Attentional modulation interacts with orientation anisotropies in contrast perception

Ilona M. Bloem\textsuperscript{1,2}, & Sam Ling\textsuperscript{1,2,3}

\textsuperscript{1} Department of Psychological and Brain Sciences, Boston University, Boston, USA.
\textsuperscript{2} Center for Systems Neuroscience, Boston University, Boston, USA.
\textsuperscript{3} Donders Institute, Radboud Universiteit, Nijmegen, the Netherlands.

Abstract

Orientation perception is not comparable across all orientations—a phenomenon commonly referred to as the oblique effect. Here, we first assess the interaction between stimulus contrast and the oblique effect. Specifically, we examine whether the impairment in behavioral performance for oblique versus cardinal orientations is best explained by a contrast- or 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 attentional load 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.

Keywords: Attention, Oblique effect, Psychophysics, Visual perception, Contrast Response Function, Orientation
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 stimuli orientations. Specifically, cardinally (0° or 90°) oriented stimuli can be judged with higher accuracy compared to obliquely (±45°) oriented edges, a perceptual anisotropy commonly referred to as the ‘oblique effect’ (Annis & Frost, 1973; Appelle, 1972; Campbell & Kulikowski, 1966; Heeley & Timney, 1988; Heeley, Buchanan-Smith, Cromwell, & Wright, 1997; Orban, Vandenbussche, & 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 overrepresentation, 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; R. L. 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 that is often found for cardinal orientations, relative to obliques (Camisa et al., 1977; 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 on 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 is a multi-factorial 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:
1) a response-gain mechanism could multiplicatively attenuate the response, leading to a lowered asymptotic
response and corresponding behavioral performance, 2) a contrast-gain mechanism could modulate the
dynamic range of the contrast response, shifting the semi-saturation towards 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/both a contrast or response gain mechanism.

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 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, 2014a; Ling, Jehee, & Pestilli, 2015a; Ling, Pratte, & Tong,
2015b). Interestingly, recent neuroimaging work found that the magnitude of attentional modulation in the
lateral geniculate nucleus (LGN) is critically dependent on stimulus orientation (Ling, Pratte, & Tong, 2015b).
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 utilize the oblique effect to examine the degree to which attentional load can modulate
behavioral performance when 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 & Tsal, 1994; Lavie, Beck, & Konstantinou, 2014; 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 multiplicative 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 impact performance to obliquely oriented stimuli to a larger extent.

**Experiment 1: Orientation anisotropies in contrast sensitivity**

**Methods**

**Participants.** Seven healthy participants (mean age = 24.2 years, SE = 1.56; four female) took part in this experiment. All participants had normal or corrected-to-normal vision and provided their informed consent. 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 R² < 0.2). Before the start of the experiment, verbal and written instruction of the experimental task was given. Participants were placed comfortably with their heads in a chinrest 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; 1280 x 1024, 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 cycles/°, a diameter of 4° of visual angle, at a randomized phase. The contrast of each stimulus varied from trial-to-trial; in total there were 8 contrast levels (spaced between 1.5 – 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 below). 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 2 independent adaptive staircases (QUEST, Watson & Pelli, 1983), which converged after 40 trials on an orientation difference that yielded 70\% accuracy (individual orientation thresholds: mean = 2.87°, STD = 1.24°), 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 gratings 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 several contrast levels. During a typical trial, participants were presented with a reference grating for 200ms oriented either cardinally (0° or 90°) or obliquely (45° or 135°), which after a short interval (1000ms) was followed by a test grating (200ms) 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 counter-clockwise, 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 1600 trials (randomly presented); 50 trials for each of the 4 orientations per contrast level, after collapsing within cardinal and oblique orientation conditions this resulted in 100 trials per condition.

**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 (CRF; Albrecht & Hamilton, 1982; Albrecht, Thorell, & Hamilton, 1981; Naka & Rushton, 1966):
\[ R(c) = (R_{\text{max}} - b) \frac{c^n}{C_{50}^n + c^n} + b \]  

where \( R(c) \) is performance as a function of contrast, \( R_{\text{max}} \) 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 \texttt{fminsearch} function by optimizing the parameter estimates for \( R_{\text{max}} \) and \( C_{50} \) (with \( n \) constrained at 2.5, \( C_{50} \) constrained between 0 and 1, and \( b \) fixed at 0.5; using nonlinear least-squares), for each individual participant. Prior to assessing psychometric functions, we determined that any observers with fits to either orientation conditions with an \( R^2 < 0.2 \) 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 (Eq. 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; 1) a response-gain mechanism will affect the \( R_{\text{max}} \) parameter,

![Figure 2. Results 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.](image)
multiplicatively attenuating the response, 2) 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/both a contrast or response gain mechanism.

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 is likely arises due to a difference in the orientation discrimination procedures. Specifically, during the staircase procedure, observers based their orientation discrimination on a reference line that was presented outside the gratings 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 response gain mechanism we compared the response saturation and the semi-saturation point parameters between each observer (average fits for all observers: cardinal $R^2$ mean = 0.93, $SE = 0.04$; oblique $R^2$ mean = 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: $t(5) = 11.82, p < .001$), the semi-saturation point ($C_{50}$ parameter), allowing 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 3.** Average parameter estimates 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 s.e.m.
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 impact the responses for both orientations equally, or does it impair responses for oblique orientations to a larger extent?

Methods

Participants. Fifteen healthy participants (seven male, eight female; 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 3 contrast levels reached 100% accuracy in one of the experimental conditions). Before the start of the experiment, verbal and written instruction of the experimental task was given. Participants were placed comfortably with their heads in a chinrest 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; 1280 x 1024, 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 cycles/º, a diameter of 4º of visual angle, and a randomized phase. The contrast of each stimulus varied from trial-to-trial; in total, there were 9 contrast levels (for the first 3 participants only 6 contrast levels were collected), spaced between 1.5 – 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 below). 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 individual differences in visual sensitivity. Specifically, fine orientation-discrimination thresholds were estimated using 2 independent adaptive staircases (QUEST, Watson & Pelli, 1983), which converged after 40 trials on an orientation tilt that yielded 80% accuracy (individual orientation thresholds: mean = 6.98º, STD = 3.66º), 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 orientated 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 accuracies while participants performed either a low or 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 (5Hz) 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 either required to attend to the target grating, or to attend to the grating and additionally pay attention to a rapid letter stream at fixation (presented at 10Hz). In the high attentional load condition one of two targets 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, instead 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 only given as feedback 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 amount of trials for 6 contrast levels: 2304 trials, collected over 2 sessions; for 9 contrast levels: 3456 trials, collected over 3 sessions on separate testing days).

*a. Task cue*  
*Figure 4.* Experiment 2 a. The beginning of a block would start with a ‘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° & 90°, or oblique: 45° & 135°), for a total duration of 1000 ms (5Hz). 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.
Analysis. Each observer’s behavioral accuracies for both orientations under low or high attentional load conditions were computed for each contrast level to reflect performance in the task as a function of contrast. The relationship between orientation anisotropies and behavioral responses in the low and high attentional load conditions were described using a Naka-Rushton function (Albrecht et al., 1981; Albrecht & Hamilton, 1982; Naka & Rushton, 1966, see Methods Experiment 1). The $R_{\text{max}}$ parameter was constrained to not exceed ceiling performance (for two observers accuracy for one contrast level was at 100%, and for one observer three contrast levels 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,

$$Attentional\ Modulation = \frac{\text{low load} - \text{high load}}{\text{low load} + \text{high load}}$$

where we take the difference between the two attentional load conditions and normalize this by the sum, for both the response saturation and the semi-saturation 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 fit 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, non-perceptual 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 from 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, Rungratsameetawee, Sprague, & Serences, 2014b; Ling & Carrasco, 2006; Ling, Jehee, & Pestilli, 2015a; 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, 2015b), 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 function. Furthermore, withdrawing attention away from the orientation discrimination task by increasing attentional load seemed to drastically impair observers’ ability to discriminate both orientations (see Figure 5 & 6), while performance on the concurrent fixation task did not differ (accuracies for both orientation conditions >90%).

Figure 5. Results 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.
Fitting these data with the Naka-Rushton (Eq. 1) allowed us to quantify how the oblique effect interacts with attentional load (average fits for all observers: cardinal-low-load $R^2$ mean = 0.95, $SE = 0.001$; cardinal-high-load $R^2$ mean = 0.88, $SE = 0.02$; oblique-low-load $R^2$ mean = 0.80, $SE = 0.05$; oblique-high-load $R^2$ mean = 0.62, $SE = 0.07$). The estimated parameters ($R_{\text{max}}$ & $C_{50}$) for each orientation and attentional load condition allowed for a direct comparison of whether attentional load affects orientation discrimination around cardinal or oblique stimulus orientations differently (see Figure 6a). Attentional load quite drastically attenuates the saturation parameter ($R_{\text{max}}$) for both cardinal and oblique orientation conditions, 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 and the semi-saturation parameters of the contrast response function. To

### a. Parameter estimates

![Graph of parameter estimates](image)

**Figure 6.** Average parameter estimates Experiment 2. **a)** Left graph illustrates the parameter estimates of the $R_{\text{max}}$ parameter, and the right graph depicts the parameter 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 $R_{\text{max}}$ 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 orientation conditions. 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 s.e.m.
quantify the strength of attentional load modulation we compared the attention modulation index for both the response saturation ($R_{max}$) and the semi-saturation ($C_{50}$) parameters of the contrast psychometric function between observers.

Interestingly, attentional load affected the performance of cardinal and oblique orientations differently, see Figure 6. While withdrawing attentional resources impairs behavioral performance for both stimuli 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: $t(8) = -3.86, p = .005$), while the semi-saturation 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 semi-saturation point less reliable. In sum, attentional load interacts with orientation anisotropies differentially. Although attentional load 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.

**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, the withdrawal of attention by increasing the load seemed to attenuate the psychometric function for oblique oriented stimuli to a larger degree.

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 towards 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; R. L. 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 this anisotropy (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 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 mid-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), impacting neuronal spatial resolution, and therefore could account for larger 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 extra-classical 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 (4° diameter) stimuli at fixation, thus the change of the underlying receptive field size with contrast is not likely to impact our interpretation of the oblique effect in these experiments.

While there is evidence suggesting that the oblique effect in orientation discrimination or contrast sensitivity does not reflect the same underlying mechanism (Heeley et al., 1997), our results are consistent with studies which 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 discernable, 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
BOLD response within primary visual cortex. While some studies find a higher mean BOLD response for
cardinals 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, 2015b; 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 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, Peterson & Freeman, 2003). Certain retinal ganglion cells (Dhande, Stafford, Lim, & Huberman,
2015; He, Levick, & Vaney, 1998; Levick & Thibos, 1982; Sanes & Masland, 2015; Shou & Leventhal, 1989)
and lateral geniculate nucleus (LGN) neurons (Cheong et al., 2013; 2013; Pisco po et al., 2013; 2013;
Vidyasagar et al., 1996; 1996; Vidyasagar & Urban s, 1982; Viswanathan et al., 2011; 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 stimulus feature a-specific, an interaction
with existing subcortical orientation anisotropies might still explain our results. Recent human neuroimaging
work illustrated that the magnitude of attentional modulation in the LGN is critically dependent on stimulus
orientation (Ling, Pratte, & Tong, 2015b). 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 impacted 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 impact behavior.
Author Contributions
I.M.B., and S.L conceived and designed the experiments, I.M.B. collected the data, and conducted data analyses. I.M.B. and S.L. wrote the manuscript.

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