Correlates of Perceptual Orientation Biases in Human Primary Visual Cortex

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Vision can be considered as a process of probabilistic inference. In a Bayesian framework, perceptual estimates from sensory information are combined with prior knowledge, with a stronger influence of the prior when the sensory evidence is less certain. Here, we explored the behavioral and neural consequences of manipulating stimulus certainty in the context of orientation processing. First, we asked participants to judge whether a stimulus was oriented closer to vertical or the clockwise primary oblique (45°) for two stimulus types (spatially filtered noise textures and sinusoidal gratings) and three manipulations of certainty (orientation bandwidth, contrast, and duration). We found that participants consistently had a bias toward reporting orientation as closer to 45° during conditions of high certainty and that this bias was reduced when sensory evidence was less certain. Second, we measured event-related fMRI BOLD responses in human primary visual cortex (V1) and manipulated certainty via stimulus contrast (100% vs 3%). We then trained a multivariate classifier on the pattern of responses in V1 to cardinal and primary oblique orientations. We found that the classifier showed a bias toward classifying orientation as oblique at high contrast but categorized a wider range of orientations as cardinal for low-contrast stimuli. Orientation classification based on data from V1 thus paralleled the perceptual biases revealed through the behavioral experiments. This pattern of bias cannot be explained simply by a prior for cardinal orientations.

Key words: fMRI; primary visual cortex; psychophysics; sensory prior; vision

Significance Statement

Our perception of the world around us is biased through prior expectations rather than necessarily reflecting the true state of our environment. Here, we investigate biases in the visual processing of spatial orientation to understand how prior expectations and current sensory information interact to generate a percept. By degrading visual input in various ways, we are able to quantify the extent to which prior experience affects both perceptual judgments and neural responses in the human visual system. We observe systematic biases in the perception of orientation that correlate with the pattern of activity in the primary visual cortex of the human brain. These results indicate that prior expectations influence neural processing right from the earliest stage of the cortical hierarchy.

Introduction

Perceptual processing must accommodate sensory representations that have a probabilistic relationship with their environmental origins. Helmholtz (1867) described as “unconscious inference” the process whereby sensory evidence is combined with prior knowledge or expectations to create an estimate of the state of the environment. Helmholtz’s classical ideas have recently inspired a body of theoretical and empirical work that considers perception as a process of Bayesian inference (for review, see Pouget et al., 2013; Ma and Jazayeri, 2014).

Within a Bayesian framework, degrading sensory input by broadening its relationship with its potential environmental causes can induce systematic departures from veridical perception biases. The challenge for the visual system is to use sensory stimulation to infer properties of the evoking stimulus. In a Bayesian conception, prior knowledge effectively acts to “pull” the sensory representation toward values that are a priori more likely (Fig. 1). It follows that our perception should not necessarily always reflect the momentary characteristics of our environment veridically, but can instead exhibit biases.

Visual images of the natural environment contain certain regularities in structure, such as a higher proportion of horizontal and vertical orientations (Coppola et al., 1998; Dragoi et al., 2001; Girshick et al., 2011), which could be used by the visual system as Bayesian priors. The human visual system is thought to be attuned to the orientation anisotropy because perceptual sensitivity to sinusoidal gratings is highest when orientations are located close to the cardinal axes (Appelle, 1972; Westheimer, 2003) and decreasing stimulus certainty shifts the perceived mean orientation of a texture array toward the nearest cardinal axis (Tomassini et al., 2010; Girshick et al., 2011). This perceptual bias has been

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Figure 1. Priors can bias perception. In the Bayesian framework, the perceptual estimate of an orientation is based on the peak of the posterior distribution, which is formed from the multiplication of the sensory evidence (the likelihood) and the prior. **A**, When the prior is uniform across orientation, the peak of the posterior (dotted line) corresponds to the maximum likelihood regardless of the certainty of the sensory evidence (top: high certainty; bottom: low certainty) and perception of the orientation is unbiased. **B**, When the prior is nonuniform, the peak of the posterior is “pulled” more toward the prior during conditions of low certainty in the sensory evidence (bottom) than during high certainty (top), as shown by the black arrow, corresponding to a larger perceptual bias.

taken to suggest the operation of a sensory prior probability distribution that peaks at cardinal orientations and is lowest for oblique orientations (Girshick et al., 2011). However, the idea that perceived orientation is biased toward the cardinals because of such a prior has been argued to be overly simplistic (Wei and Stocker, 2015). Specifically, it does not account for reports that, under conditions of high certainty, perceived orientation is biased toward the nearest primary oblique (Lennie, 1971; Tomassini et al., 2010; de Gardelle et al., 2010) in a seemingly “anti-Bayesian” manner (Wei and Stocker, 2015). Indeed, the latter appears to be the stronger effect, such that systematic biases in perceived orientation can actually be smaller under conditions of uncertainty (Tomassini et al., 2010).

Here, we first established the generality of behavioral biases in orientation perception by investigating whether patterns of bias are the same across the type of stimulus (sinusoidal grating of band-pass-filtered texture) and the method used to manipulate certainty (orientation variance, contrast, duration). The latter comparison is of particular theoretical importance because each likely has a different effect on the population response of orientation-selective neurons. Further, it has been predicted recently that manipulation of uncertainty through orientation variance and duration should have opposite effects on perceptual orientation biases (Wei and Stocker, 2015).

We then sought to determine the neural expression of such biases by examining the effect of stimulus certainty on the pattern of fMRI responses in human primary visual cortex (V1). In this way, we were able to characterize how stimulus orientation maps onto perceptual orientation, how this mapping is affected by uncertainty, and whether patterns of activity evoked in V1 show corresponding biases. Our interest in the neural mechanisms underlying perceptual biases stems from our belief that the question of how cerebral cortex deals with uncertain information is fundamental to our understanding of sensory processing. Our focus here is on V1 as the first site of significant orientation selectivity in

the primate visual processing hierarchy (Hubel and Wiesel, 1968), with the hypothesis that a correlate between behavior and the pattern of neural activity should be observable even at the earliest level of visual cortex.

Materials and Methods

Psychophysics

Participants. Six participants (one female, mean age 30.2 years) took part in Experiment 1a (sinusoidal gratings), five participants (one female, mean age 29.8 years) completed Experiment 1b (band-pass-filtered textures). The authors took part in both experiments (except for C.W.G.C. in Exp. 1b), whereas remaining participants were naive to the purpose of the experiment. All participants had normal or corrected-to-normal vision. These experiments were granted ethics approval by the local ethics review committee and all participants gave written informed consent.

Apparatus. Stimulus gratings was generated using MATLAB (The MathWorks) and Psychtoolbox (Brainard, 1997; Pelli, 1997) software and driven by a Bits# stimulus processor (Cambridge Research Systems), which provides 14-bit greyscale resolution. Stimuli were presented on a gamma-corrected 18-inch ViewSonic Graphics Series G90f CRT monitor (resolution, 1280 × 1024) operating at 75 Hz

with a background luminance of 50 cd/m². Participants completed the experiment in a dark cubicle and used a chin rest to maintain a viewing distance of 57 cm. A circular black cardboard annulus (radius, 11–29 cm) was placed over the monitor frame to provide a circular viewing aperture and to remove any external cues to vertical. Participant responses were collected using a regular computer keyboard.

Stimuli. Stimuli consisted of sinusoidal gratings (Exp. 1a) or band-pass-filtered textures (Exp. 1b) with the same mean luminance as the midgray background (Fig. 2). Stimuli were presented within an annular window of 0.75° inner radius and 7.2° outer radius, with both stimulus edges softened using a 1.5° raised cosine window.

Grating stimuli (Exp. 1a) were given a spatial frequency of 1 cycle/° with phase chosen randomly for each trial. Spatially band-pass-filtered noise textures (Exp. 1b) were generated with orientations from a wrapped normal distribution (as described by Dakin et al., 2005), with the peak of the curve located at the current trial’s orientation and its SD used to vary the level of certainty in the orientation information and spatial frequencies from a rectangular distribution from 0.35 to 3.47 cycles/°. The same method was used to introduce orientation variance into the grating stimuli, with the difference that the range of spatial frequencies was much narrower: 0.93–1.07 cycles/°.

In addition, when a backward mask was required for a trial, it was generated using the same method except that it did not contain any orientation-specific information. The backward mask was presented immediately after stimulus removal and shown for 1 s at 100% contrast.

It is possible that participants have a biased representation of cardinal and primary oblique orientations, so we provided a stable, unchanging reference onscreen throughout the entirety of the experiment. This was in the form of 1° white lines shown both above and below vertical and the 45° oblique orientation separated from the outer edge of the stimulus by 1.5°. Fixation was two centrally placed concentric white and black circles with diameters of 0.25° and 0.5°, respectively. We used a raised cosine temporal envelope for stimulus presentation ranging between 0% and the specified maximum contrast value for the trial. Participants had unlimited time to respond, during which only fixation and the reference lines were visible. The next trial commenced 500 ms after participants gave their response.

Procedure. Participants were shown a grating (Exp. 1a) or band-pass-filtered noise texture (Exp. 1b) and asked to judge whether it was oriented closer to the nearest cardinal (vertical) or oblique (45°) angle. On each trial, stimuli were given an orientation between 10° and 35° in steps of 2.5° (for our psychophysical experiments, 0° is defined as vertical and positive values indicate clockwise rotation). Participants were instructed to maintain fixation at all times and were encouraged to use the reference lines on the outside of the stimulus to assist in their judgment provided they did not break fixation.

In three separate blocks, we manipulated the level of certainty via different methods. First, we varied the SD relating to the orientation variance within the texture (see “Stimulus”) at 0°, 15°, and 25° (gratings, Exp. 1a) or between 1°, 15°, and 30° (broadband textures, Exp. 1b). Second, we varied the Michelson contrast at 100%, 5%, and 3%. Third, we varied stimulus duration across trials to be 1000, 160, or 80 ms, which was followed by a backward mask that did not contain specific orientation information (see “Stimulus”). It should be noted that, in all three blocks, the high certainty stimulus was identical (orientation variance of 1°, 100% contrast, and a 1 s stimulus presentation). Each block consisted of 10 repeats for each combination of orientation and certainty level and blocks were repeated 3 times over the course of the experiment. In all, this totaled 2970 trials (11 orientations $\times$ 3 certainty levels $\times$ 10 repeats $\times$ 3 blocks $\times$ 3 stimulus manipulations) per subject using the method of constant stimuli, with all trials and blocks presented in random order.

Data analysis. For each participant, we computed the proportion of responses that were labeled as closer to an oblique orientation for each level of certainty. We fitted logistic functions to each dataset with two free parameters: the point of subjective equality (PSE) and slope. Lapse rate was set to zero. We minimized the sum-of-squares residuals between each participant’s responses and the fit using nonlinear optimization (the Nelder–Mead simplex method implemented through MATLAB’s “fminsearch” function).

fMRI experiment

Participants. Eight participants (two females, mean age 30.6 years), including the authors, were recruited for the fMRI experiment. All participants had normal or corrected-to-normal vision. These experiments were granted ethics approval by the local ethics review committee and all participants gave written informed consent.

Apparatus. Echoplanar imaging (EPI) and T1-weighted anatomical (1 $\times$ 1 $\times$ 1 mm) data were collected using a Philips 3 T Achieva MRI scanner with an 8-channel SENSE head coil. EPI data were collected with a T2* sensitive gradient echo imaging pulse sequence [repetition time (TR) = 2 s, echo time (TE) = 32, voxel size = 2 mm isotropic, flip angle = 90°, matrix = 96 $\times$ 96, 180 volumes] in 35 slices (interleaved, near coronal) that covered the occipital lobes. A separate retinotopic mapping session was used to collect polar and eccentricity maps using an EPI sequence (TE = 32, TR = 3 s, voxel size = 1.5 mm isotropic, flip angle = 90°, matrix = 128 $\times$ 128, 132 volumes) with 46 slices (interleaved, near coronal) as well as a T1-weighted anatomical image (sagittal MP-RAGE, 1 mm isotropic resolution). We used FreeSurfer (Dale et al., 1999; Fischl et al., 1999) for segmentation, cortical surface reconstruction, and surface inflation and flattening of each participant’s anatomical image.

Stimuli were displayed on a LCD monitor (BOLDscreen; CRS) located at the head of the scanner bore and viewed via a front-surface mirror that was mounted on the head coil at a 45° angle (optical path length, 121.5 cm). Pixel resolution of the display was 1920 $\times$ 1200, subtended a visual angle of 24.3° $\times$ 15.2°, and had a temporal resolution of 60 Hz. The display had mean luminance of 384 Cd/m² and was gamma corrected to have a linear relationship with luminance intensity for each color channel. Stimulus generation and presentation was controlled using MATLAB and the PsychToolBox 3

Figure 2. Stimuli used in the psychophysical experiments. Stimuli were either sinusoidal gratings (Exp. 1a; top row) or band-pass-filtered spatial frequency noise textures (Exp. 1b; bottom row). The high-certainty stimuli (right) were the same across the three certainty manipulations. Certainty was reduced in three ways for each of our participants: (1) increasing orientation variance, (2) reducing stimulus contrast, or (3) shortening stimulus duration, which was immediately followed by the presentation of backward mask (inset) that did not contain any orientation-specific information.

extension (Brainard, 1997; Pelli, 1997). Participant behavioral responses were collected using a LU400-PAIR Lumina response pad (Cedrus).

Stimuli. Stimuli consisted of sinusoidal gratings (as in Exp. 1a) with certainty manipulated through contrast level. Stimuli with high certainty were presented at 100% contrast, whereas low certainty was shown at 3% contrast. Stimuli were presented in an annulus centered at fixation with the inner and outer radius at 0.75° and 7.2° eccentricities, respectively, with both stimulus edges softened using a 0.35° raised cosine window. Gratings had a spatial frequency of 3.35 cycle/° with phase chosen randomly for each trial and underwent a single phase reversal midway through stimulus presentation. The fixation marker consisted of two circles, a centrally located light/white circle (0.1° diameter) surrounded by a black circle (0.2° diameter).

Procedure. Each run used a condition-rich event-related design (Kriegeskorte et al., 2008) that displayed 16 orientations (0–168.75°, in steps of 11.25°) in a random order. Each trial lasted 4 s, consisting of 1 s of stimulus presentation at the maximum contrast value and a phase reversal after 500 ms to minimize retinal adaptation. This was followed by a 3 s interevent interval during which only the fixation marker was displayed. Each orientation was presented four times in each run and shown among 20 null events (24% of all trials) in which only fixation was displayed.

The first and last six trials were matched so that the initial six trials could be discarded to accommodate the time that it takes for the BOLD signal to reach a stable response while maintaining randomization across trials. Each run lasted 6 min exactly and participants completed 10–12 runs in a single session. Participants completed three sessions on different days: the first session consisted of independent retinotopic mapping scans, the second was the experiment session of gratings at full contrast (100%), and the third at low contrast (3%). Participants were given a fixation task that required them to detect luminance changes of a central fixation marker between white and light gray that changed in intensity randomly every 1500–2500 ms.

Data analysis. For each participant, we identified V1 using standard retinotopic mapping techniques (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997; Aguirre et al., 1998). Briefly, participants observed four runs of a smoothly rotating checkerboard wedge stimulus and two runs of an expanding/contracting ring stimulus (for full stimulus details, see Mannion et al., 2013), which was analyzed through phase-encoding methods (Engel, 2012) to establish preferences in the visual field over the cortical surface.

We used AFNI to correct for slice timing and to obtain estimates for head motion both within and between runs, which were then coaligned using a windowed sinc interpolation. The participant’s anatomical image was coarsely coregistered manually with the mean of all of the functional

Figure 3. Psychophysical results of an example subject. Behavioral results are shown for participant MLP for our certainty manipulations: orientation variance (**A**, **D**), stimulus contrast (**B**, **E**), and stimulus duration (**C**, **F**). The top row are the results of Experiment 1a containing the grating stimulus, whereas the bottom row are the results of Experiment 1b, which presented spatially band-pass-filtered noise textures. Each certainty manipulation was fit with a logistic function that minimized the sum-of-squares residuals. We marked the PSE with gray dotted lines for functions with the highest and lowest certainty in each manipulation.

images to provide an initial estimate for AFNI's 3dAllineate. This implemented the Pearson correlation cost function (Saad et al., 2009) with six degrees of motion (three translation and three rotation). The functional data were then projected onto the cortical surface by averaging between the boundaries of white and pial matter (identified with FreeSurfer) using AFNI/SUMA. We performed all experimental analyses on the nodes of this surface domain representation.

The response time series of each participant was analyzed in AFNI using a general linear model (GLM) that fit SPM's canonical hemodynamic response function to each of our stimulus onsets (separately), providing β -weights for all of our presented orientations. The first 12 volumes (24 s) were excluded to allow the BOLD signal to reach a steady response. For each run, we set polynomials up to the third degree as regressors to capture any fluctuations in lower temporal frequencies that were unrelated to stimulus onsets. The GLM was estimated via AFNI's 3dREMLfit, which accounts for noise temporal correlations via a node-wise ARMA(1,1) model. All subsequent data fitting used nonlinear optimization of free parameters (the Nelder–Mead simplex method implemented through MATLAB's "fminsearch" function) to minimize the sum-of-squares residuals between participant data and the current estimate of the fitted function.

We selected the nodes within the primary visual cortex to be used in the experiment according to their response (t statistic) to the comparison of all stimulus conditions versus a fixation baseline across all experimental runs. We restricted our analyses in each participant to the union of nodes in high- and low-contrast sessions that showed a significant value to this contrast ($p < 0.05$, one-tailed). This provided us with masked ROIs of nodes that were relevant to stimulus processing.

We trained a multivariate pattern classifier on the fMRI activity from each masked ROI in response to cardinal (0° , 90°) and primary oblique (45° , 135°) orientations using a leave-one-run-out cross-validation procedure. That is, for each cross-validation, one run was left out as an independent test dataset and the data from the remaining runs were used

as the training set. We tested whether activity patterns were better matched to those of the trained cardinal or oblique orientations for each of our presented stimulus orientations using binaries derived from SVM^{light} (Joachims, 1999).

We computed the mean prediction accuracy across cross-validations based on the distance to the nearest cardinal orientation (e.g., prediction accuracies for the orientations 11.25° , 78.75° , 101.25° , and 168.75° were averaged to give a single value "11.25° from cardinal"). We linearly fitted average classification performance across participants as a function of the distance to the nearest cardinal orientation for high- and low-contrast sessions separately and identified the orientation (O_{50}) at which the response pattern was equally similar to both cardinal and oblique reference stimuli. We sampled participant data over 1000 bootstraps to identify the parameter distributions for O_{50} at each certainty level. We used a kernel smoothing function to display the bootstrapped parameter distributions and a confidence interval on the difference distribution.

Results

We examined both perceptual and neural correlates of orientation biases to identify changes in cortical processing that matched any changes to perception and to establish whether they were consistent with the statistical properties of orientation in visual images of our environment.

Psychophysics

We presented stimuli within a range of orientations between vertical and oblique and asked participants to report to which of these reference orientations the stimulus was perceived to be closer. We varied the degree of certainty for two sets of stimuli using three distinct manipulations and fit each set of data with a logistic function (Fig. 3). In all six cases, we found that, for the

Figure 4. PSEs for the mean psychophysical results. Bars indicate the points of subjective equality from the fits of our mean psychophysical results. Colored markers show the PSE from each of our participants. The gray dotted line is the midpoint between cardinal and oblique orientations.

high-certainty condition, the PSE where participants were equally likely to report the stimulus into either category did not coincide with the orientation bisecting cardinal and oblique (i.e., 22.5°), but rather passed through an orientation closer to cardinal. This reveals a bias toward reporting oblique orientations because participants were more likely to respond that the stimulus was closer to oblique for a greater range of presented orientations.

Interestingly, when lower-certainty stimuli were presented, regardless of the type of manipulation or stimulus used, the bias toward reporting oblique was consistently reduced. In all cases, we found a rightward shift of the psychometric function (i.e., toward oblique) at low certainty, revealing that fewer responses were judged as oblique.

To more clearly represent the shift of the psychometric functions corresponding to differences in the certainty level, in Figure 4 we replotted the points of subjective equality from the behavioral results (Fig. 3) for all of our participants. We found a consistent monotonic increase in the PSE corresponding to lower certainty levels. This was identified to differ significantly for certainty level on the grating stimuli ($F_{(2,10)} = 17.296$, $p = 0.001$), as well as for the band-pass-filtered noise textures ($F_{(2,8)} = 13.582$, $p = 0.003$), whereas we did not find any significant differences on either set of stimuli for a main effect of the type of certainty manipulation used or for an interaction. Furthermore, *post hoc* analysis of these differences in certainty showed significant linear trends for both sets of stimuli (gratings, $F_{(1,5)} = 23.350$, $p = 0.005$; band-pass textures, $F_{(1,4)} = 18.494$, $p = 0.013$). These results show a consistent, repeated bias toward reporting orientations as more oblique than their physical orientation at high certainty, with this bias being reduced toward veridical under conditions of low certainty. This suggests that the pattern of responses reflects a generic effect of uncertainty rather than being a stimulus-specific response.

Multivariate analysis of V1 pattern information

We trained a multivariate pattern analysis (MVPA) classifier to discriminate patterns of fMRI activity from V1 for cardinal and

Figure 5. Mean classification proportions of V1 for high- and low-contrast test gratings. The mean proportion of classifications categorized as oblique is presented as a function of the distance from the nearest cardinal orientation. The horizontal dotted gray line shows where the response pattern is equally similar to those for cardinal and oblique orientations and its intersection with the fitted lines are the O_{50} orientations for each contrast level. Bootstrapped parameter distributions of O_{50} positions are shown at the bottom using kernel smoothing.

oblique orientations and provided test data from all of our presented orientations. The classifier was tasked with determining whether the fMRI activation patterns from these orientations more closely resembled those of cardinal or primary oblique orientations. Figure 5 shows the mean classifier predictions after binning test orientation dependent on the angular distance to the closest cardinal orientation.

We found that the proportion classified as oblique increases with test orientation for both contrasts, with the rate of change greater for the high-contrast session. Further, the orientation (O_{50}) at which the response pattern is equally similar to either of the two reference stimuli displays a bias toward classifying orientation as oblique at high contrast and a bias toward classification as cardinal at low contrast. We measured the reliability of this shift by performing 1000 bootstraps of the between-subjects data

and examining the O_{50} value for both high- and low-contrast datasets on each of the iterations and present the relative distribution of O_{50} values along the axes for each of the sessions (Fig. 5). We computed the O_{50} value for the high-contrast data on each bootstrapped iteration and found that the 95% confidence interval (CI) did not include 22.5°, revealing a significant bias toward classifying orientation as oblique (95% CI: 12.30–22.49°, $p < 0.05$). The corresponding 95% CI on the low-contrast O_{50} was 19.50–66.88°. We then computed the difference in the O_{50} between high- and low-contrast data, revealing that the change in the O_{50} value was significant (95% CI: 4.80–44.86, $p < 0.05$). This showed a consistent shift toward the classification of cardinal orientations in V1 for low-contrast stimuli. We also observed a significant and positive confidence interval for the slope parameter in both the high-contrast (95% CI: 0.003–0.005/°, $p < 0.05$) and low-contrast (95% CI: 0.001–0.003/°, $p < 0.05$) sessions. This is confirmation that, even though the low-contrast data have classification proportions closer to 0.5, the pattern of results was nonetheless reliable.

Our focus was on V1 as the first site of significant orientation selectivity in the primate visual-processing hierarchy (Hubel and Wiesel, 1968). We also performed exploratory analyses of the data from V2 and V3, but the shifts in O_{50} with contrast in these areas were not statistically significant.

Discussion

We used a combination of fMRI and behavioral psychophysics to investigate the effect of sensory uncertainty on the processing and perception of contour orientation in a sample of neurotypical human observers. Under conditions of high certainty, we found that perceived orientation was biased toward the obliques (Lennie, 1971), both for gratings and for band-pass-filtered noise patterns. When certainty was reduced, we consistently found that this bias away from cardinal orientations was reduced in magnitude or eliminated (Tomassini et al., 2010). This was the case regardless of whether uncertainty was introduced through increasing orientation variance, decreasing contrast, or decreasing duration. MVPA of fMRI data revealed correlates of these perceptual orientation biases in human V1. Specifically, there was a bias to classify orientation as oblique at 100% stimulus contrast, but there was a significant shift toward classification as cardinal at 3% contrast.

Our behavioral data are consistent with previous reports that perceived orientation is exaggerated toward the oblique (Lennie, 1971; Tomassini et al., 2010; de Gardelle et al., 2010; van Bergen et al., 2015) and that this bias is reduced, shifting perception closer in the direction of the nearest cardinal orientation, when certainty is reduced through an increase in orientation variance (Tomassini et al., 2010; Girshick et al., 2011). However, unlike the current study, previous studies manipulating certainty through stimulus duration rather than orientation variance have not always found the analogous pattern of results (Tomassini et al., 2010; de Gardelle et al., 2010). De Gardelle et al. (2010) manipulated stimulus duration, but reported their data as a function of subjective visibility, finding a bias in perceived orientation toward oblique that varied non-monotonically with visibility. Reanalysis of those same data in terms of stimulus duration by Wei and Stocker (2015) revealed that the bias toward oblique increased monotonically as duration was reduced. Similarly, a footnote in the Tomassini et al. (2010) paper indicates that reducing duration tended to increase the bias toward oblique, at least for stimuli with low orientation variance. This is the opposite trend to that found here.

Although we cannot explain conclusively the range of reported effects of duration on perceived orientation, there are

various points of difference between the studies. For example, in the study by de Gardelle et al. (2010), subjects indicated the perceived orientation of the test stimulus by adjusting the orientation of a “blue Gabor patch with only one visible strip.” Precise details on the luminance and chromaticity of this strip do not appear in their study, but, given the poor spatial acuity of the blue–yellow pathway in human vision (Calkins, 2001), we speculate that a method based on adjustments of a fuzzy blue strip might affect the quality of the resultant orientation reports. We also find it hard to reconcile the trends in the data as reanalyzed by Wei and Stocker (2015) (their Fig. 4E) with the data as originally reported by de Gardelle et al. (2010). Figure 2A in the original paper shows that visibility is monotonically (and inversely) related to stimulus duration, with low visibility corresponding principally to 20–40 ms, medium visibility to 80–160 ms, and high visibility to 1000 ms. However, although de Gardelle et al. (2010) (their Fig. 4A) report that orientation repulsion is a non-monotonic function of visibility, Wei and Stocker (2015) (their Fig. 4E) report a monotonic decrease in bias with duration. This leads us to question whether the results of the analysis conducted by Wei and Stocker might have been qualitatively different had the data from the shortest duration condition (20 ms) been included.

Although in our study, the three means of manipulating uncertainty yielded qualitatively similar patterns of results, this is not necessarily to be expected (Wei and Stocker, 2015) because each might be expected to have somewhat different effects on the response profile of a population of neurons coding orientation. This is a significant issue for the field because the uncertainty in a stimulus can only ever be experimentally controlled via the manipulation of some specific attribute or attributes. Rather than manipulating stimulus uncertainty, it is interesting to consider the use of a subjective judgment as a metric of uncertainty on any given trial. For example, de Gardelle et al. (2010) asked subjects to make a visibility judgment on the test stimulus as well as reproducing its orientation and then examined bias in perceived orientation as a function of subjective visibility. However, if we think about the coding of the test stimulus in the response profile of a population of orientation-tuned neurons, then judging visibility requires focusing on the height of the resulting hill of activity, whereas judging orientation requires focusing on the location of its peak (Jazayeri and Movshon, 2007) or mean (Wei and Stocker, 2015). When subjects have to do both, it is not clear what strategy they might be using. Instead, in future studies, it might be worthwhile simply to ask subjects to report their confidence in their orientation judgment and to take this as a measure of the intrinsic certainty in the stimulus.

The pattern of behavioral results observed here, whereby the bias toward obliques increases with certainty (Fig. 4), leads to the counterintuitive observation that the perception of orientation is actually closer to veridical (i.e., more accurate, although of course less precise) under conditions of uncertainty, as though our perception is in a sense “optimized” to operate in conditions of uncertainty. However, given that the distribution of contrasts in natural images peaks at low contrast (Chirimuuta et al., 2003) and that saccadic eye movements lead our visual systems to resample the environment several times per second (Ibbotson and Krekelberg, 2011), one could argue that dealing with uncertainty in the retinal image is a generic problem in vision. Therefore, there might be significant evolutionary pressure to perceive the environment accurately under conditions of uncertainty, but little cost associated with perceptual biases under the high-certainty conditions common in laboratory experiments but likely rare in natural viewing.

Convergent evidence from a range of techniques indicates nonuniformities in the coding of orientation by V1 (Chapman and Bonhoeffer, 1998; Furmanski and Engel, 2000; Li et al., 2003; Mannion et al., 2010), which appear to change with contrast (Maloney and Clifford, 2015). Our neuroimaging data from V1 reveal a significant difference in classification performance between low-contrast (3%) and high-contrast (100%) stimuli. Specifically, orientations intermediate between cardinal and primary oblique are more likely to be classified as oblique at high contrast, consistent with the observed behavioral bias. This correlate between behavior and the pattern of activity in V1 has implications for how we might think about neural coding of prior expectation.

The standard Bayesian population coding framework assumes that a perceptual variable is encoded in a population of noisy neuronal activations and that prior expectation is incorporated into a subsequent decoding stage that operates on the responses of those neurons (Zemel et al., 1998). Alternatively, it has been proposed that prior expectation might be encoded implicitly via heterogeneities within the encoding population itself rather than through an explicit decoding stage (Fischer and Peña, 2011; Girshick et al., 2011; Ganguli and Simoncelli, 2010). Specifically, in the context of orientation processing, it has been proposed that a prior expectation for cardinal orientations might be represented implicitly in the population of orientation tuning curves in early visual cortex (Girshick et al., 2011; Wei and Stocker, 2015; van Bergen et al., 2015). However, the existence of a bias to classify orientation from the pattern of V1 activity as oblique at high contrast, although consistent with our behavioral data, is not predicted by a simple prior for cardinal orientation. For a model to account for such an “anti-Bayesian” bias requires an additional layer of complexity, for example, by incorporating considerations of efficient coding into the sensory analysis (Wei and Stocker, 2015).

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