

A bias-free measure of the tilt illusion

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The perceived orientation of a central test grating is influenced by the orientation structure of the surrounding image. Measurement of this “tilt illusion” traditionally requires subjects to report the orientation of the test relative to a cardinal reference (e.g., clockwise or anticlockwise of vertical). Given that the test is presented within a surround that is itself oriented clockwise or anticlockwise from vertical, there is obvious potential for the orientation of the surround to bias the subject’s response irrespective of any perceptual effects. To avoid this bias, we ran a two temporal interval forced-choice experiment. The two intervals contained opposite surround orientations ($\pm 15^\circ$), and we manipulated the orientation of the center gratings. Participants were asked to judge which of the test gratings was closer to vertical. We found no significant difference between measurements of the tilt illusion using the traditional and two-interval procedures. We then examined interindividual differences in a larger sample and found a significant correlation between the magnitudes of the tilt illusion measured using the two procedures. Our experiments demonstrate a method free from response bias in measuring the tilt illusion although our results indicate that response biases were unlikely to factor significantly in prior tilt illusion experiments.

Introduction

Our visual perception is constantly mediated by contextual effects; the environment immediately surrounding an object is known to influence perception of its features, such as its lightness, color (Chevreul, 1839/1855), and contrast (Chubb, Sperling, & Solomon, 1989; Singer & D’Zmura, 1994). A prominent example of such contextual influence in spatial vision is the tilt illusion (Figure 1) (Gibson, 1937). Here, the perceived orientation of a center grating is shifted away from that of its surround (repulsive effect) when the difference between them is small (e.g., 10° – 20°) or shifted toward

the orientation of the surround (attractive effect) when the difference is large (e.g., 70° – 80°) (Gibson, 1937; Over, Broerse, & Crassini, 1972; Westheimer, 1990). The illusion is well established and has been studied extensively, leading to some progress in the understanding of its underlying mechanisms (for reviews, see Clifford, 2014; Schwartz, Hsu, & Dayan, 2007; Wenderoth & Johnstone, 1987).

However, the majority of findings use a paradigm that has the possibility of observers responding in a biased manner (García-Pérez & Alcalá-Quintana, 2013; M. Morgan, Dillenburger, Raphael, & Solomon, 2012), potentially influencing quantitative measurements of the tilt illusion. As shown in Figure 2A, traditionally, participants are shown a single interval of center and surround gratings and are asked to decide whether the center stimulus is tilted to the left or right of vertical (e.g., Over et al., 1972; Westheimer, 1990). Because the surround itself is oriented clockwise or anticlockwise from vertical, there is clear potential for the surround orientation to bias the participant’s response criterion independent of any genuine perceptual effect. For example, if an observer, when uncertain, tended to select the direction opposite to the current surround, then the measured tilt illusion would be artificially inflated. This standard paradigm is therefore limited in that it has no way of dissociating between perceptual and response biases and does not allow for an accurate measurement of the tilt illusion.

This shortcoming is highly relevant for application of the tilt illusion to clinical populations. Indeed, patients with schizophrenia have been observed to have abnormally low contextual effects in comparison to the general population (Dakin, Carlin, & Hemsley, 2005) and have shown dysfunctions of low-level visual processing (e.g., Chen et al., 2003; Must, Janka, Benedek, & Kéri, 2004). Additionally, fMRI reports in patients’ primary visual cortex have shown weak modulation to an orientation-specific contextual effect (Seymour et al., 2013). It appears that the functioning

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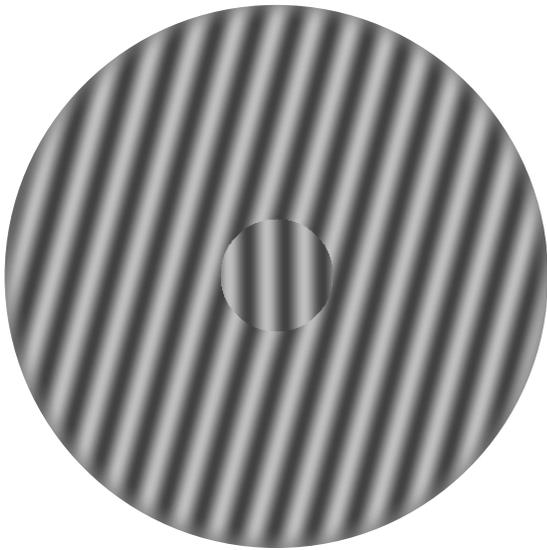


Figure 1. An example of the tilt illusion. A center grating oriented vertically is surrounded by an oriented surround ($+15^\circ$), causing a repulsion in the perceived orientation of the center grating, now appearing to be tilted left of vertical.

of basic visual processes may be systematically different in some clinical populations to that in healthy controls. However, the potential to use the tilt illusion as part of a battery of tests to identify patients with, for example, schizophrenia (Carter & Barch, 2007; Gold et al., 2012) requires accurate measurement of the perceptual effect that is not strongly influenced by response biases.

The extent to which response bias may be affecting tilt illusion measurements has not yet been ascertained. The illusion itself is readily apparent and can be observed through simple inspection (e.g., Figure 1), so we are not suggesting that the tilt illusion as a whole could be explained simply through response biases. However, it is of concern that measurements of the illusion might not accurately reflect the true perceptual effect in isolation. For example, suppressing the surround grating from conscious perception through backward masking has been shown to reduce (but not abolish) the measured effect during the repulsive tilt illusion (Clifford & Harris, 2005). This and other demonstrations (Mareschal & Clifford, 2012; Motoyoshi & Hayakawa, 2010; Pearson & Clifford, 2005; Tomassini & Solomon, 2014) show that the repulsive

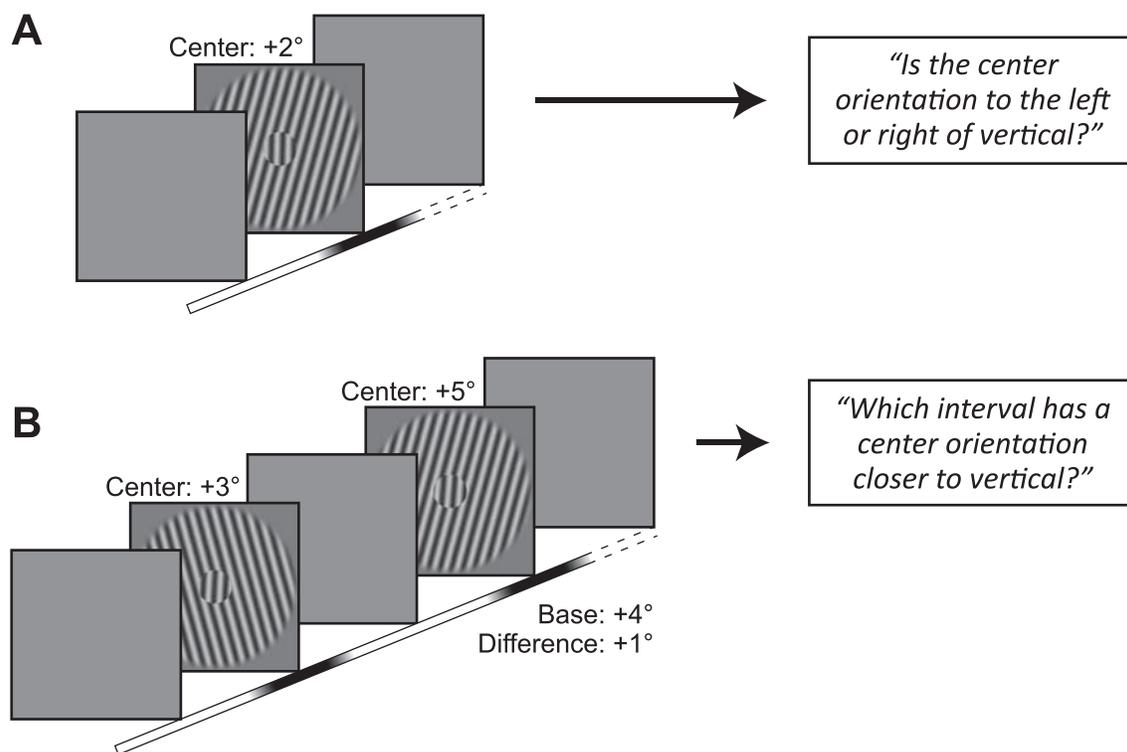


Figure 2. Task procedure for traditional one-interval and unbiased two-interval tasks. (A) The design of a traditional tilt illusion experiment and equivalently the one-interval task used in Experiments 2 and 3. The surround orientation was held constant, and we manipulated the center orientation in each trial with respect to vertical. (B) The two-interval task performed in all of our experiments (Experiments 1, 2, and 3). The surround orientations were always $\pm 15^\circ$, and the center orientations were manipulated relative to a specific base orientation. For both tasks, participants were given the instructions (right) before the experiment commenced. The grayscale lines underneath stimulus images indicate the temporal window used for stimulus presentations: Each stimulus was presented at maximum contrast for 200 ms and faded on/off with a cosine ramp over 100 ms each with 500 ms separation between intervals. Participants were given unlimited time to respond.

tilt illusion persists in the absence of higher-level processes that are suppressed alongside awareness of the surround orientation. Indeed, one could think of using the tilt illusion with a backward masked surround as a measure of the tilt illusion unaffected by response bias. However, it is not clear whether the observed reduction in the magnitude of the tilt illusion under backward masking is due to removal of a response bias or to the mask reducing the efficacy of the surround. Similar caveats apply to the use of adaptation (Motoyoshi & Hayakawa, 2010; Tomassini & Solomon, 2014) or binocular rivalry suppression (Pearson & Clifford, 2005; Rao, 1977; Wade, 1980) to render the surround invisible.

An alternative approach to removing response bias is to present two intervals containing tilt illusion stimuli with opposite surrounds in each and ask participants to judge which interval contains a center orientation closer to vertical (e.g., Figure 2B). Here, both surrounds are presented in each trial, and the response is no longer which side of vertical the stimulus is on. With this design, the center orientations could both be presented on the same side of vertical (either to the left or to the right), or alternatively, they might be placed on opposite sides of vertical, and responding consistently to a particular surround (i.e., in a biased manner) would not affect the measured value of the tilt illusion.

This methodology is similar in concept to the bias-free paradigm proposed by Morgan (2014) to measure positional aftereffects. In this study, participants underwent adaptation to two pairs of drifting Gabor patches, and in a subsequent presentation of stationary Gabors, the position of one of the Gabors was shifted. The aftereffect caused the perceived location of each Gabor to shift, and participants were asked to judge which pair of Gabors had the greater misalignment. Because adaptation affected both stimulus pairs and participants were unaware of in which direction the Gabor would shift, response bias was removed, and the effect of adaptation could be successfully measured. In our experiment, participants were simply presented with two test stimuli (in the presence of oppositely oriented surrounds) and asked to report which test appears more vertical. Our method also shares similarities with that of Jogan and Stocker (2014), who required subjects to report which of two reference stimuli was more similar to a simultaneously presented test. We, however, employed two sequential test stimuli and a single implicit reference (subjective vertical).

In three experiments, we first implemented this procedure to obtain an accurate measure of the tilt illusion, free from response biases. We then contrasted results from our bias-free measure to that of single-interval tasks and quantified the involvement of response bias in the traditional method. Finally, we examined interindividual differences using a larger

sample to scrutinize any systematic changes in measurements of the tilt illusion between one- and two-interval tasks.

Experiment 1: Two-interval tilt illusion experiment

We sought to find evidence for the tilt illusion using an unbiased design and measure its corresponding magnitude. To this end, we dissociated the surround orientation from varying systematically with task demands using a two-interval, two-alternative, forced-choice design.

Participants

Four experienced psychophysical observers (one female) with a mean age of 34.8 (range 28–47) participated in this experiment, consisting of the two authors as well as two naïve to the purpose of the experiment. All participants had normal or corrected-to-normal vision. These experiments were granted ethics approval by the local ethics review committee, and all participants gave written informed consent.

Apparatus

Stimulus gratings were generated using Matlab (Mathworks, Natick, MA) and Psychtoolbox (Brainard, 1997; Pelli, 1997) software and driven by a Bits# stimulus processor (Cambridge Research Systems, Rochester, Kent, UK), which provides 14-bit grayscale resolution. Stimuli were presented on a gamma-corrected 18-in. ViewSonic Graphics Series G90f CRT monitor (resolution, 1280×1024) operating at 75 Hz with a background luminance of 50 cd/m^2 . Participants completed the experiment in a dark cubicle and used a chin rest to maintain a viewing distance of 57 cm. A circular black cardboard annulus (radius, 11–29 cm) was placed over the monitor frame to provide a circular viewing aperture and remove any external cues to vertical. Participant responses were collected using a regular computer keyboard.

Stimuli

Stimuli consisted of two concentric sinusoidal gratings displayed simultaneously with the same mean luminance as the mid-gray background. The center stimulus had a spatial frequency of 1 cycle° and a

diameter of 3° . The surround grating (also 1 cycle/ $^\circ$) was presented in an annulus with inner and outer diameters of 3° and 15° , respectively, and given an orientation of $\pm 15^\circ$ (with respect to vertical; positive values indicate clockwise direction). We selected these orientations to maximize the magnitude of the repulsion effect (O’Toole & Wenderoth, 1977; Over et al., 1972; Wenderoth & Johnstone, 1988). The outer edge of the surround was softened using a 1° cosine window, and both gratings were given unique, randomized phases in each trial.

Stimuli were displayed using a temporal window in which the stimulus was shown at maximum (50%) contrast for 200 ms, and cosine ramping on and off both took an additional 100 ms. At all other times, the stimulus was removed, and only a blank gray screen was visible. Trials were untimed with the next trial commencing 500 ms after participants gave their response, and there was also a 500-ms delay between stimulus intervals.

Procedure

Participants were shown two sequentially presented stimuli (Figure 2B) and asked to judge which temporal interval had a center orientation that was closest to their perceived vertical. In all cases, one interval contained a left surround (-15°), and the other interval contained a right surround ($+15^\circ$). Across trials, we manipulated the orientation difference between the two center gratings in an effort to find the angular difference necessary for both intervals to appear equally close to vertical (biased by the presence of the surround grating). This difference was not necessarily centered on vertical, but from a predetermined orientation located at either 0° , $\pm 2^\circ$, or $\pm 4^\circ$ from vertical. This is referred to as the “base orientation” and was the mean of the two center orientations; differences in each stimulus pair were in equal and opposite directions from this value. We used several possible base orientations to ensure that our results did not depend on the use of a specific reference orientation (e.g., that the task was centered on the participant’s subjective vertical) and could be replicated at multiple magnitudes and on both sides of the participant’s subjective vertical.

In each trial, we manipulated the “orientation difference,” which determines the angle each center orientation is rotated from the base orientation. Specifically, the stimulus with the left surround has a center grating (θ_L) defined as

$$\theta_L = B - D \quad (1)$$

where B is the base orientation, and D is the orientation difference between each center grating and the base

orientation. Similarly, the stimulus with the right surround has a center grating (θ_R) defined as

$$\theta_R = B + D. \quad (2)$$

Using the method of constant stimuli, we manipulated orientation differences by 0° , $\pm 1^\circ$, $\pm 2^\circ$, $\pm 3^\circ$, $\pm 5^\circ$, or $\pm 7^\circ$. As illustrated in Figure 3A, a *positive* orientation difference shifts the center grating away from the base orientation toward the direction of the surround. In contrast, a *negative* orientation difference shifts the center orientation away from that of the surround, and an orientation difference of zero indicates that the center gratings were both located at the base orientation with only the surround orientation (and therefore the direction of the tilt illusion) changed between the intervals.

Each block consisted of a single base orientation magnitude, and we varied the orientation difference in each trial. Blocks with a nonzero base orientation of 2° and 4° were yoked such that we collected trials on both sides of vertical (e.g., base orientations of $\pm 2^\circ$) intermixed randomly with five repetitions for each of the orientation differences totaling 110 trials per block (2 base orientations \times 11 orientation differences \times 5 repetitions). We doubled the number of repetitions for blocks with a base orientation of 0° so that all blocks were of equal length. Over the course of the experiment, we collected 20 data points for each combination of orientation difference and base orientation (1,100 total per participant). Intervals, trials, and blocks were all shown in a randomized order.

Analysis

To estimate the magnitude of the tilt illusion and the participant’s subjective vertical, we used a maximum likelihood fit of a model based on the following assumptions and approximations:

- (1) The sensory estimate of the center orientation from each interval is corrupted independently by noise drawn from a Gaussian distribution
- (2) The level of sensory noise is independent of stimulus orientation
- (3) The magnitude of the effect of the surround on the perceived orientation of the center is independent of the precise orientation of the center over the range of orientations tested

(The limitations of these assumptions deserve some comment and will be addressed in the Discussion section.)

For each combination of orientation difference and base orientation, we computed the proportion of trials in which the participant selected the interval that contained the leftward surround. We assume that

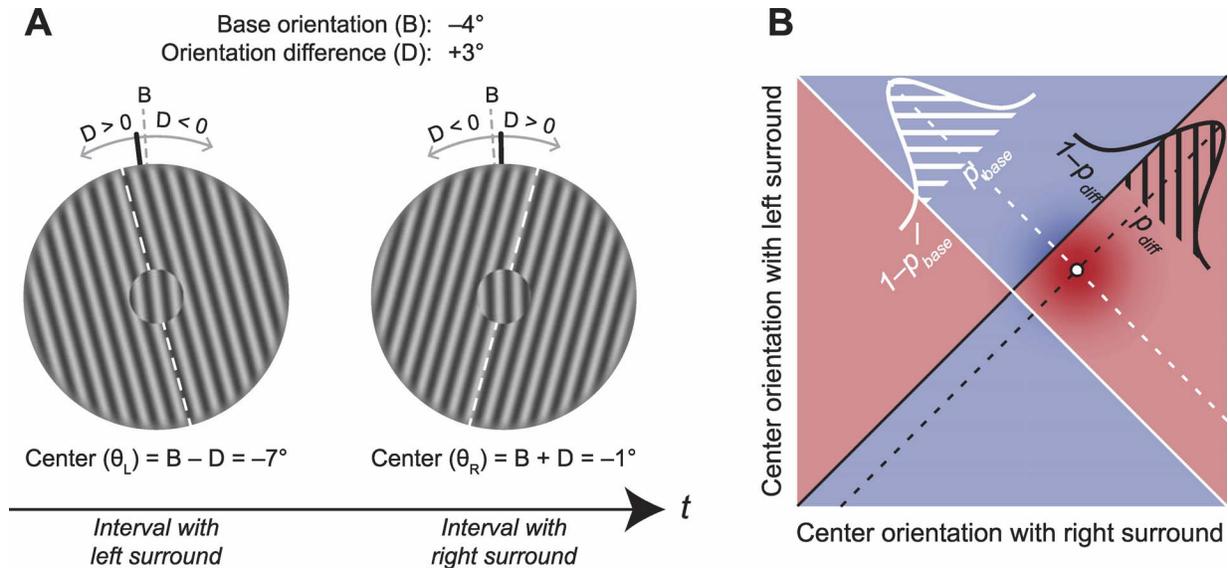


Figure 3. Conditions and analysis for the two-interval task. (A) The center orientations (solid black line) were defined relative to a base orientation (dotted gray line) and shifted by an orientation difference in both intervals that was either toward its respective surround orientation (positive difference values) or away from the surround orientation (negative difference values) as in Equations 1 and 2. Surround orientations were always $\pm 15^\circ$ (highlighted by a dashed white line). Note that order of presentation was randomized such that either of the surround orientations may have been presented first. (B) Illustration of the model used to fit the participant responses across both dimensions of difference space and base orientation space. The solid black line represents pairs of orientations that are perceived as identical. The solid white line represents pairs of orientations that are perceived as equal and opposite from subjective vertical. Red and blue shaded regions correspond to the participant's selection of the interval with the left and right surround, respectively, as containing the center orientation closer to vertical. The white circle represents the current stimulus at a base orientation indicated by the dotted white line and an orientation difference indicated by the dotted black line. The darker shading surrounding the white circle reflects the 2-D Gaussian distribution of sensory estimates of the center orientations. The probability that the participant responds to the interval with the left surround is the volume under the 2-D Gaussian that falls within either of the shaded red regions. The black and white overlaid Gaussian curves illustrate the marginal distributions of perceived orientation difference and perceived base orientation, respectively.

subjects will select the interval with the leftward surround whenever that interval has a smaller magnitude difference between the perceived center orientation and the participant's subjective vertical compared to that of the other interval (red regions in Figure 3B). As the orientation difference is defined as the angular difference between the base orientation and the center orientations presented in each of the intervals, the specific orientation difference in which the test orientations in the two intervals appear equally close to vertical is a measure of the tilt illusion. Similarly, shifts in the base orientation adjust the mean orientation of the two stimuli without affecting the orientation relative to each other. Therefore, the base orientation in which the two center gratings appear equally close to vertical is a measure of the participant's subjective vertical.

The assumptions listed above allow us to treat the joint probability distribution of perceived orientations for any given stimulus pair as a circular Gaussian distribution (see Figure 3B). As such, the marginal distributions along the dimensions of base orientation

and orientation difference (diagonals in Figure 3B) are also Gaussian distributions of equal variance. The probability of selecting the interval with the leftward surround is modeled as the area under this distribution that falls within either of the red regions in Figure 3B. These regions represent two distinct situations. The rightmost red region represents situations in which the average orientation across the two intervals (i.e., the base orientation) is to the right of subjective vertical (area above the solid white line in Figure 3B), and the center in the interval containing the leftward surround is perceived as more leftward than the center in the other interval (area below the solid black line in Figure 3B). Conversely, the leftmost red region represents situations in which the average orientation across intervals is perceived as to the left of vertical, and the center in the interval containing the leftward surround is perceived as more rightward. In both of these situations, the center orientation in the interval containing the leftward surround is perceived as the closer to subjective vertical.

Using the logistic function as an approximation to the cumulative Gaussian (Treutwein, 1995), the probability across orientation differences that the center orientation in the interval with the leftward surround is perceived as more leftward, p_{diff} , is given by

$$p_{diff} = \frac{1}{\left(1 + \exp\left(\alpha(D_0 - D)\right)\right)} \quad (3)$$

where α , the slope parameter, is inversely related to the standard deviation of the noise in the sensory estimate, D is the orientation difference between each center grating and the base orientation, and D_0 is the participant's tilt illusion.

Similarly, the probability that the average orientation across the two intervals is perceived as right of subjective vertical, p_{base} , is given by

$$p_{base} = \frac{1}{\left(1 + \exp\left(\alpha(B_0 - B)\right)\right)} \quad (4)$$

where B is the base orientation, and B_0 is the participant's subjective vertical.

According to the model, the probability of the participant selecting the interval with the leftward surround, p_{left} , is the volume under the 2-D Gaussian that falls within the red shaded area of Figure 3B, given by

$$p_{left} = p_{diff} \times p_{base} + (1 - p_{diff})(1 - p_{base}). \quad (5)$$

Simplification of this formula gives

$$p_{left} = 2 \times (p_{diff} - 0.5)(p_{base} - 0.5) + 0.5 \quad (6)$$

Finally, incorporating a lapse rate, λ , gives the function, $p'_{left}(p_{diff}, p_{base})$, used to fit each subject's data:

$$p'_{left} = (1 - \lambda) \times p_{left} + \lambda/2. \quad (7)$$

Using nonlinear optimization (the Nelder-Mead simplex method implemented through Matlab's "*fminsearch*" function), we identified parameter values that maximized the log-likelihood estimate of this fitted function (Wichmann & Hill, 2001). In this way, each subject's data were fitted in 2-D stimulus space through the use of four free parameters: (a) the subject's tilt illusion, D_0 ; (b) the subjective vertical, B_0 ; (c) the best-fitting slope across both dimensions, α ; and (d) the lapse rate of the participant, λ .

Results

We ran a two-interval, two-alternative, forced-choice experiment to measure the tilt illusion. We manipulated the angular distance between the center orientations of the two intervals and identified the size

	CC	MLP	RTM	YO
Tilt illusion magnitude (deg)	2.008	1.128	3.175	2.228
Subjective vertical (deg)	2.742	-1.045	-0.042	-1.092
Slope (deg ⁻¹)	1.472	1.721	0.681	1.240
Lapse rate (prop)	0.000	0.007	0.000	0.047
Goodness-of-fit (R^2)	0.974*	0.977*	0.902*	0.952*

Table 1. Fitted model parameters for each participant. *Notes:* Parameter values that provided the best fit for each participant (top four rows) and a goodness-of-fit test using the coefficient of determination (bottom row). * $p < 0.001$.

of the orientation difference when both gratings appeared to be oriented from vertical by a similar magnitude. This was repeated for several base orientations located on both sides of the participant's subjective vertical.

In particular, we computed the proportion of responses made to the interval with the left surround across all conditions. We then used our model to find the psychometric parameters that best represent our data across both difference space (when base orientation remained constant) and base orientation space (keeping the orientation difference the same). We used these parameters to plot logistic functions across difference space for each base orientation separately, and vice versa, as shown for one participant in Figure 4.

The fitted parameter values for all of our participants are displayed in Table 1. We measured the quality of our fits to the original data by obtaining the coefficient of determination (R^2) for each participant (Table 1, bottom row). This revealed significant fits for all of our participants. These values, coupled with inspection of the residuals, indicated the data was well accounted for across both dimensions.

To visualize our modeled data, we used the fitted parameters from Table 1 to create a heat map that describes response probabilities for all possible stimulus pairs (Figure 5). In this figure, the solid black line indicates stimulus pairs that contain an orientation difference of zero (i.e., test orientations are physically identical for both intervals) across a range of base orientations. Any shift that is parallel to this line indicates a change to the orientation difference. The cross-section along the solid black line itself reproduces our fit in the 0° base orientation plot of Figure 4B, and remaining plots from that panel are represented by data series parallel to this line. Of particular interest is the dotted black line consisting of pairs of stimuli in which both center orientations are perceived to be the same (i.e., test orientations from each interval are selected with equal probability). As orientation difference reflects the angular distance

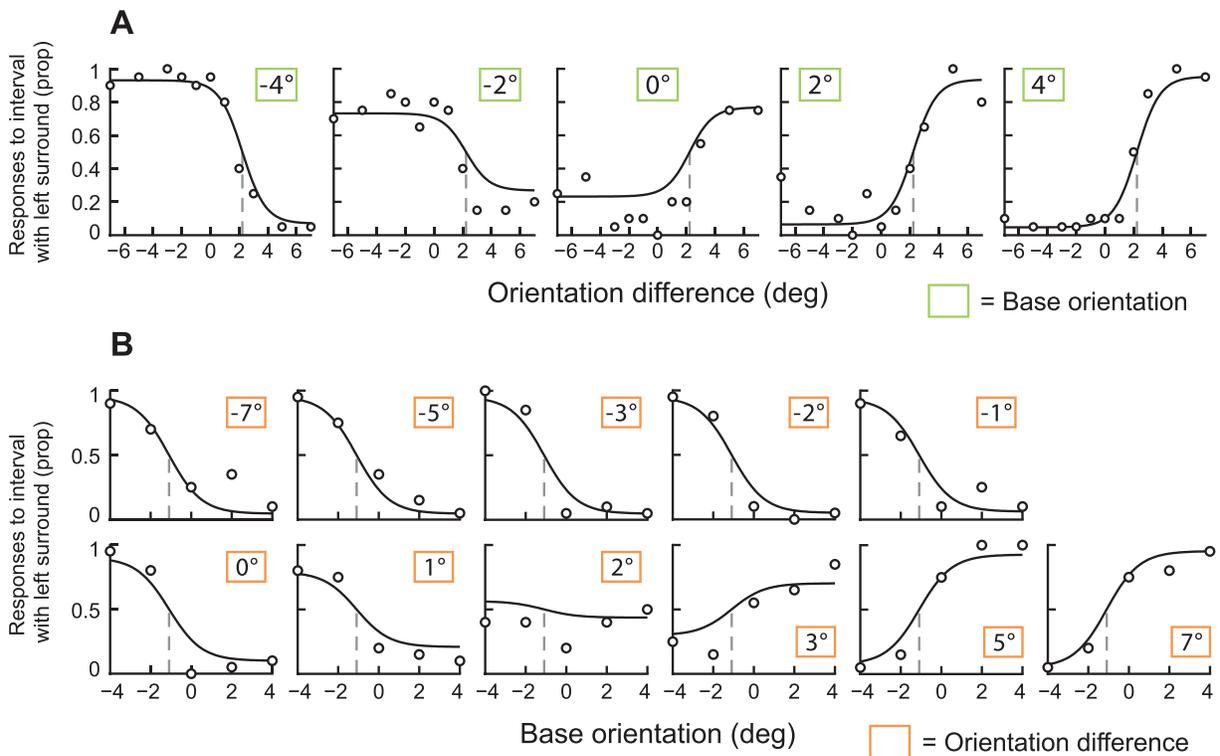


Figure 4. Fitted responses to the unbiased two-interval task for participant YO. (A) Logistic functions are fitted to difference values for each of the base orientations with the point of subjective equality (PSE; gray dotted line) representing the magnitude of the tilt illusion. (B) The inverse of (A), in which logistic functions are instead fitted to base orientations for each of the orientation differences separately. The PSE (gray dotted line) represents the subjective vertical of the participant. Note that in each set of graphs, the value where the slope changes sign is equal to the PSE in the other set of graphs.

from the base orientation to each of the test stimuli and not between the two center orientations (see Figure 3A), the distance between stimulus pairs that are physically matched (solid black line) and perceptually matched (dotted black line) is equal to *twice* the magnitude of the tilt illusion and is illustrated using a black arrow.

Similarly, the cross-section along the solid white line in Figure 5 shows stimulus pairs with a base orientation of 0° (i.e., the mean orientation of the two test gratings is vertical) and reproduces the middle plot of Figure 4A. Shifts that are parallel to this line indicate a change in the base orientation. The dotted white line represents stimulus pairs whose base orientation is equal to the participant's subjective vertical as they are equally likely to choose either interval no matter the degree of orientation difference between them. It should be noted that any given change in base orientation requires a shift in the orientation of either stimulus of twice that amount. Thus, the horizontal (or, equivalently, vertical) distance between the solid and dotted white lines (white arrow) is twice the value of the participant's subjective vertical.

Experiment 2: Across-task comparison

We have obtained an unbiased measure of the tilt illusion using a two-interval task. Our next goal was to compare results from our unbiased task with results using the traditional design to determine if response bias has influenced results in prior experiments and, if so, to what extent. For this experiment, we used an adaptive staircase procedure to run both the traditional one-interval (Figure 2A) as well as our unbiased two-interval (Figure 2B) tasks. We used the same participants as in Experiment 1 so that we could additionally compare results on the two-interval task using different procedures (adaptive vs. method of constant stimuli). Methods follow those of Experiment 1 except for those otherwise noted below.

Methods

Procedure

We used a Bayesian Psi staircase procedure (Kontsevich & Tyler, 1999) to determine the magnitude of the

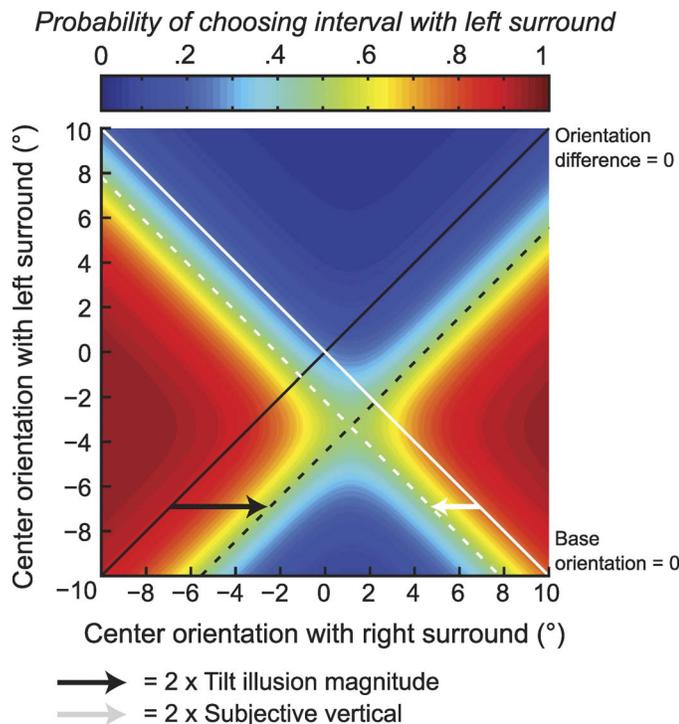


Figure 5. A heat map generated from optimized parameters in the unbiased two-interval task for participant YO. The heat map describes response probabilities of one participant to any pair of test orientations. Each color on the heat map represents pairs of center grating orientations that are equally likely to yield a particular response. The solid black line indicates when the center orientations in the two intervals are physically matched (i.e., an orientation difference of 0°), and the dotted black line shows when they are subjectively matched for this participant such that both intervals appear equally close to vertical. The change in difference space (black arrow) reveals twice the magnitude of the tilt illusion. Similarly, the solid white line is where both intervals contain orientations physically equidistant from vertical (i.e., a base orientation of 0°), and the dotted white line is where both test orientations are equidistant from the participant's subjective vertical. The difference between these lines (white arrow) is a shift in base orientation space and equal to twice this participant's subjective vertical.

tilt illusion for both one- and two-interval tasks. This method updates posterior probabilities across two dimensions (point of subjective equality [PSE], slope) in each trial and determines the stimulus value for the next trial to maximize the expected information gain. We used interleaved pairs of staircases consisting of 30 trials each. Participants completed a minimum of six staircases (maximum 10) on each task.

For the one-interval task, only a single center and surround grating were displayed, and participants were asked to judge whether its center orientation was to the left or right of vertical (Figure 2A). The orientation of the center grating varied according to the Psi adaptive

procedure while the surround orientation remained unchanged ($\pm 15^\circ$) for each staircase (interleaved pairs of staircases contained one of each left and right surrounds).

Prior to running the two-interval task, we obtained an estimate of each participant's subjective vertical by performing the one-interval task without the surround. That is, the central test orientation was presented alone, and participants were asked to indicate whether it was oriented to the left or right of vertical. We used the mean PSE from an interleaved pair of these staircases to define the base orientations for the two-interval task as $\pm 4^\circ$ away from this estimate. For example, a participant who was measured to have subjective vertical at $+1^\circ$ was tested on base orientations -3° and $+5^\circ$ for the two-interval task.

For the adaptive staircase procedure in the two-interval task, the orientation difference was manipulated to provide the best estimate of the orientation difference at which the two intervals appeared equally vertical while base orientation was held constant.

Analysis

After the completion of all trials, the marginal mean (and standard deviation) of the posterior probability distribution was used as an estimate of the PSE value (and associated standard error) for each staircase. For the one-interval task, the PSE estimates from staircases with the same surround orientation were averaged together. The magnitude of the tilt illusion was defined as half the distance between the mean of these estimates and can be expressed as follows:

$$TI = \frac{1}{2}(\mu_R - \mu_L) \quad (8)$$

where TI is the magnitude of the tilt illusion, μ_R is the mean of PSE estimates for staircases with a right surround, and μ_L is the mean of PSE estimates for staircases with a left surround. We took the mean of the error estimates from all staircases irrespective of surround orientation to produce the standard error of the mean.

The two-interval task comprises two tilt illusions per trial: one for each interval with these always occurring in opposite directions to one another (one with a left surround, one with a right surround, and center orientations always between these two surround orientations). Staircase PSE estimates are a measurement of the angular difference between the base orientation (i.e., halfway between the intervals) and the center orientation in each interval when both stimuli are perceived as equally vertical—that is, half the magnitude of two tilt illusions. As such, each staircase's PSE is simply an estimate of the tilt illusion magnitude regardless of the participant's subjective vertical or the

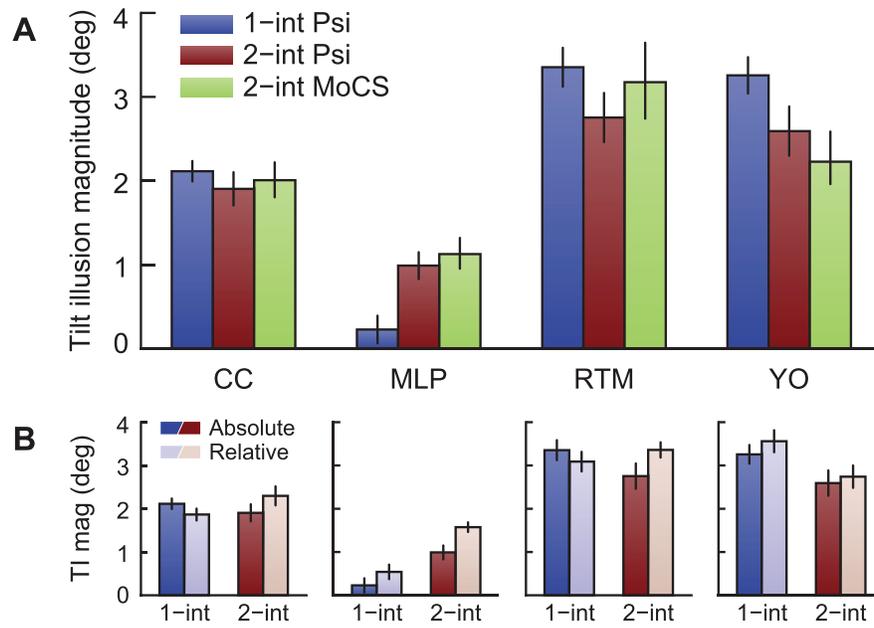


Figure 6. Comparison of tilt illusion magnitudes between different experiment designs. (A) Tilt illusion magnitudes using Psi adaptive staircases for the one-interval (blue) and two-interval (red) tasks performed in Experiment 2 alongside results of the two-interval method of constant stimuli (MoCS) task from Experiment 1 (green). Error bars show standard error of the mean, except for the two-interval MoCS results in which error bars were the 2.5th and 97.5th percentile of 1,000 fitted parametric bootstraps of surrogate participant responses. (B) Comparison of tilt illusion magnitudes for adaptive staircase methods using absolute ($\pm 15^\circ$ from vertical) or relative ($\pm 15^\circ$ from the center grating) surround orientations. Each participant is displayed on a separate graph. Data from the absolute conditions are recreated from (A) and are shown in bold colors, and relative conditions are presented in lighter colors. Error bars indicate standard error of the mean.

base orientations that were used. We therefore used the mean of all staircase PSEs as a measure of tilt illusion magnitude and the mean of the error estimates to produce the standard error of the mean.

Results

In order to compare the magnitude of the measured bias between different paradigms and quantify the extent that response bias influenced measurement of the tilt illusion, we ran adaptive staircases on both the traditional one-interval and our unbiased two-interval tasks. We used the same participants from Experiment 1 so that we could directly compare results from the two tasks as well as compare between adaptive and nonadaptive methods when running tilt illusion experiments.

Figure 6A displays the measured magnitude of the tilt illusion for one- and two-interval adaptive tasks (blue and red bars, respectively) as well as those estimated by our model using the data from Experiment 1 (green bars), which employed a nonadaptive procedure. Although clear interindividual differences exist, results for each participant are broadly stable across the different tasks. Using a repeated-measures

ANOVA on tilt illusion magnitudes from each of the three tasks, we did not find any significant difference between measurements on the tasks, ($F(2,6) = 0.165$, $p > 0.05$). First, this revealed that the faster and more efficient staircase procedure used for this experiment was not any less informative in identifying biases in perceived tilt as the more extensive testing we performed in Experiment 1 using the method of constant stimuli. Second, this revealed that both the traditional and unbiased tasks were not appreciably different in the resulting tilt illusion magnitudes, indicating that response bias was not a strong contributor to the results of prior tilt illusion experiments.

The effect of relative versus absolute surround orientation on tilt illusion magnitude

The largest repulsive effects to the tilt illusion have previously been found when the surround is oriented approximately $\pm 15^\circ$ away from the center orientation (O'Toole & Wenderoth, 1977; Wenderoth & Johnstone, 1988). We therefore used fixed (absolute) surround orientations of $\pm 15^\circ$, which was necessary to (a) provide a strong repulsive illusion and (b) ensure that the surround orientation did not provide any

extraneous cues as to the orientation of the central test grating. However, when base orientations were positioned away from vertical, the difference between center and surround orientations was reduced, and this may have had an impact upon our measure of the tilt illusion due to differences in the strength of the repulsive effect.

We therefore reran all of our participants on both one- and two-interval adaptive tasks using relative surround orientations that changed trial-to-trial as to consistently be 15° from that of the center orientation. We compared the magnitude of the tilt illusion observed here with those using absolute surround orientations (as shown previously in Figure 6A) and plotted the results together in Figure 6B. Tilt illusion magnitudes using absolute surround orientations were overall slightly lower than when using relative surround orientations with a marginal effect observed for method of surround orientation used, ($F(1,3) = 8.27, p = 0.064$). This is consistent with our suggestion that presentation of test gratings away from vertical changed the distance between center and surround orientations away from maximal repulsion.

Comparison of tilt illusion magnitudes between tasks that used relative surround orientations and that from Experiment 1 still produced no significant differences, ($F(2,6) = 0.602, p > 0.05$). Thus, even if tilt illusion magnitude differed due to the type of surround used, in both cases, we did not find any evidence of response bias influencing our measurement of the tilt illusion. Furthermore, across both surround types, we did not observe any significant differences in the tilt illusion magnitude between one- and two-interval tasks, ($F(1,3) = 0.006, p > 0.05$), nor an interaction between the task types and surround types, ($F(1,3) = 3.29, p > 0.05$). In summary, the use of surrounds fixed in absolute orientation may have caused a mild reduction in the measured tilt illusion. However, in no case did we observe a significant difference between results for the traditional one-interval method and the unbiased two-interval task (either adaptive or nonadaptive versions and regardless of how the surround orientation was defined). This indicates that response bias had minimal, if any, influence on measurements of the tilt illusion.

Experiment 3: Extensive testing for interindividual comparisons

Although the tilt illusion is a well-established phenomenon that has been readily and consistently observed across the population, the magnitude of the measured effect is observed to vary quite significantly between individuals (Song et al., 2013; Witkin & Asch,

1948). We therefore reran Experiment 2 using a larger sample size in an effort to investigate differences in the population and determine if the results for one- and two-interval tasks varied in a systematic manner. As such, methods very closely replicate Experiment 2 and are identical except as described below.

Methods

Participants

We recruited 20 right-handed, naïve participants (14 females) with a mean age of 23.9 (range 18–50) through the university research participation system and who were given monetary compensation for their time. All participants had normal or corrected-to-normal vision. This experiment was granted ethics approval by the local ethics review committee, and all participants gave written informed consent.

Procedure

The experiments and analysis methods themselves were identical to Experiment 2; however, each task was additionally preceded by 15 practice trials that contained stimuli with considerable magnitude (a center orientation of $\pm 10^\circ$ for single-interval tasks and center orientations of $\pm 2^\circ$ and $\pm 10^\circ$ for the two-interval task) simply as an additional measure to ensure participants correctly understood task instructions.

Analysis

PSE and error estimates were returned from each adaptive staircase. Individual staircases on the one- and two-interval tasks were excluded from further analysis if a significant number of trials ($p < 0.01$; one-tailed binomial test) were not in the direction consistent with this final estimate. This occurred on 22.1% of runs and resulted in the removal of three participants' data (at least one staircase was required on each side of vertical to compute a valid estimate for the magnitude of the tilt illusion).

Results

In a single session, participants performed several blocks of staircase pairs to identify subjective vertical as well as measure their perceived bias on the tilt illusion for both the traditional one-interval and unbiased two-interval tasks. We sought to examine the amount of variation found between participants in measurement of the tilt illusion and whether there was a systematic bias in the results of the different tasks.

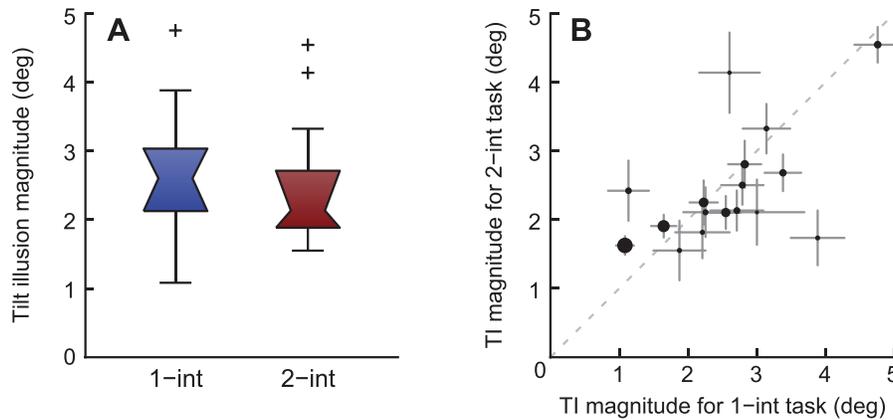


Figure 7. Comparison of measured bias between one- and two-interval tasks. (A) Each box plot is the spread of tilt illusion magnitudes across participants. The “notch” is the median with the edges of the box representing the 25th and 75th percentiles and whiskers displaying the spread of remaining points with crosses used for any outliers. (B) Relative performance of each participant on one- and two-interval tasks. Error bars in each direction are the standard error of the mean for each task. Marker size is inversely proportional to standard error, such that participants who had lower error rates are represented by larger markers. The dotted line indicates perfectly consistent performance when the tilt illusion magnitude on both tasks is identical.

Participants’ subjective vertical were reasonably evenly distributed with an average of $+0.30^\circ$ (standard deviation 0.56°) with all values within the range of $\pm 1.76^\circ$. Thus, all participants had a reasonable internal representation of vertical with mild interindividual differences.

Tilt illusion magnitudes for the two tasks are presented in Figure 7A, in which each box plot displays the distribution of tilt illusion magnitudes observed across participants for a single task. Overall, we did not find any significant difference between the measured strength of the illusion on the two tasks, ($t(16) = 0.68$, $p > 0.05$) (two-tailed paired samples t test). More specifically, magnitudes for the one-interval task were more widely distributed although the mean ($\mu_{1-int} = 2.59$) was barely larger than that of the two-interval task ($\mu_{2-int} = 2.46$). These results replicate that of Experiment 2, in which we again have not observed a significant difference between tilt illusion magnitudes for the two tasks even with a larger population sample. This provides further evidence that response bias does not significantly contribute to results in the traditional version of the tilt illusion experiment.

We wanted to examine the relative difference in each participant’s performance on the two tasks, so we plotted individual tilt illusion magnitudes from each task on separate axes (Figure 7B). We found a significant correlation between performance on the two tasks ($r = 0.57$, $p < 0.05$) even though there was considerable variability in the measured tilt illusion across participants. We note that tilt illusion magnitudes were generally higher on the traditional one-interval task than for the unbiased two-interval version (the majority of data points are located beneath the main diagonal on Figure 7B), consistent with the

results of three out of our four participants in our previous experiment using the same tasks (Figure 6A). It is therefore possible that a small response bias is present in the one-interval task, but it was below our detection power for these experiments.

Discussion

In this study, we removed the possibility of response bias influencing our measurement of the tilt illusion by developing a two-interval, forced-choice alternative task in which task demands did not coincide with changes to the inducing surround. We then compared our two-interval, bias-free measure to the traditional one-interval design using adaptive staircase procedures and found no significant difference between these methods. This was confirmed using a larger sample, in which tilt illusion magnitudes were found to correlate significantly between the two tasks across our range of participants.

The most common design used for tilt illusion experiments is the single-interval task, which, as addressed here, is susceptible to systematic response biases of the participant. This is of particular concern as there has been considerable recent interest in the possibility of using measures of contextual modulation in visual processing, such as the magnitude of the tilt illusion, as a behavioral biomarker for conditions such as schizophrenia (Butler, Silverstein, & Dakin, 2008; Carter & Barch, 2007; Dakin et al., 2005; Tibber et al., 2013; Yang et al., 2013a, 2013b). We suggest that the more accurate measure of the tilt illusion afforded by our two-interval task will be valuable if the tilt illusion

is to be used as part of a diagnostic test battery for neurological or psychiatric disorders.

To visualize how our proposed model would behave if a participant responded with a consistent bias throughout the two-interval task, consider the participant results shown in Figure 5. A bias to choose the interval with a particular surround orientation would effectively rescale the color axis on the heat map. The dotted lines representing tilt illusion magnitude and subjective vertical would remain in the same location but would now run along a different color (e.g., if biased toward responding to the interval with the left surround, the dotted lines would run through a region of yellow or red rather than green), no longer corresponding to a response probability of 0.5. This would inevitably decrease the quality of the fit of the model but would not bias the estimated magnitude of the tilt illusion.

However, as flagged in the Analysis section, our model is based on several assumptions and approximations. First, the assumption of independence between the sensory noise in the two intervals ignores the possibility of any slow drift in subjective vertical, which would tend to elongate the distribution of sensory estimates for a given stimulus pair along the leading diagonal in Figure 3B (see Klein, 1985, for discussion of psychophysical models incorporating correlated variability). This would lead to unequal variance along the dimensions of base orientations and orientation difference, which could, in principle, be modeled by using separate slope parameters in Equations 3 and 4 rather than the common slope parameter along those dimensions employed at present.

Second, the approximation that the noise in the sensory estimate is independent of stimulus orientation runs counter to the oblique effect for orientation, whereby orientation discrimination thresholds are lowest around cardinal orientations (vertical and horizontal) and higher around oblique orientations (Appelle, 1972). Indeed, in the context of the current data, we note an interesting pattern in Experiment 1 in which an occasional shift away from the psychometric function took place for some of the larger orientation separations (for example, an orientation difference of $\pm 7^\circ$ for a base orientation of 2° in Figure 4A). This behavior was typical of all of our participants and was identified more readily for base orientations closer to vertical. We posit that this unusual release from the shape of a psychometric function relates to increased task difficulty arising when the task depended on making smaller relative discriminations between the two intervals when each of the center orientations are farther, and on opposite sides, from vertical. However, although not explicitly captured by our model, such nonmonotonic performance as a function of orientation difference should not have much effect on the

resulting estimates of the tilt illusion as they would be expected to occur symmetrically for positive and negative orientation differences alike.

Third, the model assumes that the magnitude of the effect that the surround orientation has on perception of the center is independent of the precise orientation of the center over the range of orientations tested. The dependence of the magnitude of the tilt illusion on the relative orientation of center and surround is well established, and the peak effect has consistently been observed for angular differences of 10° – 20° (Clifford, 2014). Using surround orientations of $\pm 15^\circ$, we anticipated that the effect of any reduction in the strength of orientation repulsion between surround and center as a function of center orientation on the measured tilt illusion would be small. Empirical support for this assumption comes from Experiment 2, in which we compared the strength of the measured tilt illusion for fixed $\pm 15^\circ$ (absolute) surrounds with (relative) surrounds whose orientation covaried with that of the center such that the difference was fixed at $\pm 15^\circ$. Our results revealed only marginally weaker illusion magnitudes for absolute than relative surrounds.

The logic of our bias-free design has potential application well beyond the domain of orientation processing. For example, in studies of gaze perception, it has consistently been reported that the perceived direction of another's gaze is biased by the direction of his or her head (e.g., Otsuka, Mareschal, Calder, & Clifford, 2014; Otsuka, Mareschal, & Clifford, 2015; Wollaston, 1824). However, such studies typically require subjects to indicate the direction of eye gaze along the horizontal (i.e., left or right averted, sometimes with the option to respond “direct”) in the context of a head that is itself directed to the left or right. Thus, there is a straightforward correspondence with the situation in tilt illusion studies—simply substitute eye gaze direction for center orientation and head direction for surround orientation—and the associated susceptibility to response bias. To obtain an unbiased measure of the influence of head direction on perceived eye gaze, one could use a two-interval paradigm in which the heads in the two intervals were averted from straight ahead in opposite directions but by equal amounts and subjects were required to report whether the first or the second stimulus appeared to be gazing more directly at them. This is just one illustration of the potential applicability of the unbiased approach put forward here; others include unbiased measurement of direction repulsion in motion transparency (Marshak & Sekuler, 1979) and the perception of three-dimensional slant (Gillam, Sedgwick, & Marlow, 2011).

In summary, our study supports the validity of many decades of prior tilt illusion experiments. It provides

necessary confirmation that the bias measured during traditional one-interval tasks indeed reflects the perceptual bias rather than being unduly influenced by any form of response bias. By comparing results between adaptive and nonadaptive versions for the two-interval task, we confirmed consistency in tilt illusion measurements from both designs and showed that our more accurate method can be used without any notable cost of efficiency.

Keywords: orientation, psychophysics, response bias, contextual effects, center-surround.

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