

The time course of the oblique effect in orientation judgments

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It is well known that maximal sensitivity to subtle orientation differences around a cardinal axis exceeds that around an oblique axis. In principle, this oblique effect in orientation sensitivity could either be constant across stimulus durations or could evolve as stimulus durations increase. To distinguish between these possibilities, we asked participants to judge subtle (4 deg) angular differences between pairs of gratings that were presented for various durations and masked to limit neural persistence. When the gratings were presented successively and for just 8.33 ms each, the ability to judge subtle (4 deg) orientation differences was already reliably better than chance, but comparable around cardinal and oblique axes. The oblique effect emerged only at subsequent stimulus durations, and increased across the tens of milliseconds after reliable (if modest) orientation sensitivity had occurred. These additional tens of milliseconds appear to be necessary but not sufficient for the oblique effect, which was absent at these durations when the stimuli were presented simultaneously rather than successively. Relative to simultaneously presented stimuli, successively presented stimuli generated a reduction in oblique orientation sensitivity, not an enhancement in cardinal orientation sensitivity. We believe the data suggest that the oblique effect in orientation sensitivity is a dynamic phenomenon that can be influenced by the neural events occurring between two successively presented stimuli.

Keywords: orientation discrimination, oblique effect, orientation dynamics, psychophysics, duration

Introduction

This study was conducted to provide new information about the oblique effect – an anisotropy in spatial vision that is well known. Indeed, for more than 140 years (Mach 1861), it has been known that people are better able to judge subtle angular differences presented near cardinal (horizontal or vertical) axes than those near oblique (diagonal) axes. The oblique effect has also been demonstrated in many nonhuman species, including those as evolutionarily distant from each other as the octopus and the monkey (Appelle, 1972). About 30 years ago, evidence from single-cell recordings in the cat visual cortex suggested that the oblique effect arises from an overrepresentation of visual neurons tuned to cardinal axes (Mansfield, 1974). That physiological anisotropy can be construed as a steady-state explanation of the oblique effect, because the overrepresentation of cardinally tuned neurons would seem to be a static characteristic of the visual cortex. However, more recent physiological work has suggested that, within the primary visual cortex, orientation tuning itself is a dynamic rather than a static phenomenon (Ringach, Hawkin, & Shapley, 1997). Inspired by the recently found physiological dynamics, we conducted the present study to describe the time course of the oblique effect at the psychophysical level.

Because tens of milliseconds are required for orientation-tuned cortical cells to reach their maximal response (Ringach et al., 1997), we reasoned that well-timed visual masks could selectively disrupt the dynamics of orientation sensitivity. Accordingly, visual masks were used to control the duration over which oriented stimulation would persist in each participant's visual system. Given the recently found physiological dynamics (Ringach et al., 1997), orientation sensitivity at the behavioral level should be positively sloped when plotted as a function of masked stimulus duration (a psychophysical proxy for neural persistence). Additionally, the slopes associated with cardinal and oblique sensitivity can be compared to determine whether the oblique effect is static or dynamic. Specifically, when separately plotting cardinal sensitivity and oblique sensitivity as a function of masked stimulus duration, parallel slopes would indicate that the oblique effect is a static phenomenon. This is because parallel slopes have a constant difference – and the oblique effect can be defined as the *difference* between cardinal sensitivity and oblique sensitivity. By contrast, if the oblique effect were a dynamic phenomenon, then nonparallel slopes would be expected (i.e., the *difference* between cardinal and oblique sensitivities would change with masked stimulus duration).

In addition to investigating the time course of the oblique effect, we sought to have the visual masks provide new information about another intriguing aspect of the oblique effect in orientation sensitivity. Specifically, it has been shown that the oblique effect, which is salient when the two stimuli are presented successively, is much reduced when the two stimuli are presented simultaneously (Heeley & Buchanan-Smith, 1992; Westheimer, 2003). In principle, this difference in the oblique effect under successive and simultaneous stimulation could implicate the neural events occurring between the two successively presented stimuli, or those occurring after the second stimulus, or both. We believe the former possibility is especially interesting because the neural events occurring between the two stimulus presentations pertain to remembering the first orientation in the absence of “bottom-up” stimulation. A memory-related influence would be noteworthy given that the oblique effect is typically attributed not to memory but to a characteristic of the early visual pathway, namely the overrepresentation of cardinal tuned neurons in the primary visual cortex (Mansfield, 1974).

To briefly summarize the findings, data from our psychophysical masking procedure suggest that the oblique effect is a dynamic rather than static phenomenon. In particular, we found that at our briefest stimulus duration, orientation sensitivity was reliably better than chance, yet virtually identical for cardinal and oblique axes. After this initially comparable level of reliable performance, however, a difference between cardinal and oblique sensitivity emerged and grew with increasing stimulus duration. In fact, when oblique sensitivity and cardinal sensitivity were plotted separately across stimulus durations, the resultant slopes differed significantly from each other. These different slopes did not merely reflect different maximal performance levels for oblique and cardinal sensitivity; even when the comparison was restricted to the range over which oblique sensitivity improved, cardinal sensitivity increased at a faster rate. Additionally, we found that orientation sensitivity was most strongly disrupted by masks occurring between successive stimulus presentations. Because that is the interval over which the first orientation was to be remembered, the data suggest that the difference between the oblique effect in the successive and simultaneous conditions may reflect memory-related neural events.

Experiment 1: Method

Apparatus, stimuli, and task

The experiment was conducted on a 21-in (53.34 cm) ViewSonic P225 monitor that was controlled by a Macintosh G4 computer with a 733-MHz processor and software from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The vertical refresh rate of the monitor was 120 Hz, and the spatial resolution was 1024 x 768 pixels. In a well-lit room, participants viewed the monitor through a circu-

lar tube that eliminated external cues to orientation, such as the monitor's borders, and had a 15-cm inner diameter. A chin rest helped to stabilize head position at 57 cm from the monitor.

The discriminanda were Gabor patches created by multiplying a sinusoidal luminance profile by a two-dimensional Gaussian envelope. Each Gabor patch was preceded and followed by a circular bulls-eye mask. All Gabor patches and masks were 8 deg in diameter, and had a spatial frequency of 1 cycle per degree. Also, both the Gabor patches and the masks had maximum (108.00 cd/m^2) and minimum (5.83 cd/m^2) luminances that rendered high contrast (Michelson contrast = 89.76%) within the apparently gray surround (56.91 cd/m^2). To eliminate positional cues that co-vary with changes in orientation, the phase of each Gabor patch was randomized. The phase of the bulls-eye masks alternated between light- or dark-center, as pilot experiments indicated that orientation judgments were most disrupted when opposite polarity masks preceded and followed each Gabor patch. Participants foveally viewed the stimuli, and a light, circular fixation dot approximately 11 arcmin in diameter (77.83 cd/m^2 ; 15.53% contrast with the surround) helped to stabilize eye position.

The stimulus sequence is shown schematically in [Figure 1](#). On every trial, two new Gabor patches were generated and presented successively at slightly different orientations. The specific orientation differences and the duration of the Gabor patches varied and will be detailed below in the [Procedure](#). Regardless of those variations, however, each mask was 8.33 ms (one frame) in duration and the interstimulus interval (ISI) was always 500 ms. On each trial, the participant's task was to report whether the second orientation was “clockwise” or “anti-clockwise” to the first.

Participants, procedure, and data analysis

Denison University's Human Subject Committee approved all experiments. Twenty-three Denison University students with normal or corrected-to-normal vision participated in [Experiment 1](#).

We sought to establish that the limitations in our participants' performance were perceptual rather than conceptual. Accordingly, to ensure that the task was understood (i.e., could be performed at greater-than-chance levels), each participant completed an initial screening procedure. During the screening, cardinal and oblique trials were randomly interleaved. Additionally, the screening comprised stages of increasing difficulty. Specifically, although the angular difference during the screening was always 10 deg, the stimulus durations became progressively briefer. Initially, each participant was required to make five consecutively correct responses at each of the following three stimulus durations before proceeding: 500 ms, 200 ms, and 50 ms. In those initial screening trials, there were no masks. Subsequently, the masks were added (see [Figure 1](#)), and each participant was required to make five consecutively correct

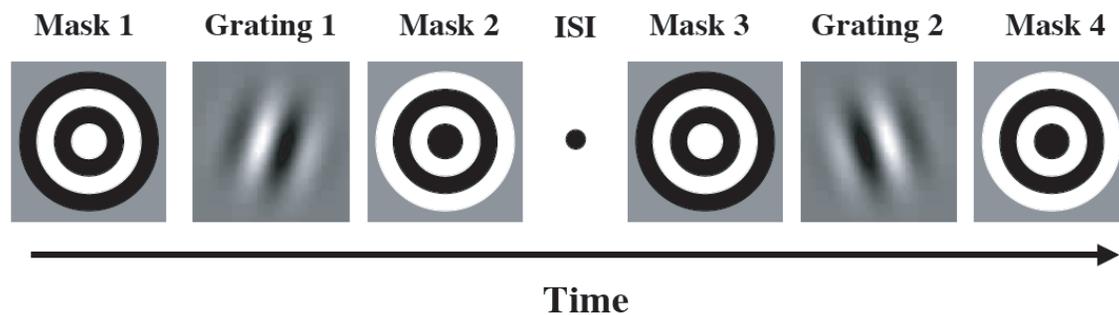


Figure 1. Stimuli and task. On each trial, two foveally viewed gratings were presented sequentially. Bulls-eye masks having opposite contrast polarity preceded and followed each grating. The two gratings on a given trial were shown for the same duration, which varied between 8.33 and 141.61 ms in 8.33-ms steps randomly across trials. The duration of each mask was always 8.33 ms, and the inter-stimulus interval (ISI) was 500 ms. Across trials the two gratings differed slightly in orientation near either a cardinal axis or an oblique axis, randomly. Participants judged the orientation of the second grating to be clockwise or anti-clockwise to the first. The correct response is anti-clockwise in the schematic above, where the magnitude of the angular difference and the spatial frequency have been selected for ease of viewing. The actual angular differences and spatial frequency are detailed in [Experiment 1: Method](#).

responses at a stimulus duration of 500 ms. Lastly, when the stimuli were masked and reduced to just 200 ms, each participant was required to make 10 consecutively correct responses, which could occur by chance less than one time in a thousand. All 23 participants successfully completed this screening, indicating that any performance limitations before the actual trials began were perceptual rather than conceptual.

After successfully completing the screening, each participant proceeded to the actual trials. On each of the actual trials, the angular difference was 4 deg, a value derived from extensive piloting of other participants from the same population tested under similar conditions. The 4-deg difference is larger than that of earlier studies on orientation discrimination (Vogels & Orban, 1985; Matthews & Welch, 1997; Matthews, Liu, Geesaman, & Qian, 1999). However, it should be noted that elevated thresholds are expected given the masks and given that on each trial there was complete uncertainty about whether the discriminanda would be presented cardinally or obliquely. To further ensure an appropriate angular difference for each participant, after every 80-trial block the computer evaluated each participant's performance, combining across the cardinal and oblique conditions. The initial angular difference (4 deg) was decreased or increased by 25% when performance respectively exceeded 80% correct or fell below 65% correct. Such adjustments prevented "floor" and "ceiling" effects, and pertained to cardinal and oblique axes alike to ensure identical angular differences in both conditions.

The procedure required each participant to complete ten 80-trial blocks. Each 80-trial block comprised four presentations from each of 20 stimulus conditions. Specifically, there were nine cardinal conditions, nine oblique conditions, and two "wide-angle" conditions, which comprised discriminanda that differed in orientation by 45 deg, rather than 4 deg in the cardinal and oblique conditions. The

nine cardinal and nine oblique conditions were defined by nine stimulus durations, which ranged between 8.33 and 141.61 ms (1 and 17 frames) in 18.66-ms (two frame) steps. The two wide-angle conditions consisted of the briefest (8.33 ms, 1 frame) and the longest (141.63 ms, 17 frames) stimulus durations. Also, the wide-angle condition comprised one Gabor patch near a cardinal axis and one near an oblique axis. Consequently, the wide-angle condition cannot be classified as exclusively cardinal or oblique. In all stimulus conditions, the orientation of the first Gabor patch was randomly jittered across a ± 5 -deg range around either the horizontal axis or the oblique axis 45-deg anti-clockwise to horizontal. The "jitter" was used to minimize the participant's ability to base judgments on implicit estimates of the primary cardinal and oblique axes, as such estimates would likely be better for the cardinal axis. Instead, the participants were forced to compare the two explicitly presented orientations to *each other*. Two clockwise and two anti-clockwise trials occurred within each of the 20 stimulus conditions, and these 80 trials were randomly re-sequenced at the start of each block.

Participants were instructed to make their clockwise/anti-clockwise judgments as quickly as possible without sacrificing accuracy. To promote accuracy, participants proceeded at their own pace, initiating each trial with a button press when ready. To maintain motivation, auditory feedback informed the participant whether their response was correct or incorrect immediately after each response, and the computer announced the overall percentage of correct responses after each 80-trial block.

In this within-subjects experiment, there were two independent variables, axis and duration. Our primary interest was the comparison between cardinal and oblique axes across the nine durations. Specifically, a significant axis-by-duration interaction would indicate that the oblique effect is a dynamic phenomenon; a nonsignificant interaction

would imply that the oblique effect is static. The interaction was investigated by a 2 x 9 (axis-by-duration) within-subjects ANOVA. The dependent variable – orientation sensitivity (d') – was computed using standard signal detection procedures (Green & Swets, 1966). Hits and false alarms were operationally defined as clockwise responses made when the second Gabor patch was, respectively, clockwise or anti-clockwise to the first. There were 20 chances to “hit” and 20 chances to “false alarm” (40 trials total) in each stimulus condition for each participant. Additionally, we computed best-fitting power functions and Pearson correlation coefficients to describe the extent to which cardinal and oblique orientation sensitivity (d') each depend on duration. We also used pair-wise ANOVAs to compare performance in the wide-angle condition to that at the much subtler cardinal and oblique angular differences (4 deg). Lastly, the error bars shown on figures throughout this study reflect 1 SEM.

Experiment 1: Results

The results from Experiment 1 are shown in Figure 2, where orientation sensitivity (d') is plotted as a function of stimulus duration. Our main finding is the differently sloped power functions for the cardinal (blue squares, solid line) and oblique (red Xs, dotted line) conditions. The slope difference is readily evident on visual inspection, and confirmed by the statistically significant interaction between axis (cardinal versus oblique) and stimulus duration, $F(8,176) = 11.31$, $p < .001$. Indeed, there is a statistically significant linear trend in the interaction, $F(1,22) = 55.16$, $p < .001$, indicating that the difference between cardinal and oblique sensitivity tends to increase across the durations. It also should be noted that not all of the slope-difference is because the cardinal and oblique sensitivities have different ranges. That is, even when the comparison is restricted to the range over which oblique sensitivity improves, the rate of improvement is faster for cardinal than for oblique stimuli. Moreover, at the earliest stimulus duration (8.33 ms), orientation sensitivity is virtually identical in the cardinal ($d'=0.20$, ± 0.05) and oblique ($d'=0.21$, ± 0.04) conditions, yet already reliably greater than chance (d' significantly greater than zero) in both conditions.¹ Taken together then, the data in Figure 2 indicate that the oblique effect in orientation sensitivity is dynamic, developing across the tens of milliseconds after reliable (if modest) orientation sensitivity to subtle (4 deg) angular differences occurs.

Further evidence that the angular resolution of the visual system depends on stimulus duration comes from the wide-angle condition (green triangles in Figure 2). The wide-angle condition comprised one cardinal grating and one oblique grating on each trial (a 45-deg angular difference), and therefore cannot be classified exclusively as either cardinal or oblique. If one takes a vertical slice on the abscissa at the briefest duration (8.33 ms), it is clear that

wide-angle sensitivity is already excellent ($d'=0.89$, ± 0.11) and significantly better than that for the smaller angular difference (4 deg) presented around either cardinal, $F(1,22) = 45.35$, $p < .001$, or oblique, $F(1,22) = 37.21$, $p < .001$, axes. This initial level of performance ($d' = 0.89$, ± 0.11) in the wide-angle condition can be matched eventually when the smaller angular difference (4 deg) is presented cardinally (blue power function), but additional tens of milliseconds are required. Indeed, sensitivity to a small, cardinal angular difference presented for 141.61 ms (our longest duration) significantly exceeds that for the wide-angular difference presented for 8.33 ms (our briefest duration), $F(1,22) = 9.02$, $p = .007$. Still, at the longest duration, sensitivity to the wide-angular difference significantly exceeds sensitivity to the small, cardinally presented angular difference, $F(1,22) = 9.12$, $p = .006$. Moreover, even within the wide-angle condition, it is clear that sensitivity at the longest duration significantly exceeds that at the briefest duration, $F(1,22) = 27.40$, $p < .001$. This indicates that orientation sensitivity depends on duration for wide angles, as well as small angles.

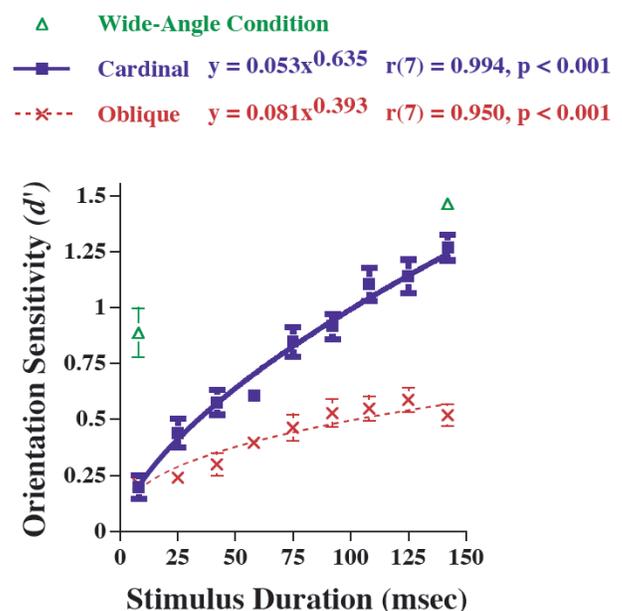


Figure 2. Data from Experiment 1. The wide-angle condition (green triangles, delta 45 deg) generated excellent performance at the briefest duration ($d'=0.89$ at 8.33 ms), and significantly better performance still at the longest duration ($d'=1.46$ at 141.63 ms). At the briefest duration (8.33 ms), sensitivity to a 4-deg angular difference is comparable in the cardinal (blue squares) and oblique (red Xs) conditions, and already reliably better than chance ($d' > 0$) in both conditions. At longer durations, however, the two conditions show different ranges, as maximal cardinal sensitivity significantly exceeds maximal oblique sensitivity. Even when the comparison is restricted to the range over which oblique sensitivity improves, the improvement occurs at a faster rate for cardinal stimuli (solid blue power function) than for oblique stimuli (dotted red power function), indicating that the oblique effect is dynamic.

| # Frames | Stimulus Duration (msec) | Cardinal Pearson r | Cardinal r-squared | Cardinal Prob. | Oblique Pearson r | Oblique r-squared | Oblique Prob. |
|----------|--------------------------|--------------------|--------------------|----------------|-------------------|-------------------|---------------|
| 1 | 8.33 | 0.963 | 0.927369 | < 0.001 | 0.99 | 0.9801 | < 0.001 |
| 5 | 41.65 | 0.981 | 0.962361 | < 0.001 | 0.992 | 0.984064 | < 0.001 |
| 9 | 74.97 | 0.995 | 0.990025 | < 0.001 | 0.991 | 0.982081 | < 0.001 |
| 13 | 108.29 | 0.996 | 0.992016 | < 0.001 | 0.991 | 0.982081 | < 0.001 |
| 17 | 141.61 | 0.998 | 0.996004 | < 0.001 | 0.994 | 0.988036 | < 0.001 |

Table 1. Statistics for psychometric functions in Experiment 2. For each of the 10 psychometric functions in Experiment 2, the Pearson correlation coefficient (r), the r-squared value, and the probability of obtaining those values by chance are shown. The stimulus durations are expressed both as the number of screen-refreshes (frames) and in ms. Values from the cardinal conditions are shown in blue, while values from the oblique conditions are shown in red. In each of the 10 stimulus conditions, the best-fitting sigmoid corresponded well with the data ($p < .001$), allowing thresholds to be fairly interpolated.

Experiment 2: Method

Twenty-four Denison University students were recruited for Experiment 2, which was conducted to determine whether the results from Experiment 1 could be replicated using a different method. The primary methodological distinction entailed tracking thresholds from a range of angular differences, rather than determining sensitivity (d') to a constant angular difference (4 deg), as in Experiment 1.

Thresholds were tracked using the method of constant stimuli. The ensemble of angular differences was $\pm 2, \pm 4, \pm 6, \pm 8,$ and ± 10 deg. These 10 angular differences were presented once per block in each of 10 stimulus conditions; two axes (cardinal versus oblique) by five durations, ranging between 8.33 and 141.61 ms (1 to 17 frames) in 33.32 ms (4 frame) steps. The resultant 100 trials in each block were randomly sequenced, and each participant completed 10 such blocks. Consequently, 2,400 trials (24 participants x 100 trials per participant) were completed in each stimulus condition. For each stimulus condition, the 10 angular differences were plotted on the abscissa of a psychometric function while the ordinate reflected the proportion of "clockwise" responses from all participants (2,400 trials per psychometric function). A least-squares procedure was then used to fit the data with a sigmoid of the form

$$1/(1 + \exp[-K(X - X_0)]), \tag{1}$$

where K and X_0 determine the slope and midpoint of the sigmoid, respectively. The correlation between the best-fitting sigmoid and the data, as indexed by the Pearson correlation coefficient (r), was statistically significant ($p < .001$) in each case (see Table 1). Because each fit was significant, it was possible to fairly interpolate from the sigmoid a 75% discrimination threshold, which was defined as half the angular difference required to alter the response rate from 0.25 to 0.75. The data were analyzed descriptively in a threshold-by-duration plot showing separate power functions and Pearson correlation coefficients for the cardinal and oblique conditions. In all other ways, the method in Experiment 2 was the same as in Experiment 1.

Experiment 2: Results

The results from Experiment 2 are shown in Figure 3, where the mean thresholds are plotted as a function of stimulus duration. Again, our main finding is the differently sloped power functions for the cardinal (blue squares, solid line) and oblique (red Xs, dotted line) conditions. It is clear from visual inspection that, although cardinal and oblique thresholds are comparable (approximately 12 deg) at the earliest duration (8.33 ms), across the remaining du-

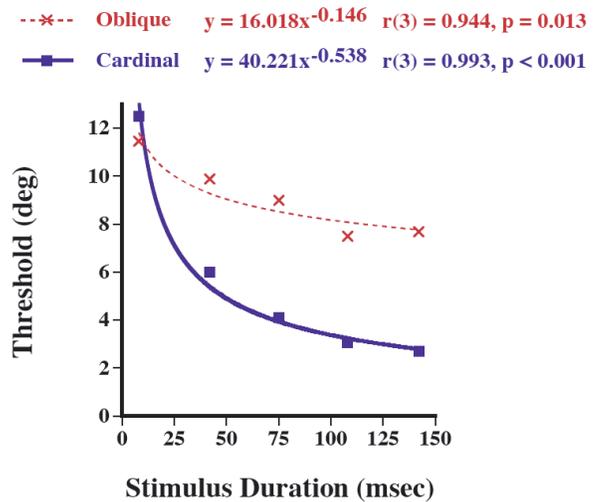


Figure 3. Data from Experiment 2. Unlike Experiment 1, Experiment 2 was based on tracking thresholds using the method of constant stimuli. Nevertheless, the data from Experiment 2 are similar to those from Experiment 1 in several ways. First, cardinal and oblique thresholds are similar at the briefest duration (8.33 ms). Second, the cardinal and oblique conditions have different ranges, as the lowest cardinal threshold is significantly lower than the lowest oblique threshold. Third, even when the comparison is restricted to the range over which oblique thresholds improve, the improvement occurs at a faster rate for cardinal stimuli (solid blue power function) than for oblique stimuli (dotted red power function), indicating that the oblique effect is dynamic.

rations cardinal thresholds decline much faster than oblique thresholds. Additionally, not all of the slope-difference can be explained by the fact that the cardinal and oblique conditions have different ranges. That is, even when the comparison is restricted to the range over which oblique thresholds decline, the decline is faster for cardinal than for oblique stimuli. Indeed, cardinal thresholds at the second briefest stimulus duration (41.65 ms) are already lower than the lowest oblique thresholds across the entire (141.61 ms) domain of durations tested. In short, although the methods in Experiments 1 and 2 differed, the findings are the same. That is, the oblique effect in the visual system's angular resolution is dynamic, developing across the tens of milliseconds after reliable if modest (approximately 12 deg with 75% accuracy) angular resolution occurs.

An additional demonstration that the oblique effect is dynamic can be seen in Figure 4, where the obliquity index – the ratio of oblique thresholds to cardinal thresholds – is plotted as a function of stimulus duration. The positive slope of the best-fitting power function clearly reveals the development of the oblique effect; at the briefest duration (8.33 ms), the obliquity index is near unity, whereas at the longest duration (141.61 ms), the obliquity index is 2.86. Also, the maximum value of the present obliquity index (2.86) is in good quantitative agreement with an earlier report by Westheimer (2003). Using the method of constant stimuli and successive stimulus presentations, as was done in the present study, Westheimer (2003) observed an obliquity index of 2.69.

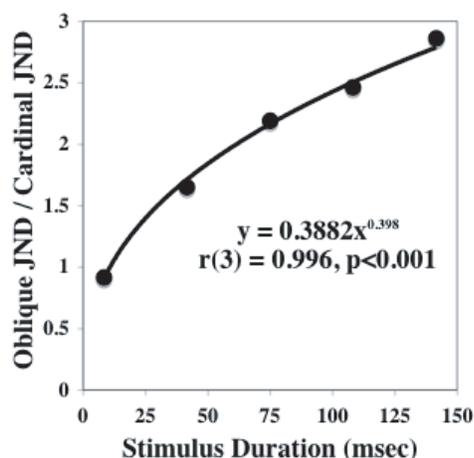


Figure 4. Obliquity index. Thresholds from Figure 3 are re-plotted here as the obliquity index: the ratio of oblique thresholds to cardinal thresholds. The best-fitting power function exposes the dynamic nature of the oblique effect in orientation sensitivity, which grows across the range of stimulus durations tested here.

Experiment 3: Method

Twenty Denison University students were recruited for Experiment 3, which was conducted to determine whether the neural events occurring at particular periods of the

stimulus sequence were essential for generating the oblique effect. To accomplish this, we systematically included and excluded masks from the stimulus sequence shown in Figure 1.

In total, there were six different mask configurations in Experiment 3. The first of these – the “all” condition – comprised the sequence of stimulation shown in Figure 1 (i.e., all four masks were presented). The second configuration – the “none” condition – was the opposite extreme, having no masks in the stimulus sequence. The “backward” condition comprised only the masks immediately following each Gabor patch (i.e., masks 2 and 4). Conversely, only masks 1 and 3, which immediately preceded the Gabor patches, were shown in the “forward” condition. Lastly, the “outer” condition comprised the first and last masks (1 and 4), and the “inner” condition comprised masks 2 and 3. These six different mask configurations were crossed with two axes (cardinal and oblique), making 12 stimulus conditions. In each trial block, the 12 stimulus conditions were presented 4 times (2 clockwise trials and 2 anti-clockwise trials) making a total of 48 trials per block. The 48 trials were randomly re-sequenced in each trial block, and each participant completed 10 such blocks. Unlike the preceding experiments, only a single stimulus duration (108.29 ms, 13 frames) was used in Experiment 3.

The data analysis consisted of *t* tests used to determine whether cardinal and oblique sensitivity differed significantly from each other in each of the six mask conditions. We also conducted various post hoc ANOVAs (see Results) to determine which mask configurations and which individual masks were most effective in disrupting orientation sensitivity overall. In all other ways, the method for Experiment 3 was the same as for Experiment 1.

Experiment 3: Results

The data from Experiment 3 are shown in the three panels of Figure 5. In each panel, orientation sensitivity (d') is plotted for a pair of mask conditions, and the gray numbers beneath the abscissa indicate the masks from Figure 1 that pertain to each condition. The parameter is axis (cardinal = blue open columns; oblique = red dashed columns). The most obvious feature in the data is the salience of the oblique effect (blue bars greater than red bars) across the mask conditions. Indeed, cardinal sensitivity significantly exceeds oblique sensitivity in each condition, $t(19) \geq 6.75$, two tailed, $p < .001$. Moreover, oblique sensitivity ranges between just 16.0% (inner mask condition) and 37.1% (outer mask condition) of cardinal sensitivity. Because the supremacy of cardinal sensitivity was consistent across the six mask conditions, it is not obvious that the oblique effect requires neural events occurring at one particular ordinal position within the stimulus sequence. It appears, instead, that the oblique effect in orientation sensitivity for successively presented stimuli can be generated from whatever neural events are able to survive the masks.

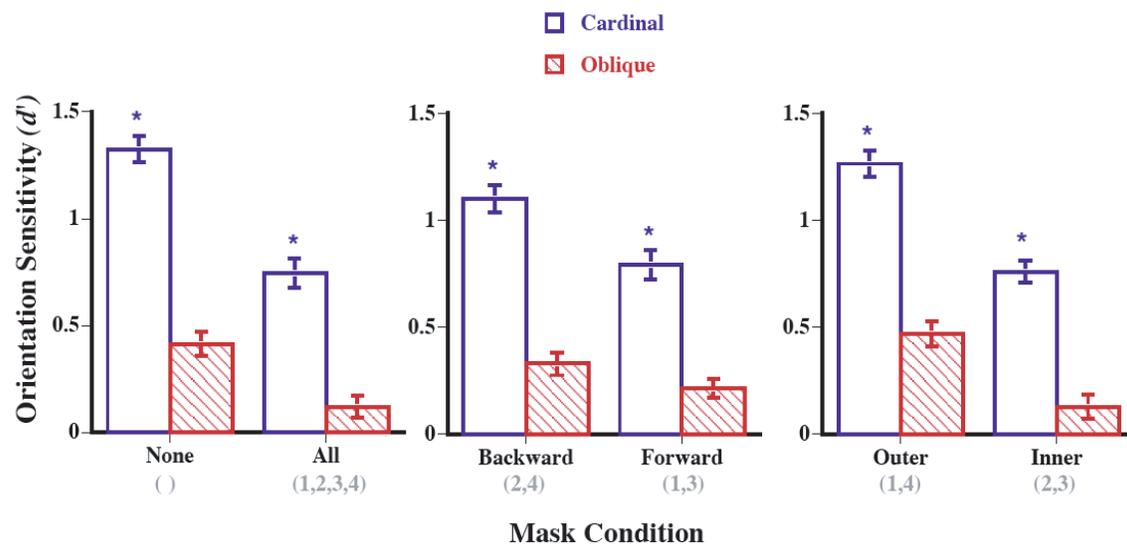


Figure 5. Data from Experiment 3. In each of the three panels, the mask condition on the right (all, forward, and inner) generated significantly reduced orientation sensitivity relative to the mask condition on the left (none, backward, and outer). The gray numbers beneath the abscissa indicate the masks from Figure 1 that pertain to each mask condition. In each mask condition, the oblique effect is readily seen, indicating the robustness of the oblique effect when stimuli are presented sequentially.

The finding that the oblique effect was robust across mask conditions cannot be explained by a general failure of the mask conditions to differentially affect orientation sensitivity overall. In fact, within each of the three panels in Figure 5, the mask condition on the right significantly reduced orientation sensitivity relative to the mask condition on the left. Specifically, orientation sensitivity overall was significantly lower in the “all” condition than in the “none” condition, $F(1,19) = 54.10$, $p < .001$; significantly lower in the “forward” condition than in the “backward” condition, $F(1,19) = 18.39$, $p < .001$; and, significantly lower in the “inner” condition than in the “outer” condition, $F(1,19) = 56.98$, $p < .001$. Despite these significant pairwise differences in mask conditions, the oblique effect remained.

Which of the four masks (see Figure 1) was most effective in impairing orientation sensitivity overall? Masks 1 and 4 (the outer masks) can be eliminated from consideration because a post hoc test indicated that orientation sensitivity was no worse, $F(1,19) = 0.002$, $p = .96$, *ns*, in the “outer” condition than when there were no masks at all (“none” condition). Masks 2 and 3 (the inner masks) are plausible candidates because a post hoc test indicated that performance was just as poor when masks 2 and 3 were presented as when all four masks were presented, $F(1,19) = 0.073$, $p = .79$, *ns*. Finally, because masks 1 and 3 (“forward” condition) were significantly more disruptive than masks 2 and 4 (“backward” condition), and because masks 1 and 4 (“outer” condition) were not disruptive, it appears that mask 3 generated the greatest impairment. We note, however, that the present analysis provides only an

indirect comparison of the four masks. A firm conclusion on the relative effectiveness of each mask requires further experimentation.

Experiment 4: Method

The robust oblique effect in Experiment 3 occurred when the two stimuli on each trial were presented *successively*. Also, only one stimulus duration was tested in Experiment 3. In Experiment 4, we investigated the oblique effect when the two stimuli on each trial were presented *simultaneously*, and several stimulus durations were tested.

Sixteen Denison University students were recruited for Experiment 4. On each trial, the participants viewed two simultaneously presented, horizontally offset Gabor patches and indicated whether the one on the right was oriented “clockwise” or “anti-clockwise” to the one on the left. The two Gabor patches were laterally separated from each other by 1 deg at the nearest edges, and each Gabor patch was 4 deg in diameter (i.e., centered 2.5 deg from fixation). The masks that preceded and followed each of the Gabor patches were also 4 deg in diameter.

Procedurally, each participant began Experiment 4 by completing a threshold-estimation phase. Thresholds were estimated using a method nearly identical to that described in Experiment 2. The only difference was that in Experiment 4, the threshold-estimation phase entailed just a single stimulus duration (83.30 ms, 10 frames). For each participant, the average of the cardinal and oblique thresholds obtained in the threshold-estimation phase was used as the angular difference to be judged at each of several durations during the actual trials.

For the actual trials, each participant was randomly assigned to one of two groups. Half of the participants viewed masked stimuli, and the other half viewed unmasked stimuli. Except for the presence or absence of the mask, the procedure was identical for the two groups. All participants completed ten 72-trial blocks. Each 72-trial block comprised eight presentations (2 cardinal/clockwise; 2 cardinal/anti-clockwise; 2 oblique/clockwise; 2 oblique/anti-clockwise) at each of nine stimulus durations. The nine stimulus durations, which varied randomly across trials, ranged between 16.66 and 83.30 ms (2 and 10 frames) in 8.33-ms (1 frame) steps. As in Experiment 1, the participant's initial angular difference was decreased or increased by 25% after a block in which performance respectively exceeded 80% correct or fell below 65% correct. Such adjustments prevented "floor" and "ceiling" effects, and pertained to cardinal and oblique axes alike to ensure identical angular differences in both conditions.

The data were analyzed via ANOVA. The within-subjects factors were orientation (cardinal versus oblique) and stimulus duration (16.66 to 83.30 ms, in 8.33-ms steps). The between-subjects factor was the presence/absence of a mask. Additionally, as in Experiment 1, we computed best-fitting power functions and Pearson correlation coefficients to describe the extent to which cardinal and oblique orientation sensitivity (d') each depend on duration. In all other ways, the method for Experiment 4 was the same as in Experiment 1.

Experiment 4: Results

The results from Experiment 4 are shown in Figure 6, where the conventions differ from those of previous figures. Here data from participants in the mask group are shown in red, and data from participants in the no-mask group are shown in blue. Perhaps the most striking feature for both groups is the absence of an oblique effect. That is, within each group, the overlap between cardinal (squares and solid lines) and oblique (Xs and dotted lines) sensitivity is readily apparent. Indeed, ANOVAs confirmed that cardinal and oblique sensitivity (d') are statistically indistinguishable from each other in the no-mask group, $F(1,7) = 0.011, p = 0.91, ns$, and in the mask group, $F(1,7) = 0.240, p = .63, ns$. Although the two groups are similar in showing no oblique effect, there are important differences. First, as is visually evident in the figure, the overall performance of the no-mask group significantly exceeds that of the mask group, $F(1,14) = 21.40, p < .001$. Also, performance in the no-mask group is already excellent at the earliest stimulus duration (mean $d' = 1.06 \pm 0.10$ at 16.66 ms), and does not improve with increases in stimulus duration. By contrast, performance in the mask group increases significantly across the stimulus durations, yet fails to reach the levels of the no-mask group even at the longest stimulus duration. These differences, we believe, suggest that the masks were effective in limiting the persistence of

oriented stimulation in the visual system. Most importantly, the data in Figure 6, which obtained when the two stimuli were presented simultaneously, contrast sharply with the salient oblique effects in Experiments 1, 2, and 3, when the stimuli were presented successively. The difference suggests that the neural events occurring between stimulus presentations can contribute to the oblique effect in orientation sensitivity.

- No Mask Cardinal $y = 1.017x^{0.017}$ $r(7) = 0.159, n.s.$
- x-- No Mask Oblique $y = 0.840x^{0.067}$ $r(7) = 0.522, n.s.$
- Mask Cardinal $y = 0.245x^{0.286}$ $r(7) = 0.821, p < 0.01$
- x-- Mask Oblique $y = 0.103x^{0.506}$ $r(7) = 0.912, p < 0.01$

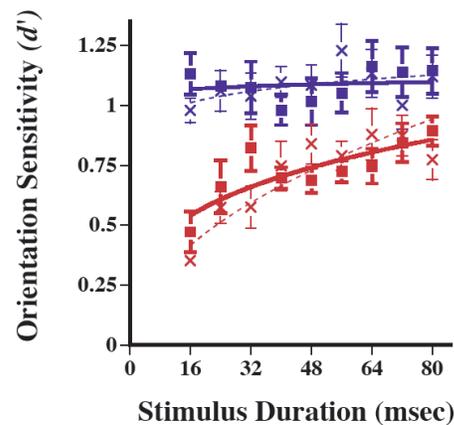


Figure 6. Data from Experiment 4. The gratings in Experiment 4 were presented simultaneously rather than successively. At each stimulus duration, orientation sensitivity (d') in the unmasked group (blue) exceeds that in the masked group (red), indicating the overall suppressive effect of the masks. For the unmasked group, performance is already excellent at the briefest stimulus duration (16.66 ms) and remains constant across stimulus durations. By contrast, performance in the masked group increases significantly with stimulus duration. For both the masked and unmasked groups, cardinal (squares and solid lines) and oblique (Xs and dotted lines) sensitivity superimpose across durations. This indicates that the oblique effect is absent across durations when the stimuli are presented simultaneously.

Because Experiment 4 was conducted in a between-subjects manner (unlike Experiments 1, 2, and 3), it is possible that the between-group differences in Figure 6 reflect preexisting group differences, rather than a mask effect. Preexisting group differences are unlikely, however, given the data shown in Figure 7 from our threshold-estimation phase. (Recall that in the threshold-estimation phase, masked stimuli were shown to all participants, including those who would subsequently not have masks in the main experiment, i.e., the no-mask group.) The psychometric functions from the mask (red) and no-mask (blue) groups clearly superimpose, and this is true for both the cardinal

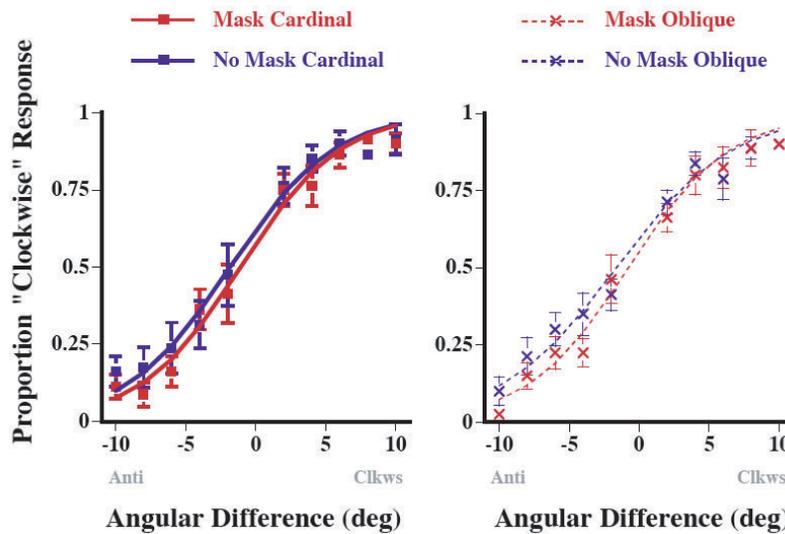


Figure 7. Initial group equivalence in Experiment 4. The participants' initial angular thresholds were tested using masked stimuli. The two grating stimuli on each trial were simultaneously presented for 83.30 ms throughout this initial phase. The mean proportion of clockwise responses is plotted against angular differences, separately for the groups that would subsequently judge masked (red) and unmasked (blue) stimuli. The psychometric functions for these two groups superimpose in both the cardinal condition (left panel, squares and solid lines) and the oblique condition (right panel, Xs and dotted lines). This initial comparability implies that the between-group differences evident in Figure 6 are due to mask effects, and not to preexisting differences between the two groups.

(left panel) and oblique (right panel) conditions. Indeed, ANOVAs confirmed that thresholds from the no-mask and mask groups are statistically indistinguishable from each other in the cardinal condition, $F(1,14) = 0.024, p = .87, ns$, and in the oblique condition, $F(1,14) = 1.01, p = 0.33, ns$. Moreover, a separate ANOVA confirmed that after combining across groups, oblique thresholds were statistically indistinguishable from cardinal thresholds, $F(1,15) = 2.90, p = .10, ns$. Thus, the data from the threshold-estimation phase rule out preexisting differences between the groups, and also replicate the main finding from Experiment 4 - that the oblique effect is reduced when the stimuli are presented simultaneously.

Relative to simultaneously presented stimuli, do successively presented stimuli generate a large oblique effect because of increased cardinal sensitivity, or decreased oblique sensitivity, or both? We addressed this question by comparing data from Experiment 4 (simultaneous stimulation) to data from Experiment 1 (successive stimulation). To ensure a fair comparison, the data from Experiment 4 were exclusively from the "mask" group, because masks had also been present in Experiment 1. Additionally, we analyzed only those data from stimulus durations that were common to both experiments. The results from our analysis are depicted in Figure 8. As is evident from visual inspection, there is a significant interaction between the axis and simultaneity variables, $F(1,29)=12.50, p = .001$. Given this significant interaction, we assessed the simple effect of the simultaneity variable separately at each axis. At the cardinal axis, orientation sensitivity is statistically indistinguishable

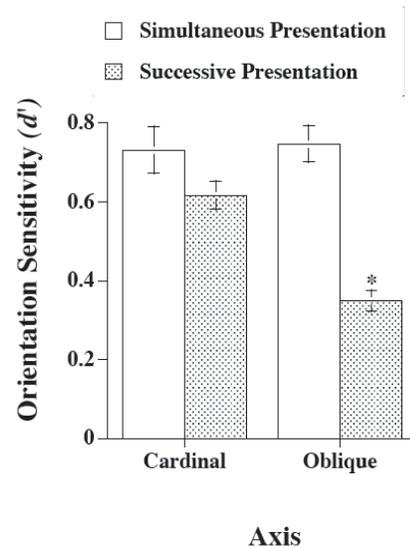


Figure 8. The interaction between simultaneity and axis. Orientation sensitivity (d') is statistically indistinguishable in the simultaneous (open bars) and successive (filled bars) groups at the cardinal axis (left). By contrast, at the oblique axis, orientation sensitivity (d') is significantly lower in the successive group than in the simultaneous group (right). This interaction between simultaneity and axis demonstrates that the oblique effect in orientation sensitivity reflects a decline in oblique sensitivity, rather than an enhancement in cardinal sensitivity.

in the simultaneous and successive groups, $F(1,29)=2.791$, $p = .10$, *ns*. By contrast, at the oblique axis, orientation sensitivity is significantly lower in the successive group than in the simultaneous group, $F(1,29)=55.40$, $p < .001$. Therefore, relative to simultaneously presented stimuli, the large oblique effect for successively presented stimuli reflects a reduction in oblique orientation sensitivity, not an enhancement in cardinal orientation sensitivity.

Discussion

This study was conducted to provide new information about the time course of the oblique effect in orientation judgments. Participants judged subtle orientation differences between two gratings, each of which was preceded and followed by a mask to limit neural persistence. When the two gratings were presented successively and each for just 8.33 ms, the ability to judge subtle (4 deg) orientation differences was already reliably better than chance. At this brief duration, performance was comparable around cardinal and oblique axes. The oblique effect emerged only at *subsequent* stimulus durations and continued to increase with stimulus duration. That finding obtained in both [Experiment 1](#) and [2](#) despite methodological differences. The robustness of the oblique effect for successively presented gratings was further demonstrated in [Experiment 3](#) when cardinal sensitivity significantly exceeded oblique sensitivity across six different mask configurations. However, in [Experiment 4](#), the oblique effect was eliminated when the gratings were presented simultaneously. Relative to the simultaneously presented stimuli, the successively presented stimuli generated a significant reduction in oblique orientation sensitivity, rather than an enhancement in cardinal orientation sensitivity. To summarize, in the present study the oblique effect was found only for successively presented stimuli, and developed across the tens of milliseconds *after* reliable (if modest) orientation sensitivity occurred. We will consider each of these points in turn.

One of our findings is that the oblique effect under successive stimulation significantly exceeded that under simultaneous stimulation ([Figure 8](#)). In principle, that difference could be attributable to factors other than successive versus simultaneous stimulation. This is because, relative to the successive condition, stimuli in the simultaneous condition were smaller and positioned further from fixation, and the oblique effect decreases with decreasing stimulus size (Vandenbussche, Orban, & Maes, 1983; Vogels, Orban, & Vandenbussche, 1984; Matthews & Welch, 1997) and decreases with eccentricity (Vandenbussche, Vogels, & Orban, 1986). However, Furmanski and Engel (2000) found a salient oblique effect using simultaneously presented stimuli that were even smaller (3 vs. 4 deg) and centered even further from fixation (4.5 vs. 2.5 deg) than those in the present simultaneous condition. That finding (Furmanski & Engel, 2000) makes it unlikely that size and

eccentricity can explain the absence of an oblique effect in the present simultaneous condition. One possible explanation for the different findings obtained in the present simultaneous condition versus those obtained by Furmanski and Engel (2000) is stimulus duration. Although the mechanism by which stimulus duration influences the oblique effect is not yet clear, across studies there is a clear correlation between the duration of simultaneously presented stimuli and the magnitude of the oblique effect. Specifically, the oblique effect was absent when our stimuli were presented simultaneously for 83.30 ms or less, whereas Furmanski and Engel (2000) found a salient oblique effect when the simultaneously presented stimuli lasted for 1,000 ms. Moreover, Westheimer (2003) presented stimuli simultaneously for an intermediate duration (300 ms) and found an oblique effect less than that reported by Furmanski and Engel (2000), yet greater than that of the present simultaneous condition.

Our finding that the oblique effect is significantly stronger for successive than for simultaneous presentations is consistent with previous studies in which the two presentation types were directly compared (Heeley & Buchanan-Smith, 1992; Westheimer, 2003).² Additionally, the present data replicate the earlier finding (Heeley & Buchanan-Smith, 1992) that the comparatively large oblique effect under successive stimulation reflects a significant decrease in oblique sensitivity and a more modest decrease in cardinal sensitivity (Heeley & Buchanan-Smith, 1992). Why would *either* cardinal or oblique sensitivity decrease under successive stimulation? To address this question, we will consider the present psychophysical masking data within the context of a recent physiological study (Orban & Vogels, 1998) that explored the neural differences underlying successive versus simultaneous orientation discrimination.

Orban and Vogels (1998) found that successive and simultaneous orientation discrimination tasks differentially affected PET data from the right fusiform gyrus of humans, and differentially affected the behavioral performance of monkeys with infero-temporal-cortex lesions. Moreover, single-cell recordings from the monkeys (Orban & Vogels, 1998) suggested that infero-temporal neurons contribute to both maintaining a memory trace of the first stimulus, and comparing the second stimulus to that memory trace. Although we do not attempt to pinpoint a neural locus from our psychophysical data, we note that the pattern of results across our mask conditions implicates the memory trace discussed in Orban and Vogels's (1998) physiological study. In particular, our "inner" masks, which preceded and followed the 500-ms ISI and were therefore temporally positioned to affect the memory trace, were especially effective at disrupting orientation sensitivity. Indeed, orientation sensitivity was statistically indistinguishable in the "inner" and "all" mask conditions, indicating that masks 2 and 3 (the "inner" masks) were as disruptive as all four masks. By contrast, masks 1 and 4 (the "outer" masks) were not temporally positioned to disrupt the memory trace and did not

impair the participants' behavior; performance in the "outer" mask condition was statistically indistinguishable from that when there were no masks at all. The ineffectiveness of the outer masks argues against the possibility that the reduced orientation sensitivity under successive stimulation arises from neural events occurring *after* the second stimulus presentation. Instead, the present psychophysical data implicate the neural events occurring *between* the first and second stimulus presentations (i.e., the interval over which Orban & Vogels's, 1998, memory trace would occur).³

The finding that the right fusiform gyrus and inferotemporal cortex are associated with successive orientation discrimination (Orban & Vogels, 1998) does not rule out the possibility that earlier visual areas contribute to the oblique effect in orientation discrimination. Indeed, Furmanski and Engel (2000) recently showed that the pattern of fMRI activity in V1 correlated strongly with the psychophysically observed oblique effect in orientation discrimination, even for simultaneously presented stimuli. Because Furmanski and Engel (2000) investigated only a single, relatively long stimulus duration (1,000 ms), their data could reflect either a steady-state overrepresentation of cardinal tuned V1 neurons (Mansfield, 1974) or a cardinal bias in the recently documented dynamics of V1 orientation tuning (Ringach et al., 1997). If there were a cardinal oriented bias in the dynamics of V1 orientation tuning, one would expect the oblique effect in orientation discrimination to increase with increasing stimulus duration. As noted earlier, that prediction has been confirmed for simultaneously presented stimuli by analyzing data across studies that used different stimulus durations (i.e., the present Experiment 4; Westheimer, 2003; Furmanski & Engel, 2000). Additionally, within the present study, the oblique effect also increased with stimulus duration for successively presented stimuli in Experiment 1 and 2. This is the topic to which we now turn.

The main finding in the present study is that, for successive presentations, the oblique effect increases with stimulus duration. This temporal summation is reminiscent of earlier psychophysical data that demonstrated the role of spatial summation. In particular, several studies have shown that the oblique effect (Vandenbussche et al., 1983; Vogels et al., 1984; Matthews & Welch, 1997), like orientation sensitivity in general (Matthews & Welch, 1997; Li, Thier, & Wehrhahn 2000; Henrie & Shapley, 2001), increases with stimulus size. We believe that the present psychophysical demonstration of the oblique effect as a dynamic phenomenon is particularly interesting given that the oblique effect is often attributed to a cause that is presumably static - namely, the overrepresentation of cardinal tuned neurons in V1 (Mansfield, 1974).

Additionally, the present study's time-dependent increases in *overall* orientation sensitivity are consistent with the claim by Ringach et al. (1997), based on the dynamics of V1-cell activity, that orientation sensitivity reflects more than a bank of static oriented filters. This is evident not

only in the present power functions that show d' increasing with stimulus duration, but also when considering the present study's briefest stimulus duration (8.33 ms). At that duration, although sensitivity to a 4-deg difference was reliably better than chance ($d' = 0.20, \pm 0.05$), sensitivity to 45 deg differences was excellent ($d' = 0.89, \pm 0.11$). Because the stimulus duration was constant in those small-angle and wide-angle conditions, the performance difference cannot be explained by a general inability to respond well to brief stimuli. Similarly, a duration-related limit in neural response strength cannot account for the data, because the duration was identical in the small-angle and wide-angle conditions (8.33 ms), and those two conditions generated very different levels of performance. Instead the performance difference must be attributed to a limit in angular resolution early in the dynamics of orientation tuning, as suggested by the physiological work of Ringach et al. (1997).

Can the dynamics of orientation tuning be hastened with practice? If so, one might expect the stimulus duration at which the oblique effect first emerges to be briefer for trained participants than for naïve participants. This would imply that the obliquity index, when plotted as a function of stimulus duration (as in the present Figure 4), would be more steeply sloped for trained participants than for naïve participants. Consistent with a practice-based hastening of orientation tuning, Karni and Sagi (1993) have shown that, with extensive training, participants can make accurate judgments about large orientation differences (90 deg) at briefer and briefer stimulus durations. However, it is also known that for subtle orientation judgments, practice improves angular resolution at oblique axes but *not* at cardinal axes (Vogels & Orban, 1985; Matthews & Welch, 1997). Therefore, the obliquity index operates over a more restricted range for trained participants than for naïve participants. Given these different obliquity ranges, it is not obvious whether the slope of the obliquity index in the present Figure 4 - based on the present naïve participants - would differ meaningfully from that of trained participants.

Finally, much physiological (Ferster, Chung, & Wheat, 1996; Shapley, Hawken, & Ringach, 2003) and computational (Somers, Nelson, & Sur, 1995; Sompolinsky & Shapley, 1997; McLaughlin, Shapley, Shelley, & Wielaard, 2000; Pugh, Ringach, Shapley, & Shelley, 2000) work on orientation sensitivity has addressed so-called "feedforward" and "feedback" mechanisms. The feedforward mechanism, which was originally proposed by Hubel and Wiesel (1962, 1968), generates orientation sensitivity through spatially aligned LGN-cell inputs to cortical cells. By contrast, feedback mechanisms generate orientation sensitivity through recurrent excitation and inhibition that sharpen a neuron's orientation tuning. This recurrent excitation and inhibition could occur in circuits that are entirely within the cortex (Somers et al., 1995), or perhaps in the reciprocal projections from the cortex to LGN (Murphy, Duckett, & Silleto, 1999). Although our psychophysical data cannot directly distinguish feedforward from feedback contributions, the

finding that both overall performance and the oblique effect increased with stimulus duration may seem more intuitively consistent with feedback mechanisms. After all, it is only the feedback mechanisms that require multiple, time-intensive network iterations. However, to the extent that increases in stimulus duration improve the reliability of the responses in LGN, the improved feedforward input from LGN could also contribute to better performance at the behavioral level. Moreover, although many cortical cells are orientation-tuned and LGN cells are not, it is possible that feedforward connections from LGN are more numerous or more efficient cardinally than obliquely. There is a further reason, too, for remaining agnostic about the neural locus of the oblique effect. Although there is evidence that implicates V1 in the oblique effect (Mansfield, 1974; Furmanski & Engel, 2000), Westheimer (2003) discovered a salient oblique effect in orientation judgments even when the stimuli comprised implicit⁴ lines “connecting” two circles. Presumably, neither the implicit lines nor the explicitly presented circles generated strong, orientation-specific responses in V1 cells. That observation, and the reduced oblique effect for successive versus simultaneous presentations, led Westheimer (2003) to speculate that some neural influences on orientation discrimination might occur in areas later than V1, and may be memory-related. That speculation is consistent with the above-described physiological data from Orban and Vogels (1998) and with the present psychophysical finding that orientation sensitivity is most disrupted by masks in the interval over which Orban and Vogels’s (1998) memory trace would occur.

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Footnotes

¹To determine whether orientation sensitivity was reliably greater than zero, we conducted one-sample *t* tests with zero as the test value. The obtained statistics were $t(22) = 3.78$, $p = .001$ for the cardinal condition and $t(22) = 5.09$, $p < .001$ for the oblique condition.

²It should be noted that Westheimer (2003) found that the oblique effect in orientation sensitivity was not completely eliminated when the stimuli were simultaneously presented. Instead, the obliquity index (i.e., the ratio of oblique to cardinal thresholds) changed from 2.69 to 1.40 when the stimulus presentation changed from successive to simultaneous.

³In the Results for Experiment 3, we suggested that mask 3 was more disruptive than mask 2 for overall orientation sensitivity. Why might this be the case? As a speculation, the memory trace would presumably be weaker at the end of the retention interval (near mask 3) than at the beginning (near mask 2), because memory decays over time. Given that masks 2 and 3 had the same physical contrast (89.76%), it stands to reason that performance would be most disrupted (pushed closest to $d' = 0$) by whichever mask occurred when the memory trace was weakest. In other words, a weak memory trace may be less able than a strong memory trace to “withstand” an 89.76% contrast mask. A more direct test of masks 2 and 3, however, is necessary to confirm this speculation.

⁴Westheimer’s (2003) implicit lines were imaginary, and unlike illusory contours, such as those seen in Kanizsa figures, did not generate percepts.

References

- Appelle, S. (1972). Perception and discrimination as a function of stimulus orientation: The oblique effect in man and animals. *Psychological Bulletin*, 78, 266-278. [PubMed]
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 433-436. [PubMed]
- Ferster, D., Chung, S., & Wheat, H. (1996). Orientation selectivity of thalamic input to simple cells of cat visual cortex. *Nature*, 380(6571), 249-252. [PubMed]
- Furmanski, C. S., & Engel, S. A. (2000). An oblique effect in human primary visual cortex. *Nature Neuroscience*, 3(6), 535-536. [PubMed]
- Green, D. M., & Swets, J. W. (1966). *Signal detection theory and psychophysics*. New York: Wiley.
- Heeley, D. W., & Buchanan-Smith, H. M. (1992). Orientation acuity estimated with simultaneous and successive procedures. *Spatial Vision*, 6(1), 1-10. [PubMed]
- Henrie, J. A., & Shapley, R. M. (2001). The relatively small decline in orientation acuity as stimulus size decreases. *Vision Research*, 41(13), 1723-1733. [PubMed]
- Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interactions and functional architecture of the cat’s visual cortex. *Journal of Physiology (London)*, 160, 106-154. [PubMed]
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology (London)*, 195, 215-243. [PubMed]
- Karni, A., & Sagi, D. (1993). The time course of learning a visual skill. *Nature*, 365(6443), 250-252. [PubMed]
- Li, W., Thier, P., & Wehrhahn, C. (2000). Contextual influence on orientation discrimination of humans and responses of neurons in V1 of alert monkeys. *Journal of Neurophysiology*, 83(2), 941-954. [PubMed]

- Mach, E. (1861). Ueber das Sehen von Lagen und Winken durch die Bewegung des Auges. Ein Beitrag zur Psychophysik. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, Wien*, 43(2), 215-224.
- Mansfield, R. (1974). Neural basis of orientation perception in primate vision. *Science*, 186, 1133-1135. [[PubMed](#)]
- Matthews, N., Liu, Z., Geesaman, B., & Qian, N. (1999). Perceptual learning on orientation and direction discrimination. *Vision Research*, 39(22), 3692-3701. [[PubMed](#)]
- Matthews, N., & Welch, L. (1997). Velocity-dependent improvements in single-dot direction discrimination. *Perception & Psychophysics*, 59, 60-72. [[PubMed](#)]
- McLaughlin, D., Shapley R., Shelley M., & Wielaard, D. J. (2000). A neuronal network model of macaque primary visual cortex. VI. Orientation selectivity and dynamics in the input layer 4Calpha. *Proceedings of the National Academy of Sciences U.S.A.*, 97(14), 8087-8092. [[PubMed](#)][[Article](#)]
- Murphy, P. C., Duckett S. G., & Sillito, A. M. (1999). Feedback connections to the lateral geniculate nucleus and cortical response properties. *Science*, 286(5444), 1552-1554. [[PubMed](#)]
- Orban, G. A., & Vogels, R. (1998). The neuronal machinery involved in successive orientation discrimination. *Progress in Neurobiology*, 55, 117-147. [[PubMed](#)]
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437-442. [[PubMed](#)]
- Pugh, M. C., Ringach, D. L., Shapley, R., & Shelley, M. J. (2000). Computational modeling of orientation tuning dynamics in monkey primary visual cortex. *Journal of Computational Neuroscience*, 2, 143-159. [[PubMed](#)]
- Ringach, D. L., Hawken, M. J., & Shapley, R. (1997). Dynamics of orientation tuning in macaque primary visual cortex. *Nature*, 387(6630), 281-284. [[PubMed](#)]
- Shapley, R., Hawken, M., & Ringach, D. L. (2003). Dynamics of orientation selectivity in the primary visual cortex and the importance of cortical inhibition. *Neuron*, 38(5), 689-699. [[PubMed](#)]
- Somers, D. C., Nelson, S. B., & Sur, M. (1995). An emergent model of orientation selectivity in cat visual cortical simple cells. *Journal of Neuroscience*, 8, 5448-5465. [[PubMed](#)]
- Sompolinsky, H., & Shapley, R. (1997). New perspectives on the mechanisms for orientation selectivity. *Current Opinion in Neurobiology*, 4, 514-522. [[PubMed](#)]
- Vandenbussche, E., Orban, G. A., & Maes, H. (1983). Influence of line length on the orientation discrimination of the cat. *Archives Internationales de Physiologie et de Biochimie*, 91, 25.
- Vandenbussche, E., Vogels, R., & Orban, G. A. (1986). Human orientation discrimination: Changes with eccentricity in normal and amblyopic vision. *Investigative Ophthalmology Visual Science*, 27(2), 237-245. [[PubMed](#)]
- Vogels, R., & Orban, G. A. (1985). The effect of practice on the oblique effect in line orientation judgments. *Vision Research*, 25, 1679-1687. [[PubMed](#)]
- Vogels, R., Orban, G. A., & Vandenbussche, E. (1984). Meridional variations in orientation discrimination in normal and amblyopic vision. *Investigative Ophthalmology & Visual Science*, 25, 720-728. [[PubMed](#)]
- Westheimer, G. (2003). Meridional anisotropy in visual processing: Implications for the neural site of the oblique effect. *Vision Research*, 43(22), 2281-2289. [[PubMed](#)]