

Attentional modulation interacts with orientation anisotropies in contrast perception

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Orientation perception is not comparable across all orientations—a phenomenon commonly referred to as the *oblique effect*. Here, we first assessed the interaction between stimulus contrast and the oblique effect. Specifically, we examined whether the impairment in behavioral performance for oblique versus cardinal orientations is best explained by a contrast or a response gain modulation of the contrast psychometric function. Results revealed a robust oblique effect, whereby asymptotic performance for oblique orientations was substantially lower than for cardinal orientations, which we interpret as the result of multiplicative attenuation of contrast responses for oblique orientations. Next, we assessed how orientation anisotropies interact with attention by measuring psychometric functions for orientations under low or high attentional load. Interestingly, attentional load affects the performance for cardinal and oblique orientations differently: While it multiplicatively attenuates contrast psychometric functions for both cardinal and oblique orientation conditions, the magnitude of this effect is greater for the obliques. Thus, having less attentional resources available seems to impair the response for oblique orientations to a larger degree than for cardinal orientations.

nally (0° or 90°) oriented stimuli can be judged with higher accuracy than obliquely ($\pm 45^\circ$) oriented edges, a perceptual anisotropy commonly referred to as the *oblique effect* (Annis & Frost, 1973; Appelle, 1972; Campbell & Kulikowski, 1966; Heeley, Buchanan-Smith, Cromwell, & Wright, 1997; Heeley & Timney, 1988; Orban, Vandebussche, & Vogels, 1984; Regan & Beverley, 1985). The oblique effect has been shown in a wide range of tasks, including contrast sensitivity (Camisa, Blake, & Lema, 1977; Campbell & Kulikowski, 1966; Campbell, Kulikowski, & Levinson, 1966; Williams, Boothe, Kiorpes, & Teller, 1981), orientation discrimination (Furmanski & Engel, 2000; Heeley & Timney, 1988; Regan & Beverley, 1985; Vogels & Orban, 1990), orientation selectivity (Campbell & Kulikowski, 1966; Orban et al., 1984), and reaction time (Bauer, Owens, Thomas, & Held, 1979; Essock, 1980). The oblique effect is typically believed to emerge from a combination of factors, many of which have early sensory origins, including an imbalance in strength between neural populations tuned for specific orientations, as well as an over-representation and narrower tuning of neurons preferring cardinal orientations (Appelle, 1972; Campbell et al., 1966; Campbell & Kulikowski, 1966; Chapman & Bonhoeffer, 1998; Coppola, White, Fitzpatrick, & Purves, 1998; De Valois, Yund, & Hepler, 1982; Li, Peterson, & Freeman, 2003; Mansfield, 1974; Rose & Blakemore, 1974; Williams et al., 1981). Previous work has attempted to link these neural signatures with the higher sensitivity, selectivity, and detection often found for cardinal orientations relative to obliques (Camisa et al., 1977;

Introduction

Our ability to discern edges and contours stands as a cornerstone property of human visual perception. However, perceptual performance is not equivalent across all stimulus orientations. Specifically, cardi-

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Campbell & Kulikowski, 1966; Furmanski & Engel, 2000; Heeley & Timney, 1988; Orban et al., 1984; Regan & Beverley, 1985; Vogels & Orban, 1990). While there is consensus that the neural properties of the visual system play a large role in the oblique effect (Li et al., 2003; Orban et al., 1984; Regan & Beverley, 1985), some have also suggested that the imbalance between neural populations within sensory cortices alone is not sufficient to explain this phenomenon; instead, it is likely that it is a multifactorial process with contributions from higher levels of processing (Heeley et al., 1997).

How does the oblique effect interact with stimulus intensity? While previous work has examined how orientation thresholds change as a function of contrast (Mareschal & Shapley, 2004; Reisbeck & Gegenfurtner, 1998; Webster, Switkes, & De Valois, 1990), little is known regarding the influence of stimulus contrast on orientation discrimination around cardinal and oblique orientations. In Experiment 1 we examined how the ability to discriminate a fixed orientation tilt around oblique and cardinal orientations changes across a range of contrasts. This allowed us to measure the psychometric function, which is believed to demonstrate a monotonic relationship between behavioral performance and the underlying neural contrast response function (Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010; Ling & Blake, 2012; Pestilli, Ling, & Carrasco, 2009). Specifically, changes in the neural contrast response function under this framework directly impacts an observer's ability to discriminate a stimulus, which would in turn be reflected in corresponding changes to the behavioral psychometric functions. We estimated behavioral contrast psychometric functions for both cardinal- and oblique-oriented gratings. Under our assumed framework, there are two possible gain mechanisms that could underlie the impaired visual sensitivity for oblique orientations: A response gain mechanism could multiplicatively attenuate the response, leading to a lowered asymptotic response and corresponding behavioral performance, or a contrast gain mechanism could modulate the dynamic range of the contrast response, shifting the semisaturation toward higher contrasts and resulting in a decrease in sensitivity (Martinez-Trujillo & Treue, 2002; Pestilli et al., 2009; Reynolds & Chelazzi, 2004; Reynolds, Chelazzi, & Desimone, 1999; Williford & Maunsell, 2006). The comparison between the model-estimated parameters for each orientation condition allowed us to directly assess whether the oblique effect is best expressed by an attenuation in either a contrast or a response gain mechanism, or both.

Despite the aforementioned orientation anisotropies, we rarely notice these imbalances in our day-to-

day interactions with our environment. What role does attention play in this? Attention is essential for human behavior; to maintain a coherent representation of our environment, our brain relies on attention to efficiently regulate between information in our environment and the limited cognitive resources available to us at any given moment. One way attention has been proposed to carry this out is by augmenting the strength of attended and unattended signals. Indeed, previous work has shown that attention alters the gain of individual neurons (Briggs, Mangun, & Usrey, 2013; Cohen & Maunsell, 2011; Desimone & Duncan, 1995; Luck, Chelazzi, Hillyard, & Desimone, 1997; Martinez-Trujillo & Treue, 2002; McAdams & Maunsell, 1999; Reynolds & Chelazzi, 2004; Reynolds, Pasternak, & Desimone, 2000; Treue, 2001; Williford & Maunsell, 2006), behavioral performance (Herrmann et al., 2010; Huang & Dobkins, 2005; Ling & Carrasco, 2006; Pestilli et al., 2009), and population responses measured using various neuroimaging techniques (Buracas & Boynton, 2007; Itthipuripat, Ester, Deering, & Serences, 2014; Ling, Jehee, & Pestilli, 2015; Ling, Pratte, & Tong, 2015). Interestingly, recent neuroimaging work has found that the magnitude of attentional modulation in the lateral geniculate nucleus (LGN) is critically dependent on stimulus orientation (Ling, Pratte, & Tong, 2015). Specifically, within the LGN oblique orientations yielded larger attentional effects than cardinal orientations—a pattern that was absent in primary visual cortex. This is consistent with electrophysiological evidence illustrating that neurons within this subcortical region are predominantly tuned for cardinal orientations (Cheong, Tailby, Solomon, & Martin, 2013; Piscopo, El-Danaf, Huberman, & Niell, 2013; Vidyasagar, Pei, & Volgushev, 1996; Viswanathan, Jayakumar, & Vidyasagar, 2011; Xu et al., 2001). Here, in a second experiment we explore whether the imbalance of attentional effects within the LGN might have an impact on behavior. Does the withdrawal of attention during orientation discrimination attenuate performance regardless of stimulus orientation, or could it have a larger effect on oblique orientations, overcoming the inherent inhomogeneities in orientation processing?

In Experiment 2 we used the oblique effect to examine the degree to which attentional load can modulate behavioral performance in discriminating a subtle tilt around an oriented stimulus. To do so, we measured contrast psychometric functions for oblique and cardinal orientations under high- and low-attentional-load conditions. Attentional load was manipulated using a dual-task design (Huang & Dobkins, 2005; Lavie, Beck, & Konstantinou, 2014; Lavie & Tsai, 1994; Lee, Itti, Koch, & Braun, 1999), allowing for a comparison of contrast psychometric

functions when full attentional resources were available for the orientation-discrimination task (low attentional load) compared to observers performing a dual task, withdrawing attentional resources away from the orientation-discrimination task (high attentional load). If the magnitude of attentional-load modulation interacts with stimulus orientation, we would expect to see larger attentional-load effects for oblique orientations, for which we have a poorer visual sensitivity, compared to cardinal orientations. We found evidence for a robust orientation-discrimination oblique effect, whereby contrast psychometric functions for oblique orientations were multiplicatively attenuated as contrast increased—a modulatory pattern consistent with a response gain mechanism. Moreover, we assessed how behavioral orientation anisotropies interact with attentional load by mapping the perceptual sensitivity for orientations under low- or high-attentional-load conditions. While attentional load affects the contrast psychometric functions for both cardinal and oblique orientations, the withdrawal of attentional resources seems to affect performance with obliquely oriented stimuli to a larger extent.

Experiment 1: Orientation anisotropies in contrast sensitivity

Methods

Participants

Seven healthy participants (four women, three men; mean age = 24.2 years, $SE = 1.56$) took part in this experiment. All participants had normal or corrected-to-normal vision and provided their informed consent. The Boston University Institutional Review Board approved the study. One participant was excluded from subsequent data analysis due to an inability to fit psychometric functions, due to a floor effect (fit $R^2 < 0.2$). Before the start of the experiment, verbal and written instruction on the experimental task were given. Participants were placed comfortably with their heads in a chin rest at a viewing distance of 57 cm from the screen, and were instructed to maintain steady fixation throughout all experimental trials.

Visual stimuli

The experiment was conducted in a dark room on a luminance-calibrated CRT screen (Sony Trinitron; $1,280 \times 1,024$ pixels, 60-Hz refresh rate). Visual stimuli were created using MATLAB (R2013a) in conjunction with the Psychophysics Toolbox-3 (Brainard, 1997;

Pelli, 1997) on a Mac Mini (OS X 10.9). Stimuli consisted of foveally presented oriented gratings with a spatial frequency of 7 c/°, a diameter of 4° of visual angle, and a randomized phase. The contrast of each stimulus varied from trial to trial; in total there were eight contrast levels (spaced from 1.5% to 80% Michelson contrast).

Orientation-threshold titration

In order to capture a suitable range of contrasts to estimate the full psychometric functions within each subject, we first ran a staircase procedure to customize the *orientation difference* used for the subsequent orientation-discrimination task (see later). Specifically, before the start of the experiment an orientation threshold was measured around an obliquely oriented grating at 60% Michelson contrast for each observer independently. Specifically, fine orientation-discrimination thresholds were estimated using two independent adaptive staircases (Watson & Pelli, 1983), which converged after 40 trials on an orientation difference that yielded 70% accuracy (individual orientation thresholds: $\mu = 2.87^\circ$, $SD = 1.24^\circ$). An auditory tone was played when the observer correctly indicated whether the grating was tilted (counter-) clockwise. As a reference for the orientation judgment, a small interrupted white line oriented at 45° was always presented outside the grating's visual-field position. Once the orientation threshold was established, we proceeded to the main experiment, in which this threshold was used as a fixed offset for all experimental conditions.

Procedure

Psychometric functions for all orientation conditions (0°, 90°, 45°, or 135°) were acquired by measuring accuracy using an orientation-discrimination task for each of the contrast levels. During a typical trial, participants were presented for 200 ms with a reference grating oriented either cardinally (0° or 90°) or obliquely (45° or 135°), which after a short interval (1000 ms) was followed by a test grating (200 ms) that had a fixed tilt relative to the reference grating (see Figure 1). The participant was required to make a button press to indicate whether this test grating was tilted clockwise or counterclockwise relative to the reference before the next trial would begin. An auditory tone was given as feedback for a correct response. In total, each participant performed 1,600 trials (randomly presented): 50 trials for each of the four orientations per contrast level; after collapsing within cardinal and oblique orientation conditions, this resulted in 100 trials per condition.

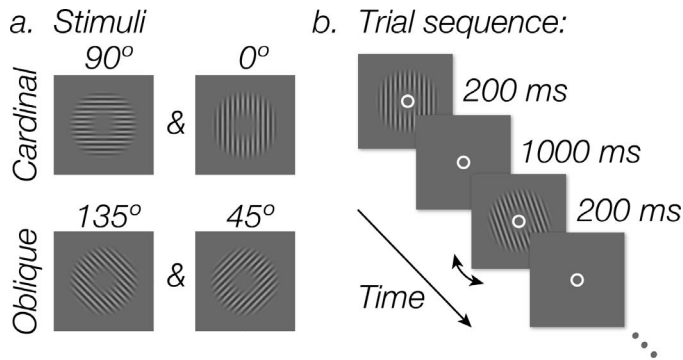


Figure 1. Experiment 1. (A) Example of the four differently oriented grating stimuli. Gratings could be either cardinally (0° or 90°) or obliquely (45° or 135°) oriented. (B) Example trial sequence. Participants viewed one of the four possible base orientations for a duration of 200 ms at the start of a trial. After a 1000-ms delay interval a test grating was presented for 200 ms, and the observer was required to indicate whether the test was rotated clockwise or counterclockwise relative to the reference grating. An auditory tone was given as feedback when the participant made a correct response. Stimuli are modified for illustrative purposes.

Analysis

Each observer's behavioral performance accuracy was computed for both cardinal and oblique orientations for each contrast level. The nonlinear relationship between contrast and behavioral responses is well described by a compressive nonlinearity, which is reflected as the Naka–Rushton contrast response function (Albrecht & Hamilton, 1982; Naka & Rushton, 1966):

$$R(c) = (R_{\max} - b) \frac{c^n}{c^n + C_{50}^n} + b, \quad (1)$$

where $R(c)$ is performance as a function of contrast, R_{\max} represents the level where the response saturates at high contrasts, C_{50} is the contrast intensity where the response has reached half of its maximum response, b is a constant reflecting baseline, and n represents the nonlinearity in the gain of the response to the input signal. The contrast response psychometric curves were estimated separately for both cardinal and oblique orientation conditions using MATLAB's `fminsearch` function by optimizing the parameter estimates for R_{\max} and C_{50} (using nonlinear least squares, with n constrained at 2.5, C_{50} constrained between 0 and 1, and b fixed at 0.5) for each individual participant. Prior to assessing psychometric functions, we determined that any observers with fits to either orientation condition with $R^2 < 0.2$ would be excluded from further analysis; based on this criterion, one observer was excluded from this experiment.

Results

Experiment 1 explored how orientation anisotropies interact with stimulus contrast by estimating psychometric functions separately for both oblique and cardinal stimulus conditions. Fitting these data with the Naka–Rushton contrast response function (Equation 1) allowed us to quantify how the oblique effect interacts with varying contrast intensities. There are two possible gain mechanisms that could explain the impaired visual sensitivity often reported for oblique orientations: A response gain mechanism will affect the R_{\max} parameter, multiplicatively attenuating the response, or a contrast gain mechanism will mainly affect the C_{50} parameter, modulating the dynamic range of the contrast response. The estimated parameters for each orientation condition allowed for a direct comparison of whether the oblique effect is best expressed by attenuation in either a contrast or a response gain mechanism, or both.

Results demonstrated a strong oblique effect; oblique orientations have a substantially attenuated psychometric function, particularly at higher contrast levels (see Figure 2). Behavioral performance for oblique orientations was lower compared to the estimated accuracy during the independent titration procedure. Although this can have multiple causes, this discrepancy likely arises due to differences in the orientation-discrimination procedures. Specifically, during the staircase procedure observers based their orientation discrimination on a reference line that was presented outside the grating's visual-field position. During the actual experiment, however, observers instead based their decision on the orientation of an earlier presented grating. To examine whether the performance difference between cardinal and oblique orientations is best explained by a contrast or a response gain mechanism, we compared the response-saturation and semisaturation-point parameters between each observer (average fits for all observers: cardinal $R^2 \mu = 0.93$, $SE = 0.04$; oblique $R^2 \mu = 0.52$, $SE = 0.11$). As illustrated in Figure 3, the oblique effect primarily interacts with the contrast psychometric function by means of a response gain mechanism. While the response saturation (R_{\max} parameter) is clearly distinct between the two orientation conditions (Figure 3a, paired t test, $t(5) = 11.82$, $p < 0.001$), the semisaturation point (C_{50} parameter), because it allows for a modulation in the dynamic range, is less affected (Figure 3b, paired t test, $t(5) = -1.14$, $p = 0.30$). In sum, these results demonstrate a robust oblique effect, consistent with a multiplicative attenuation of contrast responses for oblique orientations.

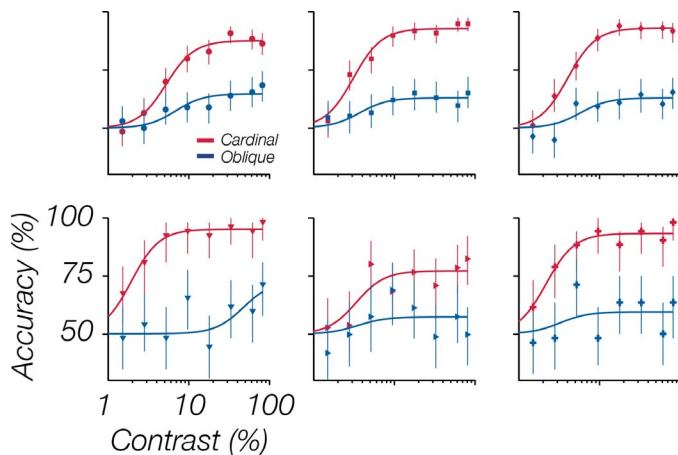


Figure 2. Results of Experiment 1. Psychometric functions for all observers. Data points reflect accuracy at each contrast level for both orientation conditions (cardinal = red, oblique = blue), and the curved lines represent the best fit. Error bars indicate the 95% bootstrap confidence interval.

Experiment 2: The influence of attentional load on orientation anisotropies

Does attentional load affect orientation discrimination of cardinal and oblique orientations differently? To test this, we measured psychometric functions for discriminating oblique and cardinal orientations, much like in Experiment 1, while varying the attentional load of the task. By estimating the contrast response for oblique and cardinal orientations while manipulating attentional load, we were able to quantify how attentional load interacts with the oblique effect. Namely, does the withdrawal of attentional resources affect the responses for both orientations equally, or does it impair responses for oblique orientations to a larger extent?

Methods

Participants

Fifteen healthy participants (eight women, seven men; mean age = 29.5 years, $SE = 1.68$) took part in this experiment. All participants had normal or corrected-to-normal vision and provided their informed consent. The Boston University Institutional Review Board approved the study. Six participants were excluded from subsequent data analyses due to such a profound oblique effect that we experienced either floor or ceiling effects across contrasts (model fit $R^2 < 0.2$; participants were excluded for ceiling effects when more than three

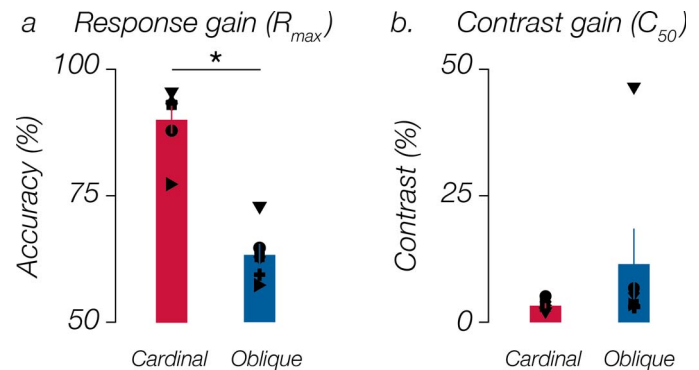


Figure 3. Average parameter estimates of Experiment 1. (A) Estimates for the R_{max} parameter for both cardinal (red) and oblique (blue) orientations. This parameter reflects the multiplicative attenuation of the response; cardinal orientations saturate at higher behavioral performance compared to oblique orientations. (B) Estimates for the C_{50} parameter for both cardinal and oblique orientations. Different symbols denote each individual observer ($N = 6$); error bars reflect ± 1 standard error of the mean.

contrast levels reached 100% accuracy in one of the experimental conditions). Before the start of the experiment, verbal and written instruction on the experimental task were given. Participants were placed comfortably with their heads in a chin rest at a viewing distance of 57 cm from the screen, and were instructed to maintain steady fixation throughout all experimental trials.

Visual stimuli

The experiment was conducted in a dark room on a luminance-calibrated CRT screen (Sony Trinitron; $1,280 \times 1,024$ pixels, 60-Hz refresh rate). Visual stimuli were created using MATLAB (R2013a) in conjunction with the Psychophysics Toolbox-3 (Brainard, 1997; Pelli, 1997) on a Mac Mini (OS X 10.9). Stimuli consisted of centrally presented oriented gratings with a spatial frequency of $7\text{ c}/^\circ$, a diameter of 4° of visual angle, and a randomized phase. The contrast of each stimulus varied from trial to trial; in total, there were nine contrast levels (for the first three participants, only six contrast levels were collected), spaced from 1.5% to 80% Michelson contrast.

Orientation-threshold titration

As in Experiment 1, we first ran a staircase procedure to customize the orientation difference used for the subsequent orientation-discrimination task (see later). Specifically, before the start of the experiment, an orientation threshold was measured around an obliquely oriented grating at 80% Michelson contrast for each subject independently to account for individ-

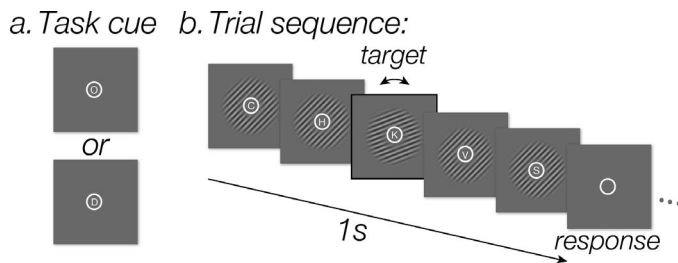


Figure 4. Experiment 2. (A) The beginning of a block would start with an *O* or *D* presented at fixation, prompting the observer whether they were required to perform a fine orientation-discrimination task (low attentional load) or whether they additionally had to report a target letter presented simultaneously with the orientation tilt (high attentional load). (B) Example trial sequence. Participants were presented with flickering gratings at one of the four possible base orientations (cardinal: 0° or 90° ; oblique: 45° or 135°) for a total duration of 1000 ms (5 Hz). The targets were always presented at the onset of the third grating in this sequence, and the observer was required to make a behavioral response. An auditory tone indicated the correct responses for both targets in the high-attentional-load task and the correct orientation discrimination in the low-attentional-load task. Stimuli are modified for illustrative purposes.

ual differences in visual sensitivity. Specifically, fine orientation-discrimination thresholds were estimated using two independent adaptive staircases (Watson & Pelli, 1983), which converged after 40 trials on an orientation tilt that yielded 80% accuracy (individual orientation thresholds: $\mu = 6.98^\circ$, $SD = 3.66^\circ$); an auditory tone was played when the observer correctly indicated whether the grating was tilted (counter-) clockwise. Observers based their decision of the tilt direction on obliquely oriented reference gratings presented before and after the appearance of the target, resulting in orientation thresholds which were larger compared to Experiment 1. The estimated orientation-discrimination angle around the oblique orientation was used as a fixed offset for all experimental conditions within this experiment.

Procedure

Psychometric functions were acquired by measuring orientation-discrimination accuracy while participants performed either a low- or a high-attentional-load task. During both attentional tasks, participants were asked to perform an orientation-discrimination task for each of the contrast levels (see Figure 4). In this experiment, participants were presented with flickering gratings (5 Hz) oriented either cardinally (0° or 90°) or obliquely (45° or 135°); the target grating was always the third grating in this sequence and had a fixed angular tilt (counter-) clockwise compared to the other gratings.

Depending on a cue presented at the beginning of a block of trials, participants were required to either attend to the target grating or attend to the grating and additionally pay attention to a rapid letter stream at fixation (presented at 10 Hz). In the high-attentional-load condition, one of two target letters (*j* or *k*) would appear at the same time as the target grating, while in the low-attentional-load condition no target letter appeared in the letter stream at fixation. At the end of a trial the participants indicated whether the target grating was rotated (counter-) clockwise and which target letter was presented (in the low-attentional-load trials, where no target letter appeared, participants were required to make a random button press). There was no imposed order in which observers made their behavioral responses; they were free to respond in an order most comfortable for them. Both tasks were stressed to be equally important; consequently an auditory tone was given as feedback only when the participant got both responses correct for the high-attentional-load condition, and the orientation task correct for the low-attentional-load condition. In total, each participant completed 96 trials for each orientation per measured contrast level for each attentional-load condition (total number of trials for six contrast levels: 2,304, collected over two sessions; for nine contrast levels: 3,456, collected over three sessions on separate testing days).

Analysis

Each observer's behavioral accuracies for both orientations under low or high attentional load were computed for each contrast level to reflect performance in the task as a function of contrast. The relationships between orientation anisotropies and behavioral responses in the low- and high-attentional-load conditions were described using a Naka–Rushton function (Albrecht & Hamilton, 1982; Naka & Rushton, 1966; see also Methods under Experiment 1). The R_{\max} parameter was constrained to not exceed ceiling performance (for two observers, accuracy for one contrast level was at 100%, and for one observer three reached perfect behavioral performance). In order to describe the strength of the attentional modulation within an orientation condition we computed the following attention modulation index:

$$\text{Attentional Modulation} = \frac{\text{low load} - \text{high load}}{\text{low load} + \text{high load}}, \quad (2)$$

where we take the difference between the two attentional-load conditions and normalize it by the sum for both the response-saturation and semisaturation-point parameters. This attention modulation index provides a proportional difference in the behavioral

response, which best reflects the magnitude of the attentional modulation.

Our data could be fitted with alternative sigmoidal models, such as a Weibull, which describe asymptotic modulation of the psychometric function with a “lapse rate” parameter (Prins, 2012; Wichmann & Hill, 2001). This class of models interprets changes in the saturation point of a psychometric function as a transient, nonperceptual source of error in performance, which could be caused by distractions during the experiment or a temporary fluctuation in sustained attention (Esterman, Noonan, Rosenberg, & DeGutis, 2013; Esterman, Rosenberg, & Noonan, 2014; Gold & Ding, 2013). Importantly, in this model the lapse rate (or saturation point) is assumed to be independent of stimulus intensity, and therefore does not commit to an underlying sensory mechanism involved in the orientation-discrimination task. In this framework one would interpret the impact of the dual task not as a withdrawal of attention away from the primary orientation-discrimination task but instead as larger fluctuations between high and low attentional states impacting behavioral performance. While this model offers an alternative account in which we could interpret the data, our experiment was based on the a priori assumption that the decrease in performance as attentional load increases reflects the underlying sensory mechanism, as the withdrawal of attention from the orientation-discrimination task either adds more noise to the representation or leads to a decrease in the effective contrast. This account is supported by a large body of research illustrating that attention alters the gain of the underlying sensory neural responses (Buracas & Boynton, 2007; Carandini & Heeger, 2012; Huang & Dobkins, 2005; Itthipuripat, Garcia, Rungratsameetaweemana, Sprague, & Serences, 2014b; Ling & Carrasco, 2006; Ling, Jehue, & Pestilli, 2015; Martinez-Trujillo & Treue, 2002; Pestilli et al., 2009; Williford & Maunsell, 2006), and work examining the simultaneous deployment of attention to multiple spatial locations (Awh & Pashler, 2000; McMains & Somers, 2004). Furthermore, this framework squares with the previously observed attentionally driven inhomogeneity within the human LGN (Ling, Pratte, & Tong, 2015; see Discussion). How asymptotic differences in psychometric functions arise from a combination of sensory and decision-related mechanisms remains an active area of research (Gold & Ding, 2013).

Results

Consistent with Experiment 1, results demonstrated a strong oblique effect; oblique orientations have a substantially attenuated contrast psychometric func-

tion. Furthermore, withdrawing attention away from the orientation-discrimination task by increasing attentional load seemed to drastically impair observers’ ability to discriminate both orientations (see Figures 5 and 6), while performance on the concurrent fixation task did not differ (accuracies for both orientation conditions > 90%).

Fitting these data with the Naka–Rushton function (Equation 1) allowed us to quantify how the oblique effect interacts with attentional load (average fits for all observers: cardinal low-load $R^2 \mu = 0.95$, $SE = 0.001$; cardinal high-load $R^2 \mu = 0.88$, $SE = 0.02$; oblique low-load $R^2 \mu = 0.80$, $SE = 0.05$; oblique high-load $R^2 \mu = 0.62$, $SE = 0.07$). The estimated parameters (R_{\max} and C_{50}) for each orientation and attentional-load condition allowed for a direct comparison of whether attentional load affects orientation discrimination differently around cardinal or oblique stimulus orientations (see Figure 6a and b). Attentional load quite drastically attenuates the saturation parameter (R_{\max}) for both cardinal and oblique orientations, and interestingly, this attenuation appears largest for orientation discrimination around oblique orientations. In order to describe the strength of attentional-load modulation within an orientation condition, we computed an attention modulation index for both the response-saturation (R_{\max}) and semisaturation-point (C_{50}) parameters of the contrast response function and compared values between observers.

Interestingly, attentional load affected performance with cardinal and oblique orientations differently (see Figure 6). While withdrawing attentional resources impairs behavioral performance for both stimulus orientations, the magnitude of this modulation is greatest for the oblique orientations. This change in the magnitude of the attentional effects is driven primarily by a change in the response saturation (R_{\max} parameter, paired t test, $t(8) = -3.86$, $p = 0.005$), while the semisaturation point is not significantly affected (C_{50} parameter, paired t test, $t(8) = 0.33$, $p = 0.75$). Although our results suggest that attentional load seems to operate through a response gain mechanism, it might be that the contribution of a contrast gain mechanism is underestimated. Psychometric functions for the high-attentional-load oblique-orientation condition, due to the sheer magnitude of the oblique effect, were close to floor performance, making the estimation of the semisaturation point less reliable. In sum, attentional load interacts with orientation anisotropies differentially. Although it affects the contrast response functions for both cardinal and oblique orientations, a higher attentional load seems to impair orientation discrimination around obliquely oriented stimuli the most.

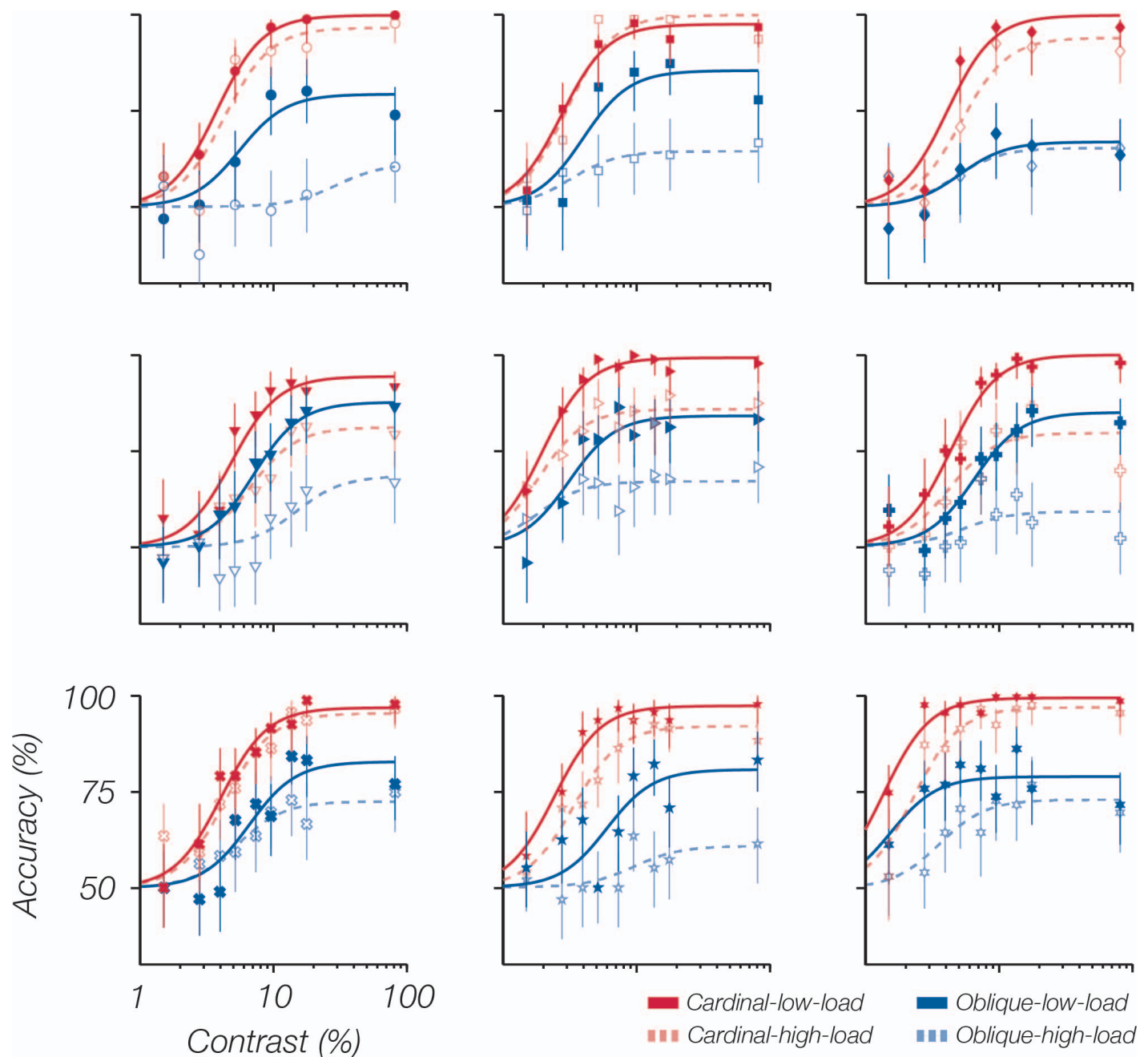


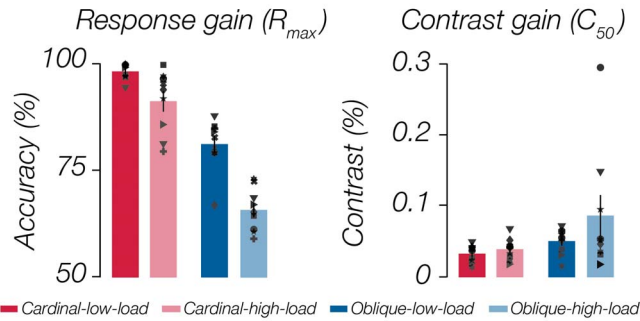
Figure 5. Results of Experiment 2. Psychometric functions for all observers. Data points reflect accuracy at each contrast level for both orientation conditions (cardinal = red, oblique = blue), and the curved lines represent the best fit. Error bars indicate the 95% bootstrap confidence interval.

Discussion

The present study mapped orientation discrimination as a function of stimulus intensity, as well as assessed the role that attention plays in modulating behavioral orientation-dependent anisotropies. We found evidence for a robust oblique effect, whereby contrast psychometric functions for oblique orientations are multiplicatively attenuated—a modulatory pattern consistent

with a response gain mechanism. Next, we explored whether withdrawing attention attenuates behavioral performance equally regardless of stimulus orientation or whether this attenuation is greater for oblique representations, partially offsetting this impairment in visual sensitivity. While attentional load affected the contrast psychometric functions for both cardinal and oblique orientations, withdrawing attention by increasing the load attenuated the psychometric function for oblique-oriented stimuli to a larger degree.

a. Parameter estimates



b. Attention modulation

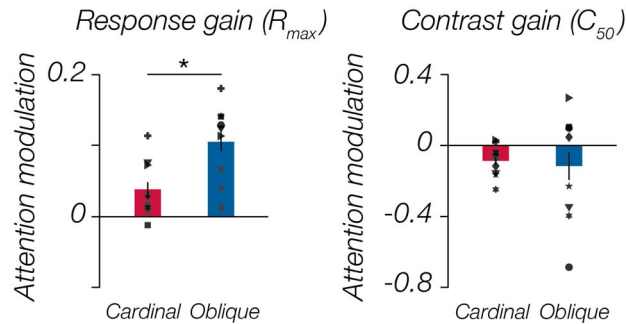


Figure 6. Average parameter estimates of Experiment 2. (A) Left graph illustrates the estimates of the R_{max} parameter, and the right graph depicts the estimates of the C_{50} parameter for both orientations for both the low- and high-attentional-load conditions. (B) Attention modulation indices. Left bar graph illustrates the attention modulation for the estimates of the R_{max} parameter for both cardinal (red) and oblique (blue) orientations. The right bar graph reflects the attention modulation for the estimates of the C_{50} parameter for both cardinal and oblique orientations. Attention modulation was computed as $(low\ load - high\ load)/(low\ load + high\ load)$. Different symbols denote each individual observer ($N = 9$); error bars reflect ± 1 standard error of the mean.

Although the oblique effect is clearly the result of some form of neural anisotropy, the precise origin of this phenomenon remains somewhat unclear, with evidence pointing toward a combination of factors including an imbalance in the cell quantity between cardinal and oblique orientations and different tuning bandwidth for certain orientations within primary visual cortex (Appelle, 1972; Campbell et al., 1966; Campbell & Kulikowski, 1966; Chapman & Bonhoeffer, 1998; Coppola et al., 1998; De Valois et al., 1982; Li et al., 2003; Mansfield, 1974; Rose & Blakemore, 1974; Williams et al., 1981). Interestingly, while these orientation anisotropies can emerge without visual experiences (Bauer et al., 1979; Gwiazda, Brill, Mohindra, & Held, 1978; Leehey, Moskowitz-Cook, Brill, & Held, 1975; Leventhal & Hirsch, 1977), exposure to natural visual inputs does seem to further exaggerate them (Annis & Frost, 1973; Gwiazda et al.,

1978). Although our psychophysical results cannot tease apart whether the oblique effect emerges as a result of an imbalance between the size of neural populations tuned to cardinal and oblique orientations or a difference in tuning bandwidth, they reveal that the magnitude of the effect scales with contrast. Specifically, the oblique effect seems driven by a response gain mechanism that multiplicatively attenuates the response for oblique orientations, leading to a lowered asymptotic response and corresponding behavioral performance.

We used an orientation-discrimination task to capture the differences in judging subtle angular differences around cardinal and oblique orientations. Previous work examining how orientation thresholds change as a function of contrast has demonstrated that orientation discrimination does not appear to be contrast invariant (Mareschal & Shapley, 2004; Reisbeck & Gegenfurtner, 1998; Webster et al., 1990). Orientation-discrimination thresholds are largest for lower contrast levels and become smaller as intensity increases, reaching a plateau around middle contrast levels (Mareschal & Shapley, 2004). It has been hypothesized that the increase of orientation thresholds at low stimulus intensity, needed to perform a task at a constant performance level, is directly related to changes in V1 receptive-field sizes. Specifically, receptive-field sizes are larger at low contrast levels (Kapadia, Westheimer, & Gilbert, 1999; Sceniak, Ringach, Hawken, & Shapley, 1999), affecting neuronal spatial resolution, and therefore could account for higher orientation-discrimination thresholds at these intensity levels (Mareschal & Shapley, 2004). However, this work also illustrates that orientation discrimination appears contrast invariant at medium to high intensities, which is the contrast range in which the multiplicative attenuation of the psychometric function is most apparent in our data. In addition, it has been shown that with an increase of stimulus size, extending into the extraclassical receptive field, orientation tuning does appear to be contrast invariant (Bowne, 1990; Liu, Hashemi-Nezhad, & Lyon, 2015; Skottun, Bradley, Sclar, Ohzawa, & Freeman, 1987). In our study, we used rather large stimuli (4° diameter) at fixation; thus, the change of the underlying receptive-field size with contrast is not likely to affect our interpretation of the oblique effect in these experiments.

While there is evidence suggesting that the oblique effect in orientation discrimination and contrast sensitivity does not reflect the same underlying mechanism (Heeley et al., 1997), our results are consistent with studies which have found an imbalance in contrast sensitivity between oblique and cardinal orientations (Williams et al., 1981). A consequence of response gain attenuation is that orientation anisotropies in visual sensitivity near detection threshold are not clearly

discernible, as the large performance differences are evident at higher contrast intensities. One practical implication of this multiplicative modulatory effect is that the oblique effect would be severely underestimated if one were measuring near the limits of visibility, as is often the case with the measurement of contrast-detection thresholds. For instance, it has been reported that the magnitude of the oblique effect is larger for higher spatial frequencies of the visual stimulus (Boltz, Harwerth, & Smith, 1979; Camisa et al., 1977; Heeley & Timney, 1988). However, contrast sensitivity is inherently higher for low spatial frequencies, so an alternative explanation for this less pronounced orientation anisotropy could be that these thresholds were in a lower contrast regime, where the oblique effect is smaller. Recent human neuroimaging work has provided some conflicting evidence regarding signatures of the oblique effect in the blood oxygen level-dependent (BOLD) response within primary visual cortex. While some studies have found a higher mean BOLD response for cardinal over oblique orientations (Furmanski & Engel, 2000), corresponding to better behavioral performance, others have found opposite patterns with a higher mean BOLD response for oblique orientations (Ling, Pratte, & Tong, 2015; Maloney & Clifford, 2015; Mannion, McDonald, & Clifford, 2010; Swisher et al., 2010). The conflicting evidence of these studies, while seemingly at odds with our results, could arise from a number of factors. For instance, the stimuli between our studies and the various neuroimaging studies vary in the location of stimulus presentation and in spatial frequency (our stimuli were presented foveally and at a much higher spatial frequency). Interpreting the relationship between the mean BOLD activity and its relationship to visual sensitivity for stimulus orientation remains an active area of research.

There is a growing body of electrophysiological evidence suggesting that cortical orientation anisotropies such as the oblique effect could be, in part, inherited by subcortical or retinal orientation-selective responses (but see Li et al., 2003). Certain retinal ganglion cells (Dhande, Stafford, Lim, & Huberman, 2015; He, Levick, & Vaney, 1998; Levick & Thibos, 1982; Sanes & Masland, 2015; Shou & Leventhal, 1989) and LGN neurons (Cheong et al., 2013; Piscopo et al., 2013; Vidyasagar et al., 1996; Vidyasagar & Urbas, 1982; Viswanathan et al., 2011) have been shown to respond to elongated stimuli especially oriented along the cardinal axes. These subcortical orientation biases could significantly contribute to the overrepresentation of neurons tuned to cardinal orientations and the sharpening of the orientation bandwidth in simple cells in primary visual areas (Orban & Kennedy, 1981; Payne & Berman, 1983; Vidyasagar & Urbas, 1982; Viswanathan et al., 2011).

We found that attention differentially attenuates the psychometric functions for cardinal and oblique orientations: The withdrawal of attention attenuates behavioral performance for obliquely oriented stimuli to a larger extent. While attentional feedback to the LGN is potentially nonspecific to stimulus features, an interaction with existing subcortical orientation anisotropies might still explain our results. Recent human neuroimaging work has illustrated that the magnitude of attentional modulation in the LGN is critically dependent on stimulus orientation (Ling, Pratte, & Tong, 2015). Specifically, within the LGN, oblique orientations yielded larger attentional effects than cardinal orientations—a pattern that was absent in primary visual cortex. These results could potentially be explained by physiological evidence illustrating that feedback projections from V1 to the LGN seem to tighten the orientation tuning of LGN neurons (Andolina, Jones, Wang, & Sillito, 2007; Vidyasagar & Urbas, 1982). Interestingly, feedback affected cardinal and oblique orientations differently, strengthening oblique representations while leaving cardinal orientations unaffected (Vidyasagar & Urbas, 1982). These studies provide a possible neural mechanism for the behavioral results of Experiment 2, suggesting that an orientation-based anisotropy in subcortical attentional modulation could affect behavior.

Keywords: attention, oblique effect, psychophysics, visual perception, contrast response function, orientation

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References

- Albrecht, D. G., & Hamilton, D. B. (1982). Striate cortex of monkey and cat: Contrast response function. *Journal of Neurophysiology*, *48*(1), 217–237.

- Andolina, I. M., Jones, H. E., Wang, W., & Sillito, A. M. (2007). Corticothalamic feedback enhances stimulus response precision in the visual system. *Proceedings of the National Academy of Sciences, USA*, *104*(5), 1685–1690.
- Annis, R. C., & Frost, B. (1973, Nov 16). Human visual ecology and orientation anisotropies in acuity. *Science*, *182*(4113), 729–731, doi:10.1126/science.182.4113.729.
- Appelle, S. (1972). Perception and discrimination as a function of stimulus orientation: The “oblique effect” in man and animals. *Psychological Bulletin*, *78*(4), 266–278, doi:10.1037/h0033117.
- Awh, E., & Pashler, H. (2000). Evidence for split attentional foci. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(2), 834–846.
- Bauer, J. A., Owens, D. A., Thomas, J., & Held, R. (1979). Monkeys show an oblique effect. *Perception*, *8*, 247–253.
- Boltz, R. L., Harwerth, R. S., & Smith, E. L., III. (1979, Month DD). Orientation anisotropy of visual stimuli in rhesus monkey: A behavioral study. *Science*, *205*(4405), 511–513.
- Bowne, S. F. (1990). Contrast discrimination cannot explain spatial frequency, orientation or temporal frequency discrimination. *Vision Research*, *30*(3), 449–461.
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 433–436, doi:10.1163/156856897x00357.
- Briggs, F., Mangun, G. R., & Usrey, W. M. (2013). Attention enhances synaptic efficacy and the signal-to-noise ratio in neural circuits. *Nature*, *499*(7459), 476–480, doi:10.1038/nature12276.
- Buracas, G. T., & Boynton, G. M. (2007). The effect of spatial attention on contrast response functions in human visual cortex. *The Journal of Neuroscience*, *27*(1), 93–97, doi:10.1523/JNEUROSCI.3162-06.2007.
- Camisa, J. M., Blake, R., & Lema, S. (1977). The effects of temporal modulation on the oblique effect in humans. *Perception*, *6*, 165–171, doi:10.1068/p060165.
- Campbell, F. W., & Kulikowski, J. J. (1966). Orientation selectivity of the human visual system. *The Journal of Physiology*, *187*, 437–445, doi:10.1113/jphysiol.1966.sp008101.
- Campbell, F. W., Kulikowski, J. J., & Levinson, J. (1966). The effect of orientation on the visual resolution of gratings. *The Journal of Physiology*, *187*, 427–436, doi:10.1113/jphysiol.1966.sp008100.
- Carandini, M., & Heeger, D. J. (2012). Normalization as a canonical neural computation. *Nature Reviews Neuroscience*, *13*(1), 51–62, doi:10.1038/nrn3136.
- Chapman, B., & Bonhoeffer, T. (1998). Overrepresentation of horizontal and vertical orientation preferences in developing ferret Area 17. *Proceedings of the National Academy of Sciences, USA*, *95*, 2609–2614, doi:10.1073/pnas.95.5.2609.
- Cheong, S. K., Tailby, C., Solomon, S. G., & Martin, P. R. (2013). Cortical-like receptive fields in the lateral geniculate nucleus of marmoset monkeys. *The Journal of Neuroscience*, *33*(16), 6864–6876, doi:10.1523/JNEUROSCI.5208-12.2013.
- Cohen, M. R., & Maunsell, J. (2011). Using neuronal populations to study the mechanisms underlying spatial and feature attention. *Neuron*, *6*, 1192–1204.
- 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, USA*, *95*, 2621–2623, doi:10.1073/pnas.95.5.2621.
- De Valois, R. L., Yund, E. W., & Hepler, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research*, *22*(5), 531–544, doi:10.1016/0042-6989(82)90112-2.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222, doi:10.1146/annurev.ne.18.030195.001205.
- Dhande, O. S., Stafford, B. K., Lim, J.-H. A., & Huberman, A. D. (2015). Contributions of retinal ganglion cells to subcortical visual processing and behaviors. *Journal of Cognitive Neuroscience*, *1*(1), 291–328, doi:10.1146/annurev-vision-082114-035502.
- Essock, E. A. (1980). The oblique effect of stimulus identification considered with respect to two classes of oblique effects. *Perception*, *9*(1), 37–46.
- Esterman, M., Noonan, S. K., Rosenberg, M., & DeGutis, J. (2013). In the zone or zoning out? Tracking behavioral and neural fluctuations during sustained attention. *Cerebral Cortex*, *23*(11), 2712–2723, doi:10.1093/cercor/bhs261.
- Esterman, M., Rosenberg, M. D., & Noonan, S. K. (2014). Intrinsic fluctuations in sustained attention and distractor processing. *The Journal of Neuroscience*, *34*(5), 1724–1730.
- Furmanski, C. S., & Engel, S. A. (2000). An oblique effect in human primary visual cortex. *Nature Neuroscience*, *3*(6), 535–536, doi:10.1038/75702.
- Gold, J. I., & Ding, L. (2013). How mechanisms of

- perceptual decision-making affect the psychometric function. *Progress in Neurobiology*, 103, 98–114.
- Gwiazda, J., Brill, S., Mohindra, I., & Held, R. (1978). Infant visual acuity and its meridional variation. *Vision Research*, 18, 1557–1564.
- He, S., Levick, W. R., & Vaney, D. I. (1998). Distinguishing direction selectivity from orientation selectivity in the rabbit retina. *Visual Neuroscience*, 15, 439–447.
- Heeley, D. W., Buchanan-Smith, H. M., Cromwell, J. A., & Wright, J. S. (1997). The oblique effect in orientation acuity. *Vision Research*, 37(2), 235–242.
- Heeley, D. W., & Timney, B. (1988). Meridional anisotropies of orientation discrimination for sine wave gratings. *Vision Research*, 28(2), 337–344.
- Herrmann, K., Montaser-Kouhsari, L., Carrasco, M., & Heeger, D. J. (2010). When size matters: Attention affects performance by contrast or response gain. *Nature Neuroscience*, 13(12), 1554–1559.
- Huang, L., & Dobkins, K. R. (2005). Attentional effects on contrast discrimination in humans: Evidence for both contrast gain and response gain. *Vision Research*, 45(9), 1201–1212.
- Itthipuripat, S., Ester, E. F., Deering, S., & Serences, J. T. (2014). Sensory gain outperforms efficient readout mechanisms in predicting attention-related improvements in behavior. *The Journal of Neuroscience*, 34(40), 13384–13398, doi:10.1523/JNEUROSCI.2277-14.2014.
- Itthipuripat, S., Garcia, J. O., Rungratsameetaweemana, N., Sprague, T. C., & Serences, J. T. (2014). Changing the spatial scope of attention alters patterns of neural gain in human cortex. *The Journal of Neuroscience*, 34(1), 112–123, doi:10.1523/JNEUROSCI.3943-13.2014.
- Kapadia, M. K., Westheimer, G., & Gilbert, C. D. (1999). Dynamics of spatial summation in primary visual cortex of alert monkeys. *Proceedings of the National Academy of Sciences, USA*, 96(21), 12073–12078.
- Lavie, N., Beck, D. M., & Konstantinou, N. (2014). Blinded by the load: Attention, awareness and the role of perceptual load. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1641), 20130205.
- Lavie, N., & Tsal, Y. (1994). Perceptual load as a major determinant of the locus of selection in visual attention. *Perception & Psychophysics*, 56(2), 183–197, doi:10.3758/BF03213897.
- Lee, D. K., Itti, L., Koch, C., & Braun, J. (1999). Attention activates winner-take-all competition among visual filters. *Nature Neuroscience*, 2(4), 375–381, doi:10.1038/7286.
- Leehey, S. C., Moskowitz-Cook, A., Brill, S., & Held, R. (1975, Month DD). Orientational anisotropy in infant vision. *Science*, 190(4217), 900–902, doi:10.1126/science.190.4217.900.
- Leventhal, A. G., & Hirsch, H. V. (1977). Effects of early experience upon orientation sensitivity and binocularity of neurons in visual cortex of cats. *Proceedings of the National Academy of Sciences, USA*, 74(3), 1272–1276.
- Levick, W. R., & Thibos, L. N. (1982). Analysis of orientation bias in cat retina. *The Journal of Physiology*, 329, 243–261, doi:10.1113/jphysiol.1982.sp014301.
- Li, B., Peterson, M. R., & Freeman, R. D. (2003). Oblique effect: A neural basis in the visual cortex. *Journal of Neurophysiology*, 90(1), 204–217, doi:10.1152/jn.00954.2002.
- Ling, S., & Blake, R. (2012). Normalization regulates competition for visual awareness. *Neuron*, 75, 531–540, doi:10.1016/j.neuron.2012.05.032.
- Ling, S., & Carrasco, M. (2006). Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision Research*, 46(8–9), 1210–1220.
- Ling, S., Jehee, J. F. M., & Pestilli, F. (2015). A review of the mechanisms by which attentional feedback shapes visual selectivity. *Brain Structure & Function*, 220(3), 1237–1250, doi:10.1007/s00429-014-0818-5.
- Ling, S., Pratte, M. S., & Tong, F. (2015). Attention alters orientation processing in the human lateral geniculate nucleus. *Nature Neuroscience*, 18, 496–498, doi:10.1038/nn.3967.
- Liu, Y.-J., Hashemi-Nezhad, M., & Lyon, D. C. (2015). Contrast invariance of orientation tuning in cat primary visual cortex neurons depends on stimulus size. *The Journal of Physiology*, 593(19), 4485–4498, doi:10.1113/JP271180.
- Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *Journal of Neurophysiology*, 77(1), 24–42.
- Maloney, R. T., & Clifford, C. W. G. (2015). Orientation anisotropies in human primary visual cortex depend on contrast. *NeuroImage*, 119, 129–145, doi:10.1016/j.neuroimage.2015.06.034.
- Mannion, D. J., McDonald, J. S., & Clifford, C. W. G. (2010). Orientation anisotropies in human visual

- cortex. *Journal of Neurophysiology*, 103(6), 3465–3471, doi:10.1152/jn.00190.2010.
- Mansfield, R. J. (1974, Month DD). Neural basis of orientation perception in primate vision. *Science*, 186(4169), 1133–1135, doi:10.1126/science.186.4169.1133.
- Mareschal, I., & Shapley, R. M. (2004). Effects of contrast and size on orientation discrimination. *Vision Research*, 44(1), 57–67, doi:10.1016/j.visres.2003.07.009.
- Martinez-Trujillo, J. C., & Treue, S. (2002). Attentional modulation strength in cortical area MT depends on stimulus contrast. *Neuron*, 35, 365–370, doi:10.1016/S0896-6273(02)00778-X.
- McAdams, C. J., & Maunsell, J. (1999). Effects of attention on the reliability of individual neurons in monkey visual cortex. *Neuron*, 23(4), 765–773.
- McMains, S. A., & Somers, D. C. (2004). Multiple spotlights of attentional selection in human visual cortex. *Neuron*, 42(4), 677–686.
- Naka, K. I., & Rushton, W. A. H. (1966). S-potentials from colour units in the retina of fish (*Cyprinidae*). *The Journal of Physiology*, 185, 536–555.
- Orban, G. A., & Kennedy, H. (1981). The influence of eccentricity on receptive field types and orientation selectivity in areas 17 and 18 of the cat. *Brain Research*, 208(1), 203–208.
- Orban, G. A., Vandenbussche, E., & Vogels, R. (1984). Human orientation discrimination tested with long stimuli. *Vision Research*, 24(2), 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(4), 1051–1072.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442, doi:10.1163/156856897X00366.
- Pestilli, F., Ling, S., & Carrasco, M. (2009). A population-coding model of attention's influence on contrast response: Estimating neural effects from psychophysical data. *Vision Research*, 49, 1144–1153, doi:10.1016/j.visres.2008.09.018.
- Piscopo, D. M., El-Danaf, R. N., Huberman, A. D., & Niell, C. M. (2013). Diverse visual features encoded in mouse lateral geniculate nucleus. *The Journal of Neuroscience*, 33(11), 4642–4656. doi:10.1523/JNEUROSCI.5187-12.2013.
- Prins, N. (2012). The psychometric function: The lapse rate revisited. *Journal of Vision*, 12(6):25, 1–16, doi:10.1167/12.6.25. [PubMed] [Article]
- Regan, D., & Beverley, K. I. (1985). Postadaptation orientation discrimination. *Journal of the Optical Society of America A*, 2(2), 147–155.
- Reisbeck, T. E., & Gegenfurtner, K. R. (1998). Effects of contrast and temporal frequency on orientation discrimination for luminance and isoluminant stimuli. *Vision Research*, 38(8), 1105–1117.
- Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience*, 27(1), 611–647, doi:10.1146/annurev.neuro.26.041002.131039.
- Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque Areas V2 and V4. *The Journal of Neuroscience*, 19(5), 1736–1753.
- Reynolds, J. H., Pasternak, T., & Desimone, R. (2000). Attention increases sensitivity of V4 neurons. *Neuron*, 26(3), 704–714.
- Rose, D., & Blakemore, C. (1974). An analysis of orientation selectivity in the cat's visual cortex. *Experimental Brain Research*, 20(1), 1–17, doi:10.1007/BF00239014.
- Sanes, J. R., & Masland, R. H. (2015). The types of retinal ganglion cells: Current status and implications for neuronal classification. *Annual Review of Neuroscience*, 38(1), 221–246, doi:10.1146/annurev-neuro-071714-034120.
- Sceniak, M. P., Ringach, D. L., Hawken, M. J., & Shapley, R. (1999). Contrast's effect on spatial summation by macaque V1 neurons. *Nature Neuroscience*, 2(8), 733–739, doi:10.1038/11197.
- Shou, T. D., & Leventhal, A. G. (1989). Organized arrangement of orientation-sensitive relay cells in the cat's dorsal lateral geniculate nucleus. *The Journal of Neuroscience*, 9(12), 4287–4302.
- Skottun, B. C., Bradley, A., Sclar, G., Ohzawa, I., & Freeman, R. D. (1987). The effects of contrast on visual orientation and spatial frequency discrimination: A comparison of single cells and behavior. *Journal of Neurophysiology*, 57(3), 773–786.
- Swisher, J. D., Gatenby, J. C., Gore, J. C., Wolfe, B. A., Moon, C.-H., Kim, S.-G., & Tong, F. (2010). Multiscale pattern analysis of orientation-selective activity in the primary visual cortex. *The Journal of Neuroscience*, 30(1), 325–330, doi:10.1523/JNEUROSCI.4811-09.2010.
- Treue, S. (2001). Neural correlates of attention in primate visual cortex. *Trends in Neurosciences*, 24(5), 295–300.
- Vidyasagar, T. R., Pei, X., & Volgushev, M. (1996).

- Multiple mechanisms underlying the orientation selectivity of visual cortical neurones. *Trends in Neurosciences*, 19(7), 272–277, doi:10.1016/S0166-2236(96)20027-X.
- Vidyasagar, T. R., & Urbas, J. V. (1982). Orientation sensitivity of cat LGN neurones with and without inputs from visual cortical areas 17 and 18. *Experimental Brain Research*, 46(2), 157–169.
- Viswanathan, S., Jayakumar, J., & Vidyasagar, T. R. (2011). Role of feedforward geniculate inputs in the generation of orientation selectivity in the cat's primary visual cortex. *Journal of Physiology*, 589(9), 2349–2361, doi:10.1113/jphysiol.2010.202317.
- Vogels, R., & Orban, G. A. (1990). How well do response changes of striate neurons signal differences in orientation: A study in the discriminating monkey. *The Journal of Neuroscience*, 10(11), 3543–3558.
- Watson, A. B., & Pelli, D. G. (1983). Quest: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, 33(2), 113–120, doi:10.3758/BF03202828.
- Webster, M. A., Switkes, E., & De Valois, K. K. (1990). Orientation and spatial-frequency discrimination for luminance and chromatic gratings. *Journal of the Optical Society of America*, 7(6), 1035–1049, doi:10.1364/JOSAA.7.001034.
- Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, 63(8), 1293–1313, doi:10.3758/BF03194544.
- Williams, R. A., Boothe, R. G., Kiorpes, L., & Teller, D. Y. (1981). Oblique effects in normally reared monkeys (*Macaca nemestrina*): Meridional variations in contrast sensitivity measured with operant techniques. *Vision Research*, 21(8), 1253–1266, doi:10.1016/0042-6989(81)90230-3.
- Williford, T., & Maunsell, J. H. R. (2006). Effects of spatial attention on contrast response functions in macaque Area V4. *Journal of Neurophysiology*, 96(1), 40–54, doi:10.1152/jn.01207.2005.
- Xu, X., Ichida, J. M., Allison, J. D., Boyd, J. D., Bonds, A. B., & Casagrande, V. A. (2001). A comparison of koniocellular, magnocellular and parvocellular receptive field properties in the lateral geniculate nucleus of the owl monkey (*Aotus trivirgatus*). *Journal of Physiology*, 531(1), 203–218, doi:10.1111/j.1469-7793.2001.0203j.x.