Aftereffect of perceived regularity

Marouane Ouhnana
McGill Vision Research Unit, McGill University, Montreal, Quebec, Canada

Jason Bell
Research School of Psychology, Australian National University, Canberra, Australia

Joshua A. Solomon
Optometry Division, Applied Vision Research Centre, City University London, UK

Frederick A. A. Kingdom
McGill Vision Research Unit, McGill University, Montreal, Quebec, Canada

Regularity is a ubiquitous feature of the visual world. We demonstrate that regularity is an adaptable visual dimension: The perceived regularity of a pattern is reduced following adaptation to a pattern with a similar or greater degree of regularity. Stimuli consisted of $7 \times 7$ element arrays arranged on square grids presented in a circular aperture. The position of each element was randomly jittered from its baseline position by an amount that determined its degree of irregularity. The elements of the pattern consisted of dark Gaussian blobs (GBs), difference of Gaussians (DOGs), or random binary patterns (RBPs). Observers adapted for 60 s to either a single pattern or a pair of patterns with particular regularities, and the perceived regularities of subsequently presented test patterns were measured using a conventional staircase matching procedure. We found that the regularity aftereffect (RAE) was unidirectional: Adaptation only caused test patterns to appear less regular. We also found that RAEs transferred from GB adaptors to both DOG and RBP test patterns and from DOG and RBP adaptors to GB patterns. We suggest that regularity is coded by the peakedness in the distribution of spatial-frequency channel responses across scale, and that the RAE is a result of a flattening of this distribution by adaptation. Thus, the RAE may be a consequence of contrast normalization, and an example of norm-based coding where irregularity is the norm.

Introduction

A regular pattern is a pattern with repeating features. Regularity—and its inverse, irregularity—may be considered a physical dimension, in that some patterns are more regular (or less irregular) than others. Patterns with a degree of regularity, that is, with a degree of repetition, are ubiquitous in our visual world, in both natural and constructed environments. In biological organisms, regularity results from specific developmental growth processes, for example the repeated substructures in an animal’s pelt (Mandelbrot, 1982). Abnormalities in such repetitions may be seen as flaws in an otherwise normal biologically planned growth process. In artificial structures, one finds that aesthetics, manufacturing ease, and functionality underpin regularity. For example, repetition of elements is often the most prominent feature in the definition of an architectural style. In vision, regularity is a pop-out feature, as shown in Figure 1, and might reasonably be considered a “gestalt”—that is, a class of visual pattern with which our visual system synergizes—similar to other gestalts such as good continuation, mirror-symmetry, common fate, and so on (Wertheimer, 1923/1938). One might therefore expect that the human visual system is especially attuned to regularity, as this would facilitate the efficient coding of an important class of visual information (Attneave, 1954; Lee & Yuille, 2007).

To our knowledge, only one study has explicitly sought to understand the mechanisms mediating the perception of regularity. Morgan, Mareschal, Chubb, and Solomon (2012) studied sensitivity to regularity in grids, circles, and lines of regularly spaced dots. The position of each dot in the pattern could be randomly perturbed from its notional regular position, and thresholds were measured for detecting this perturbation as a function of the baseline, or “pedestal,” perturbation. Based on the results, the researchers...
concluded that the visual system possesses an internal template of a regular pattern and that perceived departures from regularity occur when the amount of physical perturbation exceeds an equivalent internal noise level. The suggestion of an internal template for regularity may be taken to imply the presence of a dedicated mechanism for detecting departures from regularity.

Adaptation paradigms have long been used in vision research to identify mechanisms selective for different stimulus attributes (reviewed by Webster, 2011). If prolonged fixation of a stimulus results in a change in some behavioral measure along a particular stimulus attribute, this is taken to imply the existence of a mechanism specific to that attribute. In this article, we describe a series of psychophysical experiments, using normal human observers as test subjects, aimed at determining whether regularity is an adaptable visual feature, as evidenced by whether it produces an aftereffect. Our stimuli consist of arrays of micro-patterns (blurred dots, bull’s-eye patterns, and random binary patterns) whose positions are determined by specified random perturbations from notional grid positions (see Figure 2). We find evidence that regularity does indeed produce an aftereffect, and we on to determine a number of its perceptual properties.

One of the perceptual properties we have investigated concerns whether the aftereffect occurs in patterns whose elements are contrast–defined rather than luminance–defined. The luminance-defined elements are the Gaussian blobs shown in Figure 1 and on the left side of Figure 2; the contrast-defined elements are the random binary pattern elements shown on the bottom right half of Figure 2. Traditionally, visual mechanisms sensitive to luminance variations are termed “first-order,” whereas those sensitive to contrast variations are termed “second-order” (Graham, 2011). While these terms characterize the mechanisms involved in detecting the individual elements in our patterns, the encoding of their arrangement, which is of primary interest here, likely involves mechanisms that are at least one order higher. Thus on the one hand, neurophysiological and psychophysical evidence suggests that distinct mechanisms detect the two types of element in early vision (see, e.g., Nishida, Ledgeway, & Edwards, 1997; Schofield & Georgeson, 1999; Baker & Mareschal, 2001; see also reviews by Baker, 1999 and Graham, 2011). On the other hand, other evidence suggests that in higher stages of vision, mechanisms exist that respond to both types of stimuli (reviewed by Baker, 1999). What is the situation regarding the encoding of regularity?

**General methods**

**Observers**

Seven observers participated in the project: three of the authors (MO, JB, and FK) and four additional
observers (AK, MK, CD, and DW) who were naive to the experimental aims. All participants had normal or corrected-to-normal visual acuity. Participation was voluntary and was not financially compensated. Written consent was obtained from all test subjects, and all experimental protocols were approved by the McGill University Research Ethics Board.

Apparatus

The stimuli were created using MATLAB version 7.8 and generated using either a Cambridge Research Systems Visage or VSG2/5 video-graphics card and displayed on a Sony FD Trinitron GDM-F500 monitor. The resolution of the monitor was set to 1024 \( \times \) 768, with a refresh rate of 100 Hz. The monitor’s Z-nonlinearity was corrected using lookup tables following calibration with an Optical OP200-E photometer. The mean luminance of the monitor was 33.9 cd/m².

Stimuli

Stimuli were constructed from three types of element: Gaussian blobs (GBs), difference of Gaussians (DOGs), and random binary patterns (RBPs). The GBs were “dark” and orientationally isotropic—that is, circularly symmetric—according to the formula

\[
L(x,y) = L_{\text{mean}} \left[ 1 + \frac{1}{2\pi\sigma^2} \exp \left( -\frac{x^2 + y^2}{2\sigma^2} \right) \right] \quad (1)
\]

where \( x \) and \( y \) are Cartesian coordinates, \( L_{\text{mean}} \) is the background luminance, \( C \) is contrast (amplitude/mean), and \( \sigma \) is the standard deviation (SD). Unless otherwise stated, \( C \) was set to 1 to give maximum “dark” contrast and \( \sigma \) was set to either 3.8 or 7.7 arcmin at the viewing distance of 100 cm.

The DOGs were “dark-on-center” and isotropic, generated according to the formula

\[
L(x,y) = L_{\text{mean}} \left\{ 1 + C \left[ \frac{-1}{2\pi\sigma^2} \exp \left( -\frac{x^2 + y^2}{2\sigma^2} \right) \right] - \frac{1}{2\pi R^2 \sigma^2} \exp \left( -\frac{x^2 + y^2}{2R^2 \sigma^2} \right) \right\} \quad (2)
\]

with \( R = 1.6 \) and \( \sigma = 3.8 \) arcmin.

The RBPs were generated by the product of an array of randomly allocated binary values from a rectangular distribution (0 and 1) and a Gaussian (Equation 1) with \( SD = 7.7 \) arcmin.

Adaptor and test stimuli

The stimuli consisted of \( 7 \times 7 \) grids of elements windowed through an aperture of diameter 4°, softened by a Gaussian edge with a standard deviation of 5 arcmin. The position of each element was randomly selected from two rectangular distributions, one horizontal and the other vertical, with ranges centered on the notional grid position. The elements were displayed on a midgray background of 33.9 cd/m². For the adapting stimuli, depending on whether a single- or dual-adaptor paradigm was employed (described later), the stimuli were presented 3° above and/or below a fixation dot located in the center of the screen. In the single-adaptor condition, the adaptor element jitter was set to 0, 5, 10, 15, 20, 25, and 30 arcmin. For the dual-adaptor condition, one of the adaptors was set to a jitter range of 6 arcmin and the other at 24 arcmin. The test patterns consisted of a pair of stimuli presented above and below a fixation dot.

Procedure

Participants viewed the display in a well-lit room and were instructed to fix their gaze on the fixation dot for the entire session. Each session began with an initial adaptation period of 60 s. During adaptation, the overall position of each stimulus pattern was jittered every 500 ms over a range of 20 arcmin in a random direction, and the within-stimulus element positions were refreshed by rejittering them according to their specified degree of regularity. Both types of jitter helped to minimize the build-up of afterimages. Each test cycle began with a 500-ms blank interval with a fixation dot, followed by a 500-ms test pair, then another 500-ms blank interval, and finally top-up adaptation of 2.5 s. The onset of the test patterns was signaled by a tone.

A staircase procedure was used to determine the magnitude of the regularity aftereffect (RAE), defined as either the difference or the ratio (depending on the experiment) of the regularity of the two tests or of the test and comparison patterns, at the point of subjective equality (PSE). The exact procedure depended on whether a single or dual adaptor was employed (see Figure 3) and whether the staircase adjusted the difference or the ratio of the test-pair regularities.

Single-adaptor procedure

For the single-adaptor method, the test stimulus was located in the same position as the adaptor and was fixed at 15 arcmin of jitter, while the comparison stimulus was positioned on the other hemifield (above or below) of the fixation dot with a regularity
determined on each trial by the staircase procedure. For the difference adjustments, the initial regularity of the comparison was randomly selected from a jitter range of 10–20 arcmin, while that of the other test pattern was set to its complement such that the mean of the two regularities was a jitter of 15 arcmin. For the ratio adjustments, the initial regularity of one of the test patterns was randomly selected from a jitter range of 10–22.5 arcmin, while that of the other test pattern was set to the complement, such that the geometric mean regularity of the two test patterns was also a jitter of 15 arcmin.

During the first five trials, the regularity difference between the two test patterns was incremented or decremented by 4 arcmin of jitter, or the regularity ratio of the two test patterns was multiplied or divided by 1.25. For the remaining trials the values were 2 arcmin added/subtracted or a multiplier/divisor of 1.1. The session was stopped after 25 trials, and the RAE for that session calculated as the mean difference/ratio over the previous 20 trials.

Eight measurements were taken, four with the more regular pattern above fixation and four below. In addition, four measurements were taken in the absence of the adaptors, with all else being equal.

Calculation of the RAE

For both single- and dual-adaptor methods, an overall estimate of the RAE was calculated as follows: For the difference-adjustment experiments, the mean of the no-adaptor baseline measures was subtracted from each adaptor-present measure, and the mean and standard errors of these subtractions were calculated across measurements. In the case of the ratio-adjustment experiments, the mean of the no-adaptor baseline log PSE ratios was subtracted from each adaptor-present log PSE ratio, and the mean and standard errors of the subtractions were calculated across measurements.

Experiments

Is there a regularity aftereffect?

This experiment considered whether regularity is an adaptable feature of the visual system, by examining whether it produces a regularity aftereffect. The stimuli were made of dark Gaussian blobs (GBs) with a standard deviation of 3.8 arcmin, and the dual-adaptor method was employed.

Figure 4 shows RAEs for five observers (FK, MO, JB, CD, and AK). The figure plots the jitter-range
difference between the upper and lower test patterns at the PSE for each observer after subtracting the baseline PSE; the error bars show 95% confidence limits (i.e., not standard errors). The figure shows that all five subjects exhibited an RAE, since none of the error bars were even close to zero (no RAE). The data from the three observers were collapsed into one data set ($df = 5$ subjects $\times$ 8 measures $- 1 = 39$) and a correlated-sample $t$ test was conducted that revealed that the mean RAE was significantly different than zero, $t(39) = 17.86$, $p < 0.01$ (two-tailed). The results demonstrate that there is a regularity aftereffect.

Is the RAE unidirectional or bidirectional?

The previous experiment, by virtue of using the dual-adaptor method, does not reveal the directionality of the aftereffect. That is, it does not reveal whether (a) the more regular adaptor caused the effect by making the corresponding less regular test pattern appear even less regular, (b) the less regular adaptor caused the effect by making the corresponding more regular test pattern appear even more regular, or (c) both adaptors caused the effect by making the less regular test pattern appear even less regular and the more regular test pattern appear even more regular. If either of the first two possibilities is the case, the aftereffect may be deemed unidirectional, whereas if the third possibility is the case, the aftereffect may be deemed bidirectional.

The aim of this experiment, therefore, was to determine whether the RAE is unidirectional or bidirectional. This entailed using the single-adaptor method. Thus only a single adaptor was presented per session, with the test pattern presented in the same location as the adaptor. The “measuring stick” in the single-adaptor method was the comparison pattern that was presented in the other hemifield to that of the adaptor/test, and it was the comparison pattern only that was adjusted during the staircase procedure. The test pattern was fixed at an irregularity of 15 arcmin of jitter, and adaptor irregularities of 0, 5, 10, 15, 20, 25, and 30 arcmin of jitter were employed. The grid elements were similar to those used in the previous experiment.

Figure 5 shows the resulting RAEs for three observers (MO, JB, and DW). The figure plots the jitter-range difference between the test and comparison patterns at the PSE for each observer (after subtracting the baseline PSE) for each adaptor irregularity. All RAEs were positive, indicating that the test pattern only ever appeared less regular following adaptation, irrespective of whether the adaptor irregularity was greater than, less than, or equal to that of the test. Thus the RAE is unidirectional. Moreover, the magnitude of the aftereffect appears to decline with adaptor irregularity.

Is the RAE due to local positional adaption?

Positional adaptation produces a repulsive shift in subsequently presented elements away from their physical locations (Whitaker, McGraw, & Levi, 1997). For example, following adaptation to a three-element stimulus whose middle element is slightly offset, the middle element of a subsequent group of three aligned elements appears slightly offset in the opposite direction (Yeh, De Valois, De Valois, & Chen, 1991; Hess & Doshi, 1995). In our attempt to prevent the buildup of afterimages during adaptation, we jittered the adaptor patterns as a whole. However, it is possible that the
amount of jitter was insufficient to rule out adaptation to element modal positions. The aim of this experiment was to assess whether local positional adaptation underlies the observed RAE.

Using Gaussian blobs (GBs) with a standard deviation of 3.8 arcmin and the dual-adaptor method, two adaptor global jitter conditions were tested: 20 and 40 arcmin. Since the peak-to-peak interelement distance of the perfectly regular pattern was 41 arcmin, 20 arcmin of global jitter means that the smallest possible separation between corresponding elements in subsequent adaptor presentations is 21 arcmin. In other words there will still be regions of the retinal image that would never be stimulated by the perfectly regular Gaussian blobs during adaptation. Doubling the amount of global jitter to 41 arcmin eliminates this unadapted space, thus ensuring that every test element is subject to adaptation from elements positioned equally (on average) at all points around it, thus minimizing the effects of local positional adaptation.

Figure 6 shows RAEs for two observers (MO and JB). The figure plots the jitter-range difference between the upper and lower test patterns at the PSE for each observer after subtracting the baseline PSE, for each of the global adaptor-jitter values. The figure shows that both subjects exhibited equal amounts of RAE regardless of the amount of global adaptor jitter. The data from the two observers were collapsed into two data sets corresponding to the standard procedure and the adjusted value of global adaptor jitter. A correlated-sample t test was conducted which revealed that the mean differences were not significantly different from zero, $t(11) = 0.5723$, $p > 0.05$ (two-tailed). The results demonstrate that positional adaptation does not appear to underlie the RAE. As a conservative approach, all subsequent experiments used the global jitter value of 40 arcmin.

Figure 6. Regularity aftereffect for two observers for two values of adaptor global jitter. Dual-adaptor method. The figure shows the difference in test regularities at the PSE following adaptation minus the no-adaptation baseline PSEs. Error bars are standard errors.

Is there an RAE for contrast-defined elements?

The purpose of this experiment was to assess whether the RAE occurs with contrast-defined and not luminance-defined elements, and if it does, whether the same mechanism is involved in both. We employed two types of contrast-defined element: difference-of-Gaussian (DOG) and random-binary-pattern (RBP) elements.

RAEs were measured for all three types of element when the same element was used in both adaptor and test, termed the congruent condition, as well when adaptor and test were of different types, termed the incongruent condition. Use of both congruent and incongruent conditions enabled us to measure the amount of transfer of the RAE from one type of element to the other. The experiment was divided into two parts: (a) RAEs measured using GBs and DOGs, both with a standard deviation of 3.8 arcmin and a contrast of 33%; and (b) RAEs using GBs and RBPs, both with a standard deviation of 7.7 arcmin and presented at full contrast.

We used larger standard deviations and higher contrasts in the second part of the experiment, as the RBP elements were less salient than the other two elements at small standard deviations. The dual-adaptor method was employed, with a total of four combinations of adaptor and test in each part of the experiment. In Part 1 we tested adaptor GB/test GB, adaptor GB/test DOG, adaptor DOG/test DOG, and adaptor DOG/test GB. In Part 2 we tested adaptor GB/test GB, adaptor GB/test RBP, adaptor RBP/test RBP, and adaptor RBP/test GB. No-adaptor baselines for GBs, DOGs, and RBPs were also measured.

Results are shown in Figure 7 for Part 1 (GBs and DOGs) and Figure 8 for Part 2 (GBs and RBPs). The data for both parts of the experiment were collapsed into two groups: adaptor-test congruent, and adaptor-test incongruent. For the data in Figure 7, a two-sample dependent $t$ test revealed that the mean RAEs for the congruent and incongruent adaptor-test pairings were not significantly different, $t(47) = 0.9372$, $p > 0.05$ (two-tailed). For the data in Figure 8, the two-sample dependent $t$ test also revealed no significant difference in the mean RAEs for the congruent and incongruent adaptor-test pairings, $t(47) = 1.295$, $p > 0.05$ (two-tailed).

These results are not consistent with the idea that the RAE is mediated by separate mechanisms for luminance-defined and contrast-defined elements.

Discussion

The following summarizes the main findings of this study:
An aftereffect of perceived regularity, or RAE, can be induced in grids of Gaussian-blob (GB), difference-of-Gaussian (DOG), and random-binary-pattern (RBP) elements.

The RAE is a unidirectional aftereffect; that is, adapting to pattern regularity only ever makes a subsequent pattern appear less regular.

Positional adaptation is not sufficient to explain the RAE.

The RAE transfers from GB to DOG elements and vice versa, and from GB to RBP elements and vice versa.

A new aftereffect of perceived regularity

We have demonstrated a new aftereffect, the regularity aftereffect, or RAE. The RAE is experienced as an increase in the departure from the notional positions of elements on a grid.

Relationship to other spatial aftereffects

Other unidirectional aftereffects have been found. Adaptation to contrast only ever makes a subsequently presented pattern appear to have less contrast (Georgesen, 1985), and adaptation to density only ever makes a subsequently presented pattern look less dense (Durgin & Huk, 1997). On the other hand, the tilt aftereffect and spatial-frequency aftereffect are bidirectional. Adaptation to an oriented line invariably causes a line of slightly different orientation to appear oriented in a direction away from that of the adaptor orientation (Gibson & Radner, 1937), and adaptation to a figure of given size invariably causes a figure of slightly different size (whether bigger or smaller than the adaptor) to appear shifted away from that of the
adaptor size (Sutherland, 1954). It has been suggested that bidirectionality in aftereffects is supportive of the idea that the dimension of interest is processed by multiple channels, each tuned to a specific range of the dimension (Webster, 2011). Thus our findings provide no support for the idea that regularity is coded via multiple channels, each selective to a particular range of irregularity.

An important difference with some other unidirectional aftereffects concerns the relationship between adaptor and test regularities and the magnitude of the aftereffect. In his study of contrast adaptation using sine-wave gratings, Georgeson (1985) found that significant reductions in apparent contrast following adaptation only occurred when the test was lower in contrast than the adaptor. In the present study, as is clear from Figure 5, the apparent regularity of a test pattern is reduced by adaptors both greater and smaller in regularity than the test, though the amount of reduction is smaller for the latter. This property of the RAE is a feature of norm-based coding (Webster, 2011; H. Dennett, personal communication, December 3, 2012), where the effect of adaptation is always to shift perception towards the norm. For example, with blur adaptation, adaptation to either a blurred or a sharpened image results in the image appearing more focused, or “neutral”: In this case the norm is “focused” (Elliott, Georgeson, & Webster, 2011). For the RAE, if it is indeed a consequence of norm-based coding, then the norm that it reveals is “irregular.” This might at first seem counterintuitive, but as Figure 1 demonstrates, regularity is a pop-out feature, and therefore it is irregularity, not regularity, that would seem to be the norm in vision. The explanation of the RAE that we later provide is consistent with the idea that irregularity is treated as a norm by vision.

### Regularity coding with luminance-defined and contrast-defined elements

The data are not consistent with the idea that the RAE is mediated by mechanisms that separately

---

**Figure 8.** Top: RAEs as a function of adaptor and test-element type. Gaus. = Gaussian blobs; RBP = random binary patterns. Bottom: “Congruent” refers to the combination of adaptor and test—in this case collapsing Adaptor Gaus./Test Gaus. and Adaptor RBP/Test RBP—while “incongruent” refers to Adaptor Gaus./Test RBP and Adaptor RBP/Test Gaus. Error bars are standard errors.
process luminance-defined and contrast-defined elements. In one of their texture-density adaptation experiments, Durgin and Huk (1997) used different sizes of Gaussian blobs, as well as balanced elements (as in the DOG elements used here), to explore the spatial-frequency selectivity of texture-density coding. They found that the direction of the aftereffect was unaffected by element type; however, the aftereffect was reduced if the adaptor and test elements were different. They concluded that texture-density coding was specific to element type at an early stage of visual processing, but that information from different element types was pooled at a later stage. The data presented here for regularity are inconsistent with the first of Durgin and Huk’s conclusions, but not the second.

**Explanation of the RAE**

Here we offer an explanation of the RAE that is consistent not only with our results but with known physiology and with the concept of norm-based coding. The explanation is motivated in part by a simple demonstration shown in Figure 9, which shows the result of swapping the Fourier amplitude and phase spectra of a perfectly regular and an irregular pattern with 30 arcmin of jitter. The figure reveals that, at least in our stimuli, regularity is predominantly carried by the amplitude, not phase spectrum. The demonstration is especially pertinent when one considers that with images of natural scenes the opposite is found—that is, the recognizable structure of the scene is carried in the phase, not amplitude, spectrum (Oppenheim & Lim, 1981; Piotrowski & Campbell, 1982).

The revealed role of the amplitude spectrum in representing regularity lends itself to an explanation of the RAE in which the effect of adaptation is to alter the relationship among the response amplitudes of visual filters that respond to the stimuli. A schematic of our proposed explanation is shown in Figure 10 as it applies to the GB element patterns, and its extension to RBP element patterns is partially illustrated in Figure 11.

The basis of the idea in Figure 10 is that the grid pattern is processed by a standard filter-rectify-filter cascade (Graham, 2011), consisting of a bank of oriented first-stage filters tuned to a range of spatial frequencies, whose outputs are first rectified by squaring (or by a similar nonlinearity) to produce energy responses that are then summed across the image by a second-stage filter. To obtain a measure of the output of the putative second stage in response to our stimuli, we conducted the following simulation. Vertically oriented first-stage Gabor filters were defined by the formula

$$F(x, y) = \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right) \cos(2\pi fx),$$

(3)

where $\sigma$ is the standard deviation of the Gaussian envelope and $f$ the spatial frequency of the underlying sinusoidal modulation. These two parameters were related to produce filters with a constant bandwidth of 1.5 octaves. Gabor filters with $\sigma$ values ranging from 1 arcmin to the full width of the regularity pattern were convolved with two types of pattern, one completely regular (0 arcmin of jitter) and one irregular with an element jitter of 30 arcmin. The root-mean-square response for each filter across the convolution image was normalized to equate responses across scale by dividing the response by $\sigma^2$. Convolutions were conducted in MATLAB.

The plot in Figure 10c shows the normalized root-mean-square responses for both pattern regularities as a function of the logarithm of filter frequency $f$ in cycles per image. For both plots there is a local response peak at $f = 1.2$ log cycles per image; this peak is for the filter

![Regular and Irregular Patterns](image-url)
whose excitatory receptive-field center is matched in size to that of a single element. The plot for the fully regular pattern (blue), however, also produces a primary peak at around 0.85 log cycles per image, where the filter receptive field is matched to the duty cycle of the pattern as a whole. No such primary peak is observed for the irregular pattern (red), whose response is much reduced at this point.

We suggest that the regularity of the pattern is encoded via some measure of the peakedness of the population distribution of spatial frequency-tuned filter energy responses across receptive-field size. We suppose that the effect of adaptation is to make the responses across scale more equal, and because the response distribution to the adaptor has a band-pass characteristic, this will have the effect of flattening the response distribution. Thus after adaptation, any test pattern will be encoded as less regular than otherwise because its response distribution across scale will be flatter than otherwise.

Figure 10. Explanation of the RAE involving a standard filter-rectify-filter mechanism. Regularity is encoded via the peakedness of the population of spatially pooled energy responses of narrowband spatial-frequency filters. (a) Regular pattern made up of Gaussian elements with one scale of model Gabor first-stage filter. The filter outputs are squared and pooled across the image by a circular filter. (b) Irregular pattern with the same first-stage filter. (c) Pooled energy responses as a function of the scale of the first-stage filter, for the regular (blue) and irregular (red) patterns.

Figure 11. RAE model for patterns made from random-binary-pattern (RBP) elements.
If this explanation is correct, the RAE may be considered as a consequence of the canonical process of contrast normalization, one of whose effects is to balance the responses of visual channels across orientation and/or scale (reviewed by Carandini & Heeger, 2011; for other illusory phenomena explained by contrast normalization, see also Blakeslee & McCourt, 1999; Dakin & Bex, 2003; and Robinson, Hammon, & de Sa, 2007).

Figure 11 shows how the scheme can be extended to deal with the RBP-element patterns, by including an additional front-end stage of filtering and rectification to enable the spatial frequency-tuned filters to detect the RBP elements that fall within their receptive fields. We suggest that the final spatial-pooling stage is common to patterns made from either Gaussian blobs or random binary elements.

The second-stage filter for the GB patterns and the third-stage filter for the RBP-element patterns in our scheme is a low-pass filter because our stimuli are uniform in their regularity. In traditional filter-rectify-filter models of texture segregation, the second-stage filter is typically band-pass, because it is designed to detect changes in the texture dimension of interest within the stimulus (Graham, 2011). Indeed, if the principle behind our explanation is correct, effortless segregation of the two regions in Figure 1 is probably mediated by a band-pass, not low-pass, second-stage filter, in line with other texture-segregation models.

This explanation for the RAE is consistent with its unidirectionality, because the effect of adaptation is only ever to flatten the population response, causing all test patterns to appear less regular than otherwise. It also explains why adaptation to a pattern of given regularity will make even a more regular test pattern appear less regular (see Figure 5). This is because it is the shape of the response distribution across scale that determines regularity, irrespective of the magnitudes of the set of channel responses. In other words, it should not matter if some of the channels respond more to the test than to the adaptor: The flattening will always carry over to the test. With simple contrast adaptation, which has a significant effect only on tests that are lower in contrast, the relative magnitudes of adaptor and test are what clearly matter, not the shape of the response distribution across scale. Our explanation of the RAE is also in keeping with the idea that the visual system treats irregularity as a norm, in which the norm is a more-or-less even distribution of filter responses across scale (see, e.g., Dakin & Bex, 2003).

H. Dennett (personal communication, December 3, 2012) has suggested that regularity might be encoded by the response magnitude of neurons in the high stages of vision, as is believed to be the case for certain other high-level functions such as shape (Pasupathy & Connor, 2001; Kayaert, Biederman, Op de Beeck, & Vogels, 2005; De Baene, Premereur, & Vogels, 2007) and face (Freiwald, Tsao, & Livingstone, 2009) processing. Adaptation would have the effect of reducing the sensitivity of these neurons, shifting their responses to “less regular.” If such neurons exist, perhaps it is they that encode the peakedness of the population distribution of pooled energy responses, which we have suggested underpins the encoding of regularity (Figures 10 and 11). This explanation of the RAE shifts the proposed site of adaptation to neurons that code regularity directly via response magnitude, away from the earlier stages that provide their input. We accept this possibility; indeed, it is likely that adaptation occurs at multiple sites throughout the regularity-processing chain.

The claim that regularity is an adaptable feature in human vision might be taken to imply that the RAE should be invariant to transformations in both scale and orientation—that is, undiminished when adaptor and test differ along one or other of these dimensions. Consider in this regard some other well-known spatial aftereffects. The tilt aftereffect, in which adaptation to an oriented line or grating causes a repulsive shift in the perceived orientation of a line or grating of slightly different orientation, is universally believed to implicate orientation as an adaptable feature, yet selective for spatial frequency (Ware & Mitchell, 1974), as is also the related color-contingent tilt aftereffect (Held, Shattuck-Hufnagel, & Moskowitz, 1982). Another well-known aftereffect is the spatial-frequency aftereffect, in which adaptation to a grating of a given spatial frequency causes a repulsive shift in the perceived spatial frequency of a grating with a slightly different spatial frequency. This aftereffect implicates spatial frequency as an adaptable feature, yet it too is selective, this time for grating orientation (Blakemore, Nachmias, & Sutton, 1970). These findings imply that adaptability along one spatial dimension is often accompanied by selectivity along other spatial dimensions. Therefore, the validity of the claim that regularity is an adaptable feature is not contingent on the RAE being agnostic to transformations in scale and/or orientation.

Does our explanation for the RAE, however, lead to predictions concerning the selectivity of the RAE to scale and orientation? Since the hypothesized gain reduction that is the basis of our explanation is maximal for spatial mechanisms tuned to both the duty cycle and orientation of the pattern (see Figure 10), then indeed we would expect the RAE to show a significant degree of selectivity to both the duty cycle and overall orientation of the patterns.

Finally, as we noted in the Introduction, Morgan et al. (2012) have suggested that the visual system forms an internal representation of a regular template, be it a square grid, notional circle, or other. Our model does not preclude the existence of regularity templates for
performance tasks such as threshold discrimination, but does suggest that for appearance tasks regularity might be encoded instead via the shape of a channel-response distribution.

**Conclusion**

In this article we have demonstrated that regularity is an adaptable feature in human vision. We have demonstrated a novel unidirectional aftereffect of perceived regularity, the RAE, in which adaptation to a pattern of given regularity causes a subsequently presented pattern to appear less regular. We have presented evidence that the RAE is mediated by second-order, not first-order, mechanisms, and we have proposed a model of the RAE in which regularity is encoded by the degree of peakedness in the response distribution of oriented second-order filter responses across scale.

**Keywords:** regularity, aftereffect, adaptation, spatial vision

**Acknowledgments**

The authors thank Dr. Curtis L. Baker Jr., Dr. Aaron P. Johnson, and Dr. Michael J. Morgan for their helpful comments. This research was supported by an Australian Research Council (ARC) Discovery Project Grant (DP110101511) given to JB, an Engineering and Physical Sciences Research Council (EPSRC) Grant (EP/H033955) given to JAS, and a Natural Sciences and Engineering Research Council of Canada (NSERC) Grant (OGP01217130) given to FK.

Commercial relationships: none.
Corresponding author: Marouane Ouhnana.
Email: marouane.ouhnana@mail.mcgill.ca.
Address: McGill Vision Research Unit, McGill University, Montreal, Quebec, Canada.

**References**


