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## Rapid communication

## An inverse oblique effect in human vision

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**Abstract**

In the classic oblique effect contrast detection thresholds, orientation discrimination thresholds, and other psychophysical measures are found to be smallest for vertical or horizontal stimuli and significantly higher for stimuli near the  $\pm 45^\circ$  obliques. Here we report a novel inverse oblique effect in which thresholds for detecting translational structure in random dot patterns [Glass, L. (1969). Moiré effect from random dots. *Nature*, 223, 578–580] are lowest for obliquely oriented structure and higher for either horizontal or vertical structure. Area summation experiments provide evidence that this results from larger pooling areas for oblique orientations in these patterns. The results can be explained quantitatively by a model for complex cells in which the final filtering stage in a filter–rectify–filter sequence is of significantly larger area for oblique orientations. © 2001 Elsevier Science Ltd. All rights reserved.

*Keywords:* Inverse oblique effect; Oblique orientations; Contrast detection thresholds

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**1. Introduction**

Evidence has accumulated for over a century that the visual system of humans and many other animals is more sensitive to contour stimulation at vertical ( $0^\circ$ ) or horizontal ( $90^\circ$ ) orientations than to stimulation at the  $\pm 45^\circ$  obliques (Jastrow, 1893; Higgins & Stultz, 1950; Appelle, 1972; Heeley & Timney, 1988). This classic oblique effect manifests itself in grating sensitivity, orientation discrimination, and a variety of other tasks. Recent fMRI data indicate that the classic oblique effect is present in primary visual cortex (V1) (Furmanski & Engel, 2000), thus corroborating physiological evidence that a higher percentage of V1 neurons are tuned to horizontal and vertical than to the obliques (Mansfield, 1974; Chapman & Bonhoeffer, 1998; Coppola, White, Fitzpatrick, & Purves, 1998). Here we report a novel inverse oblique effect in which sensitivity to spatial structure in translational Glass patterns (Glass, 1969; Glass & Prez, 1973) is greater when the

dots carrying the structure are oriented at the obliques rather than at either  $0$  or  $90^\circ$ . This effect can be easily demonstrated by examining one of these patterns (Fig. 1) and then rotating it by  $45^\circ$ , which will cause the underlying spatial structure to become considerably more salient. Our experiments show that this inverse oblique effect for translational Glass patterns can be explained quantitatively by enlarged second stage pooling areas in a common model of complex cells (Movshon, Thompson, & Tolhurst, 1978; Wilson & Wilkinson, 1998).

**2. Methods**

All patterns were presented on a Macintosh IIfx computer with resolution of  $640 \times 480$  pixels and a frame rate of 67 Hz. At the viewing distance of 1.0 m each pixel subtended 1.0 arc min. Patterns were presented as white dots on a uniform gray background with mean luminance of 46 cd/m<sup>2</sup>.

Thresholds for detecting structure in random dot Glass patterns were measured using a two-interval

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forced choice procedure with 164-ms presentations to preclude multiple fixations. In the main experiments the patterns consisted of 6% dot density, with each dot being 1.0 arc min in diameter. Pairs of signal dots separated by 10.0 arc min were placed at random positions but with the same pair orientation, and the remainder of the dots were placed at random, thus forming non-oriented noise. The noise pattern, presented in the other interval, comprised the same percentage of dot pairs but randomly oriented, with the remainder of the pattern filled with noise dots. Overall pattern diameter was 4.27°. The percentage of signal dots required to detect the pattern orientation signal was measured in separate experiments at orientations from 0° up to 157.5° in 22.5° steps. In each experiment, a Quick (1974) or Weibull (1951) function was fit to the percentage correct data using a maximum likelihood procedure, and thresholds were defined as the 75% correct point estimated from this fit. All other experimental details have been reported elsewhere (Wilson, Wilkinson, & Asaad, 1997; Wilson & Wilkinson, 1998).

Basic data were obtained on three subjects, and key results were replicated on a fourth. Of these, one subject had never before participated in psychophysical research and was naive to the purposes of these experiments. A second subject, although a sophisticated psychophysical observer, had never previously participated in experiments using Glass patterns as stimuli.

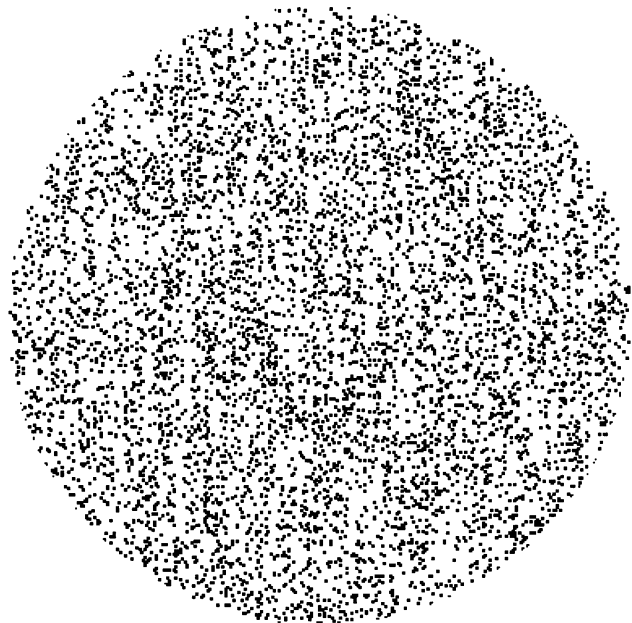


Fig. 1. Translational Glass pattern (Glass, 1969; Glass & Prez, 1973) comprising 70% signal dots and 30% noise. When viewed upright the translational structure is difficult to discern. Rotation of the page by  $\pm 45^\circ$ , however, renders the now oblique translational structure salient. This demonstrates the inverse oblique effect.

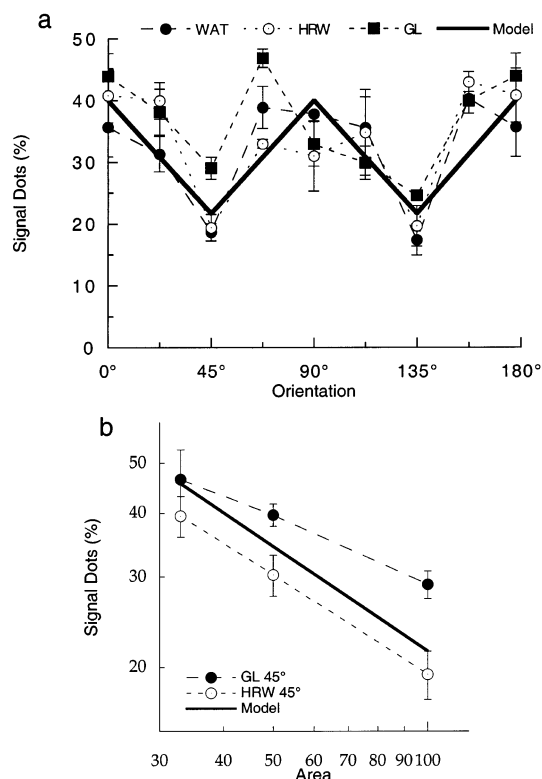


Fig. 2. Thresholds for detection of translational structure as a function of signal dot orientation and pattern area containing signal dots. (a) For all subjects thresholds for detecting translational structure were lowest at 45 and 135° signal orientations and considerably higher at 0° (vertical) and 90° (horizontal). This is the inverse of the pattern found in the classic oblique effect. (b) As the pattern area containing signal dots decreased, thresholds rose as a power function of area with exponents of  $-0.64$  (HRW) and  $-0.43$  (GL). Predictions of the complex cell model described in the text are indicated by a heavy line in each panel. Error bars plot S.E.

### 3. Results

In the major experiment, thresholds were measured for detecting translational or parallel structure in Glass (1969) patterns as a function of translational pattern orientation. Each experiment was repeated three times, and means and S.E. are plotted in Fig. 2a. It is apparent that all three subjects were able to discriminate the globally structured dot pattern from noise with the smallest percentage of oriented signal dots at orientations of 45 and 135°, and all subjects showed consistently higher thresholds at orientations at or near 0 and 90°. Thresholds for the principal meridians averaged 39% signal dots, while those for the obliques averaged 21% signal dots. Statistical analysis showed that threshold differences between the principal meridians and the obliques were highly significant ( $t_{10} = 5.81$ ,  $P < 0.0002$ ). One subject (GL) produced the highest thresholds at 67.5° rather than at either 0 or 90°, but he still showed pronounced discrimination minima at 45 and 135°. A fourth subject, tested at only 0, 45, 90, and 135°, produced the same data pattern.

In control experiments, the classic oblique effect was measured using a D6 (sixth spatial derivative of a Gaussian function; Swanson, Wilson, & Giese, 1984) with peak spatial frequency of 8.0 cpd. One experiment measured contrast detection thresholds for these patterns, while the second measured orientation discrimination at 100% contrast. All measurements were made using a two-interval forced choice procedure, and temporal presentations were 164 ms in duration. All subjects exhibited the classic oblique effect for both tasks. Across subjects, contrast detection thresholds averaged 8.75% for horizontal and vertical and 14.68% for 45° patterns. Similarly, orientation discrimination thresholds averaged 0.86° for the principal meridians but rose to 2.53° at 45°. Thus, the novel inverse oblique effect with translational Glass patterns occurred in subjects showing the traditional oblique effect for both contrast detection and orientation discrimination.

Additional control experiments investigated the effects of varying total dot density and signal dot spacing. The inverse oblique effect was obtained for densities from 6 to 12% and for signal dot spacings from 7 to 14 arc min, although the inverse oblique effect weakened at lower dot densities. In a separate experiment, viewing distance in the standard condition was doubled, but the inverse oblique effect persisted. Thus, the inverse oblique effect is robust to parameter variations.

In previous research we had found that thresholds for vertical or horizontal translational Glass patterns were significantly higher than for concentric or radial Glass patterns (Wilson et al., 1997; Wilson & Wilkinson, 1998). Area summation experiments in those studies showed that the high thresholds for horizontal or vertical translational patterns resulted from visual pooling of orientation information over a restricted area of

the pattern. Accordingly, we repeated these experiments using translational patterns oriented at 45°. Signal dots were limited to a band through the center of the pattern comprising either 50 or else 33% of the total area, all remaining area of the pattern being filled with noise dots at the same density. Experiments in which the signal dot band was parallel or else perpendicular to signal dot orientation produced indistinguishable data. The data plotted in Fig. 2b demonstrate that signal thresholds decrease with increasing signal dot area. Power functions fit to the data produced exponents of  $-0.64$  (HRW) and  $-0.43$  (GL). In contrast, comparable experiments with vertical Glass patterns produced slopes close to zero for all subjects over the same area range (Wilson et al., 1997). This provides evidence that the visual system pools information over a broader area in oblique than in vertical translational Glass patterns.

A final experiment investigated whether the visual system could pool  $+45^\circ$  signal dots in one half of the pattern and  $-45^\circ$  signal dots in the other half. This 'Glass Chevron' pattern is depicted schematically in the upper right corner of Fig. 3, where lines have been used to emphasize the orientation of the signal dot pairs in the two halves of the pattern (dots, not lines, were used to convey signal in the actual experiment). As the data in Fig. 3 show, thresholds rose by an average of 70% for the chevron pattern compared to a full field with a single oblique orientation, thus indicating that opposite obliques are not pooled by the visual system. In addition, these data provide further evidence that the visual system pools a single oblique orientation over a large pattern area, as reduction of the pattern area for a single oblique to 50% in these chevron patterns raised thresholds precipitously, as also observed in Fig. 2b.

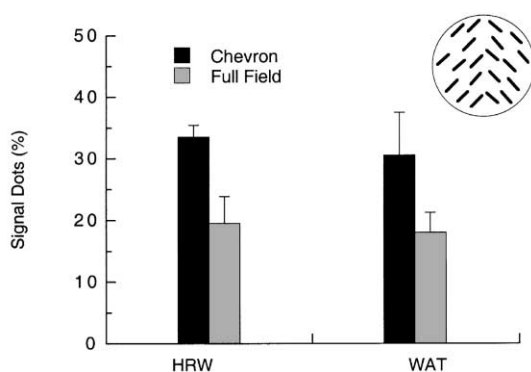


Fig. 3. Thresholds for Glass chevron patterns compared with full field oblique translational Glass patterns. As depicted in the upper right inset, a Glass chevron contains 45° oblique signal structure on one side and  $-45^\circ$  signal structure on the opposite side. (Signal dot pairs are shown by oblique lines for clarity only; actual experiments involved only dots as described in Section 2.) Thresholds averaged 70% higher for chevron than for full field translational Glass patterns, thus indicating that the visual system cannot pool both oblique orientations at the same time. Error bars plot S.E.

#### 4. Neural model

What neural processes might explain the inverse oblique effect? In an effort to obtain an answer, we applied a standard complex cell model (Movshon et al., 1978; Wilson & Wilkinson, 1998) to our patterns. This model consists of simple-cell filtering at a single orientation followed by full-wave rectification and a final pooling stage defined by a circularly symmetric Gaussian filter  $G(R)$ :

$$G(R) = \exp(-R^2/\sigma^2) \quad (1)$$

where  $R$  is radius and  $\sigma$  is the space constant. Parameters for the oriented simple cell filter were obtained from previous masking experiments and are tabulated elsewhere (Wilson, 1991). We have previously shown that this model can quantitatively account for horizontal or vertical translational Glass pattern thresholds if  $\sigma = 0.65^\circ$  (Wilson & Wilkinson, 1998). Only two changes were made to this complex cell model in order

to explain the inverse oblique effect. First, the simple cell filter was rotated from vertical to  $45^\circ$  and the sensitivity reduced to 40% of the value for a vertical filter, thus incorporating the higher detection thresholds of the classic oblique effect (also see below). Second, the final pooling stage defined by  $G(R)$  was increased in area by setting  $\sigma = 1.5^\circ$ . This produced an increase in the second stage pooling area by a factor of 5.3, which was found to produce the best fit to the inverse oblique effect data. Model responses to translational Glass patterns were determined using Monte-Carlo techniques in which each Glass pattern was convolved with a  $256 \times 256$  array of model complex cells and the maximum model response within a central  $48 \times 48$  region was determined. (Restriction to maxima in this central region was necessary to avoid edge artifacts from the fast Fourier transforms used in the model computation.) Multiple examples of translational Glass patterns with different percentages of signal dots were presented, and the mean and S.D. of the maximum model responses were calculated from the results. Similarly, multiple noise patterns were presented and the model mean and S.D. again determined. From these data signal detection theory was used to determine the 75% correct threshold for the complex cell model to detect Glass pattern structure. This is exactly the same simulation procedure used previously for vertical translational Glass patterns, and further details may be found in Wilson and Wilkinson (1998). As shown by the solid line in Fig. 2a, the larger value of  $\sigma$  at the obliques generated thresholds approximately twice as low as at  $0$  or  $90^\circ$ . As observed by Morrone, Burr, and Vaina (1995) in analogous motion experiments, this results from the improved signal-to-noise ratio generated by pooling over a larger area at the obliques. Additional complex cell model simulations produced the area summation function shown by the heavy line in Fig. 2b. The model area summation result is fit by a power law with exponent of  $-0.68$ , comparable to the data for HRW but slightly steeper than those of GL.

As data summarized in the introduction suggest that the classic oblique effect likely results from a reduced number of V1 units with preferred orientations near  $\pm 45^\circ$ , it might be objected that the simple reduction in sensitivity of simple cells employed in the model is not appropriate. Accordingly, we ran a second simulation in which the number of model simple cells tuned to  $45^\circ$  was reduced to 25% of that at vertical or horizontal, but the sensitivity of individual oblique cells was equated to that of horizontals or verticals. This was accomplished by convolving obliquely oriented simple cells with the stimulus and then setting three of the four responses in each  $2 \times 2$  patch of the neural response matrix to zero. This is equivalent to having only 25% as many oblique units spaced twice as far apart in both spatial dimensions. All other aspects of the simulation, including size of the final summation area in Eq. (1) were identical. This simula-

tion produced reductions in both maximum responses and S.D., but the model threshold was almost unchanged (22.7% signal vs. 21.7% signal in the previous simulation). Our complex cell model of the inverse oblique effect is therefore insensitive to whether the classic oblique effect results from reduced oblique sensitivity or a dearth of oblique units.

## 5. Discussion

Our results suggest that the human visual system compensates in part for the lower sensitivity to oblique orientations (the classical oblique effect) by implementing larger pooling areas for complex cells that extract oblique structure from textures (the inverse oblique effect). Furthermore, a quantitative complex cell model simultaneously accounts for the higher contrast thresholds for detection of oblique patterns and the inverse oblique effect for suprathreshold dot patterns. Despite having a 2.5 times higher detection threshold, when patterns are above threshold the larger final pooling area enhances the signal-to-noise ratio of the model response, thus enhancing detection of pattern structure. The model works equally well on the assumption that only 25% as many cells are tuned to the obliques as to the cardinal orientations. It should be emphasized that the quantitative values of the model predictions in Fig. 2 are determined by the size of the final pooling area. This is because simple scaling of overall model sensitivity increases both response means and S.D., thus leaving the response signal-to-noise ratio unchanged. Thus, the complex cell model produces a good quantitative explanation of the human data.

Several physiological studies have provided evidence that the classical oblique effect may result from a preponderance of cells preferring horizontal and vertical orientations in striate cortex (V1) (Mansfield, 1974; Chapman & Bonhoeffer, 1998; Coppola et al., 1998). In addition, recent fMRI data have localized the oblique effect in human striate cortex, which is consistent with the physiology (Furmanski & Engel, 2000). Note, however, that this does not preclude explanations of the oblique effect as resulting in part from reduced sensitivity of V1 units with oblique orientations. In particular, the increased acuity for horizontal and vertical gratings in the fovea (Jastrow, 1893; Higgins & Stultz, 1950; Appelle, 1972) implies via the Nyquist theorem that there must be more neurons tuned to these orientations than to the obliques. This, however, need only be true at high spatial frequencies; significantly below the acuity limit it remains plausible that the classical oblique effect may reflect reduced sensitivities of V1 oblique units rather than reduced cell numbers. Future physiology may help to elucidate this point.

Schoups, Vogels, and Orban (1995) have reported a dramatic improvement in oblique orientation discrimination due to perceptual learning. This cannot explain the inverse oblique effect reported here, because equal numbers of experiments were conducted at each orientation to obtain the data in Fig. 2a. In addition, there was no evidence of improvement over the course of our experiments, which were conducted in random order. Furthermore, the fact that the inverse oblique effect is easily appreciated by rotating Fig. 1 indicates that it is a general property of the adult human visual system. Nevertheless, it would be interesting to determine whether extensive training might improve oblique Glass pattern thresholds still further. If so, it would suggest the possibility of a learning-based increase in the size of the second stage pooling filter for complex cells.

Strikingly, recent evoked potential measurements have obtained a stronger signal for oblique Cyclopean gratings generated by random dot stereograms (RDS) than for horizontal or vertical Cyclopean gratings (Regan, Hong, & Regan, 2000). As both RDS and Glass patterns involve extraction of structure from dot patterns, we speculate that analogous complex cell mechanisms may be involved in both. Indeed, physiological results indicate that RDS are processed almost exclusively by complex cells (Poggio, Motter, Squatrito, & Trotter, 1985). As recent fMRI evidence localizes the classical oblique effect in human V1 (Furmanski & Engel, 2000), it will be exciting to determine whether the inverse oblique effect is also found in V1 or whether the enlarged final spatial pooling stage reflects extra-striate processing, perhaps in V2.

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