Visual motion detection sensitivity is enhanced by an orthogonal motion aftereffect

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A recent study (H. Takemura & I. Murakami, 2010) showed enhancement of motion detection sensitivity by an orthogonal induced motion, suggesting that a weak motion component can combine with an orthogonal motion component to generate stronger oblique motion perception. Here we examined how an orthogonal motion aftereffect (MAE) affects motion detection sensitivity. After adaptation to vertical motion, a Gabor patch barely moving leftward or rightward was presented. As a result of an interaction between horizontal physical motion and a vertical MAE, subjects perceived the stimulus as moving obliquely. Subjects were asked to judge the horizontal direction of motion irrespective of the vertical MAE. The performance was enhanced when the Gabor patch was perceived as moving obliquely as the result of a weak MAE. The enhancement effect depended on the strength of the MAE for each subject rather than on the temporal frequency of the adapting stimulus. These results suggest that weak motion information that is hard to detect can interact with orthogonal adaptation and yield stronger oblique motion perception, making directional judgment easier. Moreover, the present results indicate that the enhancement effect of orthogonal motion involves general motion integration mechanisms rather than a specific mechanism only applicable to a particular type of illusory motion.

Introduction

Sensitivity for visual motion detection

Although a lot of information is transmitted to the visual system, the actual performance of the human perceptual system is very limited both temporally and spatially (for a review, see Holcombe, 2009). The ability of human subjects to detect visual motion has been measured in terms of minimum-motion detection sensitivity. A few previous studies have revealed that weak motion signals become more detectable when they interact with orthogonal motion information. Derrington and Badcock (1992) used a plaid stimulus and found that the minimum-motion detection sensitivity for one component motion improved when this motion was integrated with an orthogonal motion component. This result is consistent with the previous point about directional interaction. However, the authors explained this result in terms of "feature tracking" that helps to improve the performance by detecting a second-order contrast-defined feature ('blob') necessarily contained in the plaid. Takemura and Murakami (2010) reported that vertical illusory motion induced by simultaneous presentation of a surrounding motion enhanced the detection sensitivity for the horizontal motion of a sinusoidal grating. The central grating barely moved leftward or rightward and was surrounded by another grating that moved upward or downward. The central grating was perceived as moving obliquely due to integration of horizontal physical motion and vertical illusory motion induced by the surround. In this case, the influence of feature tracking was ruled out because illusory motion does not affect the physical features of the target stimulus. The minimum-motion detection sensitivity for the central grating (leftward vs. rightward) was enhanced under this condition compared with a baseline condition in which the surround grating was stationary. These results support the theory that weak horizontal motion can combine with vertical motion and emerge as a stronger, easily detectable oblique perception. Given that vertical motion was irrelevant to the task (left/right judgment), the illusory motion itself conveyed no information about horizontal motion, but its directional interaction with horizontal stimulus motion helped subjects to judge the direction. Therefore, the results could not be explained if only local motion processing for horizontal motion was critical to directional judgment. Takemura and Murakami argued that a later motion processing stage, at which multivectorial motion integration and center-surround interaction arise, plays a critical role in determining motion detection sensitivity.

Interaction between a physical motion and motion adaptation

In the present study, we further examined whether the enhancement of motion detection by orthogonal illusory motion could be observed in conjunction with another illusory motion. We used a well-known illusory motion called the motion aftereffect (MAE), in which, after a prolonged exposure to an adapting stimulus moving in one direction, a stationary stimulus appears to move in the direction opposite to that of the adapting stimulus (Wohlgemuth, 1911). The MAE has been taken as strong evidence for a specialized mechanism for motion processing (for a review, see Mather, Pavan, Campana, & Casco, 2008; Mather, Verstraten, & Anstis, 1998).

Several previous studies have reported interactions between MAE and physical motion moving in another direction. For example, after adaptation to a unidirectional motion, the perceived direction of a moving test stimulus changes such that subjects typically overestimate the directional difference between the adapting and test stimuli (Levinson & Sekuler, 1976). This phenomenon, known as the direction aftereffect (DAE), suggests that the speed and direction of motion originating from retinal velocity can be affected by motion adaptation in another direction at some stage of visual motion processing. However, the functional stage of the DAE is still being debated, as evidence has been reported supporting the involvement of both earlier (Curran, Clifford, & Benton, 2006, 2009) and later (Schrater & Simoncelli, 1998; Wiese & Wenderoth, 2007) stages of motion processing (see Discussion section). It also remains unclear whether a weak motion signal that is hard to detect can interact with the MAE to generate a stronger DAE, which makes directional judgment easier.

The purpose of the present study

In the present study, we aimed to clarify how a slow horizontal motion signal that is hard to detect interacts with a vertical MAE to yield a change in detection performance. If detection performance is enhanced by an orthogonal, task-irrelevant MAE, a later stage of processing (after directional interaction between physical motion and the MAE) should play a critical role in determining minimum motion detection sensitivity.

To address this issue, we examined the detection sensitivity for horizontal motion in the presence of a vertical MAE. Motion detection performance was measured in terms of the rate of correct responses to questions involving two-alternative directional judgments about a stimulus that was barely moving in two opposing directions (i.e., left vs. right). Thus, "detection" in the present study refers to the ability to correctly discriminate between two directions of motion. We used a relatively weak MAE created by adaptation to relatively slow

motion because our previous study showed that slower orthogonal induced motion caused a greater enhancement effect on motion detection (Takemura & Murakami, 2010). To produce a moderate MAE, the adapting stimulus was presented for a short duration (2.5 s). In the first experiment, we examined the amount of the MAE that was produced in each subject by measuring his or her perception of the motion direction of the test stimulus moving at 0.09 deg/s after adaptation to the orthogonal motion (direction matching experiment). To eliminate individual differences in the strength of the MAE, we determined the relationship between the speed of the adapting stimulus and the MAE strength for each subject. Then, we were able to produce a vertical MAE of approximately the same strength for each subject and when the MAE was produced in the context of a test stimulus moving horizontally at a slow, barely detectable speed (0.04 or 0.02 deg/s), an oblique motion was seen as a result of interaction between horizontal physical motion and vertical illusory motion (Figure 1). We tested how the vertical motion adaptation and its aftereffect influenced the detection performance for the horizontal motion component (Motion detection experiment section).

General methods

Subjects

This study followed Declaration of Helsinki guidelines and was approved by the Ethics Committee, the College of Arts and Sciences, the University of Tokyo. The first author (HT) and five subjects who were naïve to the purpose of the experiment participated (aged 19–25 years). Each subject gave written informed consent and passed a battery of tests for visual acuity, astigmatism, and stereopsis.

Equipment

The stimulus was presented in a dark room on a 22-inch CRT monitor (Mitsubishi Electric RDF223H, 1280×960 pixels, 0.035 deg/pixel, refresh rate 75 Hz; mean luminance 34.5 cd/m^2) controlled by a computer (Apple PowerMac G5). The viewing distance was 50 cm. Subjects viewed all stimuli binocularly. The programming environment MATLAB (Mathworks) and the Psychophysics Toolbox (Brainard, 1997) were used to generate all stimuli.

Stimuli

The adapting stimulus was composed of eight sinusoidal gratings (spatial frequency 0.57 cycles/deg, contrast 99%) presented in a circular layout on a background of the
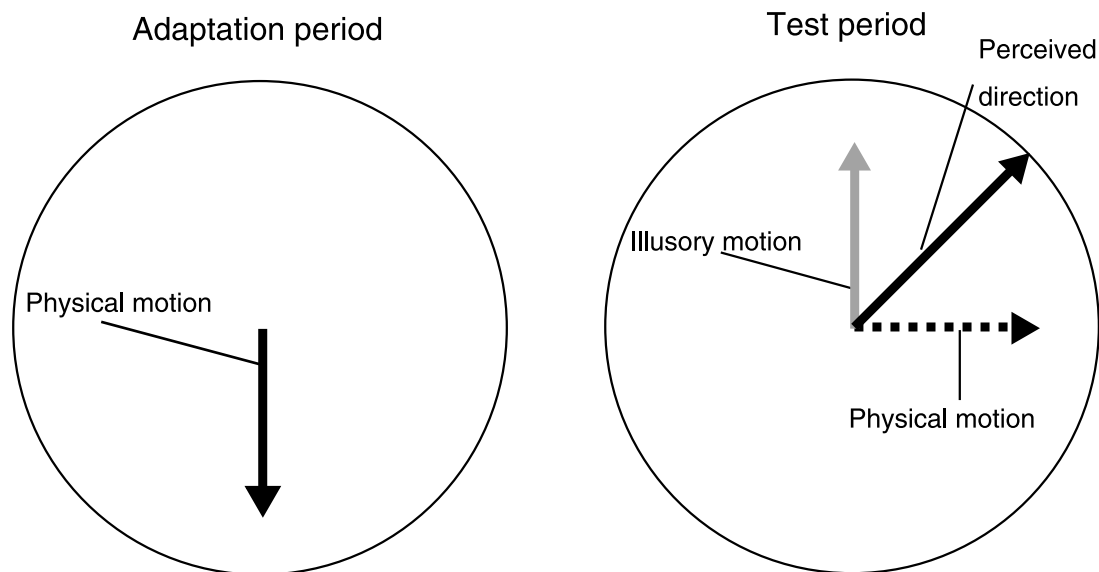
Figure 1. Schematic illustration of percept of the stimulus. Test stimulus perceived as moving in oblique direction due to the integration of a vertical MAE produced by the adapting stimulus and a horizontal physical motion component.

mean luminance (Movie 1). The distance from a central fixation point to the center of each window was 5.58 deg. Within its static window (3.72 deg diameter), each grating was moved inward or outward with respect to the central fixation point.

The test stimulus was a vertical Gabor patch (carrier spatial frequency = 0.57 cycles/deg, peak contrast = 50%, envelope SD = 0.79 deg) presented at the center of the position that the lowest of the eight gratings had occupied during adaptation (Movie 1). The carrier grating of the test stimulus moved in either a leftward or a rightward direction.

We used this eight-element grating configuration to prevent unwanted eye movements such as optokinetic afternystagmus (Cohen, Henn, Raphan, & Dennett, 1981; Kaminiarz, Königs, & Bremmer, 2009). In a preliminary experiment in which we used adapting grating moving vertically and a test Gabor patch moving horizontally in a parafoveal region, several naïve subjects made noisy vertical eye movements after adaptation to vertical motion. The variance in the eye speeds of four naïve subjects was significantly greater after motion adaptation than after viewing the same but stationary stimulus for the same period (F-test of the equality of variance: $p < 0.001$). According to previous studies (Murakami, 2004, 2010; Tong, Lien, Cisarik, & Bedell, 2008), these eye movements were able to affect the motion detection performance due to the positive correlation between eye-speed variability and motion threshold. By using eight gratings moving radially, such eye movements were suppressed (F-test of the equality of variance: $p > 0.1$). We placed all stimuli at 5.58-deg eccentricity to eliminate the unwanted eye movements toward the test Gabor patch that might have otherwise occurred in response to the appearance of more proximate stimuli.

Procedure

Each trial began with the presentation of the adapting stimulus for 2500 ms. After an inter-stimulus interval of 500 ms, the test stimulus was presented for 500 ms and was then immediately masked by random-dot noise (Movie 1). The inter-trial interval was 2500–3000 ms.
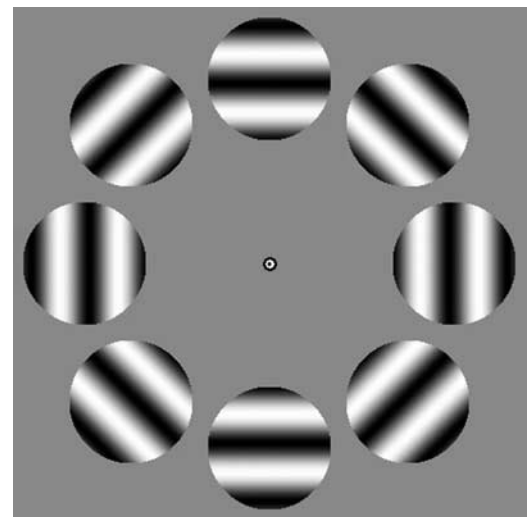
Movie 1. Stimuli. The adapting stimulus was eight sinusoidal gratings presented around the fixation point in a circle. Gratings moved in an inward or outward direction relative to the central fixation point. The test stimulus was a Gabor patch presented in a position below the central fixation point. The Gabor patch orientation was vertical, and it drifted either leftward or rightward. In the movie, the adapting stimulus is moving at 4.39 deg/s, and the test stimulus is moving at 0.09 deg/s.

The motion direction of the adapting stimulus (inward or outward) was alternated between successive trials to avoid buildup of the MAE. The direction of the test stimulus (leftward or rightward) was randomized within each experimental session. The speed of the adapting stimulus was changed in a random order from session to session. After each session, subjects took a break outside the dark room.

Direction matching experiment

Prior to the main experiment, we examined how the MAE resulting from each adapting stimulus influenced the perceived direction of the Gabor patch that was drifting above threshold.

Procedure

As described in the General methods section, the adapting stimulus (2500 ms) was followed by the test stimulus (500 ms) in each trial. After the presentation of the test stimulus, subjects were asked to match the perceived motion direction of the Gabor patch with an arrow-shaped visual icon on the screen by rotating it with a mouse cursor, or to press a canceling button when they perceived the test stimulus as being stationary.

The speed of the test stimulus was 0.09 deg/s, which was detectable well above chance for all subjects. The speeds of the adapting stimuli were 0.08, 0.14, 0.25, 0.44, 0.78, 1.39, 2.48, 4.39, 7.74, and 14.62 deg/s. Two subjects perceived a stronger MAE than others did when this range of speeds (from 0.08 to 14.62 deg/s) was used, and for these subjects an adapting stimulus moving at 0.04 deg/s was also used. Each session consisted of 20 trials, and each subject completed at least two sessions for each adapting stimulus speed. Subjects received at least one practice session under each condition prior to actual data acquisition.

Results

In a small number of trials, subjects did not report any motion direction and pressed the canceling button (8.4% on average). We excluded those trials from the subsequent analysis.

Figure 2A shows the results of directional matching for one typical subject (SY). A choice of the "0" deg direction indicated that the test stimulus appeared to move in the purely horizontal direction, and a choice of the "90" deg direction indicated that the test stimulus appeared to move in the purely vertical direction, but

opposite to that of the adapting stimulus. In all subjects, the actual results were in-between. When the adapting stimulus was slow, the influence of the MAE was extremely small and the test stimulus was perceived as moving almost horizontally (i.e., veridically). As the adapting stimulus became faster, the perceived motion direction of the test stimulus was more biased toward the direction opposite to that of the adapting stimulus, and the test stimulus was perceived as moving in an oblique direction. These results are consistent with previous studies demonstrating the DAE, namely, that the perceived direction of physical motion is influenced by motion adaptation (Curran et al., 2006, 2009; Levinson & Sekuler, 1976; Schrater & Simoncelli, 1998; Wiese & Wenderoth, 2007). For most subjects, the effect of motion adaptation was strongest when the adaptation speed was from 0.78 to 4.39 deg/s. The DAE decreased at faster or slower adaptation speeds. This is also consistent with previous findings on the DAE (Curran et al., 2006).

In Figure 2B, the median perceived direction is plotted against adaptation speed. Adaptation speed is plotted on a logarithmic scale. On the basis of these direction matching data, we determined the speed of the adapting stimulus that would produce the same perceived direction—thus presumably the same strength of the MAE—for each subject. From the linearly interpolated curves in Figure 2B, we looked up the speeds of the adapting stimulus that corresponded to the perceived directions of 15, 25, 35, 45, and 55 deg. The actual speeds of the adapting stimulus that corresponded to these five levels of MAE strength were 0.19, 0.35, 0.47, 0.53, and 0.89 deg/s, respectively, on average, across subjects. In the motion detection experiment below, we used the speeds of the adapting stimulus determined for each subject. For the sake of simplicity, we labeled these five conditions "very weak," "weak," "medium," "strong," and "very strong."

Our choice of median perceived direction as the representative index of the MAE strength shown in Figure 2A requires clarification given that one might argue that Figure 2A looks bimodal, rendering the median an inadequate index. In addition to the median, we also calculated the proportion of trials in which the perceptual bias was greater than 25 deg. This index highly correlated with the median perceived direction ($r = 0.931$, $p < 0.001$), implying that our estimation of MAE strength was not significantly affected by the choice of index.

Motion detection experiment

In the main experiment, we determined motion detection sensitivity by a two-alternative forced-response paradigm for horizontal directional judgment.
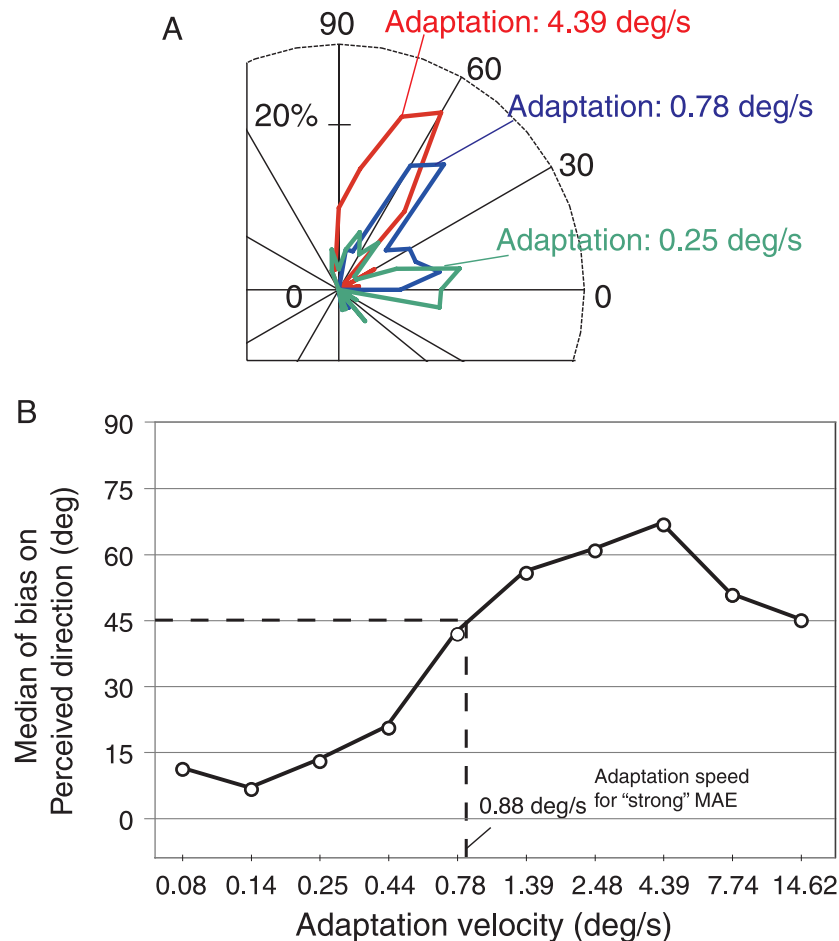
Figure 2. Results of direction matching experiment for a representative subject SY. (A) Histograms indicate the response rates (i.e., the number of completed trials over all trials) for the perceived direction of the test stimulus at each adaptation speed; "0" indicates purely rightward, and "90" indicates purely upward movement. This format was used to indicate the perceived direction of the test stimulus when it was physically moving rightward and the adapting stimulus was physically moving downward (and thus the MAE in the test stimulus was expected to occur in the upward direction). Data obtained under mirror-symmetrical conditions were reversed and merged. Each color indicates the adaptation speed. (B) Median of the perceived direction plotted against the adaptation speed. The vertical axis represents the median bias of the reported motion direction in relation to the direction opposite to the adapting stimulus expressed as deviation from horizontal. The horizontal axis represents the speed of the adapting stimulus plotted on a logarithmic scale. The strength of the MAE produced by varying adaptation speeds was calculated by matching the bias value (on a vertical axis, from 15 to 55) and horizontal axis.

Procedure

As described in the General methods section, the adapting stimulus (2500 ms) was followed by the test stimulus (500 ms) in each trial. After the presentation of the test stimulus, subjects were asked to choose the horizontal motion direction of the test stimulus from two alternatives, leftward or rightward. Only horizontal judgment was requested, although the test stimulus was perceived to move obliquely when the physical motion and the MAE were integrated perceptually. Note that the MAE component itself was task irrelevant because mathematically, the vertical direction was of no help with regard to horizontal motion detection.

For each subject, the adapting stimulus was set at five levels of speeds, described above (very weak, weak, medium, strong, and very strong). In a control condition, the adapting stimulus remained stationary in the adaptation period. In this condition, the test stimulus was seen to move horizontally (if detected) because no MAE occurred after adaptation. Also, to test whether the presence of a particular temporal frequency during adaptation was sufficient, we did another control experiment in which subjects were adapted to a counter-phase flicker of the same temporal frequency as in the condition of motion adaptation. Under this condition, the adapting stimulus appeared as a flickering grating with no impression of motion, and the test stimulus was seen to move horizontally (if detected) because no MAE occurred.

The test stimulus was equivalent across all conditions, and its speed was either 0.04 or 0.02 deg/s, randomly chosen from trial to trial. Each session consisted of

64 trials, and each subject completed eight sessions for each motion condition and for each flicker condition, and 16 sessions for the stationary control condition to stabilize the baseline performance. One subject participated under limited conditions (the MAE strengths from very weak to medium) because this subject had not perceived oblique motion steeper than 45 deg (corresponding to strong) in the direction matching experiment. Subjects received at least one practice session under each condition prior to actual data acquisition.

Results

Figure 3 shows the results under six motion adaptation conditions averaged for all subjects. The correct response rates for directional judgments were plotted across MAE strengths, with the correct response rates under the control condition of stationary adaptation as the baseline performance. The data for the easier (0.04 deg/s) and harder (0.02 deg/s) test speeds were overlaid.

After adaptation to stationary gratings, no MAE occurred. Under this condition, the average correct response rate of horizontal directional judgment was 0.71 at the easier speed and 0.62 at the harder speed of the test stimulus. Although these rates were significantly above the chance level of 0.5 (two-tailed Z-test: $p < 0.001$), they were also below 0.75, indicating that subjects discriminated poorly between leftward and rightward directions when the test stimulus was viewed alone.

Do these poor performances improve in the presence of the MAE in a task-irrelevant direction? At the easier test speed, sensitivity was not enhanced for the very weak,

weak, medium, and very strong MAE; however, motion detection sensitivity was significantly enhanced for the strong MAE (two-tailed Z-test: $p < 0.005$). Similarly, at the harder test speed, motion detection sensitivity was significantly enhanced for the weak MAE (two-tailed Z-test: $p < 0.01$), although no significant enhancement was observed for other MAE strengths.

When we varied the speed of the adapting stimulus, what we actually varied was its temporal frequency. Was the presence of a particular temporal frequency during adaptation sufficient for the enhancement to occur? Previously, Clifford and Wenderoth (1999) reported that the sensitivity to differential speed could be changed not by motion adaptation, but by adaptation to temporal modulation because the modulation effect was almost the same whether motion or counter-phase flicker was used as the adapting stimulus. To segregate these possibilities, we examined the detection performance after adaptation to counter-phase flicker that had the same temporal frequency as used under the motion adaptation condition.

Figure 4 shows the results. No significant enhancement or degradation of detection sensitivity was observed in comparison with the performance under the stationary adaptation condition. Thus, temporal frequency per se could not account for the enhancement of motion detection sensitivity observed in the main experiment; adaptation to motion and subsequent orthogonal MAE were necessary. Based on these results, we conclude that motion detection sensitivity can be enhanced when physical motion interacts with a moderate MAE in the orthogonal direction and eventually yields a sufficiently strong oblique motion percept, which makes directional judgment easier. These results suggest that a later-stage
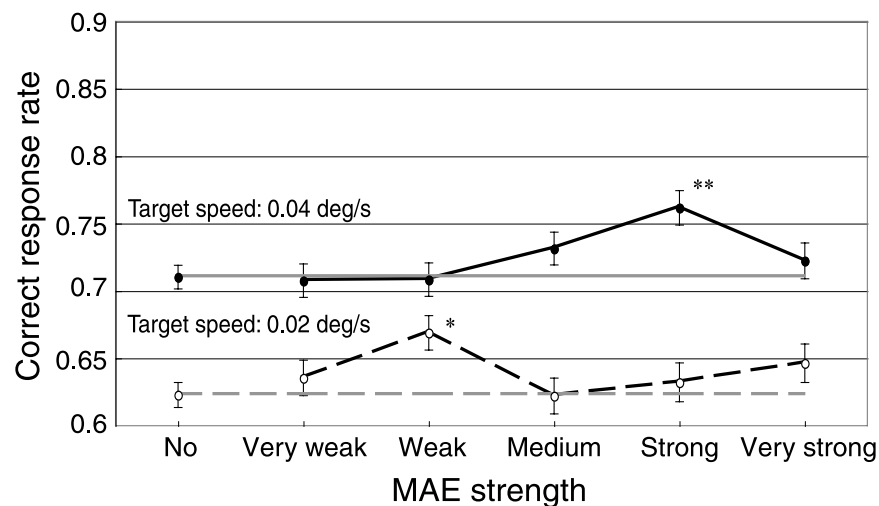

Figure 3. Effects of the vertical MAE on the detection of horizontal motion. The correct response rate is plotted against the MAE strength. "No" MAE strength indicates the stationary adaptation condition. Curves indicate the correct response rates under the motion adaptation conditions, and shaded lines indicate baseline performance (i.e., the correct response rates under the stationary adaptation condition). Error bars indicate ±1 *SEM*. Asterisks indicate the significance levels of the differences between the correct response rates under the moving adaptation versus the stationary adaptation conditions (two-tailed Z-test: $*p < 0.01$; $**p < 0.005$).
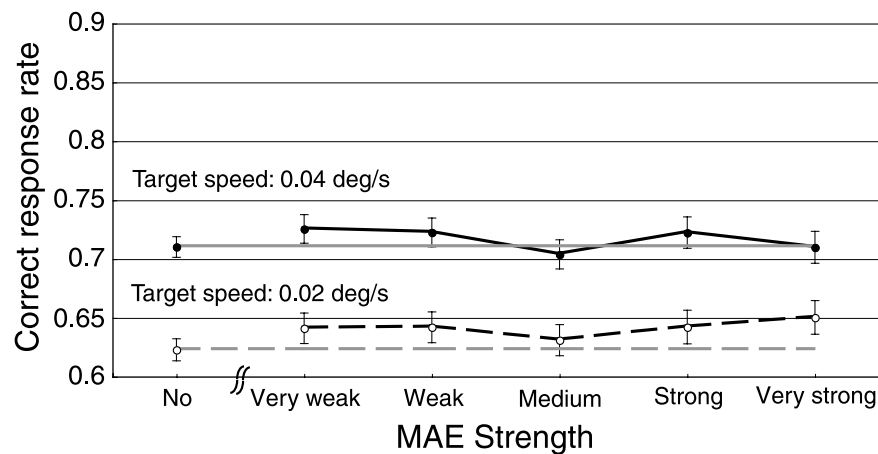
Figure 4. Effects of adaptation to counter-phase flicker on the detection of horizontal motion. The abscissa ("MAE strength") indicates the temporal frequency of the adapting stimulus showing counter-phase flicker but no motion. No MAE was perceived by adaptation with counter-phase flicker. The temporal frequency was the same as that used for moving adaptation conditions. Other conventions are identical to those used in Figure 3.

processing (after directional interactions between physical motion and the MAE) plays a critical role in determining minimum-motion detection sensitivity.

Discussion

The effect of an orthogonal MAE on motion detection sensitivity

The present results showed enhancement of motion detection sensitivity by orthogonal, task-irrelevant motion adaptation. The effect cannot be explained by the presence of a particular temporal frequency in the adapting stimulus, as shown by the finding that the effect was not observed when we changed the adapting stimulus from the moving grating to the counter-phase flickering grating. Moreover, the present results demonstrate that the enhancement effect occurs not only when the weak horizontal motion is integrated with a vertical induced motion (Takemura & Murakami, 2010), but also when it is integrated with a vertical MAE, suggesting the involvement of a more general motion integration mechanism rather than some specific mechanism only applicable to a particular type of integration between physical and illusory motions.

Relationship to previous psychophysical studies on the MAE

Raymond reported that the MAE did not enhance the motion detection sensitivity of orthogonal physical motion (Raymond, 1993a; Raymond & Braddick, 1996), a finding apparently incompatible with ours. We consider that the difference between the two studies originates in differences in their experimental paradigms.

First, in Raymond's study, the elicited MAE was much stronger than that in our study in that the adapting stimulus was faster and lasted longer than in the present study. We also confirmed that stronger MAEs did not produce the enhancement effect (Figure 3). Second, the methods of sensitivity measurement were different. We measured minimum-motion sensitivity, asking subjects to report left or right when presented with a barely moving stimulus (i.e., 1.32 or 2.63 arcmin/s). In contrast, Raymond measured the coherence threshold for a random-dot kinematogram (RDK); thus, the speed of each component dot was well above threshold. It is not appropriate to directly compare our results with experimental results for a coherence threshold in a RDK. Third, previous psychophysical results suggest a difference between the grating and RDK in terms of the characteristics of the MAE. For example, whereas the MAE seen in the grating exhibits only partial interocular transfer (Wade, Swatson, & de Weert, 1993), the MAE seen in the RDK exhibits complete interocular transfer (Raymond, 1993b).

Functional implications of the detection sensitivity

Recent reviews and investigations suggest that the visual system regards the presence of impoverished signals as equivalent to a default condition to neutralize the impact of noisy local inputs and internal noises (Morgan, Chubb, & Solomon, 2008; Ross & Burr, 2008). Morgan et al. (2008) reported a dipper function for the orientation-variance discrimination threshold of a

texture pattern as a function of pedestal orientation variance and speculated that a threshold for orientation variance exists; if this threshold is not exceeded, the pattern will exhibit a more regular appearance. Ross and Burr (2008) deemed this apparent regularity to be the default condition for texture perception in the presence of noises. The default condition for visual motion processing is arguably stationary, and can be theoretically expressed as a form of a prior probability favoring slower speeds in Bayesian estimation (Weiss, Simoncelli, & Adelson, 2002).

Based on this literature, the present results can be interpreted as suggesting that to see motion in noisy situations is to choose a non-default state on the basis of supporting evidence for the existence of a substantial motion signal, and a later processing stage of directional interaction gives a determinant positive vote for supporting evidence when bottom–up signals are very weak. However, this vote does not necessarily correspond to the neural correlate of conscious awareness of motion per se. As we discuss later, this vote mildly constrains the state of a currently unknown neuronal network that ultimately determines what type of perception is experienced. This constraint slightly but significantly raises the probability of choosing the correct motion from the two alternatives (i.e., leftward vs. rightward) in comparison with the baseline performance that would occur without this vote from the later processing stage. In the next section, we propose a simple model to account for this enhancement.

We assumed that subjects did not have access to local horizontal motion information prior to motion integration between physical and illusory motion because this information was very weak. One might argue that our assumption contradicts previous psychophysical results demonstrating that subjects can have access to both local and global motion information (Watamaniuk & McKee, 1998). Notwithstanding, the dual access revealed in this previous study is valid for stronger motion signals with a faster speed (above 10 deg/s). If motion information is sufficiently strong, we may have access to various aspects of this information depending on task demands. Our results simply indicate that when motion is extremely slow, detection sensitivity depends on the consequences of motion integration.

Our results showed that perceptual performance of horizontal motion detection depends on the motion representation after directional interaction with illusory motion. However, it is unclear how the actual conscious awareness of seen motion is constructed in the brain. Based on recent neuroscience literature on consciousness, several hypotheses are worth consideration. The first hypothesis is that conscious awareness is determined in a purely feed-forward fashion. Later-stage motion representations contribute to conscious awareness, but earlier representations (e.g., primary visual cortex) do not (Crick & Koch, 1995). This theory contrasts with recent neuro-physiological studies showing the importance of feedback connections in conscious awareness of visual motion (e.g., Pascual-Leone & Walsh, 2001). The second hypothesis is that both earlier and later representations can independently contribute to conscious awareness. For example, even if an earlier-stage motion representation is not optimal (e.g., very slow), conscious awareness of motion can be constructed based on later-stage information that is optimal, or artificially optimized, to the task demand in question (e.g., faster, oblique). The third hypothesis is that recurrent interactions between earlier and later stages, which might occur within a visual hierarchy or across distinct systems in the whole brain, necessarily constitute our conscious awareness (Lamme & Roelfsema, 2000). According to this theory, even if earlier representations are not optimal at first, they are updated by feedback signals from later stages. Our present psychophysical results are in line with all of these hypotheses.

Model of sensitivity enhancement

The MAE has been explained by a number of models. Classically, the MAE was explained by a ratio model in which motion is perceived as an imbalance of activities in a pair of oppositely tuned motion detectors (Sutherland, 1961). Later on, the ratio model was extended to a population of motion detectors tuned to different directions. This was then replaced by the distribution-shift model, which formulates the direction and magnitude of the MAE as a global shift in activities of a population of motion-encoding neurons after adaptation (Mather, 1980). Grunewald and Lankheet (1996) introduced broadly tuned inhibition among motion directions in the distribution-shift model and attributed the unidirectional MAE seen in the orthogonal direction to inhibition resulting from the adapting stimuli that moved in opposite directions. Recently, van de Grind and colleagues developed a more elaborate computational model of motion adaptation in which divisive feed-forward inhibition was introduced as a gain-control mechanism (van de Grind, Lankheet, & Tao, 2003; van de Grind, van der Smagt, & Verstraten, 2004).

One might argue that the distribution-shift model with broadly tuned inhibition could account for the enhancement effect we found by assuming that neurons tuned to the direction of the adapting stimulus decrease their activities after adaptation and disinhibit neurons tuned to the orthogonal directions. However, this is unlikely. In the first place, simple disinhibition cannot explain why the enhancement effect is confined within intermediate MAE strengths and is not observed after stronger motion adaptation (Figure 3). Moreover, even if disinhibition boosted the firing probability of the neurons tuned to the orthogonal directions, detection performance in the orthogonal direction would not change without an increase of signal-to-noise ratio. Previous models did not

explain how motion adaptation affects the neural noises, and so the simple distribution-shift model cannot explain the enhancement effect. From the computational perspective, our enhancement effect should be explained by a model evaluating signal strength in relation to neural noise by quantitative criteria, such as Fisher information (Tajima, Takemura, Murakami, & Okada, 2010).

We propose that the present results can be explained by the interaction among input motion signals, internal speed noise, and internal direction noise in the visual system (Takemura & Murakami, 2010). It has been widely accepted that the visual system has both speed tuning and directional selectivity (Cheng, Hasegawa, Saleem, & Tanaka, 1994; Maunsell & Van Essen, 1983). Classical psychophysical studies have reported independence between speed and direction representations (Ball & Sekuler, 1980). Recently, Hol and Treue (2001) used an adaptation paradigm to clarify different properties of motion detection and direction discrimination thresholds and discussed that different populations of neurons contribute to detection and to discrimination. Their idea was supported by neurophysiological and computational studies (Jazayeri & Movshon, 2006, 2007; Purushothaman & Bradley, 2005).

Based on these ideas, we hypothesize that the visual system's task in the present experiment changes from a motion detection task to a direction discrimination task depending on the speeds of the adapting and test stimuli. First, under the stationary adaptation condition, the speed of the test stimulus is extremely slow, and neuronal information for horizontal motion directions is poor. In this circumstance, the visual system cannot reliably detect the horizontal motion, and minimum-motion sensitivity for horizontal motion limits performance. Second, when the adapting stimulus moves very fast, a strong MAE is elicited, and the test stimulus appears to move almost vertically. Under this condition, subjects have to perform fine direction discrimination between two slightly oblique directions (e.g., 80 deg vs. 100 deg). In this circumstance, although the perceived speed is sufficiently fast, the perceived direction is not a reliable cue for discriminating between two oblique directions, and performance becomes no better than the baseline. Third, when the speed of the adapting stimulus is optimal, the MAE of an appropriate strength is elicited and is integrated with the slow horizontal motion of the test stimulus. Thus, the perceived speed is sufficiently fast, and the perceived direction is sufficiently oblique and away from both the purely vertical and the purely horizontal. Under this condition, the detection sensitivity for horizontal motion is enhanced because the visual system's task is to discriminate between two sufficiently oblique directions at a sufficiently fast speed. This idea is consistent with the present results showing performance enhancement with a stronger MAE (Figure 3, data labeled "strong") at the faster test speed and with a weaker MAE (Figure 3, data labeled "weak") at the slower test speed.

Neurophysiological mechanisms

A difficult question remains as to what stage of the visual pathway actually constitutes the functional stage where the local motion component and the MAE interact with each other. Several studies reported that the DAE occurs as a result of a later stage of visual motion processing. For example, the DAE shows considerable interocular transfer (Curran et al., 2006; Wiese & Wenderoth, 2007). Also, a study that examined the effect of motion adaptation on the perceived motion direction of a plaid revealed that the DAE occurred in the motion direction of the plaid rather than that of its component (Schrater & Simoncelli, 1998). On the other hand, a contribution on the DAE by an earlier stage is likely. The speed tuning of the DAE was well explained by a model based on the adaptation of motion-sensitive neurons at the local rather than at the global processing stage (Curran et al., 2006).

Current physiological knowledge suggests that motion integration occurs in area MT (Castelo-Branco et al., 2002; Huk & Heeger, 2002; Rodman & Albright, 1989) and higher visual areas (Khawaja, Tsui, & Pack, 2009). The enhancement effect found in the present study using induced motion (Takemura & Murakami, 2010) may reflect the neural activities in these areas. This idea is in line with previous studies showing a clear relationship between neuronal activities in area MT and psychophysical motion detection performances (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996; Ditterich, Mazurek, & Shadlen, 2003; Newsome, Britten, & Movshon, 1989; Salzman, Murasugi, Britten, & Newsome, 1992; Serences & Boynton, 2007). However, the neurophysiological background of integration between physical motion and the orthogonal MAE is still unclear because the physiological basis of the MAE is still under debate. Recent brain imaging studies have disputed the primacy of area MT as the underlying mechanism of the MAE, with clear indications that several brain areas are activated during the perception of the MAE (Culham et al., 1999; He, Cohen, & Hu, 1998; Taylor et al., 2000). Also, a recent neurophysiological study suggested that adaptation effects in area MT are inherited in a feed-forward fashion from V1 cells (Kohn & Movshon, 2003). Accordingly, the present results would be closely related to the neuronal activities in area MT or later cortical regions; however, our results do not rule out the involvement of other visual areas. Still, neurophysiological computation of motion integration between two directions, one physical and the other illusory, might require complex response properties, as seen in the directional selectivity of some MT neurons for pattern motion (Movshon, Adelson, Gizzi, & Newsome, 1985; Rodman & Albright, 1989; Rust, Mante, Simoncelli, & Movshon, 2006). Lastly, we are not emphasizing that all consciousness of motion must emerge only after directional interactions occur in a certain visual area, such as MT, nor are we stressing that the

minimum-motion detection sensitivity is governed by such a higher-level area. Extensive recurrent connections among various cortical areas make it difficult to locate a distinct neural correlate corresponding to each functional stage of our psychophysical model (Lennie, 1998). Relationships between the functional schema we propose and the neurophysiological stages in actual brains require examination in future investigations.

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