

Psychology & Neuroscience

ISSN: 1984-3054 landeira@puc-rio.br

Pontifícia Universidade Católica do Rio de

Janeiro Brasil

Lupón-Bas, Núria; Torrents Gómez, Aurora; Cardona, Genís; da Silva, José Aparecido; Aznar-Casanova, J. Antonio

> New evidence of visual space anisotropy with autostereograms Psychology & Neuroscience, vol. 7, núm. 3, 2014, pp. 261-267 Pontifícia Universidade Católica do Rio de Janeiro Rio de Janeiro, Brasil

Available in: http://www.redalyc.org/articulo.oa?id=207032650004



Complete issue

More information about this article

Journal's homepage in redalyc.org



Scientific Information System

Network of Scientific Journals from Latin America, the Caribbean, Spain and Portugal Non-profit academic project, developed under the open access initiative



# New evidence of visual space anisotropy with autostereograms

Núria Lupón-Bas<sup>1</sup>, Aurora Torrents Gómez<sup>1</sup>, Genís Cardona<sup>1</sup>, José Aparecido da Silva<sup>2</sup>, and J. Antonio Aznar-Casanova<sup>3</sup>

- 1. Universitat Politècnica de Catalunya, Barcelona, Spain
- 2. Universidade de Sao Paulo, Ribeirao Preto, SP, Brazil
- 3. Universitat de Barcelona, Barcelona, Spain

#### **Abstract**

Numerous research efforts have been directed toward determining the origin of anisotropies of visual space, in contrast to real space. Recent neurophysiological studies have placed the origin in the primary visual cortex (V1) or beyond. The present study sought to provide new psychophysical evidence of the origin of these anisotropies using auto-stereograms as visual stimuli in a relative depth judgment task. The observers were presented with a hidden three-dimensional shape that consisted of two pairs of parallel line segments that were located in different depth planes and oriented at 0° (horizontal line segments), 45°, and 90° (vertical line segments). The influence of orientation on the visual performance of five observers was evaluated. The encountered differences at 45° compared with cardinal orientations revealed a non-conclusive trend toward a negative impact of oblique orientation on the observers' performance. Significant differences were found in accuracy between the horizontal and vertical orientations, and the best scores corresponded to vertical line segments. This finding may be interpreted as the expression of vertical-horizontal anisotropy in depth. The perception of hidden three-dimensional shapes in auto-stereograms occurs beyond the primary visual cortex in the dorsal stream, and the present findings provide psychophysical evidence of the location of vertical-horizontal anisotropy in non-retinotopic areas beyond V1. **Keywords**: auto-stereograms, depth perception, oblique effect, line orientation, vertical-horizontal anisotropy.

Received 12 January 2014; received in revised form 27 March 2014; accepted 28 March 2014. Available online 25 November 2014.

## Introduction

Research on stereoscopic three-dimensional (3D) vision has focused on questions regarding the ability of our visual system to perform accurate and precise depth distance judgments in both real and virtual environments (Loomis & Knapp, 2003). George Berkeley asserted in the 18th century that depth could not be directly perceived by the eyes because the retinal image of any object is two-dimensional (2D), such as in a painting. Pioneering research revealed that binocular disparity plays a major role in depth perception although other mechanisms are also involved. Indeed, other depth cues such as relative accommodation and convergence and

Núria Lupón-Bas, Aurora Torrents Gómez, Genís Cardona, Department of Optics and Optometry, Universitat Politècnica de Catalunya, Spain. José Aparecido da Silva, Department of Psychology and Education, Universidade de Sao Paulo, Ribeirao Preto, Brazil. J. Antonio Aznar-Casanova, Department of Basic Psychology, Faculty of Psychology, Universitat de Barcelona, Spain. Correspondence regarding this article should be addressed to: J. Antonio Aznar-Casanova, Facultad de Psicología, Universitat de Barcelona, Passeig de la Vall d'Hebron, 171, Barcelona, 08035, Spain. E-mail: jaznar2@ub.edu.

several visual and pictorial cues need to be integrated for our brain to construct a model of the physical world (i.e., Visual Space). However, our visual system employs a series of assumptions, omissions, and biases to build easily decipherable depth relationships based on 2D retinal images (Riener & Proffitt, 2002), resulting in frequent discrepancies between physical and perceived distances and leading to illusory effects such as the "oblique effect" and vertical-horizontal anisotropy.

The "oblique effect," broadly described in the literature (for review, see Appelle, 1972; Howard, 1982; Howard & Rogers, 2002; see also Mansfield & Ronner, 1978; Mustillo, Francis, Oross, Fox, & Orban, 1988; Buchanan-Smith & Heeley, 1993; Heeley, Buchanan-Smith, Cromwell, & Wright, 1997), is associated with a decrease in the visibility of slanted oriented patterns (e.g., lines, grids, and figures) compared with patterns that are oriented in or near cardinal axes (i.e., horizontally or vertically). This effect manifests itself during diverse visual tasks such as in Vernier and Landolt C visual acuity measurements (Coppola, Purves, McCoy, & Purves, 1998a), contrast sensitivity evaluation (Essock, 1982, 1990), and orientation and movement discrimination assessment (Xu, Collins, Haytin, Kass, & Casagrande, 2006), among others.

262 Lupón-Bas et al.

The "oblique effect" has been attributed to the presence of a larger number of nerve cells that are devoted to processing horizontal and vertical, rather than oblique, orientations (De Valois, Yund, & Hepler, 1982). Indeed, Furmanski and Engel (2000) employed magnetic resonance imaging of the primary visual cortex (V1) and observed stronger responses to cardinally oriented stimuli compared with obliquely oriented stimuli. Other authors refer to the abundance of horizontally and vertically oriented lines and structures in nature as a determining factor for our visual cortex to develop increased precision in the processing of these orientations (Keil & Cristobal, 2000; Nundy, Lotto, Coppola, Shimpi, & Purves, 2000). Despite these efforts, the origin of the "oblique effect" remains largely unexplained.

Vertical-horizontal illusion (VHI), the most frequently reported type of spatial anisotropy, is responsible for overestimating the length of a vertically oriented line segment compared with an identical horizontal line segment (Prinzmetal & Gettleman, 1993). Although the magnitude of vertical overestimation is relatively small (between 3% and 6%), it remains constant in all lineal drawings and paintings in which it has been traditionally explored (Proffitt & Caudek, 2003). Notably, a few researchers have described larger VHI-related discrepancies (between 20% and 40%) when studying this effect in real-world environments (Higashiyama & Ueyama, 1988).

Traditional explanations of the VHI include hypotheses about visual field shape (Künnapas, 1959), size-constancy scaling (Gregory, 1963), and a possible neurophysiological origin (Hubel & Wiesel, 1968). Furthermore, subsequent research indicated a heterogeneous distribution of either retinal receptors (De Valois and De Valois, 1988) or caudal intraparietal neurons in monkeys, which may play an active role in the perception of 3D shapes (Sakata, Tsutsui, & Taira, 2005). Additionally, a recent study by Aspell, Wattam-Bell, Atkinson, and Braddick (2010) revealed distinct cortical activation patterns in response to horizontal and vertical global visual textures. Other authors (Mannion, McDonald, & Clifford, 2009, 2010) reported substantial anisotropy in the primary visual cortex (V1, V2, V3, and V3A/B).

To summarize, visual space anisotropy may have its origin in retinotopic areas of the visual system (retina and V1). Although early advanced imaging techniques reported that anisotropy occurs only in V1 (Furmanski & Engel, 2000), subsequent studies indicate that this occurs beyond V1 (Liu & Pettigrew, 2003; Wang, Ding, & Yunokuchi, 2003).

The present study explored both the "oblique effect" and vertical-horizontal anisotropy using a psychophysics approach with the aid of auto-stereograms and single-image random-dot stereograms (SIRDSs). A SIRDS consists of a single 2D image that contains almost identical horizontally repeating patterns. When viewed with the proper vergence, a hidden 3D shape emerges from the plane of the stereogram (Tyler & Clarke 1990). SIRDSs prevent monocular cues from taking part in depth perception because the hidden shape in the stereogram

is only visible binocularly. This 3D perception occurs beyond the primary visual cortex in the dorsal stream, including V2, V3, V5, and caudal intraparietal areas (Stidwill & Fletcher, 2011). Therefore, depth perception in a SIRDS bypasses retinotopic areas and may be used to study the origin of visual field anisotropy. Indeed, if the "oblique effect" and vertical-horizontal anisotropy appear during SIRDS perception, then this finding would support the hypothesis that anisotropy originates beyond V1.

#### Methods

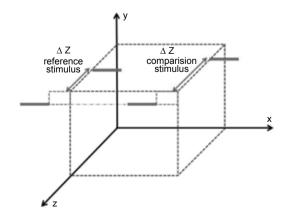
## **Participants**

A total of five subjects (two female, three male), ranging from 40 to 52 years of age, participated in the study. All of the participants had best-distance-corrected decimal visual acuity of 1 or better and stereoacuity of at least 60 arcsec measured with the TNO test. The participants provided written informed consent after the nature of the study was explained to them. The Declaration of Helsinki tenets of 1975 (revised in Tokyo in 2004) were followed throughout the study, which received approval from the Ethics Committee of the University of Barcelona.

## Stimuli and apparatus

The stimuli were 27 different SIRDSs that consisted of random dot-base patterns and a hidden 3D figure. The SIRDSs were generated using Stereogram Maker 2.1 software. A 17-inch TFT color monitor (1280  $\times$  768 resolution) was used for stimulus presentation. The viewing distance remained constant at 40 cm with the aid of a forehead and chin rest.

The hidden 3D shape followed the geometrical configuration shown in Figure 1, which consisted of two pairs of parallel line segments (i.e., reference and comparison stimuli) that were located at different distances (i.e., frontoparallel planes) from the observer. The line segments were presented at an orientation of 0°, 45°, or 90° with respect to the horizontal axis (x) and orthogonal to the depth axis (z). The SIRDS reference stimulus used in the present study, with line segments oriented at 45° with respect to the horizontal axis, is shown in Figure 2.



**Figure 1.** Geometrical configuration employed for the generation of the reference stimulus (left) and comparison stimuli (right). The line of observation follows the z axis.

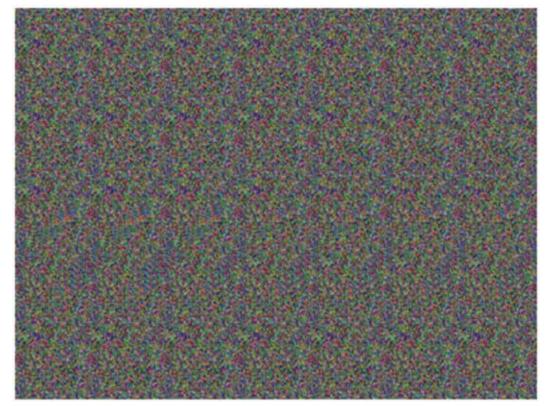


Figure 2. SIRDS that shows the reference stimulus with line segments oriented at 45° (i.e., oblique orientation).

The apparent depth of the hidden 3D shape with respect to the plane of the SIRDS was derived from depth mapping, a 2D-to-3D conversion technique based on the use of different gray levels (in increasing depth separation steps, ranging from 0 to 255 units). Thus, depth separation (\Delta Z) between reference stimulus line segments resulted from constant gray levels at 100 and 140 units, respectively, but the line segments of comparison stimuli presented nine possible different depth separation values, generated using a constant gray level of 100 in the first line segment and a variable gray level (from 120 to 160 units, in 5 unit steps) in the second line segment. Therefore, the reference stimuli provided a constant depth separation value of 40 gray levels, whereas the depth separation values ranged from 20 to 60 gray levels, in 5 unit steps, for the comparison stimuli. Stereogram Maker 2.1 software also provides the required information to allow determination of the relative depth of each part of a figure for a given value of interpupillary distance (IPD) and observation distance. Thus, although the relative depth of the reference stimulus was  $\Delta Z = 8.73$  mm, the relative depth of the comparison stimuli varied between 4.32 and 13.23 mm. These data are based on an average IPD of 62 mm, although the IPD values ranged from 58 to 69 mm, resulting in a difference of approximately 10% in perceived depth. However, given the current geometrical configuration, both the reference and comparison stimuli were similarly affected by these variations in IPD. Therefore, IPD differences should have no relevance in the evaluation of the influence of stimulus orientation on depth perception.

#### **Procedure**

The participants were tested for depth discrimination capability for different orientations using a psychophysical method of constant stimuli, with a two-alternative forced-choice (2AFC) experimental paradigm. They were asked to choose between two different options: greater or lesser separation of the oriented lines. The observers had to indicate, by pressing the right or left mouse button, whether the depth distances of the comparison stimuli were larger or smaller than those of the reference stimulus (relative depth judgments). For each of the three possible orientations, both the reference and comparison stimuli were simultaneously presented, with each of the nine possible depth distances of the comparison stimulus appearing randomly. The observers were provided with viewing strategies to facilitate SIRDS perception, consisting of relaxing their convergence beyond the plane of accommodation, which corresponded to the observation distance of 40 cm.

For each observer, six sets of trials per orientation were conducted, each consisting of randomly presenting all nine possible relative distances between the line segments of the comparison stimulus, with a fourfold repetition. Therefore, each participant performed a total of 648 depth judgment tasks (4 repetitions  $\times$  9 depths  $\times$  6 sets of trials  $\times$  3 orientations). Visual fatigue and attention decline can negatively influence the participants' performance. Therefore, such effects were avoided by limiting each experimental session to a maximum of three sets of trials, while allowing the participants to rest between sessions.

264 Lupón-Bas et al.

## Data analysis

Before the data analysis, the responses from all of the observers were pooled. A total of 1,080 data points were obtained per orientation (4 repetitions  $\times$  9 distances  $\times$  6 sets of trials  $\times$  5 observers) and fitted to a psychometric function in terms of the proportion of responses in which the participants considered the comparison stimulus to have larger depth separation than the reference stimulus. Data fitting, parameter determination, and reliability assessment were conducted within the framework of the Palamedes toolbox, a set of free Matlab routines designed by Prins and Kingdom (2009) for analyzing psychophysical data.

The psychometric Weibull function, defined by Equation 1, was found to display the best fit to our data, based on the criterion of maximum likelihood.

$$F_{W}(x;\alpha,\beta) = 1 - \exp\left(-\left(\frac{x}{\alpha}\right)^{\beta}\right)$$
 (Eq. 1)

In this Weibull function, x is a measure of the relative separation between line segments in the reference stimulus,  $\alpha$  refers to the location of the Point of Subjective Equality (PSE), and  $\beta$  is proportional to the slope of the function  $x = \alpha$ .

The present experimental settings assessed the visual performance of observers during depth judgment tasks in terms of accuracy and sensitivity, which were described by the  $\alpha$  and  $\beta$  parameters, respectively. Bootstrap analysis for 400 sets of data was also employed to determine the standard deviations (SDs) of the  $\alpha$  and  $\beta$  parameters and obtain a measure of goodness-of-fit (p > .05) within the Palamedes toolbox for MatLab.

#### Results

The experimental data points and best-fit Weibull functions for each orientation of the stimulus line segments are depicted in Figure 3.

The bootstrap analysis indicated a goodness-offit of the Weibull functions of p = .197, .007, and .133 for the horizontal, oblique, and vertical orientations, respectively, indicating that goodness-of-fit reliability was high for the cardinal orientations and poor for the oblique orientation of the stimulus line segments, which may indicate greater uncertainty in the responses of the observers at this orientation.

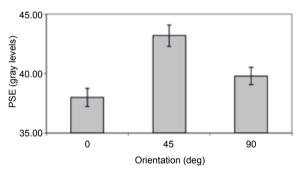
## Accuracy assessment

As previously stated, accuracy was defined by the  $\alpha$  (PSE) parameter of the Weibull function that fit the data for each particular orientation. A summary of the accuracy results is presented in Table 1, which also displays the corresponding SD values determined by bootstrap analysis and 95% confidence intervals (CIs; Figure 4).

**Table 1.** Weibull function  $\alpha$  parameter (PSE), standard deviation (SD) of  $\alpha$ , and 95% confidence interval (CI) for each orientation of the stimulus line segments.

Orientation	α (PSE) (gray levels)	SD of α (gray levels)	95% CI	
			Lower limit	Upper limit
0°	37.99	.38	37.23	38.75
45°	43.18	.45	42.29	44.08
90°	39.79	.37	39.05	40.53

## Accuracy in depth perception from SIRDS



**Figure 4.**  $\alpha$  parameter (PSE) and 95% confidence intervals of the Weibull function for each orientation of the stimulus line segments.

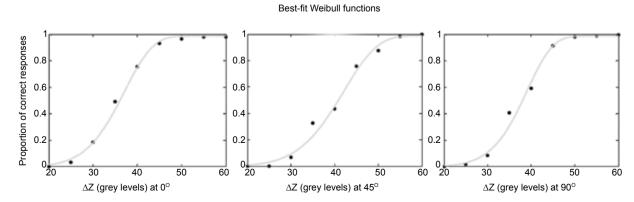


Figure 3. Best-fit Weibull functions for each orientation of the stimulus line segments. The proportion of correct responses (vertical axis) is plotted against the relative depth separation ( $\Delta Z$ ) between the comparison stimulus line segments, measured in gray levels (horizontal axis).

The accuracy of the observers when they judged relative depth distances was found to be significantly influenced by the orientation of the stimulus line segments. Although the poor goodness-of-fit at the 45° orientation prevented any inference regarding the presence or absence of the "oblique effect," the non-overlapping CIs for the horizontal and vertical orientations may be interpreted as a manifestation of vertical-horizontal anisotropy, with better accuracy scores for vertically (90°) oriented line segments than for horizontally (0°) oriented line segments.

Interestingly, the PSE values showed a trend toward underestimating the objective depth separation values between line segments at cardinal orientations (0° and 90°). Additionally, an apparent overestimation of the objective values was revealed for the oblique orientation, although the poor goodness-of-fit of the Weibull function for this orientation (p = .0007) undermines any firm interpretation of the present results, warranting further study.

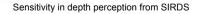
## Sensitivity assessment

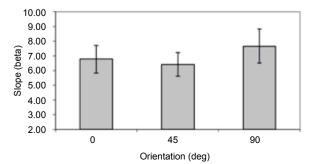
Sensitivity was defined by the  $\beta$  parameter of the Weibull function that fit the data for each particular orientation. A summary of these results is presented in Table 2, which also displays the corresponding SD values determined by bootstrap analysis and 95% CIs (Figure 5).

In contrast to the accuracy analysis, the observed overlapping of CIs failed to reveal any statistically significant influence of orientation on the sensitivity of the observers in the present depth judgment task.

**Table 2.** Weibull function  $\beta$  parameter, standard deviation (SD) of  $\beta$ , and 95% confidence interval (CI) for each orientation of the stimulus line segments.

Orientation	β		95% CI	
		SD of β	Lower limit	Upper limit
0°	6.78	.47	5.85	7.71
45°	6.42	.41	5.60	7.24
90°	7.66	.57	6.51	8.81





**Figure 5.** β parameter and 95% confidence intervals of the Weibull function for each orientation of the stimulus line segments.

## Discussion

The present study investigated the effect of stimulus orientation on the accuracy and sensitivity of observers in a depth-interval judgment task using auto-stereograms or SIRDSs, thus allowing for a novel, non-invasive, psychophysical approach to resolve the ongoing debate about the origin of visual space anisotropies, such as the "oblique effect" and vertical-horizontal anisotropy.

Interestingly, the goodness-of-fit of the selected Weibull psychometric function was acceptable only for cardinal orientations. The oblique orientation at 45° presented a significant deviation from best-fit. This finding may be interpreted as an influence of orientation on the responses of the observers (i.e., the possibility of different governing mechanisms for cardinal and oblique orientations).

In terms of accuracy, PSE values showed an overall underestimation of the actual relative depth values for the vertical and horizontal orientations of the target stimulus line segments, consistent with previous studies that utilized both virtual (Loomis & Knapp, 2003) and real (Loomis, da Silva, Fujita, & Fukusima, 1992) stimuli. Accuracy analyses revealed statistically significant differences between horizontally and vertically oriented line segments. These findings may be interpreted as a manifestation of verticalhorizontal anisotropy in depth judgment tasks, as first described in experimental settings similar to those used in the present study, for both virtual stimuli presented dichoptically (Torrents-Gomez, Cardona, & Aznar-Casanova, 2011b) and real stimuli (Torrents-Gomez, Aznar-Casanovam & Cardona, 2011a). The present findings also revealed statistically significant bias in the accuracy of the observers, with better results at the 90° orientation. The non-satisfactory goodness-of-fit for the oblique orientation of the stimuli proved detrimental for any firm conclusions to be drawn about the existence of the "oblique effect," albeit the analysis of visual performance outcomes indicated a tendency in that direction.

Sensitivity analysis revealed considerable interobserver variability (SD of approximately 7% in all orientations), which may be attributable to the choice of the parameters used in the present experimental settings, with relatively small depth differences ( $\Delta Z$ ) between the line segments of the comparison stimulus.

From a neurophysiological perspective, previous research uncovered a greater neural basis for the processing of visual information that is presented in a cardinal orientation rather than in an oblique orientation (Coppola, White, Fitzpatrick, & Purves, 1998b; Li, Peterson, & Freeman, 2003), with a correspondingly larger number of cells tuned for horizontal orientations than for vertical orientations (Furmanski & Engel, 2002; Liu & Pettigrew, 2003). Additionally, some authors have reported that only single cells in the cortex have orientation preference (Orban, Vanderbussche, & Vogels, 1984), whereas other researchers suggested that this orientation preference also occurs in complex cells

266 Lupón-Bas et al.

(Payne & Berman, 1983). Overall, the observed better visual performance for horizontal orientations remains partially unexplained, although some authors (Li et al., 2003) postulated a possible role in postural stability with reference to the horizontal line.

The present study explored visual space anisotropy in terms of its effect in a depth judgment task, indicating better accuracy for vertical rather than horizontal configurations of the stimuli. Parallel lines that contained a vertical line segment (90° orientation) displayed horizontal separation, as well as depth separation, thus requiring the observers to compare the line segments horizontally to judge their relative depth separation. The present findings revealed superior visual performance in depth judgment tasks when the target stimuli presented a horizontal rather than vertical separation between line segments (i.e., vertical over horizontal line segment configurations), which may result from the aforementioned neuronal preference for horizontal over vertical visual processing mechanisms. Additionally, daily life situations usually involve depth separation judgments about objects that present a horizontal separation and less frequently also vertical separation. Therefore, our participants had superior visual performance with experimental conditions that mimicked habitual depth assessment requirements.

The present findings may also be interpreted in the light of recent research by Mannion et al. (2010) on the human visual cortex response during the observation of vertically or horizontally oriented sinusoidal gratings in which a reduced response for the horizontal orientation of the target stimulus was reported. Similar to our experimental configuration, an horizontally oriented sinusoidal grating resulted in vertical contrast variations (i.e., required a vertical comparison task), whereas vertical gratings were associated with horizontal comparison tasks (and evoked larger cortical responses).

Finally, possible explanations for the origin of these anisotropies should be discussed because they are partly responsible for the heterogeneity of our visual space. Thus, from an ontogenetic perspective, developmental cognitive neuroscience predicts that mechanisms (i.e., neurons in the visual cortex that can detect interocular image disparities) must exist to construct psychophysical relationships and ensure a precise association between relative disparity distances in our retinal visual fields and real relative distances in the real world (Held, 1993). Furthermore, the origin of the "oblique effect" and vertical-horizontal anisotropies under study may be explained in terms of ontogenetic adjustment of the scaling for vertical and horizontal dimensions. Additionally, the "oblique effect" may derive from a combination of different scaling mechanisms for vertical and horizontal dimensions leading to larger perception errors. The rationale for this interpretation is the following. The finding of significant differences in accuracy between horizontal and vertical orientations (i.e., 0° and 90°) but no significant differences at 45° (i.e., oblique orientations) may suggest that the origin of vertical/horizontal anisotropy is in higher areas of the visual pathway. With regard to the oblique effect, however, given that the best scores corresponded to vertical rather than horizontal line segments, this result may suggest that the brain uses different scales to represent these two meridians (vertical and horizontal). In contrast, the slope of the oblique lines may be encoded from the vertical and horizontal rates that correspond to the end-points. Thus, one speculation is that combining the data from the two different scales (i.e., vertical and horizontal) may result is an increase in errors (i.e., imprecision) during depth estimation tasks.

In summary, the use of SIRDSs as a non-invasive, perceptual approach to the exploration of the origin of commonly encountered visual space anisotropies has not been previously described. The present findings support the hypothesis that the origin of these anisotropies is in non-retinotopic areas beyond V1.

# Acknowledgements

This work was supported by a grant from the Spanish Ministry of Economy and Competitiveness (MECOM; Ref. PSI-2012-35194).

## References

Appelle, S. (1972). Perception and discrimination as a function of orientation: the "oblique effect" in man and animals. *Psychological Bulletin*, 78, 266-278.

Aspell, J.E., Wattam-Bell, J., Atkinson, J., & Braddick, O.J. (2010). Differential human brain activation by vertical and horizontal global visual textures. *Experimental Brain Research*, 202(3), 669-679.

Buchanan-Smith, H.M., & Heeley, D.W. (1993). Anisotropic axes in orientation perception are not retinotopically mapped. *Perception*, 22, 1389-1402.

Coppola, D.M., Purves, H.R., McCoy, A.N., & Purves, D. (1998). The distribution of oriented contours in the real world. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 4002-4006.

Coppola, D.M., White, L.E., Fitzpatrick, D., & Purves, D. (1998). Unequal representation of cardinal and oblique contours in ferret visual cortex. Proceedings of the National Academy of Sciences of the United States of America, 95, 2621-2623.

De Valois, R.L., & De Valois, K.K. (1988). *Spatial vision*. New York: Oxford University Press.

De Valois, R.L., Yund, E.W., & Hepler, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research*, 22, 531-544.

Essock, E.A. (1990). The influence of stimulus length on the oblique effect of contrast sensitivity. *Vision Research*, 30, 1243-1246.

Essock, E.A. (1982). Anisotropies of perceived contrast and detection speed. *Vision Research*. 22, 1185-1191.

Furmanski, C.S., & Engel, S.A. (2000). An oblique effect in human primary visual cortex. *Nature Neuroscience*, *3*, 535-536.

Gregory, R.L. (1963). Distortion of visual space as inappropriate constancy scaling. *Nature*, 199, 678-680.

Heeley, D.W., Buchanan-Smith, H.M., Cromwell, J.A., & Wright, J.S. (1997). The oblique effect in orientation acuity. *Vision Research*, *31*(2), 235-242.

Held, R. (1993). Two stages in the development of binocular vision and eye alignment. In: K. Simon (Ed.), Early visual development, normal and abnormal (pp. 250-257). New York: Oxford University Press.

Higashiyama, A., & Ueyama, E. (1988). The perception of vertical and horizontal distances in outdoor settings. *Perception and Psychophysics*, 44, 151-156.

- Howard, I.P. (1982). Human visual orientation. New York: Wiley. Howard, I.P., & Rogers, B.J. (2002). Seeing in depth: depth perception (vol. 2). Toronto: I. Porteus.
- Hubel D.H., & Wiesel T.N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215-243.
- Keil, M.S., & Cristobal, G. (2000). Separating the chaff from the wheat: possible origins of the oblique effect. *Journal of the Optical Society of America*. A, Optics, Image Science, and Vision, 17, 697-710.
- Künnapas, T.M. (1959). The vertical-horizontal illusion in artificial visual fields. *Journal of Psychology: Interdisciplinary and Applied*, 47, 41-48.
- Li, B., Peterson, M.R., & Freeman, R.D. (2003). Oblique effect: a neural basis in the visual cortex. *Journal of Neurophysiology*, 90, 204-217.
- Liu, G.B., & Pettigrew, J.D. (2003). Orientation mosaic in barn owl's visual Wulst revealed by optical imaging: comparison with cat and monkey striate and extra-striate areas. *Brain Research*, 961, 153-158.
- Loomis, J.M., da Silva, J., Fujita, N., & Fukusima, S.S. (1992).
  Visual space perception and visually directed action. *Journal of Experimental Psychology: Human Perception and Performance*, 18(4), 906-921.
- Loomis, J.M., & Knapp, J.M. (2003). Visual perception of egocentric distance in real and virtual environments. In: L.J. Hettinger, & M.W. Haas (Eds.), Virtual and adaptive environments: application, implications, and human performance issues (pp. 21-46). Mahwah, NJ: Lawrence Erlbaum.
- Mannion, D.J., McDonald, J.S., & Clifford, C.W.G. (2009). Discrimination of the local orientation structure of spiral glass patterns early in human visual cortex. *Neuroimage*, 46(2), 511-515.
- Mannion, D.J., McDonald, J.S., & Clifford, C.W.G. (2010). Orientation anisotropies in human visual cortex. *Journal of Neurophysiology*, 103(6), 3465-3471.
- Mansfield, R.J.W., & Ronner, S.F. (1978). Orientation anisotropy in monkey visual cortex. *Brain Research*, 149, 229-234.
- Mustillo, P., Francis, E., Oross, S., 3rd, Fox, R., & Orban, G.A. (1988).
  Anisotropies in global stereoscopic orientation discrimination.
  Vision Research, 28, 1315-1321.
- Nundy, S., Lotto, B., Coppola, D., Shimpi, A., & Purves, D. (2000). Why are angles misperceived? Proceedings of National Academy of Sciences of the United States of America, 97(10), 5592-5597.

- Orban, G.A., Vandenbussche, E., & Vogels, R. (1984). Human orientation discrimination tested with long stimuli. *Vision Research*, 24, 121-128.
- Payne, B.R., & Berman, N. (1983). Functional organization of neurons in cat striate cortex: variations in preferred orientation and orientation selectivity with receptive-field type, ocular dominance, and location in visual-field map. *Journal of Neurophysiology*, 49, 1051-1072.
- Prins, N., & Kingdom, F.A.A. (2009). Palamedes: Matlab routines for analyzing psychophysical data. http://www.palamedestoolbox.org; accessed March 25, 2014.
- Prinzmetal, W., & Gettleman, L. (1993). Vertical-horizontal illusion: one eye is better than two. *Perception and Psychophysics*, 53(1), 81-88
- Proffitt, D.R., & Caudek, C. (2003). Depth perception and the perception of events (series title: Handbook of psychology, pp. 213-236). Hoboken, NJ: John Wiley.
- Riener, C., & Proffitt, D. (2002). Quantifying spatial presence. Paper presented at the Presence 2002 Conference: Fifth Annual International Workshop on Presence, Porto, Portugal.
- Sakata, H., Tsutsui, K., & Taira, M. (2005). Toward an understanding of the neural processing for 3D shape perception. *Neuropsychologia*, 43(2), 151-161.
- Stidwill, D., & Fletcher, R. (2011). Normal binocular vision: theory, investigation and practical aspects (pp. 152-171). Chichester: Blackwell.
- Torrents-Gomez, A., Aznar-Casanova, J.A., & Cardona, G. (2011a). Influence of background on precision of 3D depth judgment tasks in a real environment. *Perceptual and Motor Skills*, 113(3), 793-802.
- Torrents-Gomez, A., Cardona, G., & Aznar-Casanova, J.A. (2011b). The influence of background topography on stereo-acuity. *Anuario de Psicología*, 41, 9-20.
- Tyler, C.W., & Clarke, M.B. (1990). The autostereogram. *Proceedings of SPIE*, 1256, 182-197.
- Wang, G., Ding, S., & Yunokuchi, K. (2003). Difference in the representation of cardinal and oblique contours in cat visual cortex. *Neuroscience Letters*. 338, 77-81.
- Xu, X., Collins, C.E., Khaytin, I., Kass, J.H., & Casagrande, V.A. (2006). Unequal representation of cardinal vs. oblique orientations in the middle temporal visual area. *Proceedings of the National Academy of Scienes of the United States of America*, 103(46), 17490-17495.