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Visual field anisotropy revealed by perceptual filling-in

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Abstract

Four experiments were performed to investigate how the time required for perceptual filling-in varies with the position of the target in the visual field. Conventional studies have revealed that filling-in is facilitated by a target with greater eccentricity, while no systematic studies have examined the effect of polar angle. Experiment 1 examined the effect of polar angle when the target and surround differed in luminance. Filling-in was facilitated as the target position changed from the horizontal to the vertical meridian. This dependency was more prominent in the upper field than in the lower, although no asymmetry was found between the left and right visual fields. These features were observed in both monocular and binocular viewing. These results were replicated in a modified stimulus configuration, in which the surround was a circular region concentric with the target (Experiment 2). Moreover, it was confirmed that the asymmetry was not due to fluctuation in the retinal image (i.e., eye movement) (Experiment 3). Finally, Experiment 4 examined whether this anisotropy was observed when two differently oriented gratings were presented in the target and surround regions. Again, filling-in was facilitated for a target close to the vertical meridian, irrespective of the relationship between the target and surround orientations. The underlying mechanism of this anisotropy is discussed from the viewpoints of cortical magnification and neural connections in the visual cortex.

Keywords: Perceptual filling-in; Anisotropy; Brain asymmetry; Visual field; Cortical magnification

1. Introduction

When people look at a display in which a small peripheral target is presented on a uniform background, the target becomes invisible within a few seconds and the display appears uniform. This phenomenon, called "perceptual filling-in" or "perceptual fading", was first reported in the early 19th century (Troxler, 1804), and this simple, but striking, phenomenon has attracted many researchers in vision research.

The time for filling-in varies according to the stimulus and observation conditions. When the retinal image is completely stabilized, filling-in occurs quickly and strikingly (e.g., Yarbus, 1967). If the target size is suddenly reduced after filling-in is perceived, the target reappears and again fades away (Ramachandran & Gregory, 1991). These facts imply that a temporal change (or fluctuation) in the retinal image prolongs the time for filling-in, presumably by refreshing the neural activity in our visual cortex. It was also reported that filling-in was facilitated when the target/surround edge was blurred (Friedman, Zhou, & von der Heydt, 1999), and when their luminance gap was reduced (Sakaguchi, 2001). While these findings suggest that edge representation and its adaptation are important factors to determine the time for filling-in (e.g., Ramachandran & Gregory, 1991), simple edge representation does not readily explain other findings. For example, the time for filling-in was dependent not only on the target size, but also on the surround size (De Weerd, Desimone, & Ungerleider, 1998). Moreover, the time changed significantly when the luminances of the target and surround were exchanged (Sakaguchi, 2001). Although it is still unclear what mediates these phenomena, examination of the relationship between stimulus condition and the time for filling-in has provided clues to the mechanism of perceptual filling-in and related visual functions.

Incidentally, it is clear that filling-in occurs more quickly for smaller and more peripheral targets. De Weerd et al. (1998) confirmed these tendencies in a systematic study. They examined the time for filling-in while manipulating the size and eccentricity of the

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target, and observed that subjects' response times (RTs) were reduced with smaller target size and greater target eccentricity. They argued that this dependency on the target size and eccentricity was due to cortical magnification, because the effect of increasing target size on the delay in filling-in was reduced with greater eccentricity. This view was supported by the fact that a stronger linear relationship was observed between RT and the square root of the cortical projection area of the target, than between RT and the target size per se.

While the effect of target eccentricity on filling-in is clear, the effect of target direction (i.e., the polar angle) has not been examined, to our knowledge. Does the time for filling-in differ between the left and right visual fields, or between the upper and lower ones? The experiment reported here was conducted to provide empirical data for this problem by comparing RTs among various target positions.

Conventional studies have revealed asymmetry of the characteristics of human visual perception between the left and right visual fields. For example, it has been argued that the human ability to examine the local structure of a stimulus is superior in the right visual field, while the ability to examine its global structure is superior in the left visual field (e.g., Fink, Marshall, Halligan, & Dolan, 1999; Herrige & Sergent, 1986; Sergent & Hellige, 1986). Other studies suggest that the left and right visual fields are biased to the efficient use of higher and lower spatial frequencies, respectively (e.g., Kitterle, Christman, & Hellige, 1990; Proverbio, Zani, & Avella, 1997). Recently, Corballis, Funnell, and Gazzaniga (2002) clarified the difference in the performance of various visual judgment tasks between the two visual fields in split-brain patients. These differences presumably stem from the hemispheric asymmetry of human brain functioning, which causes asymmetries at various levels, including attentional control, motor performance, and linguistic processing (Davidson & Hugdahl, 1998; Hugdahl, 2000 for review). Thus, it is possible that asymmetry may also be observed in perceptual filling-in, if it is mediated by some mechanism that is affected by the hemispheric asymmetry.

In addition, recent studies have provided increasing amounts of data that indicate asymmetry exists between the upper and lower visual fields. For example, He, Cavanagh, and Intriligator (1996) showed that human performance in visual perception demanding attentional resources (e.g., a conjunctive visual search) was superior in the lower versus the upper visual field, suggesting that attentional resolution is greater in the lower visual field. Although He et al. (1996) did not find any difference in a simple (not attention-demanding) task, Leinonen and Elenius (1994) showed that perimetric sensitivity was highest in the lower temporal field and lowest in the upper nasal field. Fukusima and Faubert (2001) showed that the magnitude of underestimation of length was significantly greater in the lower versus the upper visual field, and in the right versus the left visual field. It was suggested that this asymmetry stems from ecological causes, such as the direction of gravity, the direction of sunlight, and the structure of the daily visual scene. Such causes might also affect the mechanism involved in perceptual filling-in.

This study examined whether such asymmetries are observed in perceptual filling-in. The author investigated the time required for filling-in in two stimulus dimensions: luminance and orientation. In luminance filling-in, the target and surround differed in luminance, and the screen appeared uniform when filling-in occurred. By contrast, in orientation filling-in, differently oriented gratings were presented in the two regions, and the screen appeared to have a uniform grating pattern when filling-in occurred. As will be shown below, the time for filling-in varied significantly according to the target polar angle (i.e., anisotropic), in both luminance and orientation filling-in, but it was symmetric between the left and right visual fields.

2. General method

2.1. Apparatus

Stimuli were generated by an IBM AT-compatible personal computer (Dell Optiplex575) and presented on a 17-inch color monitor (Sony GDM17seT). All experiments were run in a dimly lit booth.

Subjects observed the screen from a distance of 50 cm monocularly or binocularly (dependent on the experimental condition) with their chin resting on a chin rest. Before starting a session, the subjects looked at a gray screen (30 cd/m^2) for one minute to stabilize eye conditions.

2.2. Subjects

Graduate and undergraduate students of the University of Electro-Communications took part in the experiments. They were paid 1000 Japanese Yen (about 8 US Dollars) per hour. They all had normal or corrected-to-normal vision, and were naive to the purpose of the experiment.

2.3. Procedure

Each block started with a gray screen with a luminance of 30 cd/m^2, lasting for 15 s (preparation phase). This phase was to extinguish the afterimage of the stimulus used in the previous trial. Next, a black crosshair on which the subjects were to fixate throughout the trial appeared at the center of the screen. Shortly afterwards (2.0–2.5 s determined at random), the target and surround stimuli were presented simultaneously (test phase).

The subjects were instructed to press a key when the whole screen appeared uniform. They were asked to blink their eyes as little as possible. The time between stimulus onset and the subject's response was recorded as the RT. Although the subjective impression of filling-in may differ individually, the subjects were instructed to judge its occurrence according to a consistent criterion of their own.

The session moved on to the next trial when the subject pressed the key. If the key was not pressed within 30 s, the trial was aborted automatically. Aborted trials were recorded in the data file, and supplemental trials were inserted sometime later in the block.

The number of trials within a block was determined so that each block took 5–10 min. A 30 s rest period was inserted between successive blocks. A uniform gray screen (30 cd/m^2) was presented during the rest period. A new block started when the subject pressed the key. Sessions were repeated until the subjects had performed 15 or 16 trials for each experimental condition, with sufficient rest between sessions.

3. Experiment 1

In Experiment 1, the target and surround differed in luminance. The polar angle of the target was selected at random from 16 conditions, while its eccentricity was fixed at 8 deg.

3.1. Method

Eight subjects participated in this experiment; four observed the screen with both eyes (binocular condition) and the others observed it with the right eye (monocular condition), with an eye patch covering the left eye. The other experimental settings were as described in General Method.

Fig. 1 shows the typical stimulus configuration. A circle (i.e., the target) was presented on a uniform background (i.e., the surround). The surround size was 31.2×23.8 deg in visual angle. The target diameter and eccentricity were 1.0 and 8.0 deg, respectively. The luminances of the target and surround were 25 and 30 cd/m^2, respectively. These conditions were chosen so that RTs of most subjects were distributed around 5–20 s.[1]

In each trial, a polar angle was chosen at random from 16 alternatives: from 0 to 337.5 deg at 22.5-deg intervals, where the angle was measured counterclockwise from the right horizontal direction.

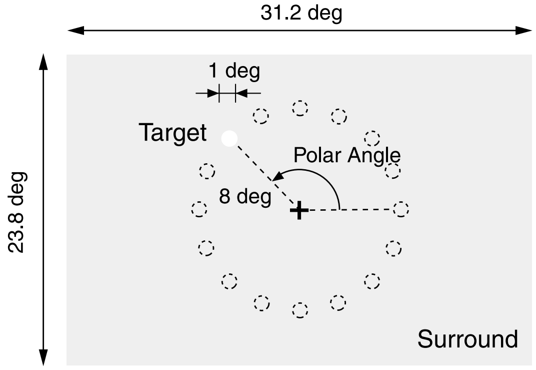

Fig. 1. Stimulus configuration in Experiment 1. A small circular patch (target) was presented on a uniform surround. Target position was chosen at random from 16 possible ones.

An experimental session consisted of three blocks of 16 trials ($= 1$ trial $\times$ 16 conditions). The subjects participated in five sessions to produce 15 results for each condition.

3.2. Result and discussion

Fig. 2 summarizes the median RTs[2] in 16 conditions for individual subjects. The scales differ among subjects, although the centers of the charts consistently correspond to the zero RT. We can see a few common tendencies from these charts, as well as considerable inter-subject variety.

First, no systematic difference was found in the overall tendency of the radar charts between the binocular and monocular conditions. This is apparent by comparing the charts in the upper and lower rows in Fig. 2. More importantly, RTs varied with the polar angle of the target. The gray regions in the charts appear to be compressed in the vertical direction: Filling-in occurred more quickly when a target was presented in the vertical direction than when it was presented in the horizontal direction. On the other hand, there was no clear asymmetry between either the right and left visual fields or the upper and lower ones.

These tendencies are clear in Fig. 3, where the inter-subject averages of median RT are indicated as a function of target direction with their standard deviation.[3]

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[1] In general, smaller eccentricity prolongs RTs while greater eccentricity makes it more difficult to judge the occurrence of filling-in. Considering their balance, the author selected 8 deg as the eccentricity in formal experiments. In a preliminary study, the result in 6-deg condition showed the same pattern as in 8-deg condition.

[2] The author used the median (instead of the mean) as the representative value because the distribution of RTs did not seem to obey a normal distribution (See De Weerd, Gattass, Desimone, & Ungerleider, 1995 or Sakaguchi, 2001 for the detailed distribution).

[3] Rather large standard deviation was mainly due to the fact that the time for perceptual filling-in was greatly different among the subjects. It should be noted that in such cases, standard deviation can be large even if the RTs for all subjects show an identical pattern for different target directions.

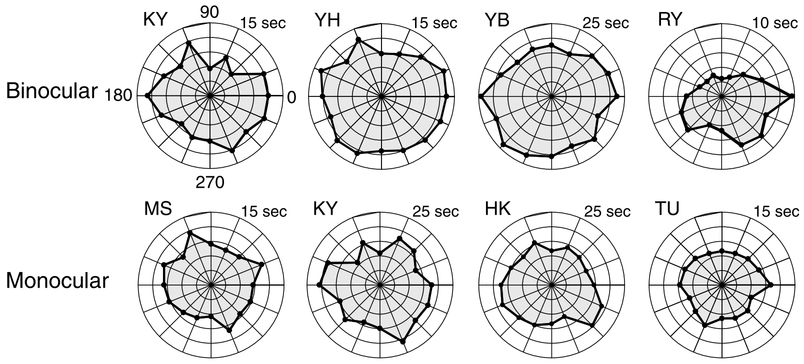

Fig. 2. Relation between polar angle and responseaction time (RT). Median RTs for different polar angles are indicated separately for each subject. The centers of the charts consistently correspond to zero responseaction time while the scales are different among the charts (the time corresponding to the outermost circle is indicated aside each chart). Upper and lower rows show the results for the subjects who participated in binocular and monocular conditions, respectively.

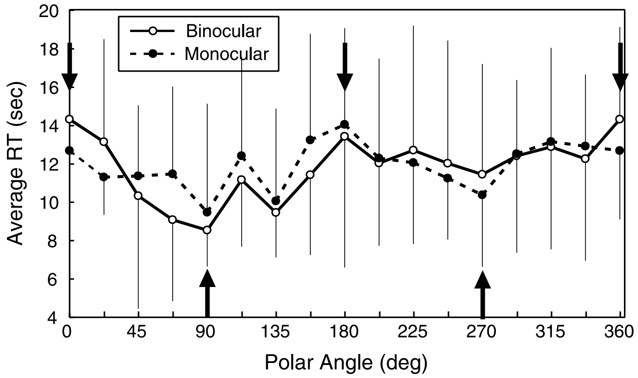

Fig. 3. Dependency of RT on the polar angle. Inter-subject average of median RTs is plotted as a function of polar angle. Response time took maximums in the horizontal direction (i.e., 0 and 180 deg conditions) and minimums in vertical condition (i.e., 90 and 270 deg conditions), as indicated by the arrows. The bars show the standard deviation.

Both curves have minimums at 90 and 270 deg (i.e., vertical direction), and maximums at 0 and 180 deg (i.e., horizontal direction), as indicated by the arrows. This was observed in both the binocular and monocular conditions. Moreover, the RT was a little shorter in the upper visual field (i.e., in the left-half of the figure) than in the lower field (i.e., in the right-half of the figure). In other words, the effect of polar angle was more remarkable in the upper visual field. Curiously, there was another local maximum at 112.5 deg. Examining the individual data in Fig. 2, this phenomenon was observed in five out of eight subjects. The reason for this local peak is not clear.

A statistical analysis was performed to test these findings. First, a two-way ANOVA was performed to test the effects of polar angle and viewing conditions. The effect of angle was highly significant ($F(15,90) = 4.603$, $p < 0.001$), while the effect of viewing condition and their interaction were not ($F(1,6) = 0.005$, $p > 0.9$ and $F(15,90) = 0.928$, $p > 0.5$). Multiple comparisons with Bonferroni adjustment showed that the difference was only significant between the 22.5 and 90 deg conditions ($p < 0.05$).

In addition, the author compared the results between the left and right visual fields, between the upper and lower fields, and between the vertical and horizontal directions. The following analysis was performed for the mixed data from the binocular and monocular conditions.

A 2 (left or right) × 7 (divergence from the upper direction (i.e., 90 deg)) ANOVA was performed to test the difference between the right and left fields, where the data for the 90 and 270 deg conditions were not used for the analysis. The effect of the field was not significant ($F(1,7) = 0.202$, $p > 0.6$), but that of the divergence was highly significant ($F(6,42) = 6.146$, $p < 0.001$). Their interaction was not significant ($F(6,42) = 0.972$, $p > 0.4$). On the other hand, the result of a 2 (upper or lower) × 7 (divergence from the right direction (i.e., 0 deg)) ANOVA (data for the 0 and 180 deg conditions were removed) showed that the effects of the field and the divergence were both significant ($F(1,7) = 7.898$, $p < 0.05$ and $F(6,42) = 4.416$, $p < 0.01$), but their interaction did not reach significance ($F(6,42) = 2.007$, $p > 0.05$). The rather high, but non-significant, interaction indicates that the effect of direction was diminished in the lower visual field (see Fig. 3).

In summary, it was revealed that the time required for perceptual filling-in was not isotropic over the visual field. It decreased consistently (except at 112.5 deg) as the target position changed from the vertical to the horizontal, even if its eccentricity was maintained. It was also found that the effect of the polar angle was more prominent in the upper than in the lower visual field, while no asymmetry was found between the left and right visual fields. This suggests that the mechanism for perceptual filling-in is evenly incorporated in the two hemispheres.

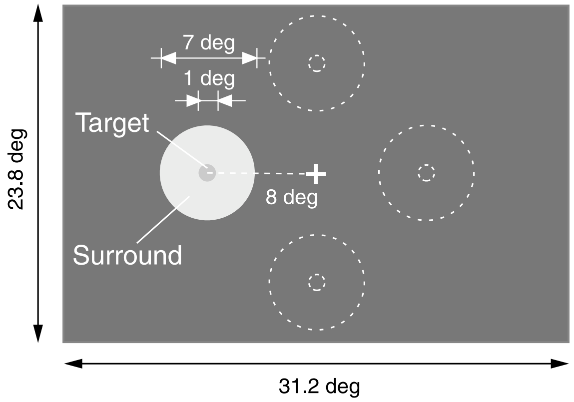

Fig. 4. Stimulus configuration in Experiment 2. A circular target was presented on a concentric circular surround to eliminate the anisotropy of the surround shape. Target location was chosen at random from four possible ones.

4. Experiment 2

The results of Experiment 1 showed that the time for filling-in differed significantly between horizontal and vertical targets. However, some might suspect that this asymmetry was due to the rectangular shape of the surround region (i.e., longer in the horizontal direction than in the vertical direction), which might cause the difference between these directions.

Experiment 2 was designed to test this. In a modified configuration (see Fig. 4), both the target and surround occupied concentric circular regions, so that the relationship between target and surround remained constant irrespective of target direction. Only four polar angles were examined to simplify the experimental procedure.

4.1. Method

The experimental procedure was almost the same as in Experiment 1; one difference was in the stimulus configuration. As shown in Fig. 4, the target and surround were concentric circles. Their eccentricity was 8.0 deg, and their diameters were 1.0 and 7.0 deg, respectively. The luminances of the target, surround, and background were 25, 30, and 0.02 cd/m^2, respectively. This stimulus was presented only in the test stimulus phase. A uniform gray display (30 cd/m^2) was presented during the preparation phase to extinguish any afterimage.

Another difference was in the direction conditions; only four polar angles (i.e., 0, 90, 180, and 270 deg) were compared in this experiment. An experimental session consisted of 2 blocks of 16 trials ($= 4$ conditions $\times 4$ trials). Subjects took part in two sessions, to produce 16 results for each condition. Six subjects participated in this experiment, and they performed the task in the binocular condition only.

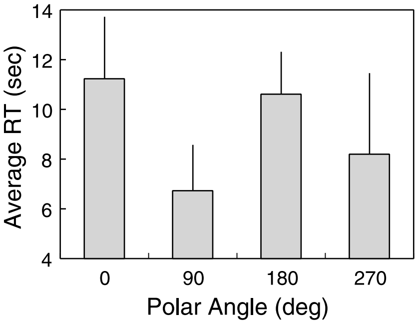

Fig. 5. Result of Experiment 2. Time for filling-in was significantly longer for the horizontal targets than the vertical targets. The bars represent the standard deviation.

4.2. Results and discussion

Fig. 5 shows the average of the median RTs of the six subjects, with their standard deviation. It is clear that filling-in was facilitated in the vertical (i.e., 90 and 270 deg) conditions compared to the horizontal (i.e., 0 and 180 deg) conditions. The RT in the 90-deg condition (i.e., upper visual field) was shorter than that in the 270-deg condition (i.e., lower visual field), as in Experiment 1. Statistical analysis supported this. A within-subject ANOVA showed that the effect of target position was significant ($F(3,15) = 12.252$, $p < 0.001$). Multiple comparison with Bonferroni adjustment showed that the difference was significant between the 0 and 90 deg conditions and between the 90 and 180 deg conditions, supporting the above.

This result rejected the view that the anisotropy observed in Experiment 1 was due to the vertical/horizontal asymmetry of the surround shape.

5. Experiment 3

Although the previous experiment rejected the effect of the surround shape on the anisotropy, it is possible that the anisotropy results from the dependency of the fluctuation of the retinal image on the target position.

As described in the Introduction, stability of the retinal image is a significant factor affecting the time for filling-in, meaning that eye movements and blinking may delay filling-in. Although the subjects were instructed to maintain strict fixation and to minimize blinking, it is practically impossible to completely eliminate involuntary eye movements and blinking. Therefore, we cannot rule out the possibility that the anisotropy of filling-in was caused because the frequency of such eye movements and blinks varied with target position.

In order to test this possibility, the author measured eye movements and examined their dependency on target position.

5.1. Method

The stimulus condition and experimental procedure were the same as in Experiment 2, except for the following points. First, the subjects wore a head-mounted eye measurement system (EyeLink, SMI Inc.) and bit on a bite-bar to produce stable measurements. Each bite-bar was made individually for each subject using a dental mold compound. Second, the eye measurement system was calibrated before every block.

The EyeLink system observes both pupils with infrared video cameras at a sampling rate (250 Hz) that is high enough to detect saccadic eye movements. Moreover, it automatically detects saccades and blinks by monitoring pupil position and size. The author set the system so that a saccade was detected when the velocity and acceleration of eye movement exceeded 30 deg/s and 4000 deg/s^2, respectively, and its amplitude exceeded 0.15 deg. In addition to these automatically detected saccades and blinks, the author added missed events manually by examining the eye position data.

An experimental session consisted of two blocks of 16 trials ($= 4$ conditions $\times$ 4 trials). Each subject took part in two sessions to produce 16 data sets for each condition. The experiment was run only in the binocular condition. Four subjects were paid to participate in this experiment.

The eye movement data for each subject were analyzed separately. In addition to the frequencies of saccades and blinks, the author calculated the range (i.e., the difference between maximum and minimum angles) of eye position and the total path length of eye movements (i.e., the cumulative sum of the distance between every succeeding eye position) as other indices. These indices were evaluated separately for 1-s time windows. Specifically, first, the author found these values for every 1-s time-bin from stimulus onset to subject response, for each trial. Then, their averages were calculated for each bin, for the four target positions.

5.2. Results and discussion

Three out of four subjects blinked only once in 32 trials, indicating that they followed the experimenter's instructions and, more importantly, that the frequency of blinking did not differ with target position. The remaining subject (TU) blinked throughout the experimental session, for a total of 13, 4, 14, and 18 blinks in the 0-, 90-, 180-, and 270-deg conditions, respectively. Although the difference in the number of blinks reached the level of significance ($\chi(3) = 8.551$, $p < 0.05$), we should not forget that the expected number of blinks increases with the duration of a trial, even if the probability of blinks is constant. Therefore, the author estimated the expected number of blinks per second by calculating the average ratio of the blink number to RT. The results were 0.0867, 0.0485, 0.0949, and 0.1438 in the 0-, 90-, 180-, and 270-deg conditions, respectively, and this time the difference did not reach the level of significance ($F(3, 60) = 2.1$, $p > 0.1$). Moreover, there was no direct correspondence between the number of blinks and RT; the number (and frequency) of blinks was greatest in the 270-deg condition, while the median RT in this condition was shorter than in the 0- and 180-deg conditions (see Fig. 6). Therefore, it is unlikely that a difference in blink frequency causes the difference in RT.

Next, the range of eye positions and total path length of eye movements showed a similar tendency among every pair of horizontal/vertical and left/right eye movements. Therefore, only the result for horizontal eye movements of the right eye is shown, excluding the data for subject TU, whose right-eye data collapsed.

Fig. 6 summarizes the eye movement and RT data. Each row gives data for each subject. The left and center columns show the temporal change in the range and path length. The upper part of the graphs in the left column indicates the timing of saccadic eye movements in the four conditions, where all events in 16 trials are superimposed in a single plot. The right column shows the median RTs in the four conditions. The results of statistical tests (i.e., Kruskal-Wallis test) are also shown in the graph.

First, the experiment replicated the finding that filling-in took significantly longer time when the target appeared in the horizontal direction (0 and 180 deg conditions) than when it appeared in the vertical direction (90 and 270 deg conditions). Within-subject statistical tests found significant differences among the RTs in the four conditions, as indicated in the figure. The RT data also show that filling-in occurred more quickly when the target was presented in the upper visual field than when it was presented in the lower visual field (see Sections 3.2 and 4.2).

Second, all the subjects made considerable saccadic eye movements during the experimental trials, although most were of small amplitude (less than 0.2 deg). The timings of the saccades varied among the subjects, and no consistent tendency was seen. In general, the total number of saccades was larger in the horizontal condition than in the vertical condition. This is presumably due to the difference in RTs, because saccades were roughly independent of the time from stimulus onset. The expected number of saccades also increases with the duration of a trial.

Third, the left and center columns show that both the range and path length differed little among the four conditions. These indices were almost constant, independent of the time from stimulus onset, except for some extraordinary values due to the small sample number. One concern is that as for subject MF, the indices were larger in the first time-bin. An extended analysis found that he tended to make small saccades in the target di-

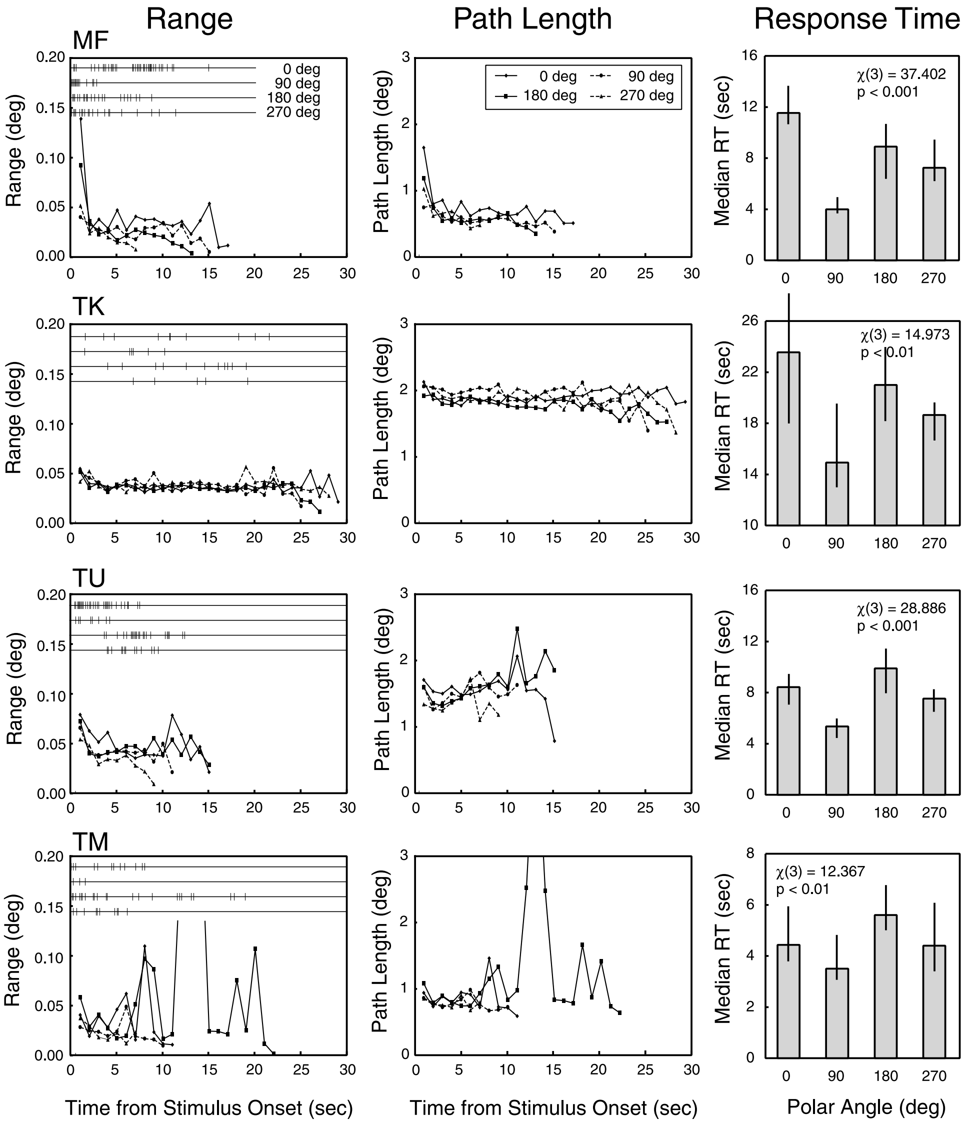

Fig. 6. Result of Experiment 3. The left and center columns show the fluctuation of eye position for individual subjects, using the range of eye position (left) and by path length of eye movement (center). Only data for horizontal movements of the right eye are shown (the left eye data was used for subject TU). The upper part of the left column indicates the timing of saccadic eye movements (superimposed for 16 trials). No consistent difference can be found in these indices among four target positions. The right column shows the median time for filling-in for four target positions, where a consistent tendency can be seen that filling-in for horizontal targets (0 and 180 deg) were slower than for vertical targets (90 and 270 deg). The bars represent inter-quartile distances (i.e., 25–50% and 50–75%).

rection just after the stimulus onset. This tendency is also seen in the saccade-timing diagram.

The *t*-test was used to examine the difference in these indices for every time-bin, and the difference reached the level of significance in only three cases (the fifth and seventh bins of subject MF and the first bin of subject TM). Therefore, the fluctuation in eye position (i.e., retinal image) did not differ among the four target positions.

In summary, the author rejects the view that the anisotropy of perceptual filling-in is due to the difference in retinal image fluctuation caused by eye movements and blinks. Instead, this anisotropy presumably stems from intrinsic characteristics of the human visual system. This will be discussed in Section 7.

6. Experiment 4

Experiment 4 asked whether the anisotropy observed in the previous experiments was observed in orientation filling-in. A Gabor patch was adopted as the target, and a uniform sinusoidal grating was presented as the surround. The Gabor patch was used to reduce the effect of the discontinuity of the pattern at the boundary of the target and surround.

Since a previous study (Sakaguchi, 2001) showed that the time for filling-in depended significantly on the orientation between the target and surround regions, four orientation combinations were used to test whether anisotropy was observed irrespective of the orientation.

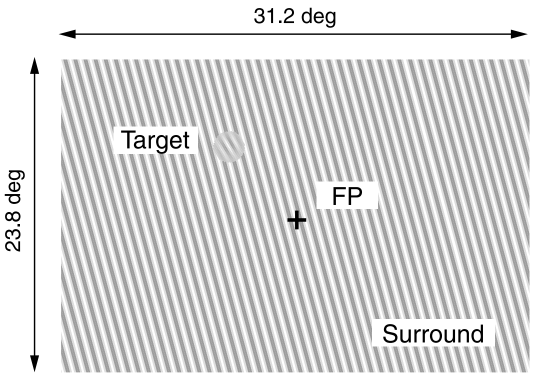

Fig. 7. Stimulus configuration in Experiment 4. A Gabor patch was presented on a uniform grating pattern. The spatial configuration of the stimulus was the same as in Fig. 1. Four pairs of target/surround orientations were examined to examine the effect of orientation difference to the anisotropy.

6.1. Method

Since the experimental procedure was the same as in Experiment 1, only the stimulus configuration is explained here.

In each trial, differently orientated gratings were presented in the target and surround regions. Specifically, a Gabor patch was presented on a uniform sinusoidal grating (see Fig. 7). The luminance of the Gabor patch was given by

$$L(x,y) = L_0 + L_a * \exp\left(-\frac{(x-x_0)^2+(y-y_0)^2}{2\sigma^2}\right) * \sin(2\pi f(n_x x + n_y y) + \theta_0),$$

where L_0 and L_a are the average luminance and amplitude, respectively, (x_0, y_0) is the center of the target, f is the spatial frequency, (n_x, n_y) is a vector representing the orientation of the grating, θ_0 is the phase, and σ is a parameter determining the scale of the pattern. In the experiment, spatial frequency (f), average luminance (L_0), the Michelson contrast (L_a/L_0), and scale parameter (σ) were 2.5 cpd, 30 cd/m^2, 33%, and 0.4 deg, respectively. The target diameter was 1.0 deg and its eccentricity was 8.0 deg. A spatial frequency of 2.5 cpd was chosen because the human visual system is most sensitive around 2–5 cpd (Campbell & Robson, 1968; De Valois, Albrecht, & Thorell, 1982a, 1982b), and because at least a few cycles of the grating pattern should be presented within the target region. The average luminance, spatial frequency, and Michelson contrast of the surround grating pattern were 30 cd/m^2, 2.5 cpd, and 33%, respectively. The phase of the target (θ_0) was fixed, while that of the surround was chosen at random in order to prevent a specific phase relationship from producing artifacts.

There were four orientation combinations: (target/surround) 15/45, 75/45, 15/−45, and 75/−45 deg, where the orientation was measured counterclockwise from the vertical. Six subjects were dedicated for each orientation combination, i.e., 24 subjects participated in this experiment, in total.

6.2. Results and discussion

Fig. 8 summarizes the results. Each line is the inter-subject average of the median RTs in each orientation condition. Although there was some variation among the four conditions, these curves share the following features. First, there are remarkable maximums at 0 and 180 deg (except in the 75/−45 deg condition). Second, there is a remarkable minimum at 90 deg, although no clear peak is found around 270 deg.

On the other hand, there does not appear to be a significant difference among the four conditions, either in the pattern of RT changes or in the absolute RTs. The lack of a difference in the latter seems to contradict a previous study showing that orientation filling-in was delayed with a larger orientation difference between the target and background (Sakaguchi, 2001). It was expected that the RTs in the 15/45 and 75/45 deg conditions (difference = 30 deg) would be shorter than in the 15/−45 and 75/−45 deg conditions (difference = 60 deg). This discrepancy presumably arises from the difference in the experimental design between the two studies. The previous experiment compared RTs in a within-subject design, while this experiment compared them in a between-subject design. Since the absolute RT of perceptual filling-in depends highly on the individual (see Fig. 2), it is reasonable that no significant difference was observed in this experiment.

Related to this point, some may be interested in the relative RT among different polar angles, rather than the absolute RT per se. To examine this problem, the author defined the normalized RT as

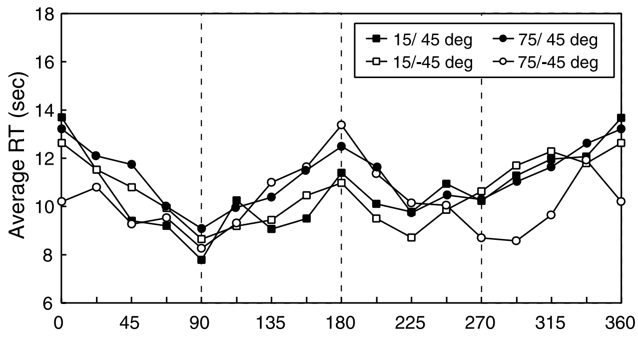

Fig. 8. Result of Experiment 4. Inter-subject averages of median RTs in four orientation conditions are plotted as a function of polar angle. Similar to the case of luminance filling-in (see Fig. 3), response time took maximal values in 0 and 180 deg conditions and minimal values in 90 deg condition. However, no clear minimum was found around 270 deg condition, implying that the effect of polar angle was diminished in the lower visual field. Standard deviation was 2–6 s (not shown in the figure for avoiding confusion).

$$\text{Normalized RT}(x\ \text{deg}) = \frac{\text{median RT}(x\ \text{deg})}{\text{median RT}(0\ \text{deg})}$$

and plotted it as a function of polar angle (x deg). The results showed that the above features were consistently preserved, although no data are shown here.

Statistical analysis was performed to test the above claims. First, a 4 (orientation condition) × 16 (polar angle) ANOVA was performed. The effect of polar angle was highly significant ($F(15,300) = 8.180$, $p < 0.001$), while the effects of orientation condition and the interaction were not ($F(3,20) = 0.030$, $p > 0.9$) and ($F(45,300) = 1.122$, $p > 0.2$). The effect of polar angle was consistently significant when the author tested it separately for each orientation condition.

Second, the author compared the results between the left and right visual fields, and between the upper and lower visual fields. These tests were performed for mixed data from all orientation combinations. A 2 (right or left) × 7 (divergence from the upper direction) ANOVA (data for the 90 and 270 deg conditions were removed) was performed to test the difference between the right and left fields, as in Experiment 1. The effect of divergence was highly significant ($F(6,138) = 9.411$, $p < 0.001$) and that of visual field was mildly significant ($F(4,23) = 4.411$, $p < 0.05$). The interaction was not significant ($F(6,138) = 2.083$, $p > 0.05$). The significant difference between the two visual fields presumably reflects the asymmetry in the lower visual field (See Fig. 8). On the other hand, the result of a 2 (upper or lower) × 7 (divergence from the right direction) ANOVA (data for the 0 and 180 deg conditions were removed) showed that the effect of divergence was quite significant ($F(6,138) = 9.723$, $p < 0.001$), but that of visual field was not ($F(4,23) = 3.283$, $p > 0.05$). Their interaction was significant ($F(6,138) = 3.299$, $p < 0.01$). This significant interaction implies that the effect of polar angle differed between the upper and lower visual fields.

Therefore, the results for orientation filling-in show the tendency seen in luminance filling-in revealed by Experiment 1. That is, (1) RTs showed clear maximums at 0 and 180 deg; (2) RTs had a minimum value at 90 deg; (3) the effect of polar angle was clearer in the upper than the lower visual field; and (4) only a slight asymmetry was found between the left and right visual fields. In addition, the effect of polar angle did not depend on the orientation between the target and surround gratings, as far as examined in this experiment.

7. General discussion and concluding remarks

This study revealed that the time for filling-in was dependent on the target polar angle, even if its eccentricity was maintained. There are at least two ways to interpret this result: the anisotropy of cortical magnification or a peculiar mechanism at the boundary between the left and right visual fields.

As described in the Introduction, the time for filling-in depends on target eccentricity and a possible cause seems to be the cortical magnification (De Weerd et al., 1998). The same explanation might hold for different target directions: The cortical magnification factor may vary with the polar angle, even if the eccentricity is maintained, which may cause anisotropy in the time for perceptual filling-in.

The cortical magnification factor has been investigated using various methodologies, including physiology (Daniel & Whitteridge, 1961), fMRI (Horton & Hoyt, 1991; Engel et al., 1994; Sereno et al., 1995), and VEP (Slotnick, Klein, Carney, & Sutter, 2001). Daniel and Whitteridge (1961) reported no significant difference in the magnification factor among six segments in the visual field, in the monkey cortex. Most of the other studies estimated the factor as an average for all directions or provided no explicit description of its relationship to the direction or polar angle. Therefore, there is no positive support for the view that the anisotropy in filling-in comes from the cortical magnification.

The second possibility is that the boundary between the left and right visual fields has some specific effect on perceptual filling-in. Needless to say, visual stimuli presented in the left and right visual fields are imposed in the right and left hemispheres, respectively, and the information brought to these hemispheres is subsequently exchanged via the corpus callosum. Accordingly, if a target is presented around the median line, the neural processing involved in perceptual filling-in must operate through the connection in the corpus callosum. Since perceptual filling-in is presumably mediated by "neural filling-in" in the visual cortex, i.e., the spread of neural activity from the surrounding field (Murakami, 1995; Pessoa, Thompson, & Noë, 1998; Spillmann & Werner, 1996), it is plausible that a singularity of neural connections may have an effect.

Although there is no strict reason to reject this view, the experimental results seem to counter it. If this view were true, then a specific effect should be observed only around the 90 and 270 deg conditions, and the RT in the other conditions should be almost constant. This was not the case, however, as seen in Figs. 2 and 8. The RT had remarkable peaks at 0 and 180 deg, and it varied only mildly around 90 and 270 deg. These results weaken the support for the second possibility.

At present, we have no clear explanation for the anisotropy found in this study. The author thinks that it is caused by anisotropy of the neural connections in the human visual system, although there are no objective grounds for this view. Nevertheless, the present findings provide a novel clue to help understand the characteristics of human visual perception, because perceptual filling-in is presumably mediated by an interaction via neural connections, common to other fundamental functions of the visual system, such as surface perception and perceptual grouping (Spillmann & Werner, 1996). It is possible that similar anisotropy will be observed in other perceptual phenomena.

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