VISUAL COGNITION, 2007, 15 (7), 765–778

Psychology Press
Taylor & Francis Group

"Filling-in" colour in natural scenes

Benjamin Balas and Pawan Sinha

Department of Brain and Cognitive Sciences, MIT, Cambridge, MA, USA

Our subjective experience of the world as being in full colour across the entire visual field is at odds with the highly fovea-biased distribution of cones in the retina. It is unclear how this percept of "pan-field colour" comes about. We use novel stimuli—"colour chimeras"—to demonstrate a related visual phenomenon in which observers perceive rich colour throughout images with large achromatic regions. This percept appears to critically depend on natural scene statistics. By separately manipulating chromatic and structural content in such images, we demonstrate that both the spatial distribution of colour and the presence of recognizable scene structure contribute to the experience of pan-field colour in these stimuli. Our results suggest that this percept is unlikely to be due to a low-level colour spreading process. Instead, we suggest that mechanisms dependent on natural scenes' chromatic and luminance statistics provide the basis for the phenomenon.

It is remarkable that during everyday scene perception human observers subjectively experience a uniform visual world. The human retina is quite heterogeneous across its surface, both in terms of spatial acuity (Anstis, 1998) and the distribution of rods and cones (Roorda & Williams, 1999). Despite this variation in resolution and colour sensitivity, observers generally perceive uniformity in colour and focus throughout the visual field. Though ubiquitous to our visual experience, this very basic phenomenon has been little examined.

In the current study, we direct our attention to the perception of what we call "pan-field colour", the name we give to the subjective experience of rich

Please address all correspondence to Benjamin Balas, Department of Brain and Cognitive Science, MIT, 43 Vassar St., Rm 46-4089, Cambridge, MA 02139, USA. E-mail: bjbalas@mit.edu

We would like to thank Roland Fleming, Dick Held, Aude Oliva, and Ruth Rosenholtz for their valuable suggestions. Tom Sanocki and an additional anonymous reviewer also provided very helpful comments. We also thank Mariko Jameson for her help in stimulus construction. BJB is supported by a NDSEG Fellowship. PS is supported by a Merck Foundation Fellowship and an Alfred P. Sloan Fellowship in Neuroscience.

http://www.psypress.com/viscog DOI: 10.1080/13506280701295453

colour across the visual field despite a rapid decrease in colour sensitivity as one moves from the fovea to the periphery.

In highly controlled psychophysical experiments subjects demonstrate the limitations placed on them due to their retinal architecture (Magnussen, Spillman, Sturzel, & Werner, 2004; Newton & Eskew, 2003), yet during normal experience the pan-field colour percept is subjectively very strong. Here, we ask why "pan-field colour" is commonly experienced in natural scenes when decreasing colour sensitivity can be measured with sparse laboratory stimuli.

One possibility is that the visual system compensates for impoverished peripheral sensitivity by applying some completion process to natural scenes. The visual system regularly receives incomplete information about the environment and must attempt to reconstruct the missing data. This process, often called "filling-in", has received much attention in recent years (Pessoa, Thompson, & Noe, 1998). Perceptual filling-in has been demonstrated in normal observers for multiple features, such as brightness (Paradiso & Nakayama, 1991), texture (Caputo, 1998; Motoyoshi, 1999; Ramachandran, Gregory, & Aiken, 1993) and colour (De Weerd, Desimone, & Ungerleider, 1998; Sakaguchi, 2001). Filling-in phenomena have also been demonstrated in patients with visual scotomas due to macular degeneration or other retinal damage (Zur & Ullman, 2003), and by using natural blind spots such as that formed by the optic nerve as it leaves the retina, or the "blue-blindness" caused by a lack of S-cones in the central fovea (Magnussen, Spillman, Sturzel, & Werner, 2001, 2004).

Within the larger domain of generic filling-in effects, there are many examples of colour-spreading phenomena. These include neon-colour spreading (Bressan, Mingolla, Spillman, & Watanabe, 1997), or the water-colour illusion (Pinna, Brelstaff, & Spillman, 2001; Pinna, Werner, & Spillman, 2003). However, it is difficult to relate these phenomena to natural scene perception due to their reliance on particular cues regarding transparency relations (Anderson, 1997; da Pos & Bressan, 2003) or edge contrast (Pinna et al., 2001). Even though illusory surfaces can interact to form more complex percepts (van Lier, 2002), it is hard to imagine such a process scaling up to the demands of spreading colour throughout real-world images. In the natural setting, pan-field colour is obtained without such cues.

We suggest that the percept of pan-field colour in natural scenes may not be the result of colour spreading into achromatic regions. Instead, we propose that natural scene statistics may make detecting a region of impoverished colour difficult in most situations, leading to the subjective experience of a fully coloured image. This proposal offers a new insight into the perceived uniformity across the visual field during scene perception. It also makes the prediction that changing the statistics of the natural world will alter observers' tendency to report colour throughout a scene. It is this prediction that we explore in this paper.

Specifically, we ask three questions:

1. Do observers complete the colour content of natural scenes when large regions of the image have had colour artificially removed?
2. If colour completion occurs, does it do so more readily from the centre of an image outwards as opposed to from the periphery inwards?
3. If colour completion occurs, does it depend on natural scene statistics?

To answer these questions, we employ a novel set of images, which we call "colour chimeras". These stimuli are composed of natural or synthetic scenes to which a colour-saturation mask has been applied. The mask either restricts colour to a central image region, or solely to the image surround (Figure 1). This manipulation is similar to the "artificial scotomas" employed by Ramachandran and Gregory (1991), in that we "lesion" the image to remove colour from a specific region. These images do not perfectly model the sensitivity to colour across the retina. Instead, they allow us to determine if colour completion occurs in the absence of chromatic information, subject to various manipulations of scene statistics. We built colour chimeras from a set of unaltered, full-colour, outdoor scenes containing a variety of objects, backgrounds, and textures.

Colour chimeras provide us with a basic means for studying colour completion in natural scenes. Regarding the questions we have posed above,

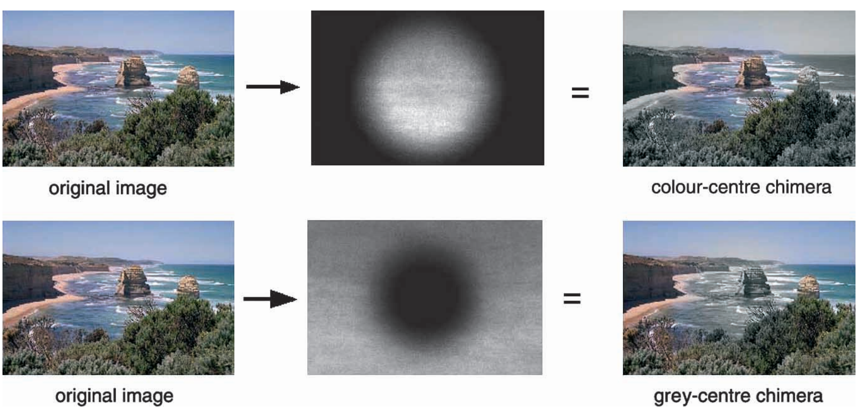

Figure 1. Constructing "colour chimeras" proceeds by applying a saturation mask (middle column) to the original full-colour image (left column). The masks displayed here are the average saturation layers across all the "colour-centre" and "grey-centre" images of intermediate mask width used in this task. The right-hand column contains examples of both colour-centre and grey-centre chimeras.

they allow us to determine both whether or not colour completion occurs in this setting and also whether or not it occurs with a centre-outward bias.

We are also interested in determining the role of natural scene statistics in our hypothesized colour completion process. By "natural scene statistics", we mean regularities in the distribution of colours, edges, and textures that occur in natural environments. To address whether or not such regularities affect colour completion, our strategy is to alter the statistics of our natural scenes in various ways and determine how difficult it is for observers to detect a colour scotoma in the new image sets. If performance is significantly modulated by our manipulations, we can conclude that colour completion is dependent on the structure of the input and thus probably not the result of a simple spreading mechanism. We carried out two manipulations on our original images, one designed to investigate the impact of natural luminance structure on colour completion and another designed to determine how chromatic variety affects the percept. Though we are not attempting to uncover the exactly how these image statistics might affect pan-field colour at present, we continue by describing two possible mechanisms by which higher order image structure and chromatic variety might influence observers' perception.

First, it is possible that recognition processes could exert a top-down influence on colour perception, leading to the experience of colour in achromatic regions. The content of natural scenes is rapidly available to observers (Potter, 1976), and the presence of coloured blobs may form the basis for the rapid recognition of scene type (Oliva & Schyns, 2000). A chimeric image of a natural scene may provide enough trace evidence in the form of coloured blobs and coarse luminance structure to bootstrap the perception of a uniformly coloured and coherent scene. There is some evidence that colour is an "intrinsic" property of objects (Naor-Raz, Tarr, & Kersten, 2003), suggesting that recognizing objects in a scene may also contribute to automatic retrieval of colour information. The presence of recognizable objects throughout a scene may thus contribute to the perception of colour across the extent of a chimeric image. If high-level recognition is an important contributor to the pan-field colour percept, we expect that our "texture" manipulation in particular should result in fewer full-colour responses to chimeric images.

Second, the global statistics of a natural scene may make detection of an achromatic region difficult, even if this region is quite large. For example, detecting a chimeric image can be formulated as a problem of detecting a statistically significant difference in chromaticity distributions between chromatic and achromatic regions of an image. Under such a model, a plausible strategy for an observer who needs to detect chimeric images is to select two candidate regions for comparison (one centrally located, the other located in the periphery) and plot chromaticity and brightness statistics from these regions in a relevant feature space. We consider here a space consisting of black–white, red–green, and blue–yellow axes, which is a useful choice for modelling human performance in many colour segmentation tasks (Rosenholtz, Nagy, & Bell, 2004). In this model, the two regions will be considered distinct (and a "mixed" image will be perceived) if the points from the two regions under consideration are linearly separable. If the points are not separable, a full-colour image will be perceived. In Figure 2 we demonstrate how this model predicts that our "colour" manipulation should have a larger effect than our "texture" manipulation. Measurements taken from the grey region of any chimera will form a cloud of points extending only along the black–white axis. Measurements from the coloured region of a multicoloured chimera then surround the origin across all three axes, making it impossible to linearly separate the two sets of points. By contrast, measurements taken from the coloured region of a "colour-manipulated" chimera form a narrow cloud translated away from the origin (due to the presence of only one hue). The grey and coloured data points are now easily separable by a plane, and the image is perceived as a chimera.

We present these two possible mechanisms (colour induction via recognition and colour induction via segmentation failure) to demonstrate that previously observed effects in other domains, such as object recognition and visual search, leave open the possibility that performance in our task could depend critically on scene statistics. The current study has not been

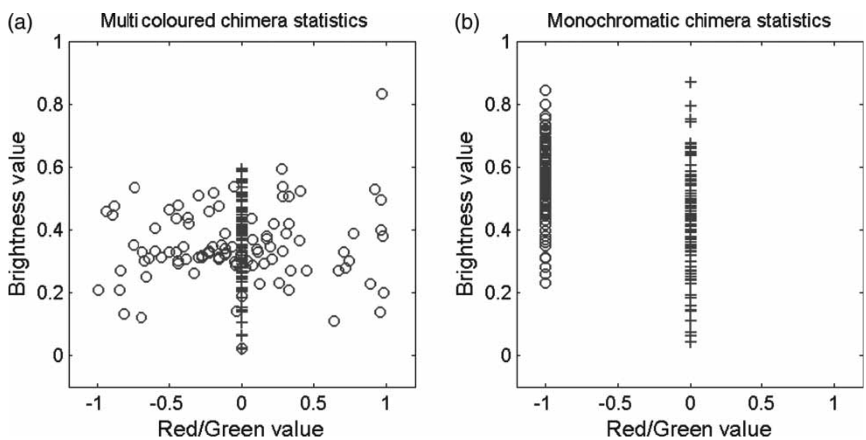

Figure 2. A schematic display of how global distributions of colour and luminance measurements in a chimeric image might make scotoma distribution more or less difficult. At left, we see how clouds of points from the chromatic and achromatic regions of a natural scene chimera are inseparable when plotted on black/white and red/green axes. At right, it is clear that the two clouds of points are easily separable when the chromatic region only contains hues drawn from a very narrow range (as in our "colour" manipulation).

designed to determine if either of these particular mechanisms is being employed by the visual system, but rather to determine if subjective colour spreading occurs in natural scenes and if the phenomenon is dependent on scene structure.

The manipulations we performed on our original images are as follows:

1. "Texture manipulation". We applied a powerful parametric texture synthesis algorithm to the original scenes (Portilla & Simoncelli, 2000). Briefly, given a target image, the algorithm characterizes the input in terms of wavelet coefficients and their neighbours in position, orientation, scale, and phase. A new image can then be synthesized, which matches the original image in terms of these statistics. The result is that local luminance and colour structure is preserved, but global layout (including recognizable objects) is not.
2. "Colour manipulation". New images were made by imposing one hue across each original image. The result is that the greyscale statistics of the image remain intact while greatly reducing colour variation. Global layout and recognizable objects are preserved in these images.

Each manipulation was carried out singly, resulting in separate "texture" and "colour" image sets. Additionally, we created another image set by carrying out both manipulations at once, resulting in a "texture + colour" condition (Figure 3)

The task for observers viewing each set of images was to detect the presence of central and peripheral colour scotomas while maintaining central fixation. For each image they were asked to respond "full-colour", "full-grey", or "mixed". To test our hypothesis that colour completion in natural scenes should be affected by manipulating luminance and colour statistics, we examined the number of false alarm responses to colour-centre and grey-centre chimeras in each set of images as a function of the size of the central saturation mask.

If the pan-field colour percept is governed by a low-level spread of activity from the fovea to the periphery, detecting the scotoma should be difficult across all conditions and reports of full-colour or full-grey images should be frequent. We also expect that "colour-centre" chimeras would be harder to detect than their "grey-centre" counterparts due to the underlying asymmetry in colour sensitivity across the retina. On the other hand, if the statistics of natural scenes play an important role in the subjective experience of pan-field colour (whether via the mechanisms we described previously or not), altering natural scenes via our "texture" and "colour" manipulations should alter the rate of false alarms.

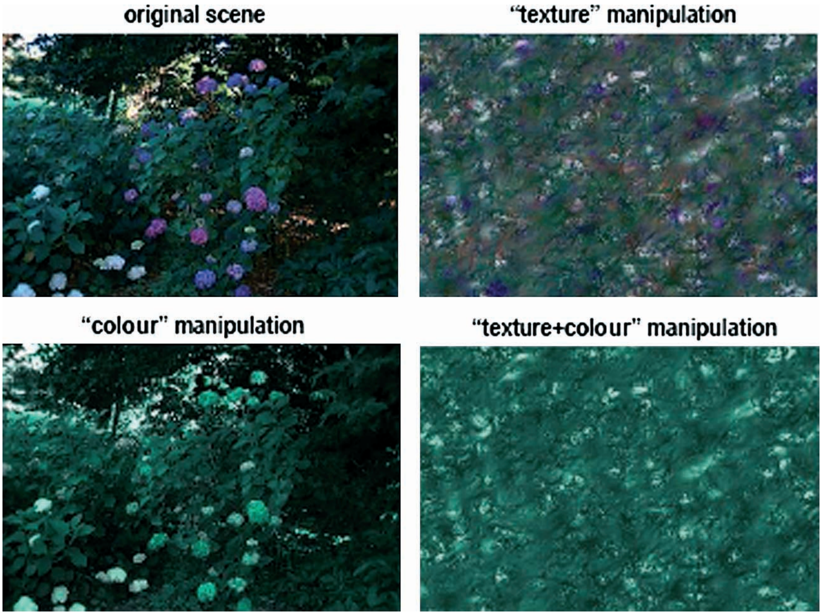

Figure 3. Examples of the "texture" and "colour" manipulations applied to a natural scene. At the lower right, both manipulations have been applied.

METHOD

Subjects

Forty-eight subjects (aged 18–40) participated in our experiments. All subjects reported having normal or corrected-to-normal visual acuity and no history of deficits in colour vision. This pool was randomly spit into four mutually exclusive groups of 12 subjects each. Each of these subgroups was assigned one image set (original, "texture" set, "colour" set, "texture+colour" set).

Apparatus and stimuli

The experiments were presented on a Dell UltraSharp 19-inch monitor, driven by a Pentium 4 computer. The Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) was used to control timing functions and stimulus display. Images subtended approximately $48^\circ \times 32^\circ$ of visual angle. Eighty unique images of natural scenes were used, depicting a range of environments (beaches, forests, mountains, and fields) and containing objects across a range of depths. Images were drawn from the University of Washington Content-Based Image Retrieval Database.

"Texture" manipulation. Portilla and Simoncelli's (2000) texture synthesis algorithm was applied to the selected images. Twenty iterations of the texture synthesis procedure were carried out per source image.

"Colour" manipulation. Red-green-blue (RGB) images were converted into hue-saturation-value (HSV) coordinates. Hue values were placed in a 20-bin histogram, and the maximally occurring value was applied across the hue layer of the HSV image before RGB conversion.

Saturation masking. A circular region centred on the image was selected, and saturation values outside (colour-centre) or inside (grey-centre) were set to zero. Region width ranged from 9° to 25° of visual angle in diameter, in steps of 4°. A soft edge was created at the mask border by linearly increasing saturation from null values to natural values over a 36-pixel range.

Design

At test, images were divided into four equal-sized categories: Full-colour, greyscale, colour-centre, and grey-centre images. Each chimeric image was presented to the subject five times during the experiment, once for each possible mask width. Full-colour and greyscale images were also presented five times each. Category membership of each image was balanced across subjects. Stimulus presentation order was individually randomized.

Procedure

Subjects sat 12 inches (30.5 cm) away from the screen, using a chin rest to stabilize head position. Before beginning, example stimuli (which were not used in the task) were presented to ensure that subjects fully understood what full-colour, grey, and both kinds of "mixed" images looked like. Subjects could freely view these stimuli as long as they wished.

Each trial began with a $0.5^\circ \times 0.5^\circ$ blue fixation dot presented at the centre of the screen for 500 ms. The test image was then presented for 50 ms, followed by a 1/f noise mask lasting 100 ms. The subject's response was then collected, using the "1", "2", and "3" keys for "colour", "grey", and "mixed" responses respectively. Breaks were scheduled every 100 trials.

To familiarize participants to the very brief presentation time used in all three tasks, subjects were given practice under experimental conditions. Eight practice trials (with feedback) were run using stimuli not included at test. Upon completion, all subjects reported feeling confident in their ability to see the images and respond accurately.

RESULTS

We examine the responses made to both grey-centre and colour-centre chimeras across all four stimulus categories. We separately analysed the number of "colour" and "grey" false alarms for these stimulus sets, to determine what factors influence observers' tendency to perceive chimeric images as completely colour or completely grey. In particular, we were interested in determining if substantial numbers of "colour" false alarms occur when viewing chimeric images, indicating colour completion. Also, given our low-level hypothesis of a centre-outward spreading to compensate for retinal asymmetry it is important to find out whether or not there is a directional bias to the rate of colour false alarms.

For each type of chimera (colour-centre and grey-centre) and each type of false alarm (reporting "colour" and reporting "grey") we carried out a $2 \times 2 \times 5$ mixed design ANOVA, with the "texture" and "colour" manipulations as between-subjects factors and mask width as a within-subject factor.

"Colour" responses in colour-centre chimeras

We see in Figure 4 that subjects who view colour-centre chimeras made from natural scenes have a strong tendency to report a full-colour image, especially as mask width increases. The proportion of chimeras reported incorrectly as being fully coloured reaches nearly 50% at the largest diameter of the saturation mask.

Our ANOVA reveals a main effect of mask width, $F(4, 44) = 58.09$, $MSE = 0.0062$, $p < .001$, as well as a main effect of the "texture" manipulation, $F(1, 44) = 41.87$, $MSE = 0.055$, $p < .001$, and a main effect of the "colour" manipulation, $F(1, 44) = 21.7$, $MSE = 0.055$, $p < .001$. There is also a marginally significant interaction between the "texture" and "colour" manipulation, $F(1, 44) = 3.89$, $MSE = 0.055$, $p = .053$, suggesting both that the presence of natural scene structure and natural colour distributions leads to an especially high rate of colour false alarms, and conversely that a lack of recognizable structure and variation in colour can significantly reduce the percept.

These results suggest that some form of colour completion is indeed taking place in this task, and that it can be affected by both of our manipulations. Importantly, colour responses to chimeric images were virtually nonexistent when both image manipulations were applied. This

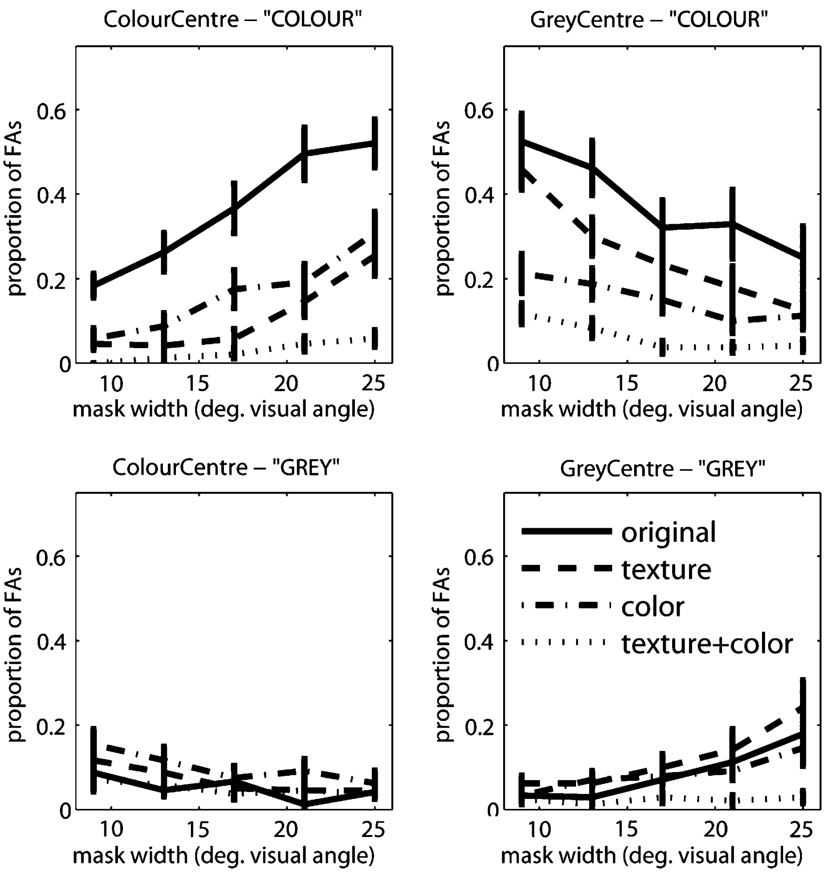

Figure 4. Top row: The incidence of "colour" responses to chimeric images as a function of scotoma width and image type for both colour-centre (left) and grey-centre chimeras (right). Bottom row: The incidence of "grey" responses to chimeric images as a function of scotoma width and image type for both colour-centre (left) and grey-centre chimeras (right). Error bars in all panels represent ± 1 *SEM*.

last finding is important since it indicates that neither task demands nor display characteristics artificially bias subjects to respond that images are fully coloured.

"Colour" responses in grey-centre chimeras

Observers viewing natural scenes show as strong a tendency to report fully coloured images in grey-centre chimeras as when viewing colour-centre chimeras. In both conditions, a smaller achromatic region produces more "colour" responses. This indicates that the percept of pan-field colour does not require colour to be spread from the centre outward.

The results of the ANOVA are very much the same as those obtained from the colour-centre images. There is a main effect of mask width, $F(4, 44) = 54.7$, $MSE = 0.022$, $p < .001$) as well as a main effect of the "texture" manipulation, $F(1, 44) = 5.8$, $MSE = 0.11$, $p = .02$, and a main effect of the "colour" manipulation, $F(1, 44) = 23.8$, $MSE = 0.11$, $p < .001$. The interaction between the "texture" and "colour" manipulations was not significant, $F(1, 44) = 0.114$, $p = .737$.

"Grey" responses in chimeric images

Overall, observers' tendency to produce grey false alarms while viewing either type of chimeric image was not as pronounced as their tendency to produce colour false alarms. The proportion of grey responses to chimeric images did not exceed .25 in any condition, in either the colour-centre or grey-centre chimeras.

Also, the proportion of grey false alarms was not very strongly affected by either our "texture" or "colour" manipulations. In colour-centre chimeras, ANOVA reveals that there is only a main effect of mask width on the proportion of grey responses, $F(4, 44) = 12.59$, $MSE = 0.002$, $p < .001$. There is no main effect of the "texture" manipulation, $F(1, 44) = 0.613$, $p = .44$, nor is there a main effect of the "colour" manipulation, $F(1, 44) = 0.55$, $p = .46$. Their interaction is also not significant, $F(1, 44) = 2.85$, $p = .10$.

For grey-centre chimeras, there is also a main effect of mask width, $F(4, 44) = 21.5$, $MSE = 0.004$, $p < .001$, as well as a main effect of the "colour" manipulation, $F(1, 44) = 5.28$, $MSE = 0.028$, $p = .029$. The main effect of the "texture" manipulation is not significant, $F(1, 44) = 0.313$, $p = .58$. There is also a significant interaction between the "texture" and "colour" effect, $F(1, 44) = 5.1$, $MSE = 0.028$, $p = .029$, which suggests that the main effect of the "colour" manipulation in this analysis is mostly driven by observers' very high accuracy in the "texture + colour" condition for grey-centre chimeras.

The mean proportions of colour and grey false alarms for each mask width and image manipulation are listed in Tables 1 and 2. The mean proportion of correct responses is also included.

Discussion

Observers in our experiment displayed a strong tendency to perceive natural images as fully coloured even when a substantial portion of the image was artificially "lesioned" to appear grey. This behaviour was

TABLE 1
Responses to colour-centre chimeras across all stimulus manipulations

Original			*"Texture"*			*"Colour"*			*"Texture" + "Colour"*		
Colour	*Grey*	*Mixed*	*Colour*	*Grey*	*Mixed*	*Colour*	*Grey*	*Mixed*	*Colour*	*Grey*	*Mixed*
0.18	0.09	0.73	0.05	0.12	0.84	0.06	0.15	0.79	0.00	0.07	0.93
0.26	0.05	0.69	0.04	0.09	0.87	0.09	0.12	0.80	0.01	0.06	0.93
0.37	0.07	0.57	0.06	0.05	0.89	0.18	0.08	0.75	0.02	0.04	0.94
0.50	0.01	0.49	0.15	0.05	0.81	0.19	0.09	0.72	0.05	0.05	0.91
0.52	0.04	0.44	0.25	0.05	0.70	0.31	0.06	0.63	0.06	0.04	0.90

observed both when colour was limited to the centre of the image and when it was limited to the periphery, indicating that pan-field colour does not depend on a radially biased completion process. Furthermore, we have found that the rate of colour false alarms is significantly influenced both by the presence or absence of natural scene structure and also by the presence or absence of a wide variety of colours in the image. Natural scene structure and colour produce the highest rates of colour false alarms, suggesting that both the presence of recognizable objects and the presence of a wide range of colours in the environment contribute to the percept of pan-field colour.

The propagation of achromaticity (or grey-spreading) was found to not be a dominant behaviour for observers in this task. Moreover, the frequency of grey false alarms was not so dramatically affected by our image manipulations as was the frequency of colour false alarms. Save for the observation that extremely low rates of grey false alarms arise during viewing of grey-centre chimeras in the "texture + colour" condition, grey-spreading is not susceptible to our manipulations of natural images.

TABLE 2
Responses to grey-centre chimeras across all stimulus manipulations

Original			*"Texture"*			*"Colour"*			*"Texture" + "Colour"*		
Colour	*Grey*	*Mixed*	*Colour*	*Grey*	*Mixed*	*Colour*	*Grey*	*Mixed*	*Colour*	*Grey*	*Mixed*
0.52	0.03	0.44	0.46	0.06	0.48	0.21	0.03	0.75	0.12	0.02	0.96
0.46	0.03	0.51	0.30	0.06	0.64	0.19	0.07	0.74	0.08	0.01	0.93
0.32	0.07	0.61	0.23	0.10	0.67	0.15	0.08	0.77	0.04	0.03	0.93
0.33	0.11	0.56	0.18	0.14	0.68	0.10	0.09	0.81	0.04	0.02	0.94
0.25	0.18	0.57	0.12	0.24	0.63	0.11	0.15	0.74	0.04	0.03	0.93

CONCLUSION

We have demonstrated that subjects experience a percept of "pan-field" colour when viewing rapidly presented scenes that contain a colour scotoma. This basic result is important on its own. Also, by evaluating the strength of the percept across different types of images, we have gained some preliminary insight into the nature of mechanisms that might contribute to this phenomenon. First, we find that there is no evidence supporting any radial asymmetry in this form of colour completion. Second, our results suggest that a low-level spreading mechanism is inadequate for explaining the percept. Instead, our data requires a mechanism that is affected by both higher order luminance statistics (such as extended contours or perhaps recognizable objects) and natural distributions of colour.

Furthermore, this work demonstrates that global image statistics can influence the perception (and possibly encoding) of complex natural scenes. Our finding that very low-level local information can be overridden by global properties of the image is intriguing beyond the "pan-field" colour percept we set out to examine. For example, it could prove interesting to consider various forms of change blindness in a similar context. Given that local colour information can be influenced by global statistics, it may be the case that local information concerning objects and textures can be similarly affected.

Our study also raises interesting questions regarding the neural correlates of the percepts obtained with colour-chimeras. Though a low-level account appears untenable, should higher level visual areas treat achromatic portions of a chimera as though they were fully coloured? Or do visual areas faithfully record the true colour content of the image only to be overridden by higher level decision processes? Further investigation into the neural basis of this phenomenon could yield potentially interesting insights into the way form, colour, and possibly the statistics of natural images (Long & Purves, 2003) interact in the human visual pathway to produce coherent percepts.

REFERENCES

Anderson, B. (1997). A theory of illusory lightness and transparency in monocular and binocular images: The role of contour junctions. *Perception*, *26*, 419–454.

Anstis, S. (1998). Picturing peripheral acuity. *Perception*, *27*(7), 817–825.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.

Bressan, P., Mingolla, E., Spillman, L., & Watanabe, T. (1997). Neon color spreading: A review. *Perception*, *26*, 1353–1366.

Caputo, G. (1998). Texture brightness filling-in. *Vision Research*, *38*(6), 841–851.

Da Pos, O., & Bressan, P. (2003). Chromatic induction in neon color spreading. *Vision Research*, *43*, 697–706.

De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Perceptual filling-in: A parametric study. *Vision Research*, *38*, 2721–2734.

Long, F., & Purves, D. (2003). Natural scene statistics as the universal basis for color context effects. *Proceedings of the National Academy of Sciences of the USA*, *100*, 15190–15193.

Magnussen, S., Spillman, L., Sturzel, F., & Werner, J. S. (2001). Filling-in of the foveal blue scotoma. *Vision Research*, *41*, 2961–2967.

Magnussen, S., Spillman, L., Sturzel, F., & Werner, J. S. (2004). Unveiling the foveal blue scotoma through an afterimage. *Vision Research*, *44*, 377–383.

Motoyoshi, I. (1999). Texture filling-in and texture segregation revealed by transient masking. *Vision Research*, *39*, 1285–1291.

Naor-Raz, G., Tarr, M., & Kersten, D. (2003). Is color an intrinsic property of object representation? *Perception*, *32*(6), 667–680.

Newton, J. R., & Eskew, R. T. (2003). Chromatic detection and discrimination in the periphery: A postreceptoral loss of color sensitivity. *Visual Neuroscience*, *20*, 511–521.

Oliva, A., & Schyns, P. G. (2000). Diagnostic colors mediate scene recognition. *Cognitive Psychology*, *41*, 176–210.

Paradiso, M. A., & Nakayama, K. (1991). Brightness perception and filling-in. *Vision Research*, *31*, 1221–1236.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Turning numbers into movies. *Spatial Vision*, *10*, 437–442.

Pessoa, L., Thompson, E., & Noe, A. (1998). Finding out about filling-in: A guide to perceptual completion for visual science and the philosophy of perception. *Behavioral and Brain Sciences*, *21*, 723–802.

Pinna, B., Brelstaff, G., & Spillman, L. (2001). Surface color from boundaries: A new "watercolour" illusion. *Vision Research*, *41*, 2669–2676.

Pinna, B., Werner, J. S., & Spillman, L. (2003). The watercolor effect: A new principle of grouping and figure–ground organization. *Vision Research*, *43*, 43–52.

Portilla, J., & Simoncelli, E. P. (2000). A parametric texture model based on joint statistics of complex wavelet coefficients. *International Journal of Computer Vision*, *40*(1), 49–71.

Potter, M. (1976). Short-term conceptual memory for pictures. *Journal of Experimental Psychology: Human Learning and Memory*, *2*, 509–522.

Ramachandran, V. S., & Gregory, R. L. (1991). Perceptual filling in of artificially induced scotomas in human vision. *Nature*, *350*, 699–702.

Ramachandran, V. S., Gregory, R., & Aiken, W. (1993). Perceptual fading of visual texture borders. *Vision Research*, *33*, 717–722.

Roorda, A., & Williams, D. R. (1999). The arrangement of the three cone classes in the living human eye. *Nature*, *397*, 520–522.

Rosenholtz, R., Nagy, A. L., & Bell, N. R. (2004). The effect of background color on asymmetries in color search. *Journal of Vision*, *4*(3), 224–240.

Sakaguchi, Y. (2001). Target/surround asymmetry in perceptual filling-in. *Vision Research*, *41*, 2065–2077.

Van Lier, R. (2002). A double neon color illusion. *Perception*, *31*, 31–38.

Zur, D., & Ullman, S. (2003). Filling-in of retinal scotomas. *Vision Research*, *43*, 971–982.

Manuscript received November 2006
Manuscript accepted January 2007
First published online June 2007