PERGAMON

Vision Research 43 (2003) 639–649

Vision Research

www.elsevier.com/locate/visres

Gaze modulation of visual aftereffects

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Received 25 June 2002; received in revised form 12 December 2002

Abstract

Physiological studies of non-human primates have suggested that the direction of gaze can modulate the gain of neuronal responses to visual stimuli in many cortical areas including V1. The neural gaze modulation is suggested to subserve the conversion from gaze-independent (eye-centered) to dependent (e.g., head-centered) representations. However, it has not been established whether the gaze modulation has significant influences on human visual perception. Here we show that gaze direction modestly but significantly modulates the magnitudes of the motion aftereffect, the tilt aftereffect and the size aftereffect. These aftereffects were stronger when the adaptation and test patterns were presented in the same gaze direction, than when they were presented in different gaze directions, even though the patterns always stimulated the same retinal location. The gaze modulation effect was not statistically significant for the post-adaptation elevation of contrast detection thresholds. The gaze modulation of visual aftereffects provides a useful psychophysical tool to analyze human cortical processes for coordinate transformations of visual space.

Keywords: Gaze direction; Motion aftereffect; Tilt aftereffect; Size aftereffect; Post-adaptation threshold elevation; Gain field

1. Introduction

We see the outer world through highly mobile sensors—our eyes. Yet our perception and action are towards objects in the environment that are stable independent of eye movements. Thus, to correctly interpret the scene projected on the retinas, the visual system has to take into account the position of the eyes in relation to the head, body and surrounding world. How the brain converts perceptual space from retinocentric to head-, body- and world-centered coordinates—the issue of spatial constancy—has been one of the major problems in cognitive neuroscience research.

Physiological evidence for cortical integration of retinal information with eye position information is the finding of gaze-dependent modulation of neuronal responses to visual stimuli: changes in the animal's gaze direction give rise to significant changes in the gain of neuronal responses to the same visual stimulus presented at the same retinal locations. The spatial tuning curve of a neuronal response to a stimulus does not change its peak retinotopic location, rather the overall amplitude (spike rate) systematically changes depending on the gaze direction. The neural gaze modulation was initially found in monkey parietal cortical areas that are important for the performance of visually guided motor behaviors (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990; Andersen, Essick, & Siegel, 1985; Andersen & Mountcastle, 1983). These "gain fields" may be important for converting visual representations from retinotopic to head-centered coordinates (Pouget & Sejnowski, 1997; Zipser & Andersen, 1988).

Is the gaze-dependent modulation of response gain limited to the sensory-motor system, or may it also be found in the perceptual system? Some recent physiological studies suggest this is the case, reporting a similar kind of neural modulation in visual cortical areas such as MSTd (Shenoy, Bradley, & Andersen, 1999; Squatrito & Maioli, 1997), V3 (Galletti & Battaglini, 1989) and V1 (Trotter & Celebrini, 1999) in the monkey. This immediately leads to the following questions: Is the gaze-dependent modulation of neuronal response indeed reflected in perception? And is it psychophysically detectable?

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doi:10.1016/S0042-6989(03)00007-5

These questions have so far remained unanswered. This is mainly because the vast majority of psychophysical experiments have been done with subjects gazing at only one eye position, or with eye position uncontrolled. We address this issue by introducing controlled gaze shifts and carefully comparing between two conditions, namely net gaze shift and no net gaze shift.

The visual effects we employ fall under the visual aftereffect paradigm. This is a natural selection because we were interested in the effect of spatial-visual context across gaze shifts, and also because aftereffects are considered to be effective and sensitive as "psychophysical microelectrodes (Frisby, 1979)" for such a purpose.

In one of the very few precursors of the current study, Mayhew (1973) provided evidence for a gaze-dependent motion aftereffect (MAE). He asked subjects to alternately gaze at a clockwise rotating disc on the left and a counter–clockwise rotating disc on the right without moving their heads, and then report the direction of the MAE seen in a static disc presented afterwards at each gaze direction. It was found that the direction of the aftereffect varied with the gaze direction, being opposite to the stimulus rotation at each gaze direction. The coexistence of aftereffects in the opposite, nulling directions clearly indicated mechanisms beyond a purely retinotopic, gaze-independent, representation. Moreover, the effect was reliably obtained with only a few minutes adaptation. This was in sharp contrast with the gaze contingent color aftereffect, which was reported to occur in some, but not all, studies (Kohler, 1962; McCollough, 1965b). Unfortunately, the lack of physiological evidence at that time prevented Mayhew from interpreting the observed aftereffect in terms of adaptation of neurons selective to both stimulus motion direction and gaze direction. The latest physiological findings mentioned above, however, have rendered his finding and the account based on gaze dependent modulation both feasible and significant.

We examine a variety of visual aftereffects known in the literature, each allegedly reflecting adaptation of different aspects and levels of visual processing. Our motivations are two-fold: (1) to determine the robustness and generality of the gaze dependent modulation of visual aftereffects and (2) to obtain some indication of the locations in the visual pathways where gaze modulation is introduced. To these ends, we used the MAE, the tilt aftereffect (TAE), the size aftereffect (SAE), and post-adaptation detection threshold elevation (DTE) (Fig. 1).

In Mayhew's experiment, the observers simultaneously adapted to opposing stimuli at different gaze directions. Although this is an elegant one-shot technique to test the existence of gaze modulation, it did not indicate the magnitude of modulation. In order to measure the gaze modulation magnitudes, and to compare it across different aftereffects, the present study employed a procedure that allowed us to determine the extent to which the base adaptation effects were modulated by gaze direction. Our observer, with eyes fixated in one gaze direction, was shown an adaptation pattern. Subsequently, the observer shifted gaze to a neutral point and then according to instruction, either shifted gaze back to the original location or to a new location. The test pattern was then presented at this final location.

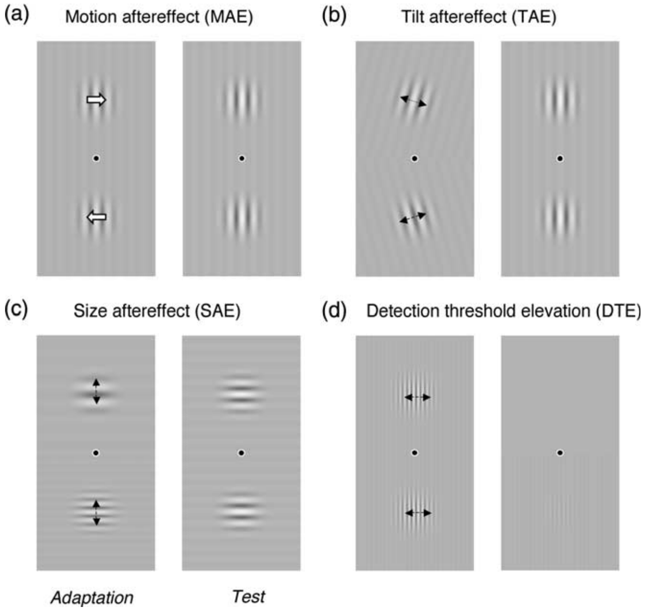

Fig. 1. Stimulus configurations used for the measurements of four types of visual aftereffects: (a) MAE, (b) TAE, (c) SAE, and (d) post-adaptation DTE. In each panel, the adaptation stimulus is shown on the left, and the test stimulus is shown on the right. A dot in the center is the fixation point. Arrows indicate the directions of movement.

To appropriately measure the gaze modulation effects, the retinal image of the test pattern, as well as its relationship with the retinal image of the adaptation stimulus, should not vary by manipulation of the gaze direction. For this purpose, first, we used two separate monitors for different gaze directions to minimize stimulus distortion by a change in the viewing direction (Fig. 2). Second, we had observers make a two-step gaze shift from adaptation to test patterns regardless of the test location (Fig. 3). Even when the test was presented at the same location as the adaptation pattern, the observer needed to make eye movements of the same distance. Third, we asked the observer to align the afterimage of the adaptation pattern with the location of the test pattern to obtain high and stable accuracy in matching retinal images even after large gaze shifts.

While these three precautions were expected to preclude conceivable artifacts, our results still indicate that the gaze direction can modulate, though modestly ($\sim$15%), a wide range of visual aftereffects.

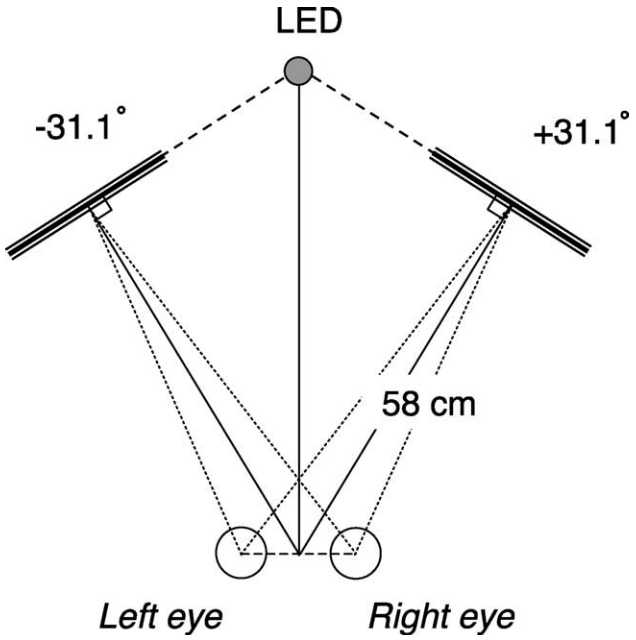

Fig. 2. The top view of the display setup. The left and right stimuli were presented by separate monitors, each facing towards the viewer, who directed his/her head to a red LED presented on the midline of the two gaze directions.

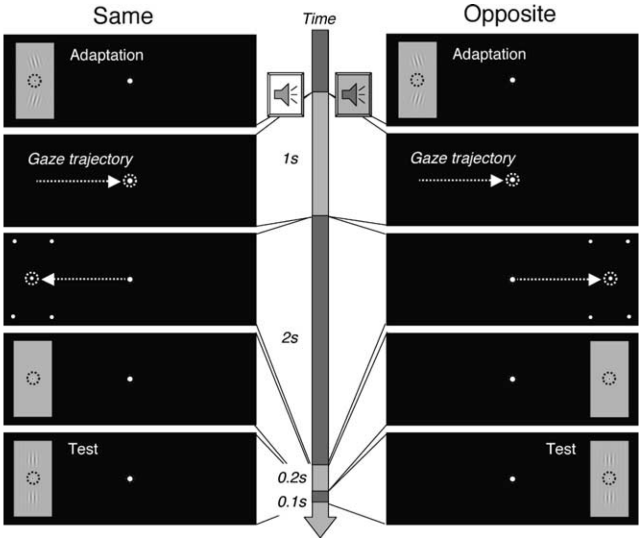

Fig. 3. The temporal sequence of an experiment. The center arrow indicates the time course. Sets of panels on the left and right illustrate the cases where the adaptation and test stimuli are shown on the same side, and opposite sides, respectively. See methods for further details.

2. Methods

2.1. Stimulus and apparatus

As shown by Fig. 1, the stimulus pattern consisted of a Gabor patch, whose luminance profile was defined as,

$$L(x,y) = L_{\text{mean}}[1 + c_{\text{peak}} \sin\{2\pi f(x\cos\theta + y\sin\theta) + \phi\} \times \exp\{(-(x^2+y^2)/2\sigma^2)\}],$$

where L_{mean} is the mean luminance (30 cd/m^2), c_{peak} is the peak contrast, f is the spatial frequency of the sinusoidal grating, θ is the grating orientation angle (0 at vertical), ϕ is the grating phase, and σ is the standard deviation of Gaussian envelope (0.8°, thus the visible size was about 4.7° in diameter). Unless otherwise stated, two Gabor patches were presented above and below a fixation bullseye with a center-to-center separation of 4.7°. The background was a gray rectangle having luminance of 30 cd/m^2, subtending 9.4° in height, 4.7° in width, surrounded by a dark field.

The stimuli were presented either 31.1° to the left or to the right from the observer's head direction. The stimuli for the two gaze directions were presented separately by two monitors (Sony GDM F500R, 120 Hz refresh). The brightness and contrast settings of the two monitors were carefully adjusted to make their Gamma functions nearly the same. The chromatic difference of the two monitors was negligibly small (in terms of CIE coordinates measured by a luminance colorimeter (TOPCON BM-5), $(x, y) = (0.2923, 0.3208)$ vs. (0.2852, 0.3079)). The screen of each monitor faced the observer and were oriented normal to the line of sight (Fig. 2). The two monitors were controlled by a VSG2/3 system. Although the same image input was given to the two monitors, only the left half of the left monitor and the right half of the right monitor were visible to the observers due to pieces of cardboard that occluded the other halves. A red LED was located at the midpoint between the two monitors. The observer viewed the stimulus at a viewing distance of 58 cm, stabilized by a chinrest. During a trial, the observer's face was always directed toward the LED marker. Observation was binocular except for the TAE monocular condition, in which the right eye of the observer was placed on the midline, and the left eye was occluded by a piece of cardboard attached to the chinrest.

2.2. General procedure

An adaptation stimulus was presented in one gaze direction, and a test stimulus was presented pseudorandomly in the same or opposite gaze direction (Fig. 3). At the end of each adaptation period, the adaptation stimulus disappeared, and a beep indicated the next test direction by pitch. For one second, nothing was presented except for the LED marker that was always on throughout the session. During this period, the observer had to shift his/her gaze to the LED marker. The test stimulus was preceded by a 2 s presentation of a grid pattern that consisted of five white dots located at the center and four corners of the test stimulus. The observer was asked not only to shift gaze to the grid pattern, but also to align it with the afterimage of the adaptation stimulus's background rectangle. In a dark experimental room, the observer could see nothing other than the stimulus patterns and the LED.

2.3. The motion aftereffect measurement

The magnitude of the MAE was determined by measuring its duration. For the adaptation stimulus, the two Gabor patches drifted horizontally in opposite directions to one another. The drift was produced by changing the spatial phase of the carrier grating (ϕ), without moving the Gaussian envelope, at a speed of 2.36 deg/s. The test stimulus was a pair of static Gabor patches. For both stimuli, the Gabor orientation was vertical ($\theta = 0°$), and the spatial frequency (f) was 1.27 cpd. The peak contrast (c_{peak}) was 60% for the adaptation stimulus and 80% for the test stimulus. In each trial, a 60 s presentation of the adaptation stimulus was followed by a 30 s test presentation. The observer was required to press a button while he/she perceived motion in the test pattern, and the duration of the button press was recorded as an MAE duration. There were four adaptation conditions that consisted of 2 gaze directions (left or right) × 2 motion directions (leftward/rightward or rightward/leftward for top/bottom Gabor patch). To see the effects of gaze change as directly as possible, we asked observers to consecutively run 2 trials of the same adaptation stimulus and different test gaze directions. In total, each observer ran 8 or 16 trials, 1 or 2 trial(s) each for eight combinations of adaptation and test conditions.

2.4. The tilt aftereffect measurement

The magnitude of the TAE was measured by employing a staircase method to determine the amount of relative tilt required to null the TAE. An experimental session started with a 100 s exposure to the adaptation stimulus, in which the upper and lower Gabor patches had opposite tilt angles (θ) of 15° (Fig. 1(a)). The spatial frequency (f) was 1.27 cpd, and the peak contrast (c_{peak}) was 60%. The spatial phase of the grating (ϕ) was smoothly oscillated between 0° and 360° at 1 Hz to minimize afterimage formation during adaptation. For test presentation, the background rectangle was first presented for 0.2 s to reduce the masking effect by an abrupt stimulus onset, then two Gabor patches ($f = 1.27$ cpd, $c_{\mathrm{peak}} = 80\%$) were presented for 0.1 s with a given tilt angle. The observer had to indicate, by pressing one of two buttons, whether the upper and lower Gabor patches appeared to be tilted clockwise and counterclockwise, or vice versa. After the observer responded, an 8 s re-adaptation period started, and then the next test stimulus was presented. Two staircases for the left and right gaze directions were randomly interleaved. Within each staircase, the tilt angle was adaptively changed by one step in the direction to null the perceived tilt. The step size was 2.0° until the first reversal, 1.0° until the second reversal, and 0.5° until the staircase terminated at the sixth reversal. The arithmetic mean of the last four reversals was taken as an estimate of the nulling tilt angle. Thus, for each session, we obtained two aftereffect estimates for different test gaze directions measured under the similar adaptation state. There were four adaptation conditions (2 gaze directions × 2 tilt directions). Each observer ran one or two session(s) for each adaptation condition. This balanced design was expected to eliminate potential artifacts related to asymmetric interaction between a particular eye and direction of gaze.

2.5. The size aftereffect measurement

The magnitude of the SAE was measured by employing a staircase method to determine the magnitude of spatial frequency change required to null the SAE. The procedure was similar to that for the TAE measurement except for the following points. In the adaptation stimulus, the upper and lower Gabor patches had spatial frequencies (f) of 0.9 and 1.8 cpd, or vice versa. The orientation was horizontal ($\theta = 90°$), and the peak contrast (c_{peak}) was 60%. In the test stimulus, upper and lower Gabor patches had spatial frequencies of f_1 and f_2, whose geometric mean was 1.27 cpd. The orientation was horizontal ($\theta = 90°$), and the peak contrast (c_{peak}) was 80%. The observer's task was to indicate which Gabor patch appeared to have a lower spatial frequency. Within each staircase, the log spatial frequency ratio, $\log_2(f_1/f_2)$, was changed in a step (0.2 and 0.1 until the first and second reversals, respectively, 0.05 thereafter) in the direction to null the perceived spatial frequency shift. There were four adaptation conditions (2 gaze directions × 2 frequency relationships). Each observer ran one or two session(s) for each adaptation condition.

2.6. The detection threshold elevation measurement

The contrast detection threshold was measured by a staircase method. The procedure was similar to those used for the TAE and SAE measurements except for the following points. The adaptation stimulus consisted of a pair of vertical Gabor patches ($f = 1.27$ cpd for IM, and 3.37 cpd for the others, $c_{\mathrm{peak}} = 60\%$). The test stimulus was a vertical Gabor patch of the same spatial frequency presented either at the upper or lower location. The observer's task was to indicate whether the test pattern appeared at the upper or lower position. Within each staircase, the test contrast was decreased by a log unit after three correct responses, and increased by the same amount after one incorrect response. The step size was 0.2 and 0.1 log units until the first and second reversals, respectively, and 0.05 log units thereafter. The adaptation duration was 100 s at the beginning, and 8 s for each re-adaptation as in the case of TAE and SAE. There were two adaptation conditions (2 gaze directions). Each observer ran two, four or six sessions for each adaptation condition. The base contrast thresholds were measured by replacing the adaptation stimulus with a uniform field that contained only a fixation point. In this case, initial adaptation lasted 30 s, and re-adaptation lasted 4 s.

2.7. Observers

At least six of seven observers (three of the authors and four naïves) participated in each experiment. All of them had normal or corrected-to-normal vision.

3. Results

3.1. The motion aftereffect

We first examined the MAE in which static patterns appear to move in the direction opposite the adapted motion direction (Mather, Verstraten, & Anstis, 1998; Wohlgemuth, 1911). The effect has been ascribed to selective reduction in sensitivity of the neural mechanisms tuned to the adapted direction (Barlow & Hill, 1963; Sutherland, 1961).

Mayhew (1973) found a gaze modulation of the MAE generated by rotating motion. (In a preliminary observation, we replicated his finding for several observers being tested.) It is suggested that global motion flows, such as rotation, are mainly processed at a higher stage of visual motion processing, area MST in the case of monkey (Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Saito et al., 1986; Tanaka & Saito, 1989), which also plays a significant role in eye movement control (Dursteler & Wurtz, 1988; Newsome, Wurtz, & Komatsu, 1988). Thus, one might expect that the use of rotation constitutes a particular case in which there is gaze modulation of the MAE. To investigate a more general condition, we used simple translational movements.

Fig. 4(a) shows the magnitude (duration) of the MAE obtained when the adaptation and test stimuli were presented in the same and opposite gaze directions. For most of the observers, the aftereffect magnitude was stronger for the same gaze direction than for the opposite gaze direction. The difference was statistically significant for two observers ($p < 0.05$ in the paired comparison t-test with the data of each session being regarded as one observation), and also for the group average ($p < 0.01$ in the paired comparison t-test with the average data of each observer being regarded as one observation). Thus, the MAE shows gaze modulation, and this is the case even when simple translation stimuli are used.

3.2. The tilt aftereffect and the size aftereffect

We next tested the TAE and the SAE. The TAE occurs after adaptation to a given orientation, and biases subsequent orientation judgments in the direction opposite to the adapted orientation (Gibson & Radner, 1937). For instance, after adaptation to a grating tilted clockwise, a physically vertical grating appears to be tilted counterclockwise. The SAE, also known as the Blakemore-Sutton effect, is an analogous effect in spatial frequency (Blakemore & Sutton, 1969). For instance, a spatial frequency slightly lower than the adapted spatial frequency appears to be lower than it actually is. These aftereffects have been ascribed to reduction in the sensitivity of the channels tuned to the orientation and spatial frequency of the adaptation stimuli (Blakemore & Sutton, 1969; Sutherland, 1961).

Many neurons in V1 are selective to these attributes, and have been regarded as the neural substrates of the adaptation (De Valois & De Valois, 1988), although contribution of higher visual areas has also been suggested in later studies (see Section 4). If the neural gaze modulation occurs in a wide range of human visual cortical areas including the earliest levels, then gaze modulation may occur even for these aftereffects.

An alternative, equally feasible, prediction is that the gaze modulation would not occur for the TAE and the SAE because of the known functional segregation of visual pathways. Motion is processed mainly by the dorsal pathway which plays a major role in visuomotor processing (Logothetis, 1994; Milner & Goodale, 1995; Ungerleider & Mishkin, 1982). The functional significance of gaze modulation is obvious in this pathway. It is therefore readily expected that the gaze modulation will occur for the MAE. On the other hand, the TAE and the SAE are aftereffects of spatial pattern judgment, which may be related more to the ventral pathway, which is more responsible for object recognition. Since conversion of retinal image information into body-centered coordinates is not a priori necessary for object recognition, the gaze modulation may not occur for the TAE and the SAE.

Fig. 4(b) shows the results of TAE. The aftereffect magnitude (nulling angle) was stronger for the same gaze direction for most of the observers. The difference was statistically significant for three observers ($p < 0.05$), and also for the group average ($P < 0.01$). Fig. 4(c) shows the nulling SAE magnitude. Although the data does not show statistically significant differences within individuals, the group average indicates

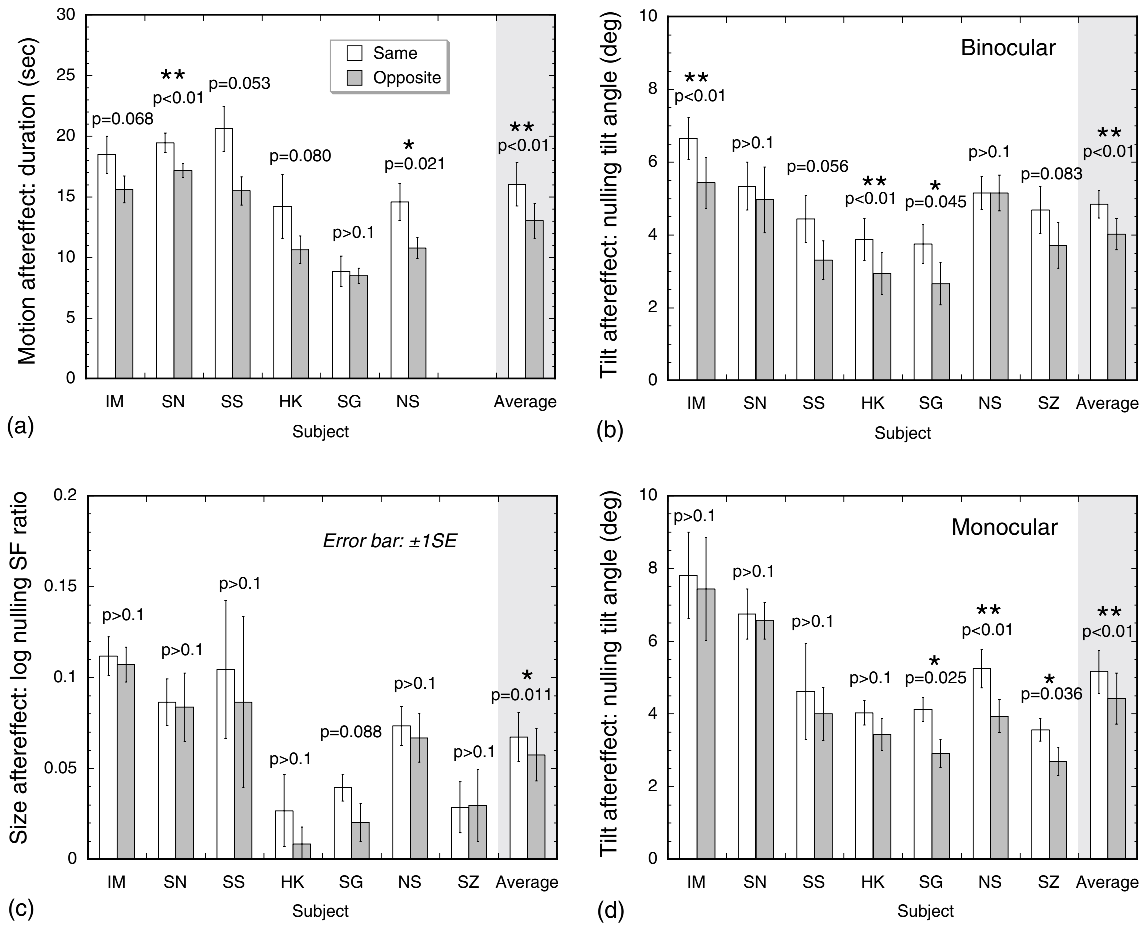

Fig. 4. The gaze direction modulates the magnitudes of suprathreshold aftereffects. (a) The magnitudes of the MAE measured in terms of duration. (b) The magnitude of the TAE measured in terms of physical tilt angle required to cancel the aftereffect. (c) The magnitude of the SAE measured in terms of physical spatial frequency change required to cancel the aftereffect. The results of (a–c) were obtained under binocular viewing, while the TAE magnitudes shown in (d) were obtained under monocular viewing. In each panel, the results of six or seven observers are shown separately, with a group average at the rightmost position. White and gray bars indicate the aftereffect magnitudes obtained when the adaptation and test stimuli were shown on the same side, and opposite sides, respectively. That the former is larger than the latter is the expected gaze modulation effect. Error bars indicate ±1 standard error between trials (for individual data) or between observers (for the group average). The *p*-value of the paired comparison *t*-test is shown for each pair of bars, with significant differences being indicated by asterisks (single for $p < 0.05$, double for $p < 0.01$). For all the aftereffects, the gaze modulation was significant in the group average.

that SAE was significantly stronger for the same gaze direction ($p = 0.011$). These results indicate that the gaze modulation occurs for the aftereffects of static spatial attributes as well as for that of motion.

3.3. The tilt aftereffect with monocular viewing

The data described above was obtained with binocular viewing. Under this viewing condition, as the observer changes gaze direction from one side to the other, the size of the retinal image slightly increases for one eye and decreases for the other eye. This implies that the gaze shift has been accompanied by a change in vertical disparity, to which the visual system is known to be very sensitive (Howard & Kaneko, 1994; Rogers & Bradshaw, 1993). In addition, the gaze shift may effect the dominance of the eyes (Khan & Crawford, 2001). The observer might show left eye dominance for the left gaze direction, and right eye dominance for the right direction. Since the degree of interocular transfer is limited (Gibson & Radner, 1937; Mohn & Van-Hof-Van-Duin, 1983; Wohlgemuth, 1911), this may account for the observed reduction of the aftereffects. To test whether the gaze modulation we obtained could be ascribed to these binocular artifacts, we replicated the TAE experiment with monocular viewing.

Fig. 4(d) shows the result. Again, the aftereffect was stronger for the same gaze direction for most of the observers. The difference was statistically significant for four observers ($p < 0.05$), and the group average ($p < 0.01$). There was no significant effect of presenting the adaptation stimulus on either the temporal or nasal side of the retina. We also found in a preliminary experiment that vertical gaze shift along the midline also had a modulation effect on the TAE. Thus, the gaze modulation of the aftereffects cannot be attributed to vertical disparity selectivity or to eye selectivity that might accompany the gaze shift.

3.4. The detection threshold elevation

Finally, we tested the gaze modulation of post-adaptation DTE. The DTE is an increase in the contrast detection threshold after adaptation to a high contrast stimulus. It is known to be selective to orientation (Blakemore & Nachmias, 1971), spatial frequency (Blakemore & Campbell, 1969) and motion direction (Sekuler & Ganz, 1963), and thus is also considered to occur at early cortical levels.

Fig. 5(a) shows the obtained DTE, defined as a logarithmic ratio of threshold elevation relative to the control threshold measured for each gaze direction. One of six observers shows a significant amount of gaze modulation. Although the group average also indicates slightly larger threshold elevation for the same gaze direction, the difference did not reach statistical significance. This is partially due to a large individual variability. In addition, for some observers, even though measured with adaptation to uniform pattern, the control threshold was slightly higher for the same direction than for the opposite direction. This results in an apparent reduction in the magnitude of the gaze modulation effect. In fact, when the DTE was estimated as a threshold elevation relative to the control threshold averaged over the two gaze directions, the gaze effect nearly reached statistical significance (Fig. 5(b)).

Fig. 6 compares the magnitude of gaze modulation across different aftereffects. The modulation ratio, defined as ('same' – 'opposite')/'same', was about 15% and nearly constant for all types of aftereffect.

4. Discussion

4.1. Implications of the present results

We found that the magnitudes of various visual aftereffects were stronger when the adaptation and test stimuli were presented at the same gaze direction than when they were presented at different gaze directions. Besides a pure gaze modulation effect, there are a few other variables that should be considered. One is retinal mismatch of the adaptation and test stimuli produced by the gaze shift. We carefully controlled for this factor by the two-step gaze shift, and the afterimage matching technique, as described above. In addition we replicated, though informally, Mayhew's (1973) observation that simultaneous adaptation of oppositely rotating stimuli at different gaze directions gave rise to a change in the MAE direction contingent with the gaze shift. This is hard to attribute to a retinal mismatch. Another possible source of artifact may be a change in binocular disparity or in eye dominance, but we rejected these as well with the results of the monocular and vertical shift control experiments.

It is known that the visual aftereffects can be made contingent on the patterns that surround the adaptation/test stimuli (Potts & Harris, 1975; Sharpe, Harris, Fach, & Braun, 1991). To minimize a potential artifact due to a change in surrounding patterns induced by a gaze shift, we ran experiments in a dark room where the observer could see nothing other than the stimulus patterns on the monitors. The only exception was the LED marker. Since it was always present, there remained the possibility that the aftereffects were contingent on the retinal LED location instead of the gaze change. To test this in an additional control experiment, we simulated retinal changes in LED location without actual gaze shifts, and examined whether it modulated

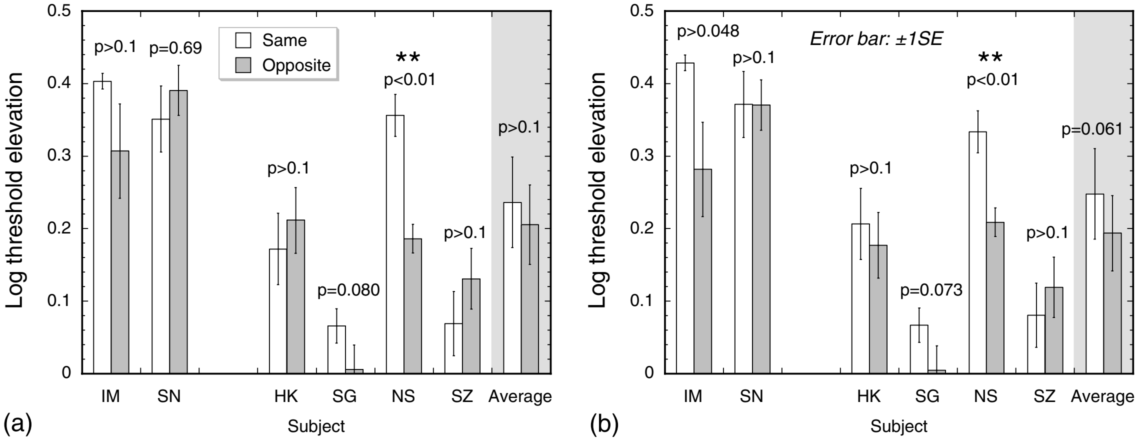

Fig. 5. The effects of the gaze direction on the magnitudes of threshold elevation. (a) The elevation was evaluated relative to the control threshold separately measured for each gaze condition. (b) The threshold elevation was evaluated relative to the control threshold averaged over the two test directions. The gaze modulation effect was not statistically significant for (a), although marginally significant for (b).

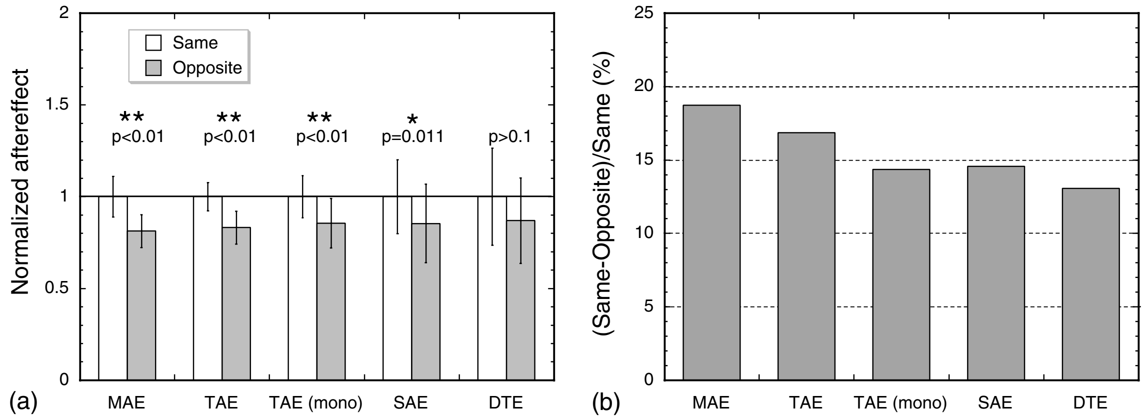

Fig. 6. The magnitude of the gaze modulation was similar between aftereffects of different types. The left graph (a) shows the aftereffect magnitude normalized relative to the same direction condition. The right graph (b) shows the modulation ratio, defined as ('same' − 'opposite')/'same'. It was about 15% and nearly constant for all types.

the TAE magnitude. Adaptation/test stimuli were always presented centrally, and a red spot was presented at 31° eccentricity. The spot location was always on one side during adaptation, but randomly varied from trial to trial. The results indicated that the TAE magnitude remains the same regardless of whether the red spot was on the same side during adaptation and test phases, or on the opposite sides.

Although it is difficult to completely exclude all possible artifacts, we believe the current data are sufficient to conclude that the differences in aftereffect magnitudes, which are small but significant for almost all of the aftereffects that we examined, are most likely due to a neural gaze dependent modulation. The neural gaze modulation found in V1, V3, MT, and MST of monkeys is thus likely found in humans as well, and is indeed reflected in perception. Interestingly, a recent fMRI experiment showed gaze direction modulation of activity in areas MT/MST and V4 of humans (DeSouza, Dukelow, & Vilis, 2002).

The findings have similarities to aftereffects that are contingent on additional variables, such as the McCollough-type orientation-contingent color aftereffect (McCollough, 1965a), and eye-contingent MAE (Anstis & Duncan, 1983). These results strongly suggest that the aftereffects are modulated by information other than retinotopic location. A unique aspect of the current findings is that, whereas the previous contingencies are limited to a particular aftereffect, a variety of aftereffects are contingent upon gaze direction.

Assuming that the aftereffects' gaze modulation is a psychophysical correlate of the gaze modulation of neural responses found by many physiological studies, what would be the implication of the present findings?

The TAE can be ascribed to response reduction of adapted orientation selective first-stage filters, or V1 orientation selective neurons, but it occurs even for orientation defined by non-luminance features, such as contrast-modulated edges and subjective contours (Paradiso, Shimojo, & Nakayama, 1989; Smith & Over, 1975; Van der Zwan & Wenderoth, 1995). This points to the involvement of V2 and/or other higher visual areas for this phenomenon.

The suggested mechanisms of the SAE are similarly distributed. Although it was initially ascribed to adaptation of spatial-frequency selective first-stage filters that can be identified with V1 neurons (Blakemore & Sutton, 1969), involvement of higher visual areas was suggested by the generation of the SAE with an orthogonally oriented adaptation stimulus (Heeley, 1979), the importance of apparent, rather than physical, spatial frequency (Parker, 1981), and the lack of clear direction selectivity as is found with the threshold elevation (Nishida, Motoyoshi, & Takeuchi, 1999).

With regard to the MAE, functional imaging studies show that area MT and its neighbors are most active during the perception of the MAE (Culham et al., 1999; Tootell, Reppas, Dale, & Look, 1995), but this does not necessarily mean that the aftereffect is due to adaptation in MT (Huk, Ress, & Heeger, 2001; Nishida & Ashida, 2000). Psychophysical properties of the MAE seen in static test patterns indicate that the underlying mechanism of this aftereffect is spatial frequency selective and mostly monocular, thus the stage of V1 direction-selective neurons is a likely candidate for the site of adaptation (Mather et al., 1998; Nishida & Ashida, 2000).

Consequently, the finding of gaze modulation for these suprathreshold aftereffects may indicate that gaze modulation occurs over a wide extent of visual cortex, possibly including V1, in the human brain. This wide range of effect would then be similar in extent to the wide range of sites for gaze modulation found in the monkey brain with single cell recording experiments. Furthermore, the modulation occurs not only for the neurons responsible for visual motion processing, but also for those responsible for static, spatial pattern analysis, thus strongly indicating modulation in multiple pathways.

The last phenomenon, the DTE, also displays selectivity with respect to orientation, spatial frequency and motion direction (Blakemore & Nachmias, 1971; Sekuler & Ganz, 1963). Moreover, cross adaptation between different types of stimuli is rarely found (Nishida, Ledgeway, & Edwards, 1997). The DTE therefore is likely to reflect adaptation of a first-stage filter or the V1 neuron, presumably more exclusively than the other suprathreshold aftereffects. Unfortunately, our DTE data was not as decisive about the existence of gaze modulation as it was for the other aftereffects. This may imply weakness of gaze modulation in V1 neurons, but an alternative interpretation is that there may be a large variation in the magnitude of neural gaze modulation among V1 neurons. Although this has a minor effect on the suprathreshold percept to which many neurons contribute, it would reduce the stability of the modulation effect for the contrast detection threshold that is supposedly determined by a small number of neurons that are most sensitive to the spatial features of the stimulus.

Our data indicate that the modulation ratio was nearly constant for all types of aftereffects. This suggests that gaze modulation occurs with a similar magnitude for a wide range of visual cortex involved in aftereffects of various sorts. Alternatively, there are intriguing possibilities such as the gaze modulation being generated in V1, which is commonly involved for all the aftereffects, or the modulation effect being generated at late visual areas and carried back to early visual areas via feedback connections.

4.2. Gaze shift paradigm

In our gaze shift paradigm, the two test patterns in different gaze directions were projected on the same position in the retinal coordinate system, but located at different positions in the head-centered coordinate system. We can interpret the present results as indicating that position change in the head coordinate system modulates early visual responses. However, the test patterns also had different locations in body- and world-centered coordinate systems, and the gain fields of some neurons in the posterior parietal cortex of monkeys are suggested to be defined in relation to these higher-order coordinates (Snyder, Grieve, Brotchie, & Andersen, 1998). It is therefore of interest to see whether head or body movement between presentations of adaptation and test stimuli also has a modulation effect on the aftereffect magnitude. Systematic investigation on this issue is under way.

It is also possible to apply the gaze shift paradigm to test whether there are visual neurons whose spatial coordinate system is converted in such a way that the receptive fields are completely defined in relation to head-, body- or world-centered coordinates. We attempted to search for such complete transformations by conducting a TAE experiment in which subjects fixated an adaptation stimulus at one location in space. They then made a gaze shift at the end of adaptation, and were shown a test pattern at various locations. It was expected that a test pattern presented at the adapted position in world coordinates, but at retinally non-adapted locations, might lead to an aftereffect stronger than that obtained at a control position that was away from the adapted location in world coordinates, but at the same retinal eccentricity as the test pattern. Although a preliminary observation showed the expected effects (Shimojo, 1996), a follow-up systematic experiment failed to confirm it.

In another experiment, to reveal object-centered coordinates in the cortex, we manipulated the location of test stimulus rather than observers' gaze direction, with an expectation that the aftereffect might indicate involvement of neurons whose receptive field is shifted with the object movement. After adaptation, a test stimulus first appeared at the adapted position, then quickly moved to a new position (in both retinal and world coordinates, since the observers kept fixation). The aftereffect was measured at the new test position. The pattern of the results we expected to find was that the aftereffects measured by this procedure were stronger than those measured for the test stimulus that suddenly appeared at the same position, or moved to this position from a non-adapted position. The result obtained so far was however negative.

At a theoretical level, this may be interpreted to mean that a complete transformation from the retinotopic to a non-retinotopic representation may never occur for visual perception. Instead, the "gain field", mentioned above may in effect serve as a functional alternative (Pouget & Sejnowski, 1997; Zipser & Andersen, 1988). Lack of robust effects in these experiments might be due to our use of the TAE that mainly reflects the adaptation of early visual processing. Recent fMRI studies suggest that the adaptation paradigm is effective even for the analysis of high-level object representations (Buckner et al., 1998; Kourtzi & Kanwisher, 2001). There may be a better chance to obtain positive results if we use aftereffects that mainly reveal adaptation of visual processing at higher levels or at levels closely linked to motor systems.

5. Conclusion

Gaze direction modulates a wide range of visual aftereffects. This modulation is modest, but highly reproducible. The results suggest that the gaze modulation of neural response may occur early in the human visual cortex. This modulation is most likely relevant to perceptual functions in the natural environment, the exploration of which involves eye saccades. The gaze shift paradigm with visual aftereffects may provide a useful psychophysical tool to analyze cortical processes for coordinate transformations of visual space.

Acknowledgements

We thank Drs. T. Hirahara, K. Ishii and Y. Tohkura of NTT CS Labs for their support. IM was supported by a JSPS fellowship for Japanese Young Scientists and by Tohoku University. RAA and SS were supported by the National Eye Institute (R01 EY13274-02).

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