Perceptual asymmetry in vernier offset discrimination
—a similar trend between the cardinal and oblique orientations—

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Our previous study has demonstrated that in the cardinal orientation, offset detection depends on the relative position of the vernier bars, i.e., how the left and right or upper and lower vernier bars are displaced from each other in space (Karim & Kojima, 2008, 2010). The present study examined whether the fact can be generalized to the oblique orientation. Experiment 1 demonstrated that for a pair of vernier bars, one displaced from the other and arranged side-by-side with a large gap between them at $+45^\circ$ orientation observers were, on average, somewhat better at discriminating an offset if the relative position of the lower right-hand bar was to the right of the upper left-hand bar than vice versa. A similar asymmetry was evident in Experiment 2, where observers judged vernier offset for a pair of bars at $-45^\circ$ orientation. In that case, average acuity was significantly better when the relative position of the upper right-hand bar was to the right of the lower left-hand bar than the opposite. The asymmetries in performance were consistent across the two orientations and did not diminish with learning, thus indicating configuration-specific processing of the vernier stimuli.

Key words: perceptual asymmetry, vernier, configuration, cardinal, oblique, invariance

Introduction

Early studies in visual psychophysics have demonstrated that perception of line or dot segments and gratings depends on their alignment relative to the cardinal axes (i.e., horizontal and vertical). Perhaps Jastrow (1893) was the first to show this kind of fact, asking subjects to view a line segment and then immediately set another segment to lie at the same orientation. He found that the judgments of horizontal or vertical segments were more accurate and less variable than oblique segments. Craig and Lichtenstein (1953) claimed that oblique segments that were viewed with steady fixation disappeared more readily and for longer durations than did horizontal or vertical segments. Leibowitz, Meyers, and Grant (1955) reported that single dots that were flashed to an eccentric position (i.e., relative to fixation) were more accurately localized if they were positioned on or near a cardinal axis. Leibowitz (1953), Campbell, Kulikowski, and Levinson (1966), and Regan and Price (1986) found that grating resolution/acuity was better for horizontal and vertical orientations than when the gratings were at a tilt. This has been replicated in a more recent fMRI study with gratings (Furmanski & Engel, 2000) and in psychophysical studies on stereo-acuity (Mustillo, Francis, Oross, Fox, & Orban, 1988) and vernier acuity (Saarinen & Levi, 1995b; Skrandies, Jedynak, & Fahle, 2001; Westheimer & Beard, 1998).

The superior accuracy, perceptibility and discriminability can be accompanied by differentials in variance. For example, Sulzer and Zener (1953) observed variability in orientation judgment to be minimal for horizontal, near minimal for vertical and maximal for oblique segments. Bouma and Andriesen (1968) found minimal variability in collinearity judgment at horizontal and vertical positions and maximal variability at $45^\circ$. This has been confirmed in a more recent study on collinearity judgment
(Greene, Frawley, & Swimm, 2000). All these asymmetries or differentials are collectively known as the “oblique effect” (Appelle, 1972).

In addition to the oblique effect, there is evidence of some other kinds of perceptual asymmetry. For example, in orientation and angular position judgments line segments or dots are seen as being closer to the horizontal or vertical than is true (Bouma & Andriessen, 1968; Jastrow, 1893; Sittig & De Graaf, 1994). It has been reported that subjects are good at finding a target when the light is lit from the top-left (Sun & Perona, 1998). This perceptual asymmetry is most prominent in foveal vision (Mamassian, Jentzsch, Bacon, & Schweinberger, 2003) and can be modified or reduced by training or visual experience (Adams, Graf, & Ernst, 2004; Champion & Adams, 2007).

In a recent study, we tested humans' perception of spatial offset by means of alignment judgment (Karim & Kojima, 2008, 2010). The study indicated within-cardinal asymmetry depending on how the left and right or upper and lower vernier lines were displaced from each other. Specifically, we demonstrated that for a pair of horizontal line segments arranged side-by-side with a large gap between them observers were, on average, somewhat better at discriminating a vertical offset if the right-hand segment was below the left-hand segment than vice versa. We observed a similar kind of asymmetry when observers judged horizontal offset for a pair of vertically oriented line segments, one above the other. In that case, performance was better when the lower segment was to the left of the upper segment than the opposite. Consistent with other studies (Adams et al., 2004; Champion & Adams, 2007) we also showed that perceptual asymmetry reduced more or less with training. This means that the asymmetric phenomena are modifiable through learning. These findings motivated us to carry out the present study with a two-fold purpose: to see (1) whether the within-cardinal configurational asymmetry in line alignment judgment can be generalized to the oblique orientation and (2) whether it can be shaped by learning as in the cardinal orientation. To achieve these purposes, we conducted two experiments using the line vernier stimuli at +45° and -45° orientations respectively.

**Experiment 1**

**Method**

**Observers.** Eight paid undergraduate students of normal, or corrected to normal vision, participated in this experiment. All the observers were naive to the experimental purpose and did not have any history of psychophysiological or neurological illness.

**Stimuli and apparatus.** Vernier stimuli, each comprising of two light bars either aligned or misaligned at a +45° orientation, were generated using Borland C++ Builder 6. The offset sizes of the misaligned verniers were ±30, ±90, ±150, ±210 and ±270 arcsec. One of the bars was displaced to the right (−) or left (+) at right angles to the other, constant, bar. The stimuli were white against a black background, with a feature separation of 15 arcmin (Figure 1). The width and length of each bar were 0.5 and 15 arcmin respectively. The luminance of the stimulus and background were measured by a luminance meter (TOPCON, BM-3). The Michelson contrast of each stimulus was 0.98 (Lmax = 90.43 cd/m²; Lmin = 0.81 cd/m²). For displaying the stimuli we used a 21-inch color monitor (Eizo, FlexScan T962) of 1280×1024 pixels and 85 Hz with a high-speed graphic card (3 Diabs, Wildcat III 6110). From a viewing distance of 1.82 m, the angular resolution of each pixel was 30 arcsec.

**Procedures.** At the beginning, observers took a few practice trials to get some practical knowledge of how to respond with a keyboard. Then they were run in two experimental sessions using the method of constant stimuli. In one session, we presented five possible vernier stimuli of the rightward offset (−) and five aligned (null offset) verniers in random order, each one repeating 80 times, at the centre of the visual field. Similarly, we presented five possible stimuli of the leftward offset (+) and five aligned verniers in another session. The order of the two sessions was counterbalanced between the observers and between the training days for each observer. In each session, the stimulus duration and response stimulus interval were 100 ms and 1000 ms respec-
Observers in a dark room viewed the stimuli binocularly using a chin and forehead rest from the distance mentioned above. Because there was no additional fixation point in order to avoid unwanted positional cues available from that point, we asked observers to always attend to the gap between the vernier features (the centre of the display). They indicated by a key press (F or J) whether the features were aligned or misaligned, where incorrect responses were followed by an auditory feedback. The two response keys were counterbalanced between the observers.

The experiment was continued for six days, each day covering 1600 trials in total (800 in each session). A half of the observers were introduced to the stimuli with the lower-right bar being displaced rightward or leftward (Figure 1a,b) and the remaining half with the upper-left bar being displaced in either direction (Figure 1d,e). From the point of intersection of the polar axes (0, 0), the constant bar was always at the same distance across the left-upper and right-lower visual fields. However, observers were not informed of which bar would be constant and which one be displaced.

Data processing and statistical analysis. In any psychophysical experiment, the first hand data include perceiver sensitivity, but often confounded with normal guessing habit and response bias. The habitual guess or guessing bias and response bias are reflected in observer's false alarm-such as responding to a null-offset vernier as an offset one. So, we calculated in each experimental session the proportion of false alarm and the proportion of correct offset detection at each offset for individual observers. Then, we excluded each observer’s guessing bias and response bias following two crucial steps as below.

First, to exclude potential guessing bias we converted subjective data in each training day using Equation 1.
The corrected number of "Yes" responses to a vernier stimulus, and \( Y_0 \) and \( FA \) represent the observed proportion of "Yes" responses to a vernier stimulus and the proportion of false alarm ("Yes" response to a null-offset) respectively, in an experimental session. Here, "Yes" response indicates responding to any vernier stimulus as offset. This equation converts any false alarm to '0' and 100% correct offset detection to '100'.

Second, if an observer response were biased toward a particular vernier configuration (non-uniform distribution of response biases between the two configurations) the proportion of false alarm would be ultimately higher in that session as compared to the session of an opposite configuration. So, we calculated subjective response biases in each training day using Equation 2.

\[
Y_C = \frac{Y_0 - FA}{1 - FA} \times 100
\]

Where, \( Y_C \) represents the corrected number of "Yes" responses to a vernier stimulus, and \( Y_0 \) and \( FA \) represent the observed proportion of "Yes" responses to a vernier stimulus and the proportion of false alarm ("Yes" response to a null-offset) respectively, in an experimental session. Here, "Yes" response indicates responding to any vernier stimulus as offset. This equation converts any false alarm to '0' and 100% correct offset detection to '100'.

The response bias score could thus range between -100 and +100, with negative and positive values reflecting leftward and rightward biases respectively. A score approaching zero indicates no response bias.

The response bias scores so obtained were analyzed in a series of one sample t-tests. If any observer's response bias toward a particular displacement/configuration were found to be significant, the frequency of biased responses was subtracted on day-by-day basis from the guess-free frequency (see Equation 1) of "Yes" responses to an offset vernier.

After such exclusion of guessing bias and response bias, each observer's data in the rightward and leftward displacements were separately fitted by the probit model (using XLSTAT; Addinosoft USA). According to Yes/No paradigm, offset detection thresholds were calculated at 50% correct detection of the vernier misalignment. In order to minimize the effect of presentation order (of the configuration) on any pair of subjective scores, we averaged the threshold data on every two successive days. Thus in six days of training we obtained three pairs of scores for each observer. We analyzed each observer's threshold data in matched sample t-test and group data in repeated measures ANOVA followed by the post-hoc LSD test where appropriate. If the sphericity assumption was violated for repeated measures data we carried out these ANOVA using the Greenhouse-Geisser (when \( \varepsilon < .75 \)) or Huynh-Feldt (when \( 1 > \varepsilon > .75 \)) correction.

Results

Response bias. Figure 2 shows mean subjective response biases calculated over the training days (left panels) and mean daily response biases for the two observer groups (right panels). When subjected to a series of one-sample t-tests we found that the average response bias scores were significantly different from zero for O2 \((t(5) = -6.217, p = .002)\) and O6 \((t(5) = -2.572, p = .040)\) only. So, before fitting any psychometric functions for determining the offset detection thresholds we excluded, on day-by-day basis, the response biases for these two observers.

As shown in the right panels, the mean response bias scores obtained on every two successive days were not significantly different from zero for the two observer groups who were introduced to the upper-left bar (Figure 2a; \( t(3) = -0.231, p = .832 \) in d1, d2; \( t(3) = -0.511, p = .645 \) in d3, d4 and \( t(3) = .196, p = .857 \) in d5, d6) and lower-right bar (Figure 2b; \( t(3) = -1.197, p = .317 \) in d1, d2; \( t(3) = -1.404, p = .255 \) in d3, d4 and \( t(3) = .015, p = .989 \) in d5, d6) displacements respectively.

Offset direction, spatial configuration and training effects. Figure 3a, b displays the daily offset detection thresholds for individual observers and the corresponding aggregates for the two groups who experienced stimuli with the upper-left and lower-right bar displacements respectively. A series of matched sample t-tests applied to the individual observer data demonstrated that one (O2) of the four observers experiencing the upper-left bar displacement (Figure 3a) had significantly lower thresholds if the offset was rightward rather than leftward \((t(2) = 16.806, p = .004)\). Two of them (O1 and O3) showed a fairly similar trend \((t(2) = 2.848, p = .104 \) for O1; \( t(2) = 4.023, p = .057 \) for O3). One (O6) of the four observers expe-
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Figure 2. Response biases (Mean±CIs) in Experiment 1. (a) Percent biases in the upper-left bar displacement; Left panel—subjective biases of four observers; Right panel—group mean biases on every two successive days of training. (b) Percent biases in the lower-right bar displacement; Left panel—subjective biases of four observers; Right panel—group mean biases on every two successive days of training. The positive (+) and negative (−) values indicate biases to rightward and leftward offsets respectively. Error bars reflect 95% confidence intervals (CIs) of the mean differences.

The positive (+) and negative (−) values indicate biases to rightward and leftward offsets respectively. Error bars reflect 95% confidence intervals (CIs) of the mean differences.

We analyzed the observers’ threshold data in two-way repeated measures ANOVA with offset direction and training as within-subjects factors. The sphericity assumption was violated for training factor and interaction, so the Greenhouse-Geisser correction was applied. It revealed that the main effect of training was significant (Greenhouse-Geisser corrected F(1.285, 8.996)=8.578, ε=0.643, p=.013). But the mean effect of offset direction (F(1, 7)=5.14, p=.013) and the effect of interaction between offset
Figure 3. Observer performances by offset direction, configuration, and training in Experiment 1. (a) Four observers' individual thresholds averaged on every two successive days and their aggregate in the upper-left bar displacement. (b) Other four observers' individual thresholds averaged on every two successive days and their aggregate in the lower-right bar displacement. (c) Offset direction-wise mean thresholds for all observers on every two successive days irrespective of which bar was displaced. (d) Configuration-wise mean thresholds for all observers on every two successive days irrespective of which bar was displaced. Error bars reflect standard errors (SEs) of the means.
direction and training were not significant (Greenhouse-Geisser corrected $F(1.462, 10.232)=.693, \epsilon = .731, p=.478$). We also analyzed the data by the same statistical procedures considering configuration and training as within-subjects factors. We found that the main effect of configuration was fairly large ($F(1, 7)=4.324, p=.076$) and that of training was significant (Greenhouse-Geisser corrected $F(1.285, 8.996)=8.578, \epsilon = .643, p=.013$). But the effect of interaction between the two factors was not significant (Huynh-Feldt corrected $F(1.940, 13.583)=.864, \epsilon = .784, p=.440$). A further analysis of the training effect done by the post hoc LSD test revealed that the threshold was, fairly lower on the 3rd and 4th day ($M=187.890, SE=4.867, p=.066$) than on the 1st and 2nd day ($M=202.139, SE=8.608$), the effect being significant on the 5th and 6th day of training ($M=177.721, SE=6.493, p=.012$).

Finally, we examined the configurational differences in both pre- and post-training. We considered the first two days' training as pre-training and the last two days' training as post-training. The pre-training mean difference between the two configurations was about 15 arcsec ($SE=8.67$) and the post-training difference was about 21 arcsec ($SE=9.26$) (Figure 3d). Matched sample $t$-test revealed that the pre-training mean difference was fairly large ($t(7)=1.726, p=.128$) and the post-training difference was nearly significant ($t(7)=2.244, p=.060$). The post-training higher mean difference was unexpected, however, it was not significantly different from the pre-training mean difference ($t(7)=1.157, p = .285$).

### Experiment 2

#### Method

**Observers.** Twelve naive and paid adults of normal, or corrected to normal vision, participated in this experiment.

**Stimuli and apparatus.** We used line vernier stimuli, either aligned or misaligned, at $-45^\circ$ orientation (Figure not shown). The offset sizes, stimulus contrast, feature separation, feature width and length were all identical to the first experiment.

**Procedures.** Following the setup and procedures identical to the first experiment, this experiment was run for twelve days.

#### Data processing and statistical analysis.** The data were fitted by the probit model after excluding subjective guess and response bias where necessary following the same procedures as in Experiment 1. Then, offset detection thresholds were calculated at 50% correct detection of the vernier misalignment. In order to reduce the effect of presentation order (of the configuration) on any pair of subjective scores, the threshold data were averaged on every two successive days. Thus in twelve days of training six pairs of scores were obtained for each observer. Then, inferential analyses of the data were done following the same statistical tools as in Experiment 1. One of the observers (O9) showing higher false alarm than correct detection even at larger offsets (i.e., response by guessing) was considered unreliable and hence excluded from the analysis.

### Results

**Response bias.** Figure 4 shows mean subjective response biases calculated over the training days (left panels) and mean response biases for the two observer groups on every two successive days (right panels). When subjected to a series of one sample $t$-test we found that the average bias scores were significantly different from zero for O1 ($t(11)=-2.710, p=.020$), O2 ($t(11)=-3.395, p=.006$) and O10 ($t(11)=2.877, p=.015$) only. So, before fitting any psychometric functions for calculating the offset detection thresholds we excluded, on day-by-day basis, the response biases for these three observers.

As shown in the right panels, the response bias scores obtained on every two successive days were not significantly different from zero for the two observer groups who were introduced to the upper-right bar (Figure 4a; $t(5)=-1.358, p=.232$ in d1.d2; $t(5)=-.326, p=.758$ in d3.d4; $t(5)=-.599, p=.575$ in d5.d6; $t(5)=-1.640, p=.162$ in d7.d8; $t(5)=-.489, p = .645$ in d9.d10 and $t(5)=-1.301, p=.250$ in d11.d12) and lower-left bar (Figure 4b; $t(4)=.660, p=.546$ in d1.d2; $t(4)=.324, p=.762$ in d3.d4; $t(4)=.336, p=.754$ in d5.d6; $t(4)=2.643, p=.057$ in d7.d8; $t(4)=1.379, p = .240$ in d9.d10 and $t(4)=-.665, p=.543$ in d11.d12)
Figure 4. Response biases (Mean±CIs) in Experiment 2. (a) Percent biases in the upper-right bar displacement; Left panel—subjective biases of six observers; Right panel—group mean biases on every two successive days of training. (b) Percent biases in the lower-left bar displacement; Left panel—subjective biases of other five observers; Right panel—group mean biases on every two successive days of training. The positive (+) and negative (−) values indicate biases to rightward and leftward offsets respectively. Error bars reflect 95% confidence intervals (CIs) of the mean differences.

Displacements respectively. The right panels also indicate that the distribution of mean response bias scores across the training days (whatever the degree) was constantly leftward when the upper-right bar was displaced (Figure 4a) and almost rightward when the lower-left bar was displaced (Figure 4b). These refer to the response biases toward an identical vernier configuration which did not reduce with training.

Offset direction, spatial configuration and training effects. Figure 5a, b displays the daily offset detection thresholds for individual observers and the corresponding aggregates for the two groups who experienced stimuli with the upper-right and lower-left bar displacements respectively. A series of matched sample t-tests applied to the individual observer data demonstrated that three (O1, O2 and O5) of the six observers experiencing the upper-right bar displacement (Figure 5a) had significantly lower thresholds if the offset was rightward rather than leftward (t(5) = 5.832, p = .002 for O1; t(5) = 6.051, p = .002 for O2 and t(5) = 9.210, p < .001 for O5). One (O10) of the six observers experiencing the lower-left bar displacement (Figure 5b) had significantly lower thresholds if the offset was leftward rather than rightward (t(5) = −6.925, p = .001). Though other observers of the two groups did not show any significant difference a few of them showed a differential trend to some degree (e.g., O3, O4 and O11). The line graphs of the aggregated data for the two groups show that aver-
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Figure 5. Observer performances by offset direction, configuration, and training in Experiment 2. (a) Six observers' individual thresholds averaged on every two successive days and their aggregate in the upper-right bar displacement. (b) Other five observers' individual thresholds averaged on every two successive days and their aggregate in the lower-left bar displacement. (c) Offset direction-wise mean thresholds for all observers on every two successive days irrespective of which bar was displaced. (d) Configuration-wise mean thresholds for all observers on every two successive days irrespective of which bar was displaced. Error bars reflect standard errors (SEs) of the means.
Average thresholds were lower when the upper-right bar was displaced to right (Figure 5a; right most last panel) and the lower-left bar was displaced to left as compared to the opposite displacements (Figure 5b; right most last panel). This asymmetry was significant in the upper right bar displacement ($F(1,5)=10.902, p=.021$) and non-significant in the lower left bar displacement $F(1,4)=1.912, p=.239$ scenarios. However, the trends were configurationally identical irrespective of which bar was displaced. This led us to plot the grand averages by configuration (Figure 5d) in addition with plotting by offset direction (Figure 5c), taking training as a common factor.

As in Experiment 1, we analyzed the observers’ threshold data in two-way repeated measures ANOVA which revealed that the main effect of offset direction was non-significant ($F(1,10)=.611, p=.453$). However, the main effects of both configuration and training were significant ($F(1,10)=10.595, p=.009$ for configuration, Greenhouse-Geisser corrected $F(2.628, 26.278)=21.862, \epsilon=.526, p<.001$ for training). The effect of their interaction was non-significant (Greenhouse-Geisser corrected $F(2.740, 27.402)=1.881, \epsilon=.548, p=.160$). A further analysis of the training effect done by the post hoc LSD test revealed that the 5th and 6th days’ mean threshold ($M=166.999, SE=8.102$) was significantly lower than the 1st and 2nd days’ mean threshold ($M=202.065, SE=7.295, p<.001$). This improvement was maintained, on average, at the 7th and 8th ($M=157.974, SE=8.512, p<.001$), 9th and 10th ($M=155.247, SE=8.590, p<.001$) and 11th and 12th ($M=151.246, SE=7.425, p<.001$) days’ follow-ups.

Finally, we examined the configurational differences in both pre- and post-training. We considered the first two days’ training as pre-training and the last two days’ training as post-training. The pre-training average threshold difference between the two configurations was about 36 arcsec, the difference being reduced to 22 arcsec in the post-training (Figure 5d). Matched sample t-testrevealed that both these mean differences were statistically significant ($t(10)=4.309, p=.002$ for pre-training, ($t(10)=2.393, p=.038$ for post-training).

![Figure 6. Schematic of the vernier configurations in comparison. (a) 0°, 90°, +45° and -45° oriented configurations in which average performance was better. (b) 0°, 90°, +45° and -45° oriented configurations in which average performance was worse (Source of 0° and 90° oriented configurations: Karim & Kojima, 2010).](image)

**General Discussion**

In this study, experiments at the oblique orientation showed that there might be significant or nearly significant effect of spatial configuration, but no effect of offset direction on average vernier acuity. Specifically, Experiment 1 demonstrated that for a pair of bars arranged side-by-side with a large gap between them at +45° orientation, observers were somewhat better at discriminating an offset if the relative position of the upper left-hand bar was to the right of the lower right-hand bar than vice versa, regardless of which bar they experienced as displaced. That is, vernier acuity was better when the Upper Left bar was to the Right of the Lower Right bar (ULR-LRL configuration) than when the Upper Left bar was to the Left of the Lower Right bar (ULL-LRR configuration) (Figure 3d). Similarly, Experiment 2 which was conducted at -45° orientation revealed that performance was significantly better when the Upper Right bar was to the Right of the Lower Left bar (URR-LLL configuration) than when the Upper Right bar was to the Left of the Lower Left bar (URL-LLR configuration) (Figure 5d). The results are in consistent with what we demonstrated in a previous study at cardinal orientations (Karim & Kojima, 2010). A rotation of the vernier configurations (Figure 6) 45° clockwise indicates that configuration LU-RD (a, horizontal) corresponds to config-

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urations ULR-LRL (a, +45°), UR-LL (a, vertical), and URR-LLL (a, -45°) directly in mental representation. Similarly, configuration LD-RU (b, horizontal) represents configurations ULL-LRR (b, +45°), ULLR (b, vertical), and URL-LLL (b, -45°). Thus there is no difference between the cardinal and oblique trends of the configurational asymmetry.

Possible mechanisms of the asymmetry. As we have excluded observers’ guessing bias and response bias prior to fitting psychometric functions and calculating thresholds, the asymmetry can be explained by neither of these variables. The contribution of eye movement is also unlikely as the stimulus duration was very brief (100 ms). Nevertheless, if there had been any eye movements it might not have any role in vernier acuities (Kessy, 1960), because vernier lines have internal orientation information and may, therefore, be less susceptible to orientational or angular noise created by head tilt or eye torsion (Waugh & Levi, 1993). So, the present results definitely refer to perceptual bias or preference.

As vernier acuity is accomplished by the activity in orientation tuned neural channels (Campbell & Kulikowski, 1966; Phillips & Wilson, 1984), such perceptual bias might originate from neural selectivity for a specific orientation created by the feature offset or for a specific vernier frame created by the luminance edges and other surrounding spatial cues. Visual response properties are thought to develop in two distinct phases: an experience independent phase in which the basic neural circuits become established and organized into cortical maps, and a subsequent phase of plasticity in which initial circuits are elaborated and refined by experience (Cairn, Gillespie, & Stryker, 1998; Hubel & Wiesel, 1963; Katz & Crowley, 2002; Sengpiel & Kind, 2002). However, it is not clear in the present study whether the reported perceptual bias/preference can be attributed to the first candidate because until today we do not know any inborn corresponding asymmetry of neural organizations in the visual cortex. The second candidate instead explains the asymmetry better because most aspects of spatial vision (e.g., vernier acuity, grating acuity) are quite immature in the human neonate (Skoczenski & Norcia, 1999) and neural organization of the human visual system may be influenced by early visual experience (Freeman, Mitchell, & Millodot, 1972; Freeman & Thibos, 1973; Mitchell, Freeman, Millodot, & Haegerstrom, 1973).

In our study, when a roughly 50% of the observers showed more or less better performances in a particular vernier configuration, 10% of them (05 in Exp.1 and 08 in Exp.2) showed fairly an opposite trend and the remaining 40% did not show any asymmetry at all (Figure 3a,b; Figure 5a, b). This might be because the experiential worlds which play a critical role in visual development (Chapman, Gödecke, & Bonhoeffer, 1999; Coppola & White, 2004) are not necessarily equal for all.

The above statistics also remind us of an incidence of handedness. Annett (1967) reported that the proportions of left-handers, mixed-handers and right-handers are approximately 2–5%, 25.1–37%, and 58.4–71.5%. As is often argued on the causality of handedness, some kind of genetic factors, environmental/developmental factors such as language laterality, as well as cultural factors such as the prejudice against left-handed, might be related to perceptual asymmetry. However, because the present study lacks in handedness data it is difficult to answer whether the asymmetric vernier performance can be associated with handedness or cerebral lateralization. The existing literature in visual psychophysics or visual neurology also cannot explain the phenomenon directly. Nonetheless, we can get important clues of the underlying reason from some related studies (Freimuth & Wapner, 1979; Levy, 1976; Mead & McLaughlin, 1992). These studies have shown importance of handedness in other visuospatial tasks, with considerable performance variation being found between dextrals and sinistrals. Specifically, in a study of aesthetic judgment of pictures Levy (1976) found that asymmetric pictures judged to have centers of interest to the right of the center were preferred over their enantiomorphs (mirror-reversed pictures), the effect being true for dextrals, but not for sinistrals. Levy (1976) explained her findings by the hemispheric activation model which suggests that differential activation of a hemisphere produced an attentional orientation bias to the con-
trilateral visual field (cf. Kinsbourne, 1974). Assuming that the right hemisphere is more activated than the left hemisphere when a dextral is engaged in visuospatial task, she argued that such an attentional bias to the left visual field would make a symmetrical picture look unbalanced. If, on the other hand, a picture were asymmetric in the direction opposite to the attentional bias, the net perceptual result would be a state of balance and the aesthetic response would be positive. Pictures that have areas of greater interest or weight in their right halves are then preferred because their asymmetries counteract the asymmetry produced by the attentional bias to the left visual field. Freimuth and Wapner (1979), on the other hand, reported that dextral subjects preferred paintings with left-to-right directional properties. According to them, directional cues that suggest a left-to-right sequence may draw attention to the rightward portions of the picture, but unlike Levy’s view such an attentional draw need not necessarily create the perceptual balance. Freimuth and Wapner’s model can explain the results of the present study better than does the model of Levy. In our study, we have shown that a large part of the observers performed better in the rightward asymmetry (offset) of the vernier stimuli at both $+45^\circ$ and $-45^\circ$ orientations. In addition, a small part of the observers showed an opposite trend. This led us to assume that for a visuospatial stimulus suggesting directional cues, visual attention probably becomes clockwise (left-to-right directional) biased in the dextrals and anticlockwise (right-to-left directional) biased in the sinistral. In line with this hypothesis, McLaughlin, Dean, and Stanley (1983) reported that dextral subjects preferred asymmetric paintings that contained a rightward position of the area of major interest and that sinistral behaved in an exactly opposite fashion. Similarly, Mead, and McLaughlin (1992) demonstrated that paintings containing left-to-right directional cues were preferred by both dextrals and inverted sinistral. However, the phenomenon is still unclear and needs further investigation to generalize to other visuospatial stimuli as such as vernier stimuli.

Possible mechanisms of the orientation-invariance. By definition, the line vernier features represent categorical (e.g., above/below, left/right), not coordinate (exact distances) spatial relation (cf. Kosslyn, 1987). The categorical spatial relations afford invariant abstract spatial relations useful for viewpoint independent object recognition and prototypical spatial location coding (Bullens & Postma, 2008; Jager & Postma, 2003; Kosslyn, 1987). This invariance is possibly achieved at some stage(s) of higher level of cortical processing. Early cortical neurons having small receptive fields show selectivity for specific stimulus orientation and motion direction (Hubel & Wiesel, 1968) and for specific spatial and temporal frequency of luminance gratings (DeValois, Albrecht, & Thorell, 1982; Foster, Gaska, Nagler, & Pollen, 1985; Holub & Morton-Gibson, 1981). Higher cortical neurons, in contrast, have large receptive fields and respond preferentially to particular shapes, textures or patterns of complex objects (e.g., David, Hayden, & Gallant, 2006; Hegdé & Essen, 2000; Kobatake & Tanaka, 1994; Logothetis, Pauls, & Poggio, 1995; Merigan & Pham, 1998; Pasupathy & Connor, 2001; Sheinberg & Logothetis, 2001; Tamura & Tanaka, 2001). In addition, unlike early visual (lower level) processing which is orientation-specific in favor of the cardinal (e.g., Campbell et al., 1966; Furmanski & Engel, 2000; Saarinen & Levi, 1995b; Skrandies et al., 2001; Westheimer & Beard, 1998), late (higher level) processing is normally orientation-invariant (e.g., Biederman & Cooper, 1991; Biederman & Gerhardstein, 1993; McMullen & Farah, 1991; Murray, Jolicoeur, McMullen, & Ingleton, 1993; Takano, 1989; Tarr & Pinker, 1990). These differential response properties of lower and higher level cortical neurons led us to assume two possibilities for the orientation-invariant configurational preference in our study. One possibility is that the preference might occur primarily at early stages of processing the spatial frame structured by the luminance edges of the vernier bars and other surrounding spatial connections. Once the preference is thus gained for a specific configuration the signal is then dispatched to subsequent higher stage(s) where it is controlled by orientation-invariant mechanism. Alternatively, the preference might be directly mediated by configuration-
selective higher order processing which is orientation-invariant. The higher cortical neurons respond not only to complex objects, but also to simple stimuli such as edges and bars (Cadieu, Kouh, Pasupathy, Connor, Riesenhuber, & Poggio, 2007; Desimone & Schein, 1987; Desimone, Albright, Gross, & Bruce, 1984; Pollen, Przybyszewski, Rubin, & Foote, 2002) as in our study. The role of higher cortex to achieve vernier acuity has also been suggested in previous studies (c.f., Beard, Levi, & Klein, 1997; Saarinen & Levi, 1995a,b; Sterken, Toet, & Yap, 1994) claiming that the neurons on higher levels of processing may use complex features to discriminate vernier offsets (Fahle, 2004). Thus, a higher order mechanism is suggested to operate either directly or indirectly to achieve configuration preference invariantly at different orientations.

Learning vernier acuity and configurational asymmetry. Training improved vernier performance significantly, but inter-individual differences were striking in our study. In the first experiment, for example, O2, O3 and O5 showed remarkable fall of vernier thresholds in the course of training whereas O1 and O7 did not show any improvement (Figure 3a,b). The large individual variations were also observed with extended period of training (Figure 5a,b; Exp.2). This is in agreement with the previous similar kind of studies (Fahle & Edelman, 1993; Karim & Kojima, 2010; McKee & Westheimer, 1978; Saarinen & Levi, 1995a). For instance, McKee and Westheimer (1978) reported that after 2000–2500 trials, the range of the individual decrease in vernier thresholds was from 2% to 70%. An important aspect of the present findings is that average vernier acuity improved with training, but configurational differences persisted from the beginning to the end of training course in both the experiments (Figure 3d; Figure 5d). In addition, we unexpectedly found a little higher post-training mean difference than the pre-training mean difference in Exp.1 (not in Exp.2). These demonstrations make an important difference from our previous study in which the mean asymmetry markedly decreased with at least extended period of training (Karim & Kojima, 2010). This implies that the asymmetry in oblique orientation is less sensitive to training than the asymmetry in cardinal orientation. It can be interpreted by the same mechanism of the oblique effect (Furmanski & Engel, 2000). That is, a much lower percentage of V1 neurons are tuned to oblique than to cardinal orientation (Coppola, White, Fitzpatrick, & Purves, 1998; DeValois, Yund, & Hepler, 1982; Furmanski & Engel, 2000; Li, Peterson, & Freeman, 2003). In addition, neurons with oblique preferences exhibit wider orientation tuning widths than neurons with cardinal preferences (Kennedy & Orban, 1979; Nelson, Kato, & Bishop, 1977; Orban & Kennedy, 1981; Rose & Blakemore, 1974). Thus, the asymmetry might reduce with training at a slower rate in the oblique than in the cardinal orientation.

In brief, consistent with our previous study in cardinal orientation (Karim & Kojima, 2008, 2010) the present study demonstrated configuration-specific response property in oblique orientation. However, unlike the previous study we did not find here any diminishing trend of the average asymmetry with training, indicating a cardinal versus oblique orientation difference in response to training. Though we do not know clearly about the origin of the asymmetric response, the results advance our understanding that the relationship between vernier elements even of simple configuration might be crucial for visual spatial judgment.

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