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Oblique stimuli are seen best (not worst!) in naturalistic broad-band stimuli: a horizontal effect

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Abstract

People with normal eyesight typically see horizontal and vertical gratings better than oblique gratings (*Psychological Bulletin 78* (1972) 266; *Perception 9* (1980) 37). In the present study we investigated whether this oblique effect anisotropy is still observed when viewing more complex visual stimuli that better correspond to the content encountered in everyday viewing of the world. We show that the ability to see oriented structure in an image consisting of broadband spatial content is indeed anisotropic, but that the pattern of this orientation bias is completely different from that obtained with simpler stimuli. *Horizontal* stimuli are seen worst and oblique stimuli are seen *best* when tested with more realistic broadband stimuli. We suggest that this "horizontal effect" would be useful in an evolutionary capacity by serving to discount the horizon and other oriented content that tends to dominate natural scenes and thereby increase the salience of objects contained in typical outdoor scenes.

1. Introduction

When resolution acuity or contrast sensitivity is evaluated at different stimulus orientations, visual performance is often best for horizontal and vertical orientations and worst for oblique orientations; an anisotropy referred to as the "Class 1 oblique effect" (Appelle, 1972; Essock, 1980; Essock, Krebs, & Prather, 1997). This anisotropic performance is due to a neural, rather than optical, bias (Campbell, Kulikowski, & Levinson, 1966; Mitchell, Freeman, & Westheimer, 1967) and has been related to a corresponding anisotropy in the number of early cortical neurons tuned to different orientations (De Valois, Yund, & Hepler, 1982; Mansfield, 1974; Mansfield & Ronner, 1978; Orban & Kennedy, 1980; see reviews in Essock, 1980 and Essock et al., 1997). Both the physiological numerical bias and the associated behavioral anisotropy have often been linked to the preponderance of horizontal and vertical content in the visual environment. Specifically, it has often been proposed that early experience in a "carpentered world" leads to the physiological anisotropy by biasing development in individuals (e.g., Annis & Frost, 1973; Yoshida, Iwahara, & Nagamura, 1975). The alternative view, that an innate physiological bias has evolved that matches the preponderance of horizontal, and vertical (although less so for vertical: Baddeley & Hancock, 1991; Hansen & Essock, submitted for publication; Keil & Cristóbal, 2000) content in natural outdoor scenes, is also common (Chapman, Stryker, & Bonhoeffer, 1996; Frégnac & Imbert, 1978; Leehey, Moscowitz-Cook, Brill, & Held, 1975; Switkes, Mayer, & Sloan, 1978; Timney & Muir, 1976). However, when assessing the evidence for either the "nurture" or "nature" view of the oblique effect, it is important to realize that although human performance is inferior for oblique orientations when tested with simple stimuli (e.g., isolated grating patterns), it is not presently known whether the anisotropic performance found when vision is tested with simple stimuli should be assumed to also exist in the perception of more realistic images such as those that contain spatial content composed of a range of spatial scales and orientations. Indeed, in light of findings demonstrating psychophysical and neurophysiological interactions between the components of a

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multi-element stimulus, one might expect a difference in the ability to detect a lone grating as opposed to detecting the grating embedded in rich natural-scene content; that is, the content at other spatial scales and orientations in a scene is likely to alter the processing of a given single spatial component due to various types of adaptation, suppression or gain control mechanisms demonstrated to exist (see e.g., Albrecht, Geisler, Frazor, & Crane, 2002; Carandini, Heeger, & Senn, 2002; Wainwright, Schwartz, & Simoncelli, 2001 for reviews and further references).

This issue was addressed in the present study by testing the ability of humans to perceive oriented structure in images consisting of broadband spatial content tested as a function of orientation (Fig. 1). Noise images were used to allow us to mimic natural scenes in terms of spatial content without introducing any semantic meaning inherent in real-world scenes that might introduce higher-level effects. Preliminary reports of this work have been presented elsewhere (DeFord, Hansen, Sinai, & Essock, 2001, 2002; Hansen, DeFord, Sinai, & Essock, 2002).

2. Methods

2.1. Stimuli

The stimulus patterns were constructed in the frequency domain by taking a broad amplitude spectrum containing a large range of spatial scales (Fig. 2a) and combining this with different random phase spectra to make broadband isotropic noise images (0.35 root mean square (rms) contrast and 40 cd/m^2 mean luminance). Four amplitude spectrum slopes were used, 0.0, −0.5, −1.0 and −1.5 to evaluate a spectrum typical of natural scenes (i.e., −1.0; Van der Schaaf & van Hateren, 1996) and both steeper (‘‘blurred’’), and flatter (‘‘whitened’’) slopes. The isotropic noise images were then filtered to create an increment of amplitude within an orientation band (45° or 20° extent) centered at one of four orientations (0°, 45°, 90° or 135°). Thus content was incremented in the frequency domain within a ‘‘wedge’’- or ‘‘bowtie’’-shaped region creating an oriented test stimulus consisting of a range of orientations (45° or 20°) and a range of spatial frequencies (e.g., 0.2–17 cpd) contained in an otherwise isotropic broad-spectrum background (Fig. 2b, left column). This was done by weighting the spectrum with a triangle filter centered on the nominal test orientation, and retaining the mean luminance and rms contrast of the images. An inverse Fourier transform was then used to convert these frequency-domain representations to the space domain for display (Fig. 2b, right column) on a conventional monitor (SGI 420C) by standard means.

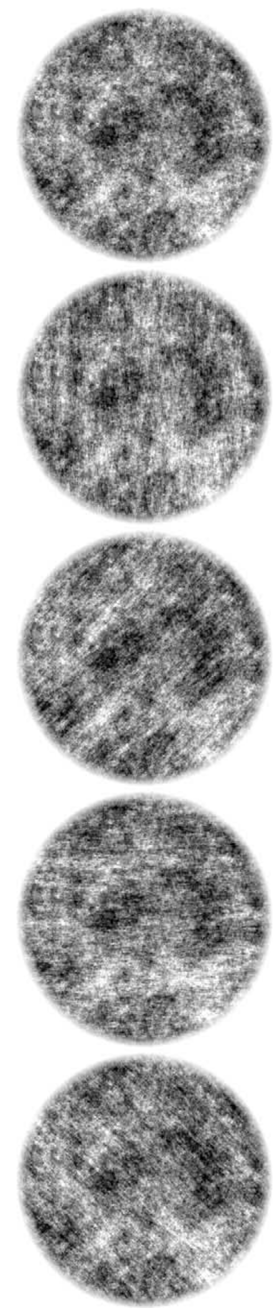

Fig. 1. The top stimulus patch shows a noise pattern with no oriented component for comparison purposes. Underneath the un-oriented pattern is an example of the stimuli used shown at the four orientations tested, each with an oriented increment of an identical amount. Typical observers find the oriented component to be most salient when at the oblique orientations and least salient at the horizontal orientation.

2.2. Psychophysical procedures

Subjects were asked to adjust the test stimulus to ‘‘match the perceived ‘strength’ or ‘salience’ of the oriented structure’’ that they perceived in a standard stimulus. Subjects made keypresses to increase or decrease the physical magnitude of the oriented increment

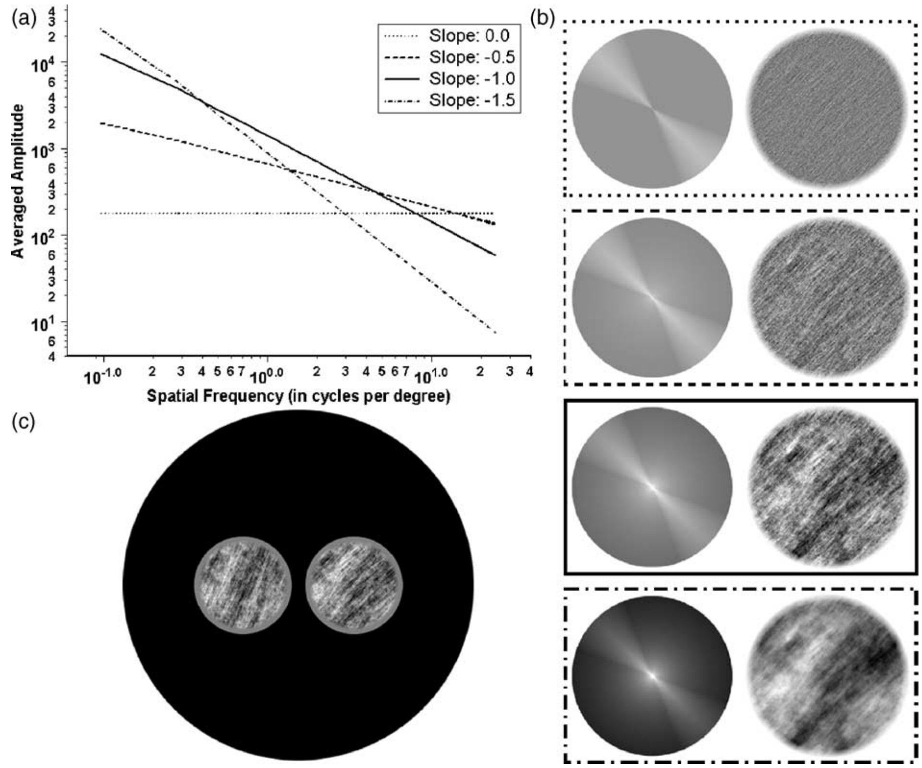

Fig. 2. (a) Amplitude spectra of different slopes (0.0, −0.5, −1.0 and −1.5) that were used to construct the stimuli. (b) For each slope (indicated by the type of line, as defined in Fig. 2a, forming the rectangular box), the two-dimensional frequency spectrum of the stimulus (left), and the corresponding image as presented to the observers after the inverse FFT was performed (right) are shown. (c) An approximation of how the stimulus field appeared to the subject. The subject assessed the perceptual salience of oriented structure presented in the "standard" stimulus pattern on the left (shown at 22.5°) and varied the magnitude of the oriented increment in the test pattern at the right (shown at 45°) to make a perceptual match.

contained in the test pattern in order to make the perceptual match (i.e., they adjusted the amplitude of the frequency-domain "wedge"; see Fig. 2b, left). The test stimulus (centered at 0°, 45° 90°, or 135°) and the standard stimulus (centered at 22.5° or 112.5°) were presented simultaneously as depicted in Fig. 2c. The two 10° stimuli, separated by 1.5°, were isolated from the monitor bezel and room contours by a large 59° black circular mask. Control conditions varied the orientation of the lateral placement of the two stimuli and also of the raster orientation itself (by physically rotating the monitor and mask) and showed that these factors had no effect on the results (i.e., an equivalent [$F_{(3,6)} = 0.56, p > 0.05$] horizontal effect [$F_{(3,6)} = 59.40, p < 0.01$] was obtained in both positions). Across four sessions, subjects made 40 matches of the test pattern (at each of the four test orientations), with 20 trials for each of the two orientations of the standard stimulus. (The orientation of the standard stimulus was found to have no effect on the pattern of results ($F_{(1,3)} = 1.58, p > 0.05$) and results were combined for presentation below.) The phase spectrum used was selected at random on each trial for both the standard and the comparison stimuli. Four experienced and four naive observers, all corrected (as needed) to 20/20 acuity and no residual astigmatism, were tested after IRB-approved informed consent was obtained.

3. Results

The perceptual salience of the oriented structure measured at the four test orientations is shown in Fig. 3. The results demonstrated a strong anisotropy ($F_{(3,18)} = 81.29, p < 0.001$) that was highly different from the oblique effect that occurs with grating stimuli: instead of targets at oblique orientations being seen most poorly, *horizontal* stimuli were seen most poorly and oblique stimuli were seen *best*, with vertical performance intermediate. This was true whether the amplitude spectrum mimicked the content of natural scenes (a slope of −1.0; Fig. 2b, third row) or deviated considerably in terms of the relative content at the different scales of spatial structure (Fig. 2b). Thus, when tested with broadband stimuli a *horizontal* effect is observed rather than the well-known oblique effect, and it does not vary with the distribution of the scale of the broadband content across spatial scale.

We next evaluated how much broadband spatial content must be present in the oriented test pattern to

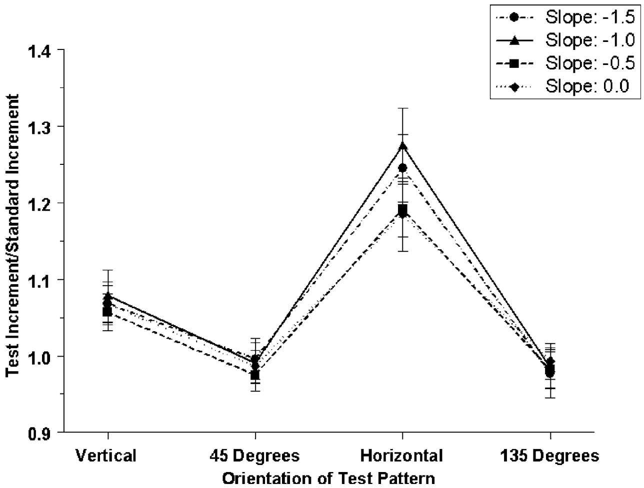

Fig. 3. Means (±SEM) of the eight observers are plotted in terms of the ratio of the percentage of the oriented increment in the test pattern to that in the standard pattern. Values greater than 1.0 indicate that the test orientation was less salient than the standard. Individual data (not shown) showed a pattern of results very similar to the mean data.

change the perceptual bias from an oblique effect to a horizontal effect. The results (Fig. 4a) show that for an oriented component consisting of a single spatial frequency (16 c/deg) and a 20° band of orientations presented on broad-spectrum content (−1.0 slope), a typical *oblique effect* pattern is indeed still observed ($F_{(3,12)} = 3.78$, $p < 0.05$) even though the test stimulus contains multiple orientations. [3] When the content of this test stimulus is broadened to include a 1-octave band of spatial frequencies (8–16 cpd), a clear *horizontal* effect ($F_{(3,12)} = 5.48$, $p < 0.05$) is obtained (Fig. 4c) and when the range of spatial frequencies is reduced to one-half octave (12–16 cpd) performance shows an intermediate pattern suggestive of a transition between the two anisotropies (Fig. 4b). Thus the visual system shows one anisotropy, the well-known oblique effect, with test stimuli consisting of a modest range of spatial content (e.g., a squarewave grating as shown in other studies or the 20° band of orientations reported above), but when the test's content contains a broader range of spatial content (specifically, an octave of spatial frequencies across the 20° orientation band), the perceptual bias becomes a horizontal effect.

Finally, we note that this horizontal effect is a robust effect. In addition to these suprathreshold results, the horizontal effect is also obtained at detection threshold with comparable 1/f noise stimuli on a 2-AFC method of constant stimuli paradigm (Fig. 5a), and just above threshold on another criterion-free measure of sensitivity (Fig. 5b). Furthermore, we report elsewhere that the horizontal effect is also obtained with stimuli made of natural scenes filtered to be isotropic (DeFord et al., 2001; Hansen et al., 2002; Hansen & Essock, submitted for publication).

4. Discussion

The results of this study indicate that when humans view structure similar to that of real-world scenes, their perception is highly anisotropic, with horizontal structure appearing much less salient and oblique content most salient. Thus, compared to the perception of an isolated grating, or a stimulus with a small range of content, the presence of additional spatial components in a visual stimulus results in interactions that strongly alter the relative visibility of oriented content at various orientations. That is, the oblique effect obtained with simple stimuli does not extend to naturalistic viewing situations as many have presumed. A horizontal effect is obtained instead.

We suggest that this dramatic change in the orientation anisotropy obtained with broad-spectrum stimuli actually is to be expected from standard models of contrast gain control (e.g., Bonds, 1991; Geisler & Albrecht, 1992; Heeger, 1992; Wilson & Humanski, 1993) in consideration with the oblique effect literature. Typical models propose that the output of V1 cortical units is modulated by division of their response by the summed activity of other units pooled across a range of preferred orientations and spatial frequencies. We suggest that the present data indicate that the weights for various orientations contributing to the normalization pool are not equal. Specifically, when the broadband test pattern in the present study is oriented obliquely it causes gain to be turned down less than when it is oriented horizontally. Consistent with this proposal, numerous studies have indicated that among striate cortical neurons mediating central vision, horizontal and vertical preferred orientations are somewhat more prevalent than oblique orientations (Chapman et al., 1996; Coppola, White, Fitzpatrick, & Purves, 1998; De Valois et al., 1982; Furmanski & Engel, 2000; Mansfield, 1974; Mansfield & Ronner, 1978; Orban & Kennedy, 1980; Tiao & Blakemore, 1976). Thus, when the output of units is pooled across orientation, the divisive signal would be weaker at oblique orientations, resulting in the stronger response at oblique orientations when viewing broadband patterns such as demonstrated here. In other words, the test-plus-background stimulus would cause more total pooled activity when at the horizontal test orientation than when at an oblique orientation, and would turn down the output of the units detecting the test pattern at horizontal more than when the pattern is at oblique orientations, thereby producing a relatively smaller perceptual response for horizontally oriented content compared to obliquely oriented content in a

[3] A similar effect was obtained with an 8 c/deg grating (and 20° orientation band) when checked with two observers.

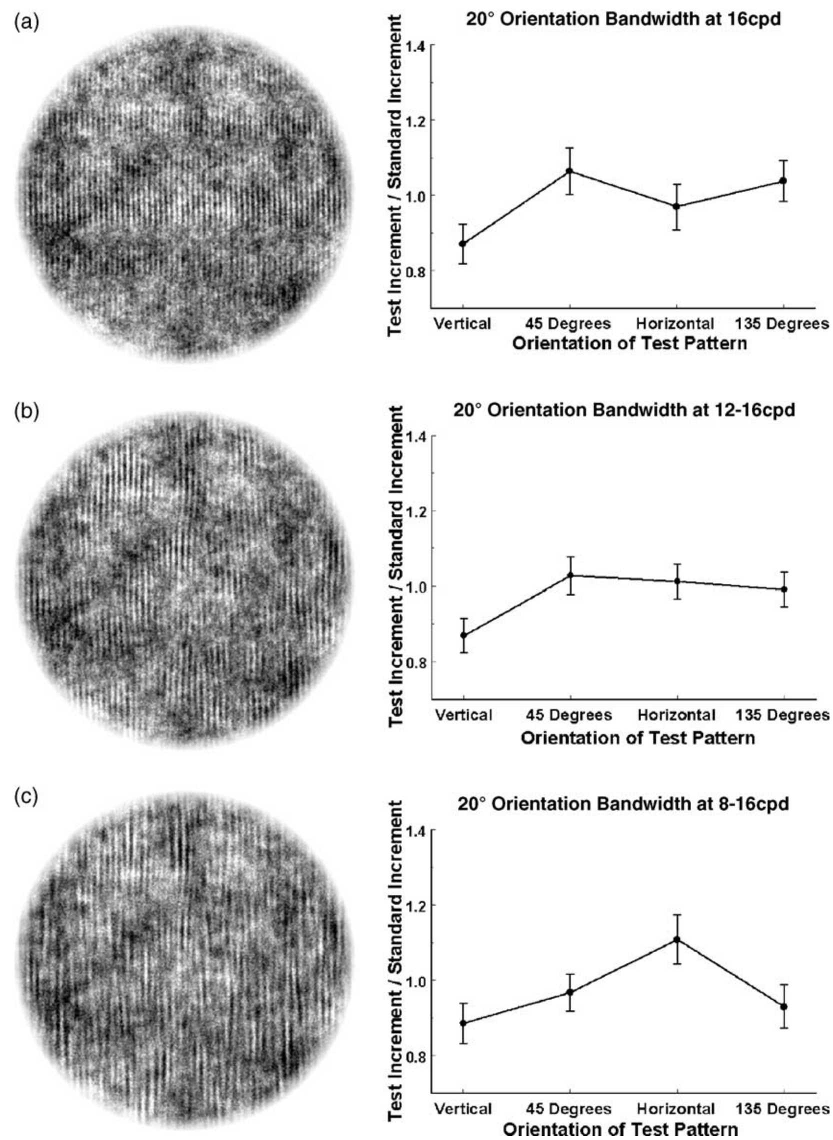

Fig. 4. Stimuli in these different test conditions varied in terms of the range of the spatial frequencies contained in the oriented test component: (a) a single spatial frequency of 16 cpd; (b) a one-half octave band (12–16 cpd); (c) a 1-octave band (8–16 cpd). Orientation bandwidth was 20°. Patch size was 5°. All other details were as described earlier.

broadband pattern. It is also noteworthy that the effect of the background alone, without the much higher amplitude wedge increment, would be to create a weak horizontal effect bias. Indeed the results of the single-frequency sinewave test stimulus on the broadband background (Fig. 4a) appear to reflect an oblique effect due to the 16 c/deg sinewaves in combination with a weak horizontal effect presumably due to the background (and to the multiple sinewaves of the test).

Most models of contrast normalization are dynamic, in the sense that the contribution to the normalization pool by a given filter depends upon its current activity which is determined by the particular content of the currently/recently viewed scene,. However, the horizontal effect reported here must be due to a *static* anisotropy inherent in the divisive signal since the test patterns used here consist of isotropic noise with an oriented test component that itself is identical when presented at different test orientations. That is, any content-based dynamic contribution would be equal when the ‘‘wedge’’ test pattern is presented at one or another test orientation because the content is otherwise equal at each test orientation. Thus we propose that a static weighting factor needs to be added to normalization models to capture this intrinsic orientation bias associated with the unequal neurophysiologic representation of the different orientations.

At the present time we cannot definitively answer why performance is worse for horizontal than vertical, when dogma presumes that these orientations are treated

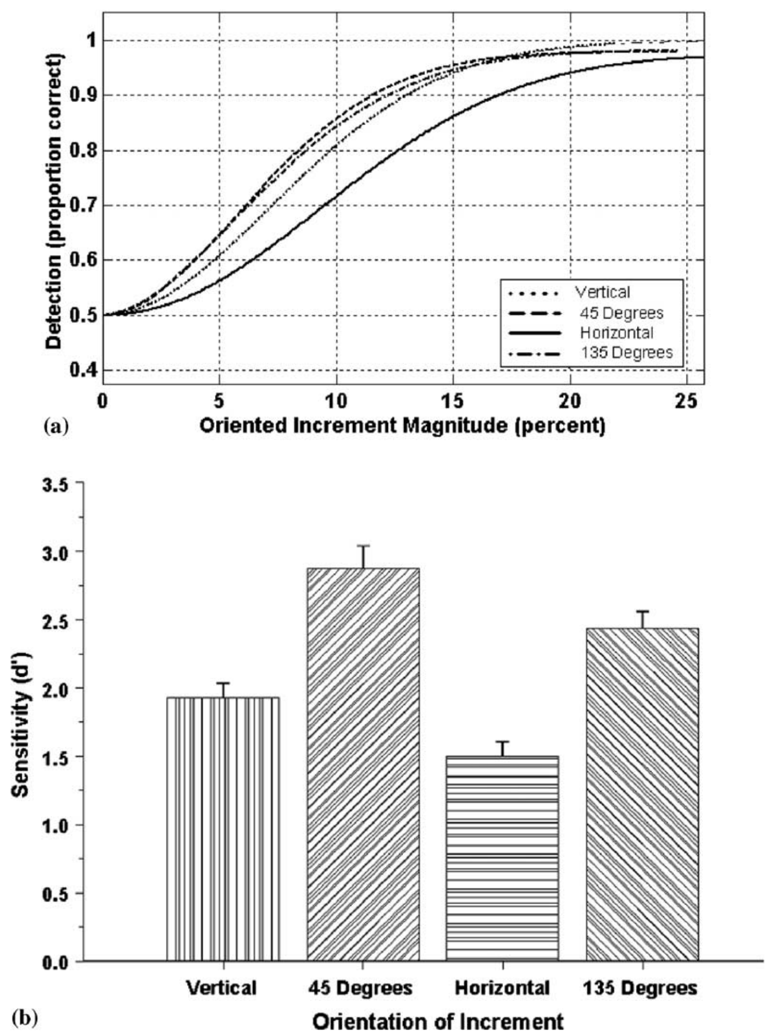

Fig. 5. Ability to detect oriented content at the four test orientations measured on increment threshold (a) and detection sensitivity (b) tasks. (a) Results from a temporal 2AFC paradigm; one of the 240 ms intervals contained a 1/f noise pattern like those described in the text, and the other also contained an amplitude increment of oriented content (a 45° "wedge") of the indicated percentage (relative to the unaltered 0% background noise). Weibull curves fit to mean data obtained from three observers (two experienced, one naïve) indicate detection thresholds (75%) of 8.4, 7.0, 10.6, and 7.2, for 0°, 45°, 90° and 135°, respectively. (b) Sensitivity to an oriented amplitude increment (12%) centered at the four orientations measured on a single-interval (1000 ms) Yes/No task. Average sensitivity (d') and ±1 SEM shown for four observers (three naïve).

equally at a physiological level. However, we suggest that, contrary to current dogma, such a physiological difference between horizontal and vertical very well may actually exist, but that it has not been apparent in most single-unit studies due to the difficulty in obtaining an unbiased sample of adequate size to truly address this issue. Suggestions of a greater prevalence of neurons with a horizontal preferred orientation are actually apparent in the data of several reports (Tiao & Blakemore, 1976; Chapman et al., 1996 (Figs. 1 and 2); Chapman & Bonhoeffer, 1998 (Figs. 1 and 2); Coppola et al., 1998; Mansfield, 1974; Mansfield & Ronner, 1978) and, moreover, a recent characterization of a very large sample of neurons (Li, Peterson, & Freeman, 2003) most clearly indicates this finding. A second way in which a horizontal-vertical disparity is observed is that when they are analyzed separately, horizontal contours are more prevalent in natural scenes than vertical contours due to the presence of the horizon and due to the foreshortening in the vertical direction in the ground plane which creates horizontal image components (Baddeley & Hancock, 1991; Hansen & Essock, submitted for publication). The horizontal effect reported here is highly parsimonious with both of these findings. Finally, given this horizontal-vertical bias in typical natural scenes, it is noteworthy that the anisotropy in the normalization pool (i.e., the "static" orientation weights) that we propose here would be an efficient neural coding strategy, serving to "whiten" the neural representation of natural scenes with respect to orientation.

We conclude that this horizontal effect observed with relatively broadband stimuli would have the consequence of minimizing the perceptual saliency of the horizontal content (and, to a lesser extent, vertical content) that often predominates natural scenes, and enhancing the relative salience of objects containing structure consisting of a range of orientations. Thus, this horizontal effect may serve to discount the horizon and foreshortening in a natural scene so that predators and other broad-spectrum objects are more salient when viewed against the anisotropic background of a typical natural scene.

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