shown that the static MAE is sensitive to global motion while the flicker MAE is not (Shioiri & Matsumiya, 2007; Shioiri, Matsumiya, & Tamura, 2008). These facts suggest that the hypothesized fast and slow motion detectors are qualitatively different. However, this is not conclusive, and further studies are necessary to understand how these two motion detectors differ.

The slow and fast motion detectors that we assumed are psychophysical concepts. One important question is how the slow and fast motion detectors correlate with physiology. It is not easy to answer the question. Their physiological counterparts may be in different visual pathways or in different brain areas while these detectors may also be two among a variety of motion detectors with continuous differences in spatiotemporal and other properties in a brain area.

The difference in spatiotemporal frequency tuning between the fast and slow motion detectors are similar to that of the differences between the magno and parvo pathways in early vision. The magno pathway is considered to convey spatially low and temporally high frequency contents of retinal images while the parvo pathway is considered to convey spatially high and temporally low frequency contents. One may think that the slow motion detector is the motion detector in the parvo pathway while the fast motion detector is that in the magno pathway. This is consistent with the fact that isoluminant color motion signals, which are likely to be conveyed through the parvo pathway, contribute to perceiving slow motion stimuli (Cavanagh & Favreau, 1985; Gegenfurtner & Hawken, 1996b; Hawken & Gegenfurtner, 2001; Hawken et al., 1994).

However, the dichotomy of the parvo and magno pathways might be too simple to characterize the motion system (De Valois, Cottaris, Mahon, Elfar, & Wilson, 2000; Merigan & Maunsell, 1993). Indeed, the difference in orientation tuning found in Experiment 2 is not consistent with the dichotomy. Direction selective cells are mainly found in layers 4B, 4Cα and 6 in V1, which either receive inputs from magnocelluer layers of LGN (lateral geniculate nucleus) or send output to MT. The cells in the layers have been reported to have narrow orientation tunings (Gur, Kagan, & Snodderly, 2005). This suggests that motion sensitive mechanisms in the magno pathway have a narrow orientation tunings. Since Experiment 2 showed a narrow orientation tuning for the static MAE, the slow motion detector is possibly in the magno pathway, or at least more likely so than the fast motion detector as far as orientation tuning concerned. It should also be noted that some cells within MT/MST are sensitive to motion slower than 1°/s (Palanca & DeAngelis, 2003), while cells sensitive to such slow speeds may be rare (Krekelberg, van Wezel, & Albright, 2006; Palanca & DeAngelis, 2003; Perrone & Thiele, 2001). Further investigation is required in order to identify the physiological counterparts of the slow and fast motion detectors.

Finally, the differences between the hypothesized slow and fast motion detectors suggest that they play different roles in motion analysis. For example, the slow motion detector may be important for a variety of motion analyses with detailed features, such as detecting of motion border, perceiving depth from motion and identifying human movements. In contrast, the fast motion detector, on the other hand, may be important for a variety of quick motion analyses, such as estimating of time to contact of object approaching, identifying the direction of motion of dangerous animals, and catching moving objects. Whatever the ecological meaning of the differences, the sensitivity differences between the slow and the fast motion detectors are perhaps related to the difference in their functions.

Conclusions

Using a novel technique, we revealed that there are the fast and slow motion detectors that differ in spatial and temporal properties, in orientation tunings, and in sensitivity to relative motion. This suggests that motion mechanisms sensitive to slow speed or low temporal frequencies may be more important than has been considered.

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Footnotes

[i]Shioiri, S., Sakurai, K., Tashiro, T. & Yaguchi, H. (2003). *VISION* 15, 41.
[ii]Shioiri, S., & Matsumiya, K. (2006) in *Journal of Vision* 6(6), 1086a.

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