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The oblique effect depends on perceived, rather than physical, orientation and direction

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Abstract

Observers can better discriminate orientation or direction near the cardinal axes than near an oblique axis. We investigated whether this well-known oblique effect is determined by the physical or the perceived axis of the stimuli. Using the simultaneous tilt illusion, we generated perceptually different orientations for the same inner (target) grating by contrasting it with differently oriented outer gratings. Subjects compared the target orientation with a set of reference orientations. If orientation discriminability was determined by the physical orientations, the psychometric curves for the same target grating would be identical. Instead, all subjects produced steeper curves when perceiving target gratings near vertically as opposed to more obliquely. This result of orientation discrimination was confirmed by using adaptation-generated tilt aftereffect to manipulate the perceived orientation of a given physical orientation. Moreover, we obtained the same result in direction discrimination by using motion repulsion to alter the perceived direction of a given physical direction. We conclude that when the perceived orientation or direction differs from the physical orientation or direction, the oblique effect depends on perceived, rather than physical, orientation or direction. Finally, as a by-product of the study, we found that, around the vertical direction, motion repulsion is much stronger when the inducing direction is more clockwise to the test direction than when it is more counterclockwise.

Keywords: Orientation discrimination; Direction discrimination; Simultaneous tilt illusion; Tilt aftereffect; Motion repulsion

1. Introduction

The oblique effect refers to the well-established fact that our discriminability of orientation or direction is significantly better around the cardinal (horizontal or vertical) axes compared to an oblique axis (Appelle, 1972; Howard, 1982). A question for understanding this phenomenon is exactly how the cardinal axes are defined. This question has been addressed in a major class of psychophysical experiments that employ whole-body tilt of observers. The goal of these experiments was to determine whether the cardinal axes are defined by the gravitational field or by the retina/body orientation. The rational is straightforward: if observers' best performances are found around the gravitationally (or retinally) defined horizontal and vertical axes, then the oblique effect must follow the gravitational (or retinal) coordinates. The results, however, are mixed, with some studies favoring the gravitational coordinates (Buchanan-Smith & Heeley, 1993) while others favor the retinal coordinates (Chen & Levi, 1996; Saarinen & Levi, 1995). It has been suggested that the discrepancy may result from the differences in detailed experimental conditions such as the presence/absence of visual references,

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the control (or the lack of it) for the eye counter-torsion caused by the body tilt, the lengths of oriented stimuli, and the psychophysical tasks (Chen & Levi, 1996; Howard, 1982).

Recently, Luyat and Gentaz (2002) revisited the coordinate-frame question for the oblique effect. Unlike the earlier experiments that focused on gravitationally or retinally defined vertical or horizontal axes, these investigators first measured observers' *subjective* gravitational vertical, which could be different from both the gravitational vertical and retinal vertical under the whole-body tilt condition. They then found that observers' performances on an orientation task were significantly better around the subjective vertical than around 45° away. They thus conclude that the cardinal axes of the oblique effect follow neither retinal nor gravitational frame, but the subjective gravitational frame.

In this study, we addressed a different but closely related question about the oblique effect, namely whether the effect is determined by the perceived or physical orientation/direction of the stimuli in the absence of whole-body rotation. We altered the perceived vertical axis through three visual manipulations: simultaneous tilt illusion (STI), tilt aftereffect (TAE), and motion repulsion (MR). STI and TAE are orientation illusions. In STI, an oriented stimulus is surrounded by a differently oriented stimulus (Gibson & Radner, 1937). The perceived orientation of each stimulus shifts away from the orientation of the other. Similarly, TAE is the observation that after adaptation to a given orientation, the perceived orientation of a subsequently presented stimulus shifts away from the adapted orientation (Gibson & Radner, 1937). MR is a related illusion in motion perception: when two sets of nearby or overlapping dots move in different directions, each set appears to move in a direction further away from the other direction (Hiris & Blake, 1996; Marshak & Sekuler, 1979). Using these illusions, we generated two different perceived orientations (or directions) from the same physical orientation (or direction), with one perceived orientation (or direction) near vertical while the other more oblique. We found that the orientation (or direction) discrimination was always better when the stimuli were perceived more vertically than more obliquely. Preliminary results have been reported in abstract form (Meng & Qian, 2003).

2. Experiment 1

In this experiment, we used simultaneous tilt illusion (STI) to investigate whether the oblique effect is determined by the physical or the perceived orientation of the stimuli.

2.1. Methods

2.1.1. Observers

The observers included the first author (X.M.) and three individuals (L.D., Z.M., and H.T.) who were naïve about the purpose of the study. All had normal or corrected-to-normal vision. The experiments were undertaken with the written consent of each observer.

2.1.2. Apparatus and stimuli

The experiment was conducted on a 21 in. ViewSonic P225f monitor controlled by a Macintosh G4 computer. The vertical refresh rate was 120 Hz and the spatial resolution was 1024 by 768 pixels. In a well-lit room, observers viewed the monitor through a black circular viewing tube from a distance of 76 cm, using a chin rest to stabilize head position. The viewing tube had an inner diameter of 10 cm and extended from the observers' eyes to the computer screen, thereby preventing observers from using external references to determine the orientation of the stimuli.

The screen had a constant veiling luminance of 37.6 cd/m^2. The stimuli were made of square-wave gratings with a fundamental frequency of 0.5 cycle/deg. The luminance of the gratings was 0.27 and 82.7 cd/m^2 for the black and white stripes, respectively. The Michelson contrast was 99.3%. Each trial consisted of a test stimulus, a reference stimulus, and a noise mask. A test stimulus was made of an inner (target) grating of 5° in diameter and an outer (inducing) grating with a diameter of 8°. The orientation of the inner grating (target orientation) was either 85° or 95°. For each inner grating, the outer grating was oriented 12° away, either in the clockwise or counterclockwise direction, to generate a nearly vertical or a more oblique perceived orientation for the same physical target orientation. (These orientation values were determined in pilot studies, and worked well for all observers in this experiment.) There were thus a total of four different test stimuli (Figs. 1A and B). For each physical target orientation of the test stimuli, we generated a set of nine reference stimuli, which contained the inner grating only and whose orientations were 0°, ±2°, ±4°, ±6° or ±8° away from the physical target orientation. For all stimuli, a random phase was assigned to each grating. The noise mask consisted of six fields of random pixels. The luminance of each pixel was drawn from a uniform distribution between 0.27 and 82.7 cd/m^2.

The stimuli were generated in advance by our anti-aliasing program in Matlab, using Psychophysics Toolbox extensions generously provided by Brainard and Pelli (Brainard, 1997; Pelli, 1997).

2.1.3. Procedure

Subjects initiated each trial by pressing any of the two mouse buttons. Each trial consisted of a test and a

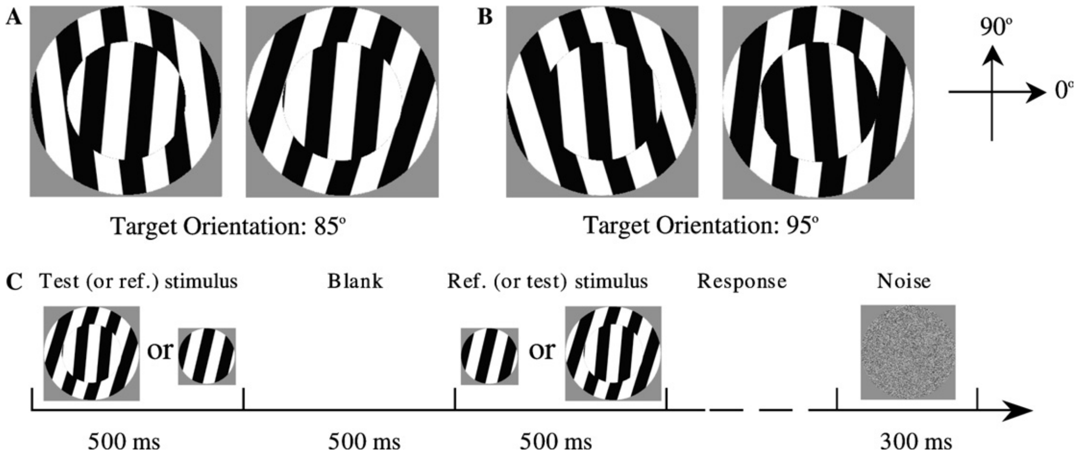

Fig. 1. Stimuli and procedure for Experiment 1. (A and B) The test stimuli (not the actual size) used in Experiment 1. The orientation of the inner target grating was either 85° (A) or 95° (B). The 90° orientation is vertical. The outer grating was oriented 12° counterclockwise or clockwise to the inner grating. (C) The time course of one trial.

reference stimulus in random order, each lasting 500 ms, with an inter-stimulus interval of 500 ms (Fig. 1C). Subjects were required to report, by pressing the left or right button, whether the orientation of the second stimulus was clockwise or counterclockwise from that of the first stimulus. They were instructed to use the inner (target) orientation of the test stimuli to perform this discrimination task. After the response, six noise patterns, each lasting 50 ms, were presented for a total of 300 ms to mask the retinal afterimages of the stimuli before the next trial. No fixation point was shown during the experiment. There were 24 trials for each combination of the reference and test stimuli, resulting in a total of $24 \times 9 \times 4 = 864$ trials. During the experiment, the 432 trials for each of the two physical target orientations were randomly interleaved, and were divided into eight blocks, with a break of at least 10 s between every two blocks. The trials were self-paced and observers were encouraged to take breaks between trials if desired.

For each observer, the proportion of 'clockwise' responses for the test stimulus under each condition was plotted as a function of the reference orientation, and fitted with the logistic function ($f(x) = \frac{1}{1+\mathrm{e}^{-k(x-x_0)}}$).

2.2. Results

The psychometric curves for comparing the inner (target) orientations of the test stimuli (Fig. 1A and B) with a set of reference orientations are shown in Figs. 2, for four observers. The results for the two test patterns in Fig. 1A (target orientation 85°) and for the two test patterns in Fig. 1B (target orientation 95°) are shown in the top and bottom rows of Fig. 2, respectively. The two curves in each panel are for the target grating of the same physical orientation, but different perceived orientations due to the different surrounds and STI. The perceived orientations correspond to the 50% points (given by the x_0 parameters of the fitted logistic functions) of the curves; these points shift away from the physical orientation in opposite directions for the two curves in each panel as expected from the different surround orientations. The average magnitude of STI is around 2°, comparable with those measured by others (Smith, Clifford, & Wenderoth, 2001; Wenderoth & Johnstone, 1988). The slope at the 50% point provides a measure of orientation discriminability, and is equal to a quarter of the k parameter of the fitted logistic function. If the orientation discriminability was determined by the physical target orientation, the slopes of the two curves in each panel would be identical. Instead, across all panels, the slopes were steeper when the targets were perceived closer to the vertical (solid curves) than when they were perceived more obliquely on either side of the vertical (dashed curves). After removing consistent individual differences (Loftus & Masson, 1994), the slopes of the fitted logistic functions for all the observers were tested by a one-way ANOVA for each physical target orientation. The difference between the solid and dashed curves is statistically significant ($p = 0.01$, $F = 11.7$ for the target orientation of 85°; $p = 0.03$, $F = 8.5$ for the target orientation of 95°). These results indicate that the oblique effect depends on the perceived, rather than physical, orientation.

In this experiment, the observers were instructed to use the inner target orientations of the test stimuli to perform the discrimination task. One could argue that observers might accidentally use the outer grating orientations of the test patterns in a small number of trials, and the difference between the two curves in each panel might be explained by the different outer grating orientations. This alternative explanation can be readily ruled out. For example, for the target orientation of 85° (the top row of Fig. 2), the solid and dashed curves correspond to an outer grating orientation of 73° and 97°,

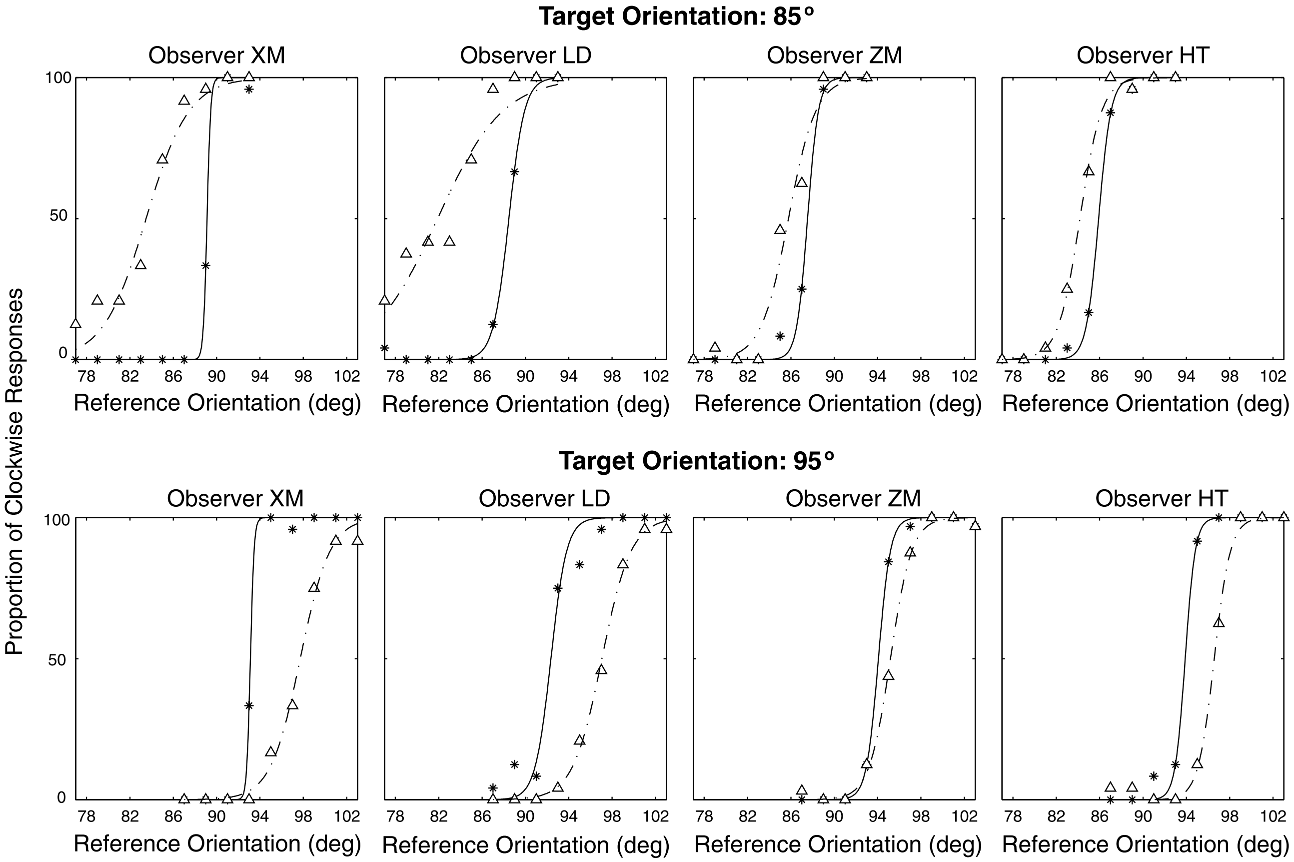

Fig. 2. Psychometric curves from Experiment 1 showing the proportion of trials where the (target) orientation of the test stimuli appeared more clockwise than the orientation of reference stimuli. The physical target orientation of the test stimuli is 85° for the top row and 95° for the bottom row. The two curves in each panel are for the target grating of the physical orientation, but different perceived orientations, with the solid curve (*) representing near vertical perception and the dashed curve (△) representing more oblique perception. Each point reflects 24 trials. The nine points of each are fitted by a logistic function.

respectively. If observers used the outer grating for discrimination, the 50% points of the two curves would have the opposite order of what was observed. Moreover, the dashed curves would be steeper than the solid curves because 97° is closer to vertical than 73°, again the opposite of what was observed. A similar argument applies to the case of 95° target orientation (the bottom row of Fig. 2).

3. Experiment 2

To further rule out the possibility that the results in Experiment 1 were due to the observers' occasional use of the outer gratings of the test patterns, we employed the tilt aftereffect (TAE) to manipulate the perceived orientation in the second experiment.

3.1. Methods

3.1.1. Observers

The first author (X.M.) and three naïve subjects (Y.C., C.Q., and L.D.) served as observers in this experiment. All had normal or corrected-to-normal vision and provided written consent.

3.1.2. Apparatus and stimuli

The apparatus was identical to that for Experiment 1. All stimuli were square-wave gratings with the same parameters as in experiment 1 but without any outer gratings. Each trial consisted of an adapting, a test and a reference grating in this order. As in Experiment 1, the orientation of the test grating (target orientation) was either 85° or 95°. For each test grating, the adapting grating was oriented 12° away, either in the clockwise or counterclockwise direction, to generate different perceived orientations for the same physical target orientation. The set of reference gratings differed from each physical target orientation by 0°, ±2°, ±4°, ±6° or ±8°.

3.1.3. Procedure

The strategy was to first create different perceived orientations for the same physical target orientation (of a given test stimulus) via adaptation-induced TAE, and then measure a psychometric curve under each perceptual condition by comparing the test and reference stimuli.

For each of the four combinations of the adapting and target orientations, 24 trials were run at each of the nine reference orientations, resulting in 216 trials. (There were a total of $216 \times 4 = 864$ trials as in Experiment 1.) During the experiment, these 216 trials were randomly divided into four 54-trial blocks. The eight blocks for each physical target orientation but different adapting orientations were randomly interleaved, with at least a 5 min break between every two blocks. Each block started with a 2 min initial adaptation, and followed by 54 trials (Fig. 3). Each trial started with a 500 ms re-exposure to the adapting grating to keep the TAE at full strength. It was then followed by a 500 ms blank, a 100 ms test grating, another 500 ms blank, and finally a 500 ms reference grating. The observers were required to report whether the orientation of the reference grating was clockwise or counterclockwise from the test grating by pressing the left or right button of the mouse, respectively. The response of the observer then started the 500 ms re-adaptation period of the next trial. As in Experiment 1, for each observer, the proportion of 'clockwise' responses for the test grating under each condition as a function of the reference orientation was fitted with the logistic function. No fixation point was shown during the experiment.

Previous studies indicate that a longer duration of the test stimuli reduces the TAE (Harris & Calvert, 1989; Wolfe, 1984). That was why we chose a short duration of 100 ms in this experiment. The reference grating must also subject to TAE. We chose a 500 ms blank period and a relatively long duration (500 ms) for the reference grating to reduce its TAE. However, the TAE of the reference grating was probably not eliminated, and any residual TAE on the reference gratings must reduce the difference between the two perceived target orientations for the same physical orientation. Fortunately, the effect we found was still highly significant (see below).

3.2. Results

The psychometric curves for comparing the test and reference orientations are shown in Fig. 4 for four observers. The presentation format is identical to that of Fig. 2 for Experiment 1. The average magnitude of TAE is around 1.8°, comparable with those measured by others (Greenlee & Magnussen, 1987; Wolfe, 1984). It should be clear from the figure that for the same physical target orientations of the test gratings, all observers showed steeper curves when the test gratings were perceived near vertically (solid curves) than when they were perceived more obliquely (dashed curves). After removing consistent individual differences (Loftus & Masson, 1994), the slopes of the fitted logistic functions for all the observers were tested by a one-way ANOVA for each physical target orientation. The differences in slopes between the solid and dashed curves are statistically significant ($p = 0.05$, $F = 6.0$ for the target orientation of 85°; $p = 0.01$, $F = 12.6$ for the target orientation of 95°). These results confirm the conclusion in Experiment 1 that the oblique effect is determined by the perceived, rather than physical, orientation.

4. Experiment 3

In Experiments 1 and 2, the psychometric curves were obtained from comparing the target orientations with a set of reference stimuli. The slope of each psychometric curve at the 50% point was taken as the measure of orientation discriminability. Due to the illusions (STI, or TAE) used to generate the two different perceptions for the same physical target, the 50% points (the points of subjective equivalence) for the two perceptual conditions were necessarily different. This means that the reference stimuli around the 50% points for the two perceptual conditions were also necessarily different. For example, although the two curves in each panel of Fig. 2 were obtained with the same physical target orientation and the same set of reference orientations, the 50% points of the two curves corresponded to different reference orientations. Since the reference orientations around the 50% point for the solid curve in each panel are closer to vertical than that for the dashed curve, this difference in reference orientations per se might account for the different slopes of the two curves. To rule out this possibility, we performed another control experiment for Experiment 1. Specifically, we used reference stimuli with surround just like the test stimuli in Figs. 1A and B to equate the 50% points of the two different perceptual conditions for the same physical target orientation.

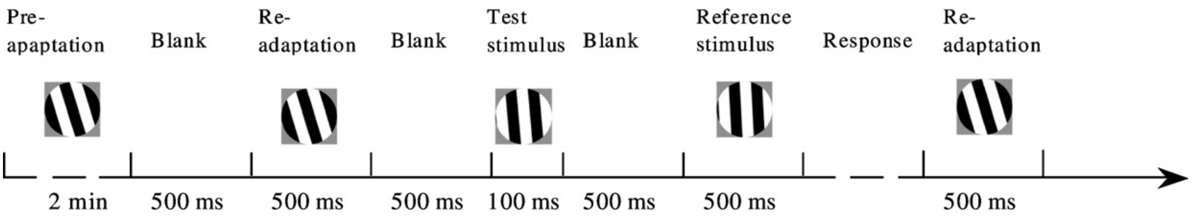

Fig. 3. Time course of Experiment 2.

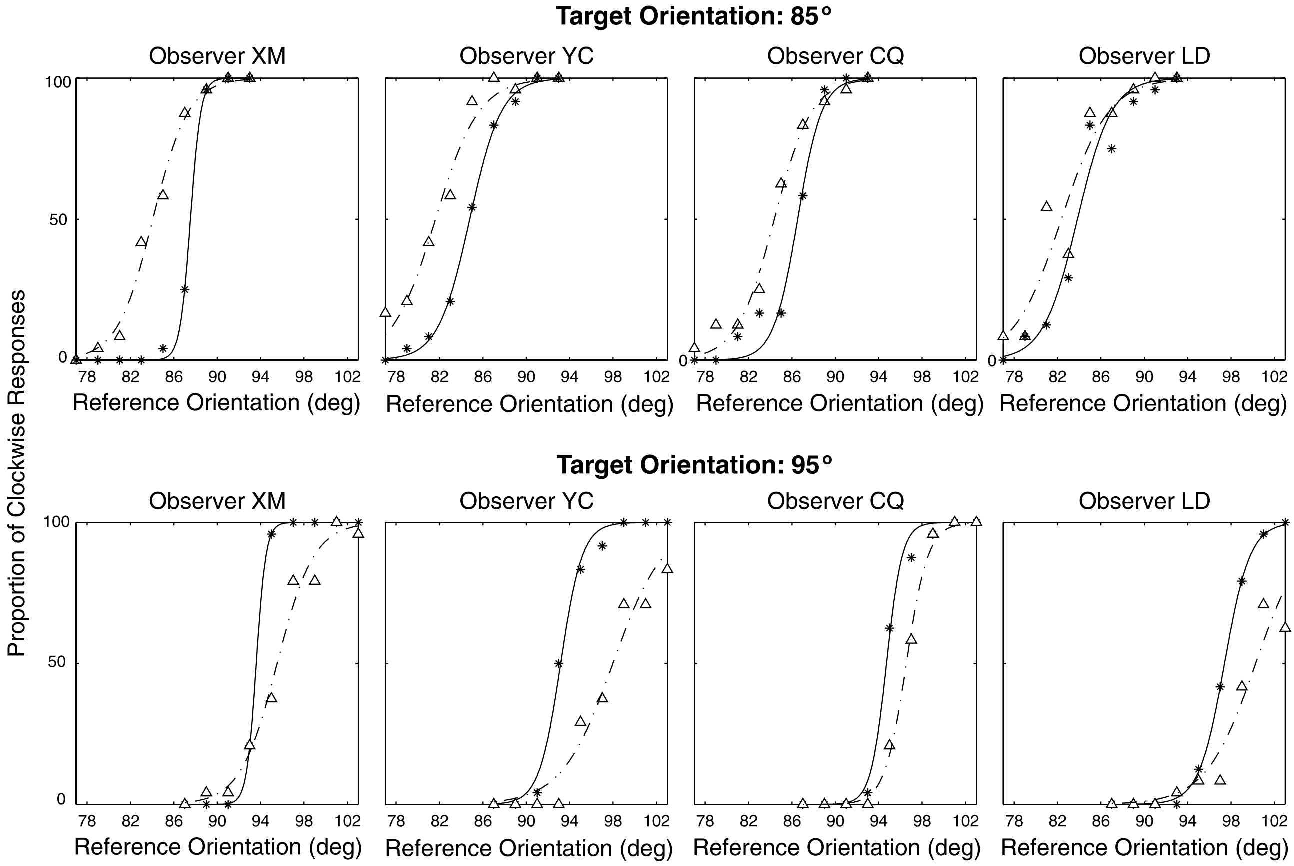

Fig. 4. Psychometric curves showing the proportion of clockwise responses in Experiment 2. The format is identical to that of Fig. 2.

4.1. Methods

4.1.1. Observers

The first author (X.M.) and three naïve observers (C.Q., Y.Y., and M.X.) served as observers in this experiment. All had normal or corrected-to-normal vision, and provided written consent.

4.1.2. Apparatus and stimuli

The apparatus was identical to that for Experiment 1. The test stimuli were identical to those in Figs. 1A and B for Experiment 1. Unlike Experiment 1, however, each reference stimulus had both an inner grating and an outer grating just like the test stimuli, and the angular difference (both the magnitude and the sign) between the inner and outer orientations was identical to that for the test stimulus in the same trial. The inner orientations of the reference stimuli for each test stimulus covered the same range as the reference stimuli in Experiment 1. One of the reference stimuli was identical to the test stimulus, while the other eight reference stimuli were the rotated versions of the test stimulus. As in Experiment 1, each physical target orientation of the test stimuli had two perceived orientations, one close to vertical and another more oblique, due to STI. However, since the reference stimuli here had the same configuration as the corresponding test stimulus, STI was also present in the reference stimuli. Therefore, the 50% points of the two different perceptual conditions for the same physical target orientation should be the same. Then, any difference in slopes at the 50% points must be due to the different perception even though the perceptual differences are not reflected in the 50% points in this experiment.

4.1.3. Procedure

The procedure was identical to Experiment 1 except that a central fixation point was shown between trials, but not during a trial. The fixation point disappeared when observers clicked the mouse to start a trial and reappeared after the response. We did not use a fixation point in the first two experiments because it does not affect the illusions (e.g., STI has similar magnitudes with (Smith et al., 2001) or without (Wenderoth & Johnstone, 1988) the fixation point), and we did not want to introduce an extra visual reference into the discrimination task. In this experiment, since both the test and the reference stimuli contained two orientations, we used the central fixation to remind observers that the inner orientations of the stimuli should be used in the discrimination task. Since the fixation point was not shown during the stimulus presentation, it should not affect the discrimination process.

4.2. Results

The psychometric curves for comparing the inner orientations of the test and reference stimuli are shown in Fig. 5 for four observers. The presentation format is identical to that of Fig. 2 for Experiment 1. Again, the two curves in each panel correspond to the two different perceptual conditions for the same physical target orientation. However, unlike Fig. 2, the 50% points of the two curves are similarly located. This is expected since in this experiment, the reference stimuli had the same type of surround as the corresponding test stimulus (see Section 4.1). Although the 50% points do not reflect the perceptual difference between the two curves, we use the inferred perceptual difference from Experiment 1. Just like Fig. 2 for Experiment 1, Fig. 5 shows clearly that for the same physical target orientations of the test gratings, all observers showed steeper curves when the target gratings were perceived near vertically (solid curves) than when they were perceived more obliquely (dashed curves). After removing consistent individual differences (Loftus & Masson, 1994), the slope of the fitted logistic function for all the observers was tested by a one-way ANOVA for each physical target orientation. The differences in the slopes are statistically significant ($p = 0.001$, $F = 35.1$ for the target orientation of 85°; $p = 0.02$, $F = 9.8$ for the target orientation of 95°). In this experiment, the slope difference at the 50% points of the two curves in each panel must be due to perceptual difference only because the physical target orientation and the physical reference orientations for the two conditions were identical or nearly so. Together with Experiments 1 and 2, the results confirm the conclusion that the oblique effect is determined by the perceived, rather than physical, orientation.

5. Experiment 4

Experiments 1 to 3 were concerned with the oblique effect in the orientation domain. In this experiment, we extend our above results to motion direction discrimination using motion repulsion (MR) to manipulate the perceived direction.

5.1. Methods

5.1.1. Observers

The first author (X.M.) and two naïve observers (Y.C. and Z.M.) served as observers in this experiment.

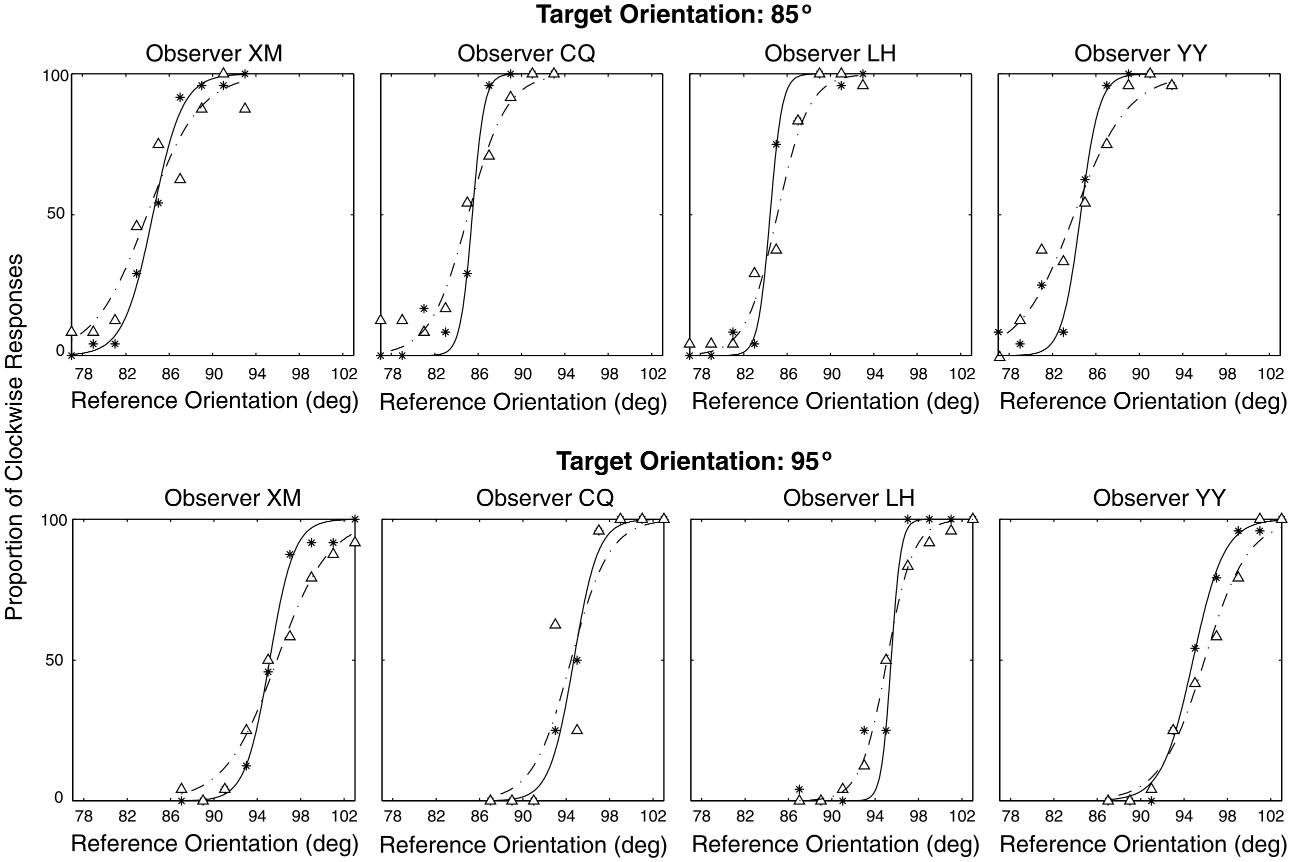

Fig. 5. Psychometric curves showing the proportion of clockwise responses in Experiment 3. Here, the 50% points of the solid and dashed curves in each panel were made approximately equal. The format is identical to that of Fig. 2.

All had normal or corrected-to-normal vision, and provided written consent.

5.1.2. Apparatus and stimuli

The apparatus was identical to that for Experiment 1. The stimuli were random dot kinematograms (RDKs). Each stimulus contained 100 dots within a virtual circular aperture of 4° in diameter; half of dots were red while the other half were blue. The dot density was thus 7.96 dots/deg^2. Each dot was a 2-pixel × 2-pixel square (approximately 3.6 arc min on each side). All dots moved at 4 deg/s, a speed within the range for optimal direction discrimination (De Bruyn & Orban, 1988). The red and blue dots moved in different directions. The red-dot direction (target direction) was determined via a staircase procedure before the main experiment (see below), while the blue-dot direction (inducing direction) was 25° away, either clockwise or counterclockwise to the target direction. Therefore, the blue dots generated two different perceived directions for the each physical red-dot (target) direction via MR. We used 25° as the angle between the two directions because according to previous studies, the magnitude of repulsion was largest when the angle was between 20° and 40° (Hiris & Blake, 1996; Marshak & Sekuler, 1979). The reference RDKs were similar to the test RDKs, except that only the red dots were moving and the blue dots were all stationary. The directions of the red dots in the reference RDKs differed from that of the corresponding perceived target direction for each subject (measured via a staircase procedure, see below) by 0°, ±4°, ±8°, or ±12°. Here, the reference directions were chosen relative to the perceived, instead of physical, target direction because the MR strength is highly variable among different subjects. No fixation point was shown in this experiment.

5.1.3. Procedure

Since direction discriminability is poorer than orientation discriminability (De Bruyn & Orban, 1988; Gros, Blake, & Hiris, 1998; Heeley & Timney, 1988), it may be more difficult to see a slope difference between the two perceptual conditions generated by MR. In addition, our experience suggests that compared with STI and TAE, the magnitudes of MR are more variable among different observers. It is thus important to make sure that for each physical target direction, one of the two perceived directions generated by MR was close to vertical. We applied a double randomly interleaved staircases procedure (Levitt, 1971; Wetherill & Levitt, 1965) to each observer to estimate the two physical directions, one on each side of the vertical (90°), that led to a perceived vertical direction when an appropriate inducing direction 25 ° further away was added.

We first estimated, for each subject, the physical target direction less than 90° that was perceived as vertical when the inducing direction was 25° more clockwise. Subjects pressed any button on a mouse to start a trial. On each trial, observers viewed, in random order, a test and a reference RDK, each lasting 1 s, with a 1 s interstimulus interval between them. Using the red-dot directions of the stimuli, the subject reported whether the direction of the second RDK was clockwise or counterclockwise from that of the first RDK. The direction of the reference RDK was always 90°. If the target direction of the test RDK was judged more clockwise (or counterclockwise) than the reference direction, both the target and inducing directions of the test RDK were adjusted counterclockwise (or clockwise) by the same amount. In one staircase, the target direction started at 30° clockwise to 90°, while in the other, it started at 10° clockwise to 90°. The trials from the two staircases were randomly interleaved. Each staircase followed a 1-up 1-down schedule. For each staircase, the step size was a random number between 0° and 3° at the beginning, and after 2 reversals, the step size was reduced to a random number between 0° and 1°. After the two staircases crossed, we ran another 27 reversals per staircase before termination. The final 50 reversals (25 from each staircase) were averaged to obtain the estimation of the physical direction that would appear vertical in the presence of the 25° more clockwise inducing direction. This physical direction was used as a target direction in the main experiment for the same subject. We also determined the perceived direction of the same physical target direction when the inducing direction was 25° more *counterclockwise* using a similar staircase procedure. In the main experiment, the reference directions were 0°, ±4°, ±8°, or ±12° away from each perceived target direction.

We then similarly determined the physical target direction *greater* than 90° that appeared vertical when the inducing direction was 25° more counterclockwise. In addition, we determined the perceived direction of the same physical target direction when the inducing direction was 25° more clockwise.

In the main experiment, psychometric functions for discriminating the target directions of the test stimuli and the reference directions were measured by a constant stimuli procedure similar to that for Experiment 1. Observers were instructed to use the red-dot directions to perform the task. Each trial contained a test and a reference RDK in random order. The target direction was set to each of the two values measured in the above staircase procedure for each observer. The test and reference RDKs each lasted for 1 s, separated by a 1 s inter-stimulus interval. There were 24 trials for each of the 7 reference RDKs and each of the 4 combinations of the target and inducing directions, with a total of 672 trials. During the experiment, the 336 trials for each physical target direction were randomly interleaved. At the end of a trial, observers were required to report whether the red-dot direction of the second RDK was clockwise or counterclockwise to that of the first RDK by pressing the left or right button of the mouse, respectively. The proportion of 'clockwise' responses as a function of the reference direction was fitted by the logistic function as before.

5.2. Results

The psychometric curves for comparing the target directions of the test stimuli and the reference directions are shown in Fig. 6 for three observers. The presentation format is again identical to that of Fig. 2 for Experiment 1. The physical target directions used, as determined by the staircase method for each observer, were 75.3°, 79.5°, and 77.4° for the top panels, and 95.0°, 93.6°, and 90.5° for the bottom panels, respectively. The average MR magnitude was 7.5° from the 12 staircase measurements, and was 7.3° from the 12 psychometric curves in Fig. 6. These values are larger than the STI and TAE magnitudes for orientation in the first two experiments but consistent with the previous work from our laboratory (Chen, Matthews, & Qian, 2001) and the report of Rauber and Treue (1999) with similar procedures. As in the orientation case, all observers showed steeper curves when the target directions were perceived near vertically (solid curves) than when they were perceived more obliquely (dashed curves). After removing consistent individual differences (Loftus & Masson, 1994), the slope parameters of the fitted logistic function for all the observers were tested by a one-way ANOVA for each row. The differences in slopes between the solid and dashed curves are statistically significant ($p = 0.007$, $F = 26.5$ for the target directions less than 90°; $p = 0.004$, $F = 35.4$ for the target directions larger than 90°).

This experiment also revealed an unexpected asymmetry of MR. Recall that for each observer, we used two different physical target directions, one on each side of vertical. For each physical target direction, MR was generated with the inducing direction either 25° more clockwise to the target (clockwise MR) or 25° more counterclockwise to the target (counterclockwise MR). We found that for a given physical target direction, the clockwise MR was always much larger than the counterclockwise MR, regardless of whether MR was measured with the staircase method in the pilot study or with the constant stimuli method in the

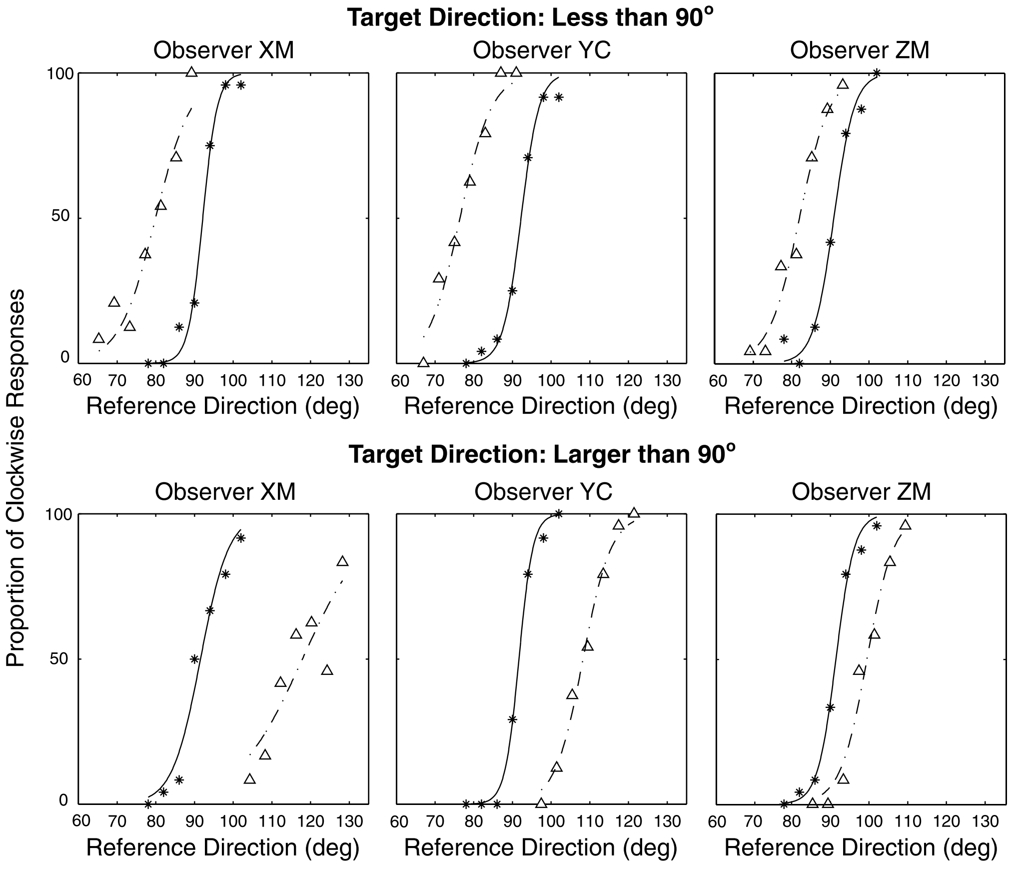

Fig. 6. Psychometric curves showing the proportion of clockwise responses in Experiment 4. The physical target directions were 75.3°, 79.5°, and 77.4° for the top panels, and 95.0°, 93.6°, and 90.5° for the bottom panels, respectively, measured by a staircase method for each observer. The format is identical to that of Fig. 2.

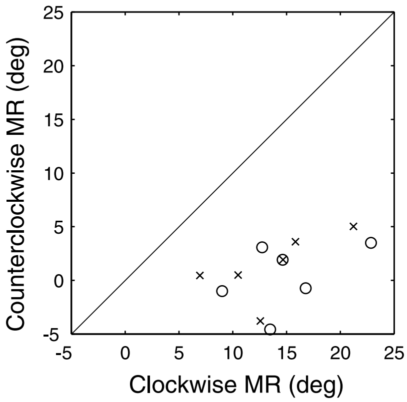

Fig. 7. Comparison of the clockwise MR and the counterclockwise MR measured in Experiment 4. Each point represents the clockwise MR and the counterclockwise MR for the same physical target direction. The points from on the staircase method are shown as (x), while those from the constant stimuli method are shown as (○).

main experiment. This is shown in Fig. 7, where the clockwise MR and counterclockwise MR for the same physical target direction are plotted against each other. All 12 data points (6 from the staircase method and 6 from the constant stimuli method) are well below the diagonal line. The mean clockwise MR and counterclockwise MR were 14.3° and 0.8°, respectively, and the difference is highly significant ($p = 2 \times 10^{-8}$, $F = 72.4$). This strong asymmetry is unrelated to the perceived direction. When we only consider the cases where the perceived target direction was always vertical, the mean clockwise MR and counterclockwise MR were 13.9° and 2.2°, respectively, again a highly significant difference ($p = 0.0009$, $F = 21.7$).

6. Discussion

In this study, we performed a set of experiments to test the hypothesis that the oblique effect is determined by the perceived, rather than physical, orientation or direction. In Experiment 1, we generated two different perceived orientations from the same physical target orientation by contrasting the inner target with different surround orientations (STI). We found that the orientation discrimination was significantly better when the target was perceived near vertically than when it was perceived more obliquely. In Experiment 2, we demonstrated the same result using orientation adaptation to generate two different perceived orientations for the same physical target orientation (TAE). Experiment 2 also served as a control for Experiment 1: one could argue that the surround orientation in Experiment 1 not only affects the perceived orientation of the target but also influences the orientation discrimination task directly. This problem was avoided in Experiment 2 as there was no surround orientation and a single test orientation was compared with a single reference orientation during the discrimination task. Experiment 3 served as a further control for Experiment 1. In Experiment 1, even though the physical target orientation and the set of reference orientations for comparison were identical between the two different perceptual conditions (the two curves in each panel of Fig. 2), the reference orientations at the 50% points where the discriminability (slope) was measured were not the same. This problem was eliminated in Experiment 3 where we used reference stimuli with the same surround as the test stimuli to equate the 50% points for the different perceptual conditions.[1] Finally, Experiment 4 was a similar experiment in the domain of direction discrimination. We used MR to generate different perceived directions from the same physical target direction and again found that the oblique effect follows the perceived, instead of physical, direction. The last experiment also generated an interesting side observation: around the vertical direction, MR was much stronger when the inducing direction is more clockwise to the test direction than when it is more counterclockwise.

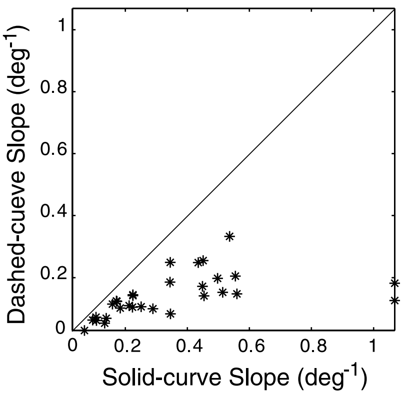

Fig. 8. Summary of orientation or direction discriminability (measured by the slopes at the 50% points) from the four experiments. The horizontal axis represents the slopes when perceived orientations or directions were near vertical, while the vertical axis represents the slopes when perception was more oblique. The slopes were obtained from the fitted curves in Figs. 2, 4, 5, and 6.

To summarize all data across the four experiments, we plot in Fig. 8 the slope (at the 50% point) of the dashed curve against that of the solid curve for each panel of Figs. 2, 4, 5, and 6. Recall that the solid and dashed curves in these figures are for the near-vertical and more-oblique perceptual conditions, respectively, corresponding to the same physical target orientation or direction. Fig. 8 shows that every point falls below the diagonal line, indicating that in all cases, the slope

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[1] Note, however, that Experiment 3 cannot replace Experiment 1. The reason is that Experiment 3 was designed to keep together the 50% points for the two different perceptual conditions, and thus could not show directly that the perceived target orientations were different under the two conditions.

was greater when the same physical orientation or direction was perceived near vertically than more obliquely.

Our conclusion that the oblique effect is determined by the perceived, not physical, orientation or direction is consistent with the study of Luyat and Gentaz (2002) who found that the oblique effect follows subjective gravitational frame. It is also consistent with a study by Li and Westheimer (1997). These investigators used two oblique lines to form a cross pattern with an overall orientation (called the implicit orientation in their paper) equal to the mean of the two line orientations. They found that the oblique effect of the whole cross pattern depends on its implicit orientation instead of the physical orientations of its two component lines. Since the implicit orientation is likely the perceived orientation of the whole pattern, their results can be interpreted as that the oblique effect is determined by the perceived orientation. Our experiments provide a more direct demonstration of the same conclusion by generating two different perceived orientations from the same physical orientation.

The underlying physiological mechanism for the oblique effect is still not clear. Some studies found the origin in the biases of the primary visual cortex. For example, more V1 neurons were found tuned to horizontal and vertical than to oblique orientations (Chapman & Bonhoeffer, 1998; Coppola, White, Fitzpatrick, & Purves, 1998; Li, Peterson, & Freeman, 2003; Mansfield, 1974; Yu & Shou, 2000). It was also found that stimuli around the cardinal axes evoke larger cortical potentials (Bonds, 1982; Campbell & Maffei, 1970; Mansfield & Ronner, 1978) or generate narrower tuning curves (Li et al., 2003; Nelson, Kato, & Bishop, 1977; Rose & Blakemore, 1974). However, other studies failed to find significant orientation anisotropy in the number of neurons or in the width of tuning curves (Finlay, Schiller, & Volman, 1976; Wilson & Sherman, 1976). In addition, whether a given reported anisotropy contributes to the oblique effect depends on the specific model and the psychophysical task. For example, if one believes that orientation discrimination depends on the cells' differential responses to the two orientations being compared, then the discriminability should be mostly determined by the cells with the largest slopes of tuning at the stimulus orientations, and a larger number of cells tuned to the cardinal axes will not help to enhance the discrimination at the cardinal axes (Regan & Beverley, 1985; Teich & Qian, 2003). On the other hand, if the task is to detect the presence of a low-contrast orientation, a larger number of cells tuned to the cardinal axes will likely enhance the detection at the cardinal axes (Teich & Qian, 2003).

Psychophysical results on the oblique effect, particularly those with whole-body tilt paradigm, have often been discussed in the context of whether the phenomenon occurs in an early visual cortical area such as V1 or a later area where vestibular information is combined with the visual inputs. Our results suggest the oblique effect must occur at or after the stage that encodes the perceived, rather than the physical, orientation and direction. Whether this implies an involvement of an early or late visual cortical area depends on whether V1 encodes physical or perceived orientation or direction. The physiological evidence is mixed. On the one hand, the long-range horizontal connections among V1 cells tuned to similar orientations can explain many perceptual interactions between a stimulus and the surrounding context (Gilbert, 1998). In particular, a V1 network model has been proposed to explain the tilt illusion used in this study (Sakai, 2003). On the other hand, V1 appears to be a primitive stage of processing for many visual attributes including direction of motion, and responses in higher visual cortical areas are often found to better correlate with the perception (Movshon, Adelson, Gizzi, & Newsome, 1986; Qian & Andersen, 1994). A related point is that although extraretinal information such as gaze angle and vergence state (Trotter & Celebrini, 1999; Trotter, Celebrini, Stricanne, Thorpe, & Imbert, 1992) modulates V1 activities, we are not aware of any reports on vestibular inputs to V1; this suggests that the gravitational influence reported by some of the whole-body tilt studies can only be explained at the level of parietal cortex where vestibular signals are found (Andersen, Shenoy, Snyder, Bradley, & Crowell, 1999). Further investigations are obviously required to clarify the role of V1 in the oblique effect.

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