



## Randomly oriented edge arrangements dominate naturalistic arrangements in binocular rivalry

Jonathan J. Hunt<sup>a</sup>, Jason B. Mattingley<sup>a,b</sup>, Geoffrey J. Goodhill<sup>a,c,\*</sup>

<sup>a</sup> Queensland Brain Institute, University of Queensland, St. Lucia, Queensland 4072, Australia

<sup>b</sup> School of Psychology, University of Queensland, St. Lucia, Queensland 4072, Australia

<sup>c</sup> School of Mathematics and Physics, University of Queensland, St. Lucia, Queensland 4072, Australia

### ARTICLE INFO

#### Article history:

Received 13 February 2012

Received in revised form 4 May 2012

Available online 9 June 2012

#### Keywords:

Co-circularity

Binocular rivalry

Natural scene statistics

Saliency

### ABSTRACT

Biological visual systems are highly adapted to the image statistics of the natural world. A particularly important aspect of the statistics of natural scenes is the arrangements of edges they contain. Here, we examined how different arrangements of edges influence human perceptual saliency using a binocular rivalry paradigm. We constructed fields of randomly positioned Gabor patches with orientation arrangements containing co-oriented, co-circular and naturalistic structure. We rivalled these against arrangements with random orientations, which have higher entropy. Surprisingly, we found that fields with randomly oriented edges consistently dominated over the more ordered arrangements. These results suggest that visual scene entropy may be a key variable in early perceptual saliency.

© 2012 Elsevier Ltd. All rights reserved.

### 1. Introduction

Biological visual systems are adapted to the statistics of their input at multiple feature levels and timescales (Geisler et al., 2001; Field and Hayes, 2004; Geisler, 2008). The spatial arrangement of edges is one of the most important features in natural scenes. Edges are not arranged randomly, and the structure in their arrangements is important for shape recognition (Kruger, 1998; Geisler et al., 2001; Elder and Goldberg, 2002; Ledgeway et al., 2005; Geisler, 2008) and texture discrimination (Grossberg & Pessoa, 1998; Wolfson, Orientation, & Landy, 1995; Ben-Shahar, 2006). The relative arrangement of edge pairs can affect their perception (Polat & Sagi, 1993) or grouping (Geisler et al., 2001; Geisler and Perry, 2009). A well-known statistical property of edge pairs is that they tend to be co-linear, i.e. arranged in straight lines. A more recently discovered property is a tendency for edge pairs in natural scenes to be co-circular (Sigman et al., 2001; Geisler et al., 2001). Edges are co-circular if they lie tangent to a common circle; this is the natural generalisation of co-linearity. However, the extent to which the property of co-circularity influences human perception is largely unknown. Here we used a binocular rivalry paradigm to examine how the statistics of edge arrangements, particularly co-circularity, affects low-level salience in humans.

Binocular rivalry is a powerful technique for measuring low-level salience in humans which minimises subjective bias or the need for

complex and potentially confusing feedback from participants. In binocular rivalry, incompatible stimuli are presented to each eye, causing the subjective perception to oscillate between the two conflicting inputs. If one stimulus is perceived for a significantly larger fraction of the viewing time it is said to “dominate” the rivalry. This can be used to probe the effect adaptations to naturalistic statistics impose on the conscious experience of stimuli. While the mechanisms underlying binocular and other perceptual rivalry are still under debate (Blake, 2001; Clifford, 2009), it has been demonstrated that attentional mechanisms play an important role (Blake, 2001; Chong, Tadin, & Blake, 2005; Paffen, Alais, & Verstraten, 2006). Changes in stimulus features such as contrast, which enhance low-level saliency, increase the dominance of stimuli (Whittle, 1965; Hollins, 1980; Blake, 2001). In a particularly relevant recent study, Baker and Graf (2009) demonstrated that noise with naturalistic spatial and temporal power spectra dominated in binocular rivalry over stimuli with less naturalistic power spectrum, suggesting that the human visual system is adapted to find naturalistic spatial frequencies more salient. However, this study did not examine higher level statistics such as edge orientations.

We examined saliency of edge orientations by creating test stimuli consisting of fields of randomly positioned Gabor patches. These fields allowed us to manipulate the statistics of the edge arrangements while leaving other factors, such as spatial frequencies and contrast, unaffected. We rotated the orientations of the Gabors in the field to synthesise random, co-oriented and co-circular stimuli, and also used arrangements obtained directly from natural images. We then rivalled the structured stimuli with the random stimuli. If we consider the information entropy of the stimuli, which is a

\* Corresponding author at: Queensland Brain Institute, University of Queensland, St. Lucia, Queensland 4072, Australia.

E-mail address: [g.goodhill@uq.edu.au](mailto:g.goodhill@uq.edu.au) (G.J. Goodhill).

measure of uncertainty in a random variable, the random stimuli have greater entropy than the competing stimuli. This is because the orientation of each Gabor is independent in the random case, so that the amount of information required to describe the arrangement of the Gabors is proportional to the number of Gabors. In contrast, in the co-oriented case, observation of a single Gabor removes all uncertainty about the stimuli, so it has lower entropy, and similarly for the less-extreme cases of co-circular and naturalistic stimuli. Surprisingly, random edge arrangements consistently dominated over more ordered arrangements. This was true for every condition we considered. The dominance of the higher entropy random stimuli suggests that, unlike spatial frequencies, entropic edge arrangements may be more salient.

## 2. Methods

### 2.1. Ethics statement

All participants provided informed consent to participate in the study, the procedures of which were approved by the University of Queensland Human Research Ethics Committee (Brisbane, Australia).

### 2.2. Gabor fields

We created simple, well-defined stimuli we termed “Gabor fields” for the rivalries (Fig. 1). Each field was constructed from 300 Gabor patches, positioned stochastically within a circle of diameter  $10^\circ$ . The orientation of the Gabors could be modified to introduce well-defined statistical structure into the arrangement independent of other properties such as spatial frequencies or

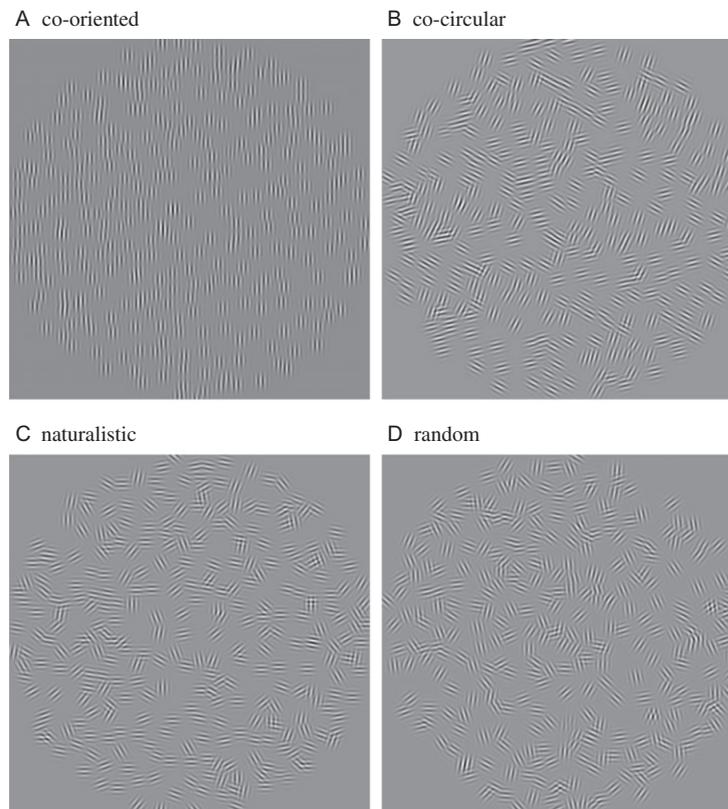
contrast. Gabors were used as the basic building block because they are both a good description of V1 simple cell receptive fields (Jones et al., 1987) and the independent components of natural images are Gabor-like (Bell & Sejnowski, 1997; Van Hateren & Van der Schaaf, 1998). A symmetric envelope was used for the Gabors so that each Gabor was parametrized as

$$g_{x_0, y_0, \theta, \sigma, f}(x, y) = \exp \left[ \frac{-(x - x_0)^2 - (y - y_0)^2}{2\sigma^2} \right] \cos [2\pi f(x \cos \theta + y \sin \theta)] \quad (1)$$

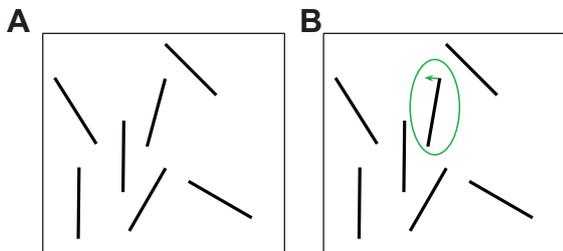
described by a spatial position  $x_0$ , and a spatial frequency  $f$ ,  $y_0$ , orientation  $\theta$ , a Gaussian envelope with variance  $\sigma^2$ . The spatial frequency of the Gabors was chosen to be near the expected peak spatial frequency of the majority of V1 simple cells (Valois, Albrecht, & Thorell, 1982):  $f = 4^{\text{cycles}/\rho}$ . The Gaussian envelope was fixed at  $\sigma = 1/f$ . Overlaps were avoided by randomly placing the first Gabor anywhere in the field and selecting each subsequent Gabor position by stochastically choosing free positions with a probability inversely proportional to the distance to the nearest Gabor.

Different edge statistics were then introduced into the fields by rotating the Gabor patches. The random stimuli were the simplest to generate. After the Gabors were positioned as described above, each Gabor was assigned an orientation  $\theta$ , chosen uniformly between  $[0, \pi)$ . Co-oriented stimuli were generated in a similar fashion, except each Gabor in a field was assigned the same orientation.

Co-circular Gabor fields were created by optimising a quantitative measure of co-circularity using simulated annealing (Kirkpatrick, Gelatt, & Vecchi, 1983) to find co-circular arrangements (Fig. 2). To quantify co-circularity we used  $D_{\text{diff}}$ , a measure of co-circularity which we introduced in previous work and demonstrated to be robust (Hunt



**Fig. 1.** Example stimuli. Four stimulus types were generated for the rivalry experiment. (A) co-oriented stimuli containing edges of a single orientation, (B) co-circular stimuli with strong co-circularity ( $D_{\text{diff}} = 30^\circ$ ), (C) natural edge arrangements (described earlier) (D) and randomly oriented stimuli. Note that each nonrandom stimulus was only ever paired during rivalry with a random stimulus. The arrangement of the stimuli here does not indicate pairing. The stimuli are shown here at high contrast without tinting.



**Fig. 2.** Generating co-circular edges using simulated annealing. (A) Co-circular edge arrangements were created using an optimisation method, simulated annealing, to rotate a set of randomly oriented edges until the desired co-circularity was achieved. (B) At each step of the annealing process, one of the edges was chosen at random and its orientation was rotated slightly. The direction of the rotation was also chosen at random. The co-circularity between all the edges was calculated both before and after the edge was rotated. If the proposed random change increased the co-circularity of the edges it was accepted. The changed edge set was then used as the starting point for the next step of the annealing. If the change decreased the co-circularity it was rejected probabilistically. This occasional acceptance of “backward” steps helps avoid getting stuck in poor local minima (Kirkpatrick et al., 1983).

et al., 2009; Hunt, Bosking, & Goodhill, 2011).  $D_{\text{diff}}(r)$  is defined as the mean deviation from co-circular over all pairs of edges separated by distance  $r$ . Randomly oriented edge arrangements have  $D_{\text{diff}}$  values near  $45^\circ$ , with lower values indicating increasing co-circularity. To remove the dependence on  $r$  in order to obtain a scalar value for simulated annealing we calculated a weighted mean

$$D = \int_0^\infty dr D_{\text{diff}}(r) K(r) \quad (2)$$

We used a Gaussian weighting function  $K(r) \propto \exp(-(r - r_0)^2 / (2\sigma^2))$  with  $r_0 = 5^\circ$  and  $\sigma = 1^\circ$ . This weighting introduces little co-circularity at short separations in order to avoid creating nearby edges with a large degree of co-linearity, while introducing co-circularity over long range separations. Simulated annealing was used to optimise randomly oriented fields with starting  $D_{\text{diff}} \approx 45^\circ$  to generate arrangements with  $D_{\text{diff}} \approx 30^\circ$ . New states were generated by adjusting a randomly chosen Gabor patch’s orientation by  $\pm 1^\circ$ . State changes during annealing were accepted with a probability:

$$p = \min(\exp((D_{\text{old}} - D_{\text{new}})/k_b), 1) \quad (3)$$

where  $D_x$  denotes the co-circularity of the old and new states. The annealing temperature was adjusted after each round of annealing to be:

$$k_b(n) = 3 \exp[-n/3000] \quad (4)$$

where  $n$  is the number of annealing steps taken. The initial value of 3 was chosen so that non-optimal steps were commonly taken during the early stages of the annealing. Annealing was halted as soon as a solution  $D \leq 30^\circ$  was achieved. With these parameters, we reliably found solutions with  $D$  values of  $\approx 30^\circ$  from randomly oriented starting points.

In order to ensure that the results we found were not due to some statistical artefact induced in the generation of co-circular scenes, we also created Gabor fields using edge arrangements extracted directly from natural images. This had the disadvantage of introducing wider variation in the statistics of the edge arrangements, but ensured that the statistics were closely modelled on natural scenes. The reason natural scenes could not be used directly is that we needed to separate the statistics of the edge arrangements from other confounding factors, such as changes in amplitude spectrum or high-level salience. To achieve this, we randomly picked a scene fragment from the Van Hateren image dataset (Van Hateren & Van der Schaaf, 1998) for each stimulus (Fig. 3A). Gabor positions were chosen stochastically as described

earlier. The scene fragments were filtered, using 3-level steerable pyramids (Simoncelli & Freeman, 1995) to find the power in each orientation at each pixel. The use of steerable filters allowed a multi-scale filter to be calculated efficiently so that orientation was considered at multiple length scales in the original scene. Each pixel was then assigned the orientation of the filter with the strongest power at that position. Fig. 3B shows an example orientation image. Finally, each Gabor was assigned the orientation of the underlying pixel. Fig. 3C shows the resulting Gabor field. This method allowed us to source the underlying image edge orientation statistics while maintaining stochastic edge arrangements and fixed spatial frequencies.

The only variation between each class of stimuli was in the statistics of the edge orientations. All Gabor fields contained the same number of Gabors. Fig. 1 shows an example of each type of stimulus (including tinting, which was independently varied as described below). The creation of these synthetic stimuli ensured that only the variable of interest was modified when comparing different stimulus types; there were no correlations with spatial frequency, contrast or contours which could confound our results. The generated stimuli were not matched during rivalry. Each eye’s stimulus had differently positioned Gabors.

### 2.3. Binocular rivalry displays

Once the stimulus sets were created, a standard mirror stereoscope setup was used to measure dominance. Stimuli were displayed on either a Dell 2407 WFP or a Dell U2410 LCD monitor (both  $1920 \times 1200$  pixels, 32-bit colour) running at 60 Hz driven by an ATI Radeon 2400 Pro graphics card<sup>1</sup> controlled by a Dell PC running Windows XP.<sup>2</sup> The Psychophysics toolkit (Brainard, 1997) with MATLAB<sup>3</sup> was used to drive the display. Participants viewed the display through a standard mirror stereoscope 600 mm from the display monitor. Participants performed the experiment in a dark room. All participants had normal, or corrected to normal vision.

Each experiment consisted of 20 trials of a non-random stimulus rivalled with a random stimulus. One stimulus was tinted red and the other blue for each trial (tinting was performed by using only the corresponding pixel colour of the RGB display). Each stimulus was used only once per participant. Participants reported which colour they were experiencing by holding down one of two mouse buttons. They were instructed to release both buttons if they were unsure which colour was dominant. The trial was counterbalanced across eye and tint condition. Each trial consisted of a 40 s rivalry followed by a 20 s blank screen and then the next trial. The 40 s trial length was chosen because it was long enough to allow a number of rivalry switches but mitigated “bleaching” that occurred due to visual adaptation. Participants performed blocks of 5 trials and then the experiment paused until participants were ready to continue. This allowed participants to stretch and reduced fatigue and eye strain.

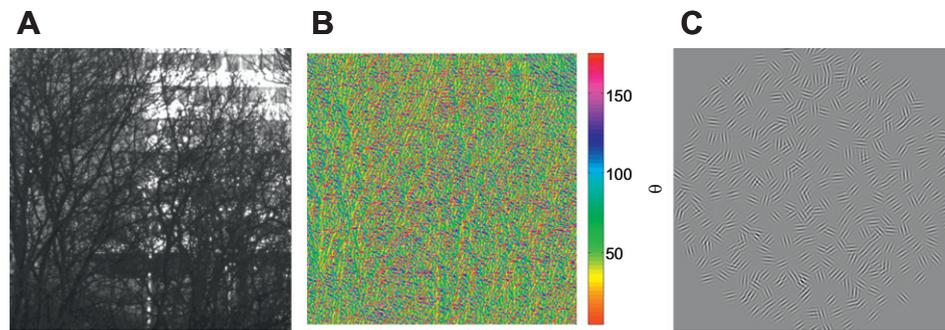
Since rivalry dominance is affected by perceived contrast, each participant did calibration trials where two random stimuli were rivalled and the contrast of the red stimulus was adjusted until the stimuli were reported as dominating approximately equally. This ensured that the perceived contrast of each tint was equivalent for each participant.

Fusion was aided by surrounding the stimuli with a small ring of white noise, identical in both eyes. Participants placed their heads on a chin-rest during the experiment and before each exper-

<sup>1</sup> Advanced Micro Devices, Inc., Sunnyvale, CA, USA.

<sup>2</sup> Microsoft, Redmond, WA, USA.

<sup>3</sup> Version 2009b. The Mathworks, Natick MA, USA.



**Fig. 3.** Creating natural edge fields. (A) Natural scene edge arrangements were created by randomly selecting a region of a picture from the van Hateren dataset (the image brightness has been increased for ease of viewing). (B) The orientation of each pixel was then determined using multi-scale filtering. (C) Gabor patches positions were chosen at random and were overlaid and the orientation of the underlying pixel was assigned to the Gabor. These Gabor fields were then used as the natural edge arrangement stimuli for the rivalry experiments. Note: In order to facilitate comprehension, the natural image and the Gabors have been contrast-enhanced in this figure. This enhancement is for viewing clarity only and was not used in the experiments.

iment participants used a mouse to select the display position which maximised fusion.

#### 2.4. Statistical analysis

For each rivalry experiment we used a two-sided, one-sample *t*-test to determine if the fraction of time random stimuli dominated the rivalry was significantly different from 0.5 (the amount expected if the edge arrangements did not affect rivalry). For the primary findings in this study, we treated each participant as a single observation by calculating the median dominance of random stimuli for each participant ( $n - 1$  degrees of freedom for  $n$  participants). For the second part of the study, a partial reproduction of Baker and Graf (2009), we treated each trial as an independent sample (with  $20n - 1$  degrees of freedom for  $n$  participants). To determine if degree of dominance of random stimuli was significantly different between the different conditions a one-way ANOVA was performed with stimulus type as the condition.

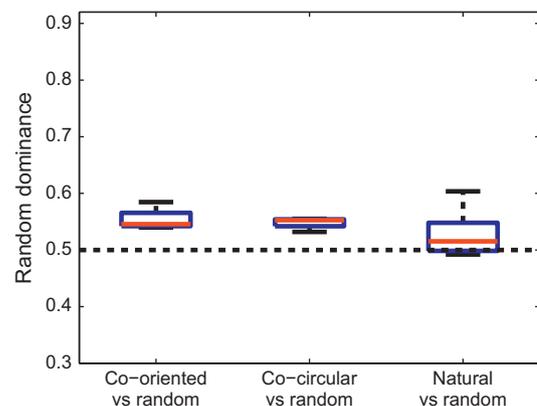
Additionally, we fitted a 2-way ANOVA to test whether eye and tint colour affected our results. This was to measure the noise that these confounding factors contributed to the results. It is important to note that even if these factors are significant, they cannot contribute to a non-null result due to the counterbalancing in our experimental design. We fitted the ANOVA across all participant's results together. We reported both the *p*-value and the effect size  $\eta^2$  (the effect size measures the amount of variance in the results explained by a variable).

For all tests  $p < 0.05$  was considered to indicate significance. All statistics were calculated using MATLAB built-in functions.

### 3. Results

Four types of stimuli were generated for testing in rivalry (Fig. 1): co-oriented, with all edges oriented identically; co-circular, with edges optimised to contain co-circularity at long distances (Fig. 2); naturalistic, with edge arrangements following those of a natural scene (Fig. 3); and random, with each edge orientation chosen independently. All non-random stimuli were rivalled against the random stimuli.

The random stimuli consistently dominated over all other stimulus types (Fig. 4) by a small, but statistically significant amount (random stimuli dominated 0.56, 0.55, 0.53 fraction of the time ( $p = 0.01$ ,  $p = 0.003$ ,  $p = 0.04$ ) for co-oriented, co-circular and natural stimuli respectively). Every test had a least 2 naive participants and at least 4 participants (Table 1). An ANOVA found no significant difference in the dominance between the three conditions.



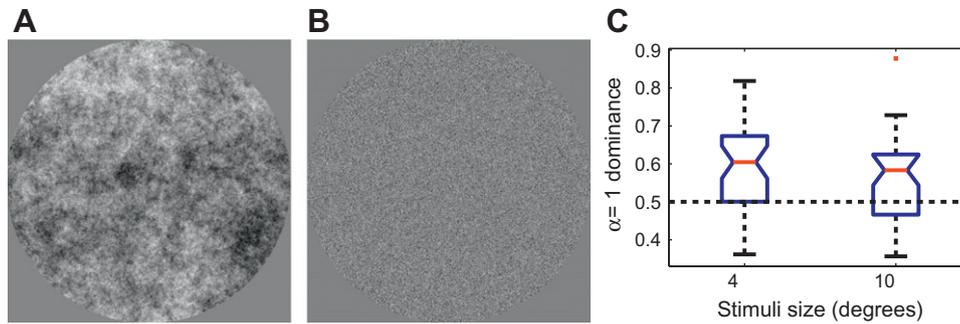
**Fig. 4.** Binocular rivalry of Gabor fields. Box and whisker plot showing the fraction of time for which the random stimuli were dominant. Box shows median (red bar) and quartiles (blue bar) and the range (black bar). In this experiment each participant was summarised as a single observation. For all conditions, the random stimuli dominated ( $p = 0.01$ ,  $p = 0.003$ ,  $p = 0.04$ ). The mean dominance of random stimuli was 0.56, 0.55, 0.53 for co-oriented, co-circular and natural stimuli respectively. The ANOVA reported no significant difference in random dominance between the three experimental conditions ( $p = 0.007$ ). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

Number of participants per experiment. Each participant performed 20 binocular rivalry trials. All results were used in the analysis. Some participants participated in all 3 experiments.

Stimulus type	<i>n</i> Naive	<i>n</i> Total participants
Co-oriented	2	4
Co-circular	2	4
Natural	7	10

Although random edges consistently dominated, they did not do so by a large amount. However, the random dominance was robust across conditions. In addition to the pooled analysis, we also analysed each participant's individual results separately, and we found that in every experiment in which the participant had a statistically significant deviation from 50% dominance, randomly oriented edges dominated (this was the case for 3, 4, and 3 participants in the co-oriented, co-circular and natural experiments respectively). Additionally, only 3 participants had a mean dominance below 50%, and this only occurred in the natural scene case, which had a larger variability, possibly because the stimulus statistics cannot be as well controlled in this case. The effect of edge arrangements on



**Fig. 5.** Stimulus size does not significantly affect dominance in binocular rivalry. To test if the size of the stimulus was likely to have played a role in our findings we repeated one part of the Baker and Graf (2009) experiment on spatial noise using two different sizes of stimuli. (A) shows an example stimulus with a naturalistic power spectrum ( $\alpha = 1$ ) contrasted with (B) which has a flat power spectrum ( $\alpha = 0$ ) (stimuli are shown without tint). (C) The box and whisker plot shows the dominance of naturalistic spatial noise over the white noise. In this experiment each observer trial was counted as an independent observation. For both the small ( $4^\circ$ ) and large stimuli ( $10^\circ$ ), naturalistic noise dominated the rivalry ( $p < 0.006$ ) with a dominance of 0.59 and 0.57 respectively. There was no significant difference ( $p = 0.29$ ) between the two stimulus sizes.

dominance had a comparable effect size to the effect of naturalistic spatial noise we found when we replicated Baker and Graf's results (see below, Fig. 5). The strength of dominance was lower for the naturalistic stimuli compared with co-oriented and co-circular stimuli (Fig. 4). Overall, these results demonstrate a robust dominance of higher entropy edge arrangements.

We used ANOVA to measure the contribution of noise from confounding factors such as eye and tint. Our counterbalanced design ensures that these factors cannot contribute to a non-null result, but they may add noise to the results. A 2-way ANOVA was performed, with the fraction of time participants indicated the random stimulus was dominant as the result variable and stimulus position and tint as treatment conditions. In the co-oriented experiment the ANOVA showed a small dependence on tint  $p = 0.008$ ,  $\eta^2 = 0.09$ , and in the natural stimuli experiment a small dependence on position  $p = 0.01$ ,  $\eta^2 = 0.07$ . No other trials had a statistically significant dependence on either tint or stimulus position. This indicates that the majority of the variance in the trials is not due to eye position or tint colour, but in two experiments these factors contributed a small amount of noise. These factors are not an exhaustive list of noise sources.

In order to contain a large number of edges we made our stimuli relatively large ( $10^\circ$ ). This meant that, as expected (Kang, 2009), dominance was sometimes partial. Participants were instructed to press a key when one colour dominated clearly so the partial switching should not confuse the results. In all experiments, one colour dominated approximately 80% of the time (Table 2), indicating that participants perceived clear dominance the majority of the time. We examined whether stimulus size might play a role in our results by repeating the Baker and Graf (2009) experiment on the dominance of spatial noise with varying stimulus sizes. Using both small ( $4^\circ$ ) stimuli similar to their original experiment and larger stimuli ( $10^\circ$ ), we found, in agreement with their results, that spatial noise with naturalistic power spectrums dominated (Fig. 5). There was some reduction in dominance of the larger stimuli but it was not statistically significant. This indicates that, although lar-

ger stimuli may have longer switching transitions, this was not an important factor in our results. Additionally, it demonstrates the dominance of the random Gabor fields is comparable to the dominance of naturalistic spatial noise.

#### 4. Discussion

Here we have found that subtle changes in the statistics of Gabor-field edges affects their dominance during binocular rivalry. Although our rivalry tests showed only small shifts in binocular dominance based on edge statistics, these small changes may indicate important differences in the early visual processing of edges. Binocular rivalry experiments are inherently noisy due to the stochastic nature of binocular switching (Walker, 1975; Blake et al., 1990; Lehky, 1995; Brascamp et al., 2006; Tong et al., 2006; Kim et al., 2006; Krips and Furst, 2009) in addition to noise in the participant's reporting. This is exacerbated because the Gabor fields are necessarily large (to incorporate a large number of edges), which means that binocular switching is often incomplete. Another consideration is that the changes in edge statistics used in our stimuli are relatively subtle and, in the case of the co-circular stimuli, only present over large distances. Therefore, despite the small change in magnitude, the dominance of random edges may indicate important differences in low-level saliency.

The Gabor fields stimuli used in the experiments differ from natural scenes in several aspects such as their power spectrum. However, the only differences between stimulus types is the statistics of their edge arrangements. Although it would be desirable to use more naturalistic stimuli, this would make it difficult to modify just the edge statistics without affecting other confounding factors. Although naturalistic scenes are more complex, it is likely that the mechanisms exposed by these simplified stimuli continue to play an important role.

The dominance of randomly oriented edges may indicate that saliency for higher-level features, such as edges, is assigned to areas of high entropy. This idea finds theoretical support in recent models of predictive coding which posit that deviations from the expected attract the most attention (Schultz & Dickinson, 2000; Hosoya, Baccus, & Meister, 2005; Zhaoping, 2006; Schwartz, Hsu, & Dayan, 2007; Lesica et al., 2007), and recent work demonstrating that surprise is a good predictor of saliency (Itti & Baldi, 2009) and a Bayesian model of saliency that finds uncommon visual features are good predictors of attention (Zhang, Tong, Marks, Shan, & Cottrell, 2008). There is some evidence that primary visual cortex lateral connectivity may contain anti-co-circular connections involved in this process (Hunt, Bosking, & Goodhill, 2011).

**Table 2**

Fraction of dominance. The mean fraction of trial time that participants pressed a mouse button, indicating clear dominance, for each condition. In every condition, the levels of clear dominance were similar.

Co-oriented	0.84
Co-circular	0.83
Natural	0.87
Spatial noise (small)	0.86
Spatial noise (large)	0.77

Other groups have used eye-tracking as a method for measuring low-level saliency. This approach has the advantage of corresponding more closely to natural viewing conditions but the disadvantage of providing more scope for individual idiosyncrasies (Leonards & Scott-Samuel, 2005; Lorigo et al., 2006), habitual search patterns, task specific behaviours or external biases (Parkhurst et al., 2002; Najemnik and Geisler, 2005; Williams et al., 1997; Bindemann, 2010). Additionally, high-level visual features may play a role (Cerf et al., 2008; Johnson et al., 1991). Several groups have found that observers tend to direct their gaze at regions of natural scenes with less spatial correlation (higher entropy) (Reinagel and Zador, 1999; Renninger, Verghese, & Coughlan, 2007; Itti and Baldi, 2009) and eye-movements are preferentially in directions which maximise the reduction in entropy (Bruce et al., 2006; Renninger, Verghese, & Coughlan, 2007). Although these groups considered local spatial correlations rather than edge arrangements, both of these findings are consistent with the notion that entropy is key in assigning input saliency.

Baker and Graf (2009) found that stimuli with naturalistic spatial amplitude spectrums dominated over other stimuli, including the most entropic choice: white noise. However, these findings do not conflict with our result that high entropy edge arrangements dominate during rivalry. It is not surprising that naturalistic amplitude spectrum may be treated differently from naturalistic edge arrangements during rivalry. Edges arise from appropriate combinations of differing spatial frequencies, in this sense edge arrangements are higher-level statistics than the amplitude spectrum. The dominance of stimuli with naturalistic amplitude spectrum could be understood as a narrow prior on the input amplitude spectrum, which causes input with non-naturalistic spatial frequencies to be discounted. The different treatment of naturalistic edge statistics may reflect a higher-variance prior belief about edge statistics so that non-naturalistic edge arrangements attract attention rather than being discounted. This difference in processing is reasonable since the amplitude spectrum remains relatively near  $1/f$  across most natural images (Field, 1987; Ruderman & Bialek, 1994; Dong & Atick, 1995) (although there is still significant variation (Langer, 2000)), while edge arrangements in individual natural scenes are highly variable (Sigman et al., 2001; Hunt, 2011). Regarding possible mechanisms, if the differences in binocular dominance are arising in V1, both lateral connections and predictive feedback from other visual areas provide scope to explain the dominance of stimuli with naturalistic amplitudes and high entropy edge arrangements.

Alais and Blake (1999) and Alais et al. (2006) showed that Gabor patches with Gestalt grouping cues (good continuation and common fate) tended to temporally correlate during rivalry. This grouping effect did not alter the rivalry dominance of the stimuli and does not explain the effects seen here. Any grouping effect of our stimuli would aid full rivalry switching, but it does not explain the dominance of random stimuli.

Motoyoshi and Kingdom (2010) recently examined the role of co-circularity in texture discrimination. They created textures containing pairs of edges, visually similar to our Gabor fields and asked participants to distinguish between different textures. They found that participants could distinguish textures containing co-circularity from random textures relatively easily compared to other textures. This result is complementary to our finding that randomly arranged edges dominate during rivalry. Motoyoshi and Kingdom measured discriminatory ability to show that co-circularity is a key statistic in texture discrimination. However, our results show that the saliency of edge arrangements is increased by removing statistical regularities, thus increasing entropy. Both these findings are compatible with the view that the brain is tuned to deal quickly with co-circular structure, while devoting attention to less-predictable structure. In agreement with our findings, Bonnef and Sagi

(1999), using short-duration binocular rivalry, showed that random texture arrangements are more salient than co-linear textures.

Binocular rivalry provides a straightforward method for estimating low-level visual saliency accurately. Here we have used the dominance of edge arrangements to indicate their saliency. An avenue for future work that may elucidate the role lateral connections play in edge saliency would be to examine asymmetries in the spread of rivalry switching, as has been done for other types of stimuli (Knappen, van Ee, & Blake, 2007; Arnold, James, & Roseboom, 2009). Such asymmetries may indicate underlying asymmetries in the neural circuitry. There is also wide scope for further work examining visual processing of other types of edge statistics using binocular rivalry. Such work may provide further insights into the role of edge arrangements in early scene comprehension.

## References

- Alais, D., & Blake, R. (1999). Grouping visual features during binocular rivalry. *Vision Research*, 39(26), 4341–4353.
- Alais, D., Lorenceau, J., Arrighi, R., & Cass, J. (2006). Contour interactions between pairs of Gabors engaged in binocular rivalry reveal a map of the association field. *Vision Research*, 46(8–9), 1473–1487.
- Arnold, D., James, B., & Roseboom, W. (2009). Binocular rivalry: Spreading dominance through complex images. *Journal of Vision*, 9(13), 1–9.
- Baker, D. H., & Graf, E. W. (2009). Natural images dominate in binocular rivalry. *Proceedings of the National Academy of Sciences of the United States of America*, 106(13), 5436–5441.
- Bell, A. J., & Sejnowski, T. J. (1997). The independent components of natural scenes are edge filters. *Vision Research*, 37(23), 3327–3338.
- Ben-Shahar, O. (2006). Visual saliency and texture segregation without feature gradient. *Proceedings of the National Academy of Sciences of the United States of America*, 103(42), 15704–15709.
- Bindemann, M. (2010). Scene and screen center bias early eye movements in scene viewing. *Vision Research*, 50(23), 2577–2587.
- Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain and Mind*, 2, 5–38.
- Blake, R., Westendorf, D., & Fox, R. (1990). Temporal perturbations of binocular rivalry. *Perception and Psychophysics*, 48(6), 593–602.
- Bonnef, Y., & Sagi, D. (1999). Configuration saliency revealed in short duration binocular rivalry. *Vision Research*, 39, 271–281.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436.
- Brascamp, J. W., van Ee, R., Noest, A. J., Jacobs, R. H. A. H., & van den Berg, A. V. (2006). The time course of binocular rivalry reveals a fundamental role of noise. *Journal of Vision*, 6(11), 1244–1256.
- Bruce, N., & Tsotsos, J. (2006). Saliency based on information maximization. *Advances in Neural Information Processing Systems*, 18, 155.
- Cerf, M., Harel, J., Einhäuser, W., & Koch, C. (2008). Predicting human gaze using low-level saliency combined with face detection. *Advances in Neural Information Processing Systems*, 20, 241–248.
- Chong, S., Tadin, D., & Blake, R. (2005). Endogenous attention prolongs dominance durations in binocular rivalry. *Journal of Vision*, 5(11), 1004–1012.
- Clifford, C. W. G. (2009). Quick guide: Binocular rivalry. *Current Biology*, 19(22), 1022–1023.
- Dong, D. W., & Atick, J. J. (1995). Statistics of natural time-varying images. *Network: Computation in Neural Systems*, 6, 345–358.
- Elder, J. H., & Goldberg, R. M. (2002). Ecological statistics of Gestalt laws for the perceptual organization of contours. *Journal of Vision*, 2(4), 324–353.
- Field, D. J. (1987). Relations between the statistics of natural images and the response properties of cortical cells. *Journal of the Optical Society of America A*, 4(12), 2379–2394.
- Field, D. J., & Hayes, A. (2004). Contour integration and the lateral connections of V1 neurons. *The Visual, Neurosciences*, 1069–1079.
- Geisler, W. S. (2008). Visual perception and the statistical properties of natural scenes. *Annual Review of Psychology*, 59, 167–192.
- Geisler, W., & Perry, J. (2009). Contour statistics in natural images: Grouping across occlusions. *Visual neuroscience*, 26(01), 109–121.
- Geisler, W. S., Perry, J. S., Super, B. J., & Gallogly, D. P. (2001). Edge co-occurrence in natural images predicts contour grouping performance. *Vision Research*, 41(6), 711–724.
- Grossberg, S., & Pessoa, L. (1998). Texture segregation, surface representation and figure-ground separation. *Vision Research*, 38(17), 2657–2684.
- Hollins, M. (1980). The effect of contrast on the completeness of binocular rivalry suppression. *Perception and Psychophysics*, 27(6), 550–556.
- Hosoya, T., Baccus, S., & Meister, M. (2005). Dynamic predictive coding by the retina. *Nature*, 436(7047), 71–77.
- Hunt, J. J. (2011). *Natural scene statistics and the development of the primary visual cortex*. Ph.D. thesis. University of Queensland.
- Hunt, J. J., Bosking, W. H., & Goodhill, G. J. (2011). Statistical structure of lateral connections in the primary visual cortex. *Neural Systems and Circuits*, 1(1), 3.

- Hunt, J. J., Giacomantonio, C. E., Tang, H., Mortimer, D., Jaffer, S., Vorobov, V., et al. (2009). Natural scene statistics and the structure of orientation maps in the visual cortex. *Neuroimage*, 47(1), 157–172.
- Itti, L., & Baldi, P. (2009). Bayesian surprise attracts human attention. *Vision Research*, 49(10), 1295–1306.
- Johnson, M. H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition*, 40(1–2), 1–19.
- Jones, J. P., & Palmer, L. A. (1987). An evaluation of the two-dimensional Gabor filter model of simple receptive fields in cat striate cortex. *Journal of Neurophysiology*, 58(6), 1233–1258.
- Kang, M.-s. (2009). Size matters: A study of binocular rivalry dynamics. *Vision Research*, 9(1), 1–11.
- Kim, Y.-J., Grabowecy, M., & Suzuki, S. (2006). Stochastic resonance in binocular rivalry. *Vision research*, 46(3), 392–406.
- Kirkpatrick, S., Gelatt, C. D., & Vecchi, M. P. (1983). Optimization by simulated annealing. *Science*, 220(4598), 671–680.
- Knapen, T., van Ee, R., & Blake, R. (2007). Stimulus motion propels traveling waves in binocular rivalry. *PLoS One*, 2(1), e739.
- Krips, R., & Furst, M. (2009). Stochastic properties of coincidence-detector neural cells. *Neural Computation*, 21(9), 2524–2553.
- Kruger, N. (1998). Collinearity and parallelism are statistically significant second-order relations of complex cell responses. *Neural Processing Letters*, 8, 117–129.
- Langer, M. S. (2000). Large-scale failures of  $f^{-\alpha}$  scaling in natural image spectra. *Journal of the Optical Society of America A*, 17(1), 28–33.
- Ledgeway, T., Hess, R. F., & Geisler, W. S. (2005). Grouping local orientation and direction signals to extract spatial contours: Empirical tests of association field models of contour integration. *Vision Research*, 45, 2511–2522.
- Lehky, S. R. (1995). Binocular rivalry is not chaotic. *Proceedings of the Royal Society, London, Series B*, 259(1354), 71–76.
- Leonards, U., & Scott-Samuel, N. E. (2005). Idiosyncratic initiation of saccadic face exploration in humans. *Vision Research*, 45(20), 2677–2684.
- Lesica, N. A., Jin, J., Weng, C., Yeh, C.-I., Butts, D. A., Stanley, G. B., et al. (2007). Adaptation to stimulus contrast and correlations during natural visual stimulation. *Neuron*, 55(3), 479–491.
- Lorigo, L., Pan, B., Hembrooke, H., Joachims, T., Granka, L., & Gay, G. (2006). The influence of task and gender on search and evaluation behavior using Google. *Information Processing and Management*, 42, 1123–1131.
- Motoyoshi, I., & Kingdom, F. A. A. (2010). The role of co-circularity of local elements in texture perception Isamu Motoyoshi. *Journal of Vision*, 10(3), 1–8.
- Najemnik, J., & Geisler, W. S. (2005). Optimal eye movement strategies in visual search. *Nature*, 434(7031), 387–391.
- Paffen, C. L. E., Alais, D., & Verstraten, F. A. J. (2006). Attention speeds binocular rivalry. *Psychological Science*, 17, 752.
- Parkhurst, D., Law, K., & Niebur, E. (2002). Modeling the role of salience in the allocation of overt visual attention. *Vision Research*, 42(1), 107–123.
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. *Vision Research*, 33(7), 993–999.
- Reinagel, P., & Zador, A. M. (1999). Natural scene statistics at the centre of gaze. *Network*, 10(4), 341–350.
- Renninger, L. W., Verghese, P., & Coughlan, J. (2007). Where to look next? Eye movements reduce local uncertainty. *Journal of Vision*, 7, 1–17.
- Ruderman, D., & Bialek, W. (1994). Statistics of natural images: Scaling in the woods. *Physical Review Letters*, 73(6), 814–817.
- Schultz, W., & Dickinson, A. (2000). Neuronal coding of prediction errors. *Annual Review of Neuroscience*, 23, 473–500.
- Schwartz, O., Hsu, A., & Dayan, P. (2007). Space and time in visual context. *Nature Reviews. Neuroscience*, 8(7), 522–535.
- Sigman, M., Cecchi, G. A., Gilbert, C. D., & Magnasco, M. O. (2001). On a common circle: Natural scenes and Gestalt rules. *Proceedings of the National Academy of Sciences of the United States of America*, 98(4), 1935–1940.
- Simoncelli, E. P., & Freeman, W. T. (1995). The steerable pyramid: A flexible architecture for multi-scale derivative computation. In *2nd Annual international conference on image processing*.
- Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, 10(11), 1364–6613.
- Valois, R. L. D., Albrecht, D. G., & Thorell, L. G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. *Vision Research*, 22(5), 545–559.
- Van Hateren, J. H., & Van der Schaaf, A. (1998). Independent component filters of natural images compared with simple cells in primary visual cortex. *Proceedings of the Royal Society, London, Series B*, 265(1394), 359–366.
- Walker, P. (1975). Stochastic properties of binocular rivalry alternations. *Perception*, 18(6), 467–473.
- Whittle, P. (1965). Binocular rivalry and the contrast at contours. *The Quarterly Journal of Experimental Psychology*, 17(3), 217.
- Williams, D., Reingold, E., Moscovitch, M., & Behrmann, M. (1997). Patterns of eye movements during parallel and serial visual search tasks. *Canadian Journal of Experimental Psychology*, 51(2), 151–164.
- Wolfson, S. S., Orientation, T., & Landy, M. S. (1995). Discrimination of orientation-defined texture edges. *Vision Research*, 35(20), 2863–2877.
- Zhang, L., Tong, M., Marks, T., Shan, H., & Cottrell, G. (2008). SUN: A Bayesian framework for saliency using natural statistics. *Journal of Vision*, 8(7), 1–20.
- Zhaoping, L. (2006). Theoretical understanding of the early visual processes by data compression and data selection. *Network: Computation in Neural Systems*, 17(4), 301–334.