Contour adaptation

Stuart Anstis

Department of Psychology,
University of California–San Diego, La Jolla, CA, USA

It is known that adaptation to a disk that flickers between black and white at 3–8 Hz on a gray surround renders invisible a congruent gray test disk viewed afterwards. This is contrast adaptation. We now report that adapting simply to the flickering circular outline of the disk can have the same effect. We call this "contour adaptation." This adaptation does not transfer interocularly, and apparently applies only to luminance, not color. One can adapt selectively to only some of the contours in a display, making only these contours temporarily invisible. For instance, a plaid comprises a vertical grating superimposed on a horizontal grating. If one first adapts to appropriate flickering vertical lines, the vertical components of the plaid disappears and it looks like a horizontal grating. Also, we simulated a Cornsweet (1970) edge, and we selectively adapted out the subjective and objective contours of a Kanisza (1976) subjective square. By temporarily removing edges, contour adaptation offers a new technique to study the role of visual edges, and it demonstrates how brightness information is concentrated in edges and propagates from them as it fills in surfaces.

Introduction

How does the visual system code the luminance and contrast of objects? Experiments on visual adaptation can help us here. Adaptation to luminance is well established: It is well known that adapting to a black square will yield a light-colored negative afterimage, and a white square a dark negative afterimage. Adaptation to luminance contrast has been discovered more recently; for example, after adaptation to a contrast defined by modulations between light red and dark green, an equiluminant red appears darker, whereas an equiluminant green appears lighter. Light adaptation adjusts sensitivity to mean luminance, while adaptation to contrast (flicker) adjusts sensitivity to variations in luminance (Webster & Mollon, 1993).

Here we study adaptation to luminance contrast in achromatic stimuli. We now report that adaptation to just the flickering edges or outline of an achromatic shape can reduce the perceived contrast of the whole shape when viewed subsequently.

It is known that virtually any visual dimension can be adapted to give an aftereffect. These dimensions include color, luminance, spatial frequency, orientation, stereo depth, motion, and contrast (Frisby & Stone, 2010, pp. 75–110). To this list we now add a new one: contour adaptation, which includes aspects of perceptual filling-in and of contrast adaptation, which we shall now briefly review.

Filling-in

The normal process of perceiving surfaces may depend upon filling-in from the edges of a surface, and disruption of these edges may lead to anomalous filling-in, in which surfaces perceptually disappear. For instance, during strict fixation, peripherally viewed objects may fade out and disappear from view (Troxler, Himly, & Schmidt, 1804). Since Troxler et al. (1804), ways to increase peripheral fading have proliferated. Schieting and Spillmann (1987) and Anstis (1996) found that flickering spots viewed peripherally appeared to stop flickering and then disappeared. Spillmann and de Weerd (2003) ascribed this kind of filling-in to an interaction between interpolation processes and boundary representations. Thus, after slow adaptation of boundary representations, background information is rapidly interpolated across the bounded region.

Filling-in can be accelerated by optically stabilizing an image on the retina. The color and lightness of such a stabilized image fade away until it is no longer visible, and the area fills in with the color and lightness of the surrounding area (Gerrits, De Haan, & Vendrik, 1966). Thus, if a red disk is surround by a green annulus, and the red/green border is retinally stabilized, the green spills into the area of the disk and the whole display looks uniformly green (Krauskopf, 1963; Yarbus, 1967; Nerger, Piantaneda, & Larimer, 1993).

Retinal stabilization is not the only way to disrupt edges. Backward masking can do it (Breitmeyer &

Citation: Anstis, S. (2013). Contour adaptation. *Journal of Vision*, *13*(2):25, 1–14, http://www.journalofvision.org/content/13/2/25, doi:10.1167/13.2.25.

doi: 10.1167/13.2.25 Received June 15, 2012; published February 27, 2013 ISSN 1534-7362 © 2013 ARVO

Ogmen, 2006). If a white disk is flashed up on a black surround, followed by a white annulus whose inner border is congruent with the outer border of the disk, the interior of the annulus looks black since the disk is never seen. This backward masking is far less effective if the disk and annulus are different colors (Becker & Anstis, 2004). Contour adaptation, as described in this paper, also disrupts edges, but it does so with prolonged flicker before presentation of the test disk, not by a single flash just after the disk is exposed. Thus contour adaptation and backward masking have similar effects, but no common mechanism has been found.

Paradiso and Nakayama (1991) used backward masking of a very different kind. They reasoned that if brightness is perceived by a filling-in process initiated by luminance boundaries, then some response initially biased toward the boundaries fills in to represent the interior of uniform surfaces. If so, there should be some measurable time in which the surface representation is incomplete. They interrupted this process by flashing up a large white disk on a black surround, followed after a stimulus onset asynchrony (SOA) of 50–100 ms by a white outline circle of smaller diameter (say, half the diameter of the disk). The percept was of a white disk, with the region inside the outline circle looking like a black hole. They assumed that the contours of the masking outline circle would interfere with the brightness filling-in of the uniform disk if the circle were presented at a time before the filling-in was complete. In other words, brightness contours serve to start and stop filling-in, as previously suggested by Walls (1955), Gerrits and Vendrik (1970), and Grossberg (2003).

By varying the diameter of the outline circle, and the SOA between the presentation times of the disk and the circle, Paradiso and Nakayama (1991) were able to estimate the speed with which the filling-in process travelled. For monoptic stimulation (disk and circle seen by the same eye), the optimal SOA was 50–100 ms. For dichoptic stimulation (disk and circle seen by opposite eyes) the masking effect was, surprisingly, much greater, with an optimal SOA of zero. This differs from our results in Experiment 2, which showed no interocular transfer for our contour adaptation. The estimated velocity of the spread of filling in was 100°/s–150°/s.

Rossi and Paradiso (2003) found a second way to examine this propagation speed. They argued that when a bright disk is flashed up, there must be a wave of brightness propagating inwards from the periphery to the center. Ordinarily this is not visible, but they found that if a bright disk was rapidly dimmed, the brightness changes over the center of the disk appeared to lag behind changes at the edge of the disk, so the center of the disk looked much brighter than the edge, and darkness swept into the center.

Contrast adaptation takes many forms. An adapting window filled with a drifting grating leaves no afterimage, since each retinal area receives the same time-averaged luminance, but the adapted area shows a reduced sensitivity to test gratings that have about the same orientation and spatial frequency. This reduced sensitivity manifests itself both as a threshold elevation (Kelly, 1972; Blakemore & Campbell, 1969) and also as a reduction in the perceived contrast of test gratings (Kelly & Burbeck, 1980). Since this kind of contrast adaptation is selective for both orientation and spatial frequency (Movshon & Blakemore, 1973) and in addition shows interocular transfer (Bjorklund & Magnussen, 1981), its origins are probably cortical—unlike the contour adaptation described in this paper.

A simpler form of contrast adaptation involves no gratings and is not tuned to orientation or spatial frequency. Instead, observers adapt to a spatially uniform flickering patch that leaves behind no afterimage, provided that the time-averaged luminance of the flicker matches the background luminance, but it does leave behind a patch of reduced sensitivity to contrast, such that a low-contrast test object presented on this adapted patch looks even lower in contrast (Webster & Mollon, 1993; Webster & Wilson, 2000). Incidentally, these authors also found that adaptation to a patch that flickers between complementary hues such as blue and yellow also yields chromatic contrast adaptation, but in this paper we shall confine ourselves to achromatic stimuli.

These conditions demonstrate contrast adaptation, whereas a simple afterimage demonstrates luminance adaptation. Luminance adaptation refers to adaptation to the mean luminance of a stimulus, while contrast adaptation refers to adaptation to the variance of luminance, over either space or time or both. In this paper we are more interested in adaptation to temporal variance, which might be termed adaptation to flicker rather than to texture. Adaptation alters the appearance of an achromatic stimulus by adjusting visual sensitivity both to the average luminance in the stimulus (through light adaptation) and to the variations in luminance (through contrast adaptation; Webster & Mollon, 1993; Webster & Wilson, 2000). Thus, contrast adaptation is thought to optimize visual performance by increasing contrast sensitivity for changing stimuli while possibly decreasing it for unchanging stimuli (Pestilli, Viera, & Carrasco, 2007). Visual adaptation occurs for any stimulus feature and involves a continuous adjustment of the neuronal contrast gain. These adjustments maintain our visual system at maximum sensitivity for the prevailing ranges of stimulus features that are processed at a given time (Pavan, Marotti, & Campana, 2012). In general, adaptation matches visual gain to the stimulus intensity.

In this paper we added a spatial factor to this temporal adaptation. Whereas in previous studies the adapting and test stimuli were windows filled with drifting gratings (Blakemore & Campbell, 1969; Kelly, 1972) or were spatially congruent patches (Webster & Mollon, 1993; Webster & Wilson, 2000), we now adapted to *a thin flickering outline* that delineated the test stimulus. For instance, we found that adapting for a few seconds to a flickering outline circle could make a whole low-contrast test disk disappear from view.

For the sake of completeness we shall now mention some other studies, showing an improvement in contrast sensitivity (Kwon, Legge, Fang, Cheong, & He, 2009), a mismatch between contrast adaptation and contrast sensitivity (Langley & Bex, 2007), and examples of very slow and very fast contrast adaptation (Bao & Engel, 2012; Pavan et al., 2012).

Kwon et al. (2009) reported an *improvement* in contrast sensitivity and contrast discrimination after observers wore contrast-*reducing* goggles for 4 hrs. They interpreted this as an adjustment in the gain of the contrast-response in the presence of a reduced range of stimulus contrasts, which is consistent with a response-gain mechanism. The adaptation appeared to be compensatory, such that the precision of contrast coding was improved for low retinal-image contrasts. On the other hand, our contour adaptation produced a systematic *decrease* in contrast sensitivity. Also, unlike our contour adaptation, their adaptation to reduced contrast appeared to be cortical, since it transferred interocularly.

Langley and Bex (2007) pointed out that contrast gain control models of flicker adaptation should predict that the effects of contrast adaptation correlate with contrast sensitivity. This is not what they found. Adaptation was greatest at a flicker rate of 19 Hz, which is more than twice the peak frequency for contrast sensitivity.

The time course of contrast adaptation varied widely in different studies: Pavan et al. (2012) reported subsecond contrast adaptation to very brief stimuli, while Bao and Engel (2012) found long-term processes of adaptation and "de-adaptation" when they adapted their observers to contrast for 4 hrs and then tested them on natural stimuli for 15 min. However, these processes are much shorter or longer than the ones that we report here.

Ratliff and Sirovich (1978) proposed the concept of "equivalence classes" of visual stimuli that produce the same, or nearly the same, neural response. One could arguably extrapolate this idea to filled and outline versions of the same shape, which do not look alike but are equally good adaptors for reducing the perceived contrast of the test shape. This implies that outlines and solids can produce different neural responses at the level of conscious awareness (they look very different) but have underlying similarities (adaptive power) at a level that does not reach consciousness.

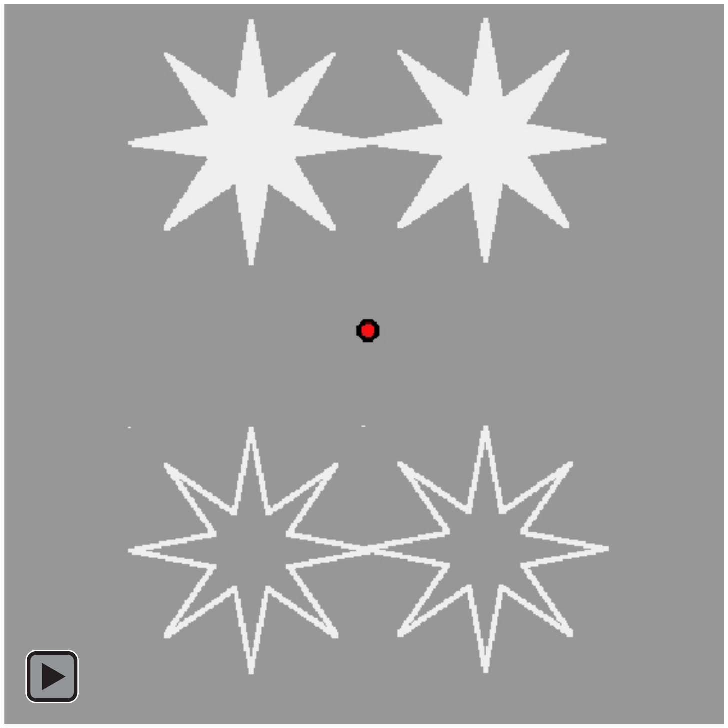
Qualitative observations

We shall first show qualitative demonstrations of contour adaptation, followed by some quantitative measurements. All stimulus movies were programmed in Director 11 (Adobe, San Jose, CA) and displayed on the monitor of a 2700 iMac computer (Apple, Cupertino, CA). They were viewed from a distance of 57 cm in a dimly lit room. All screen luminances were calibrated with a Minolta Chromameter II photometer (Konica Minolta, Ramsey, NJ). (In this article, all the movies have been exported into Quicktime [Apple, Cupertino, CA]. All movies should be run in a loop mode).

Movie 1 demonstrates contour adaptation. Six contour-rich eight-pointed stars are grouped around a central fixation point. The three light-gray stars on the right are all the same, with a Michelson contrast of about +7% (depending on your monitor). The three dark-gray stars on the left are all the same, with a Michelson contrast of about −7%. (We use positive and negative numbers for the Michelson contrast of spatial increments and decrements.) All stars are about equally salient. But now run the movie. First you see a dynamic adapting field, in which the two top stars flicker between black and white at 5 Hz, while below it the edges that outline the two bottom stars also flicker between black and white. Since the time-averaged black and white have the same mean luminance as the mid-gray surround, these flickering stimuli generate no visible afterimages. However, they do leave an invisible area of reduced sensitivity to contrast.

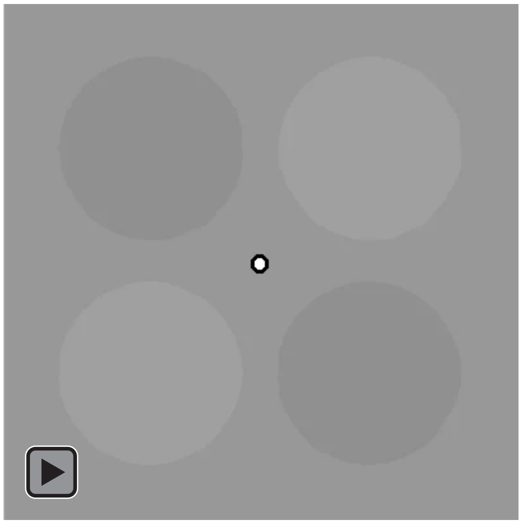
After a few seconds of adaptation the original static test stars reappear in Movie 1 (after which the adapting cycle restarts.) The two unadapted lateral stars, positioned at nine and three o'clock, are kept visible for comparison purposes, but adaptation makes the other four test stars disappear from view, even though they are still present on the screen. Note that both types of adapting fields—flickering solid stars and flickering outlines—reduce the sensitivity of the visual system enough to make both the light and dark test stars subjectively disappear.

It is not necessary to use thin spiky stars in which all parts of the star are near to an edge. In Movie 2, outline circles that flicker at different rates are fixated for 3 s, followed by low-contrast gray test disks of the same size and of Michelson contrast ~5%. Result: The test disks completely disappear from view. This works for disks of radii between 1° and 10°. Test disks of higher contrast (not shown) look like very blurry blobs following adaptation.



Movie 1. Fixate the central red spot. The two solid flickering stars at the top and the two flickering outline stars at the bottom obliterate the four corresponding gray test stars, even though these are still on the screen.

More complex shapes can adapt. Movie 3 shows two identical test patterns side by side, namely low-contrast lith portraits of Dr. Michael Webster. Fixate the central red spot while a flickering *outline* of the right-hand portrait adapts your visual system. When the two test portraits reappear, the right-hand one will have apparently vanished, though it is still present on the screen.



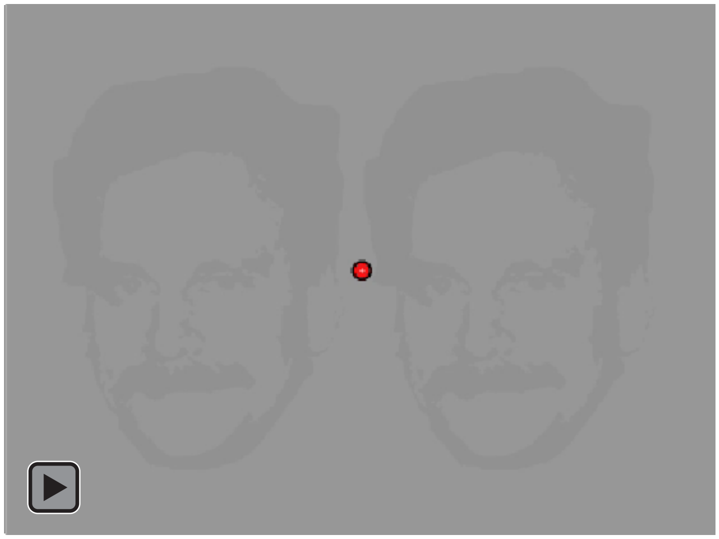
Movie 2. As in Movie 1, adapting to the flickering outline circles makes the test disks disappear from view. Adapting circles flicker at 1, 2, and 4 Hz, and the rotating dashed circle is also an effective adaptor; clearly flicker rate is not crucial.

Selective adaptation

It is possible to adapt only some of the contours of a test pattern selectively, leaving other edges unaffected. Movie 4 shows four test stars, each divided into light and dark quadrants. The two stars on the left are identical, but look radically different following adaptation. The same is true for the two stars on the right. Run the movie four times, fixating each time on the red spot in the center of a different star. In the top row, adapting to the external edges of the stars makes these edges disappear in each test star, leaving only an intersection of four disembodied quadrants. In the bottom row, adapting to an internal cross suppresses the internal structure and makes the individual quadrants disappear, making each test star look like a uniform gray.

Movie 5 shows a faint plaid, made by transparently superimposing a vertical and a horizontal square-wave grating. When the movie is run, the adapting pattern consists of flickering black/white lines on a gray surround. These lines are horizontal in the top left half, and vertical in the bottom right half of the adapting pattern. Pay attention only to the appearance of the test plaid. After adaptation it will look like a series of capital letter Ls, comprising vertical stripes in the top left half, and horizontal stripes in the bottom right half, because the other stripes have adapted out.

We conclude that in the top-left half the horizontal test contours are weakened and suppressed by the horizontal adapting lines, so that the plaid is perceived

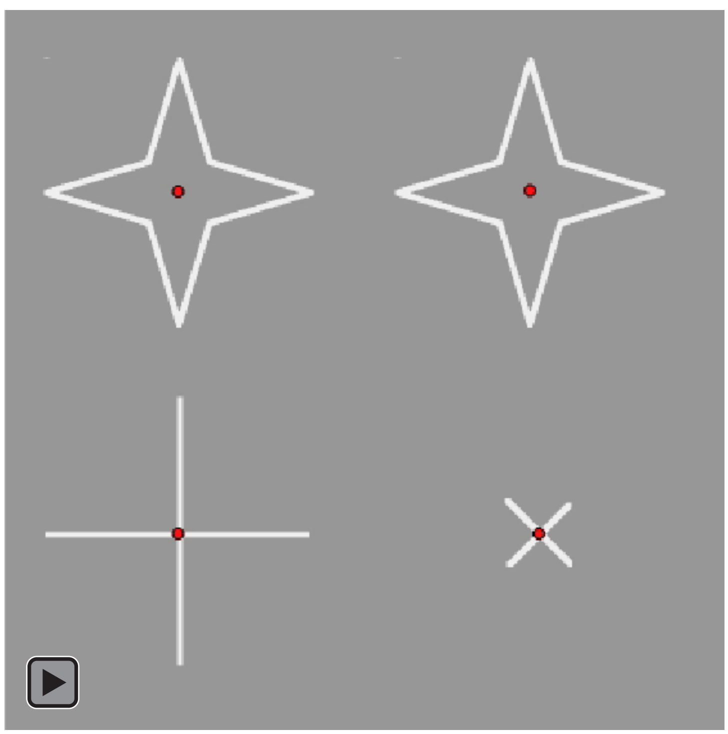


Movie 3. Adapting to Webster's outlined face on the right makes the right-hand test Webster disappear.

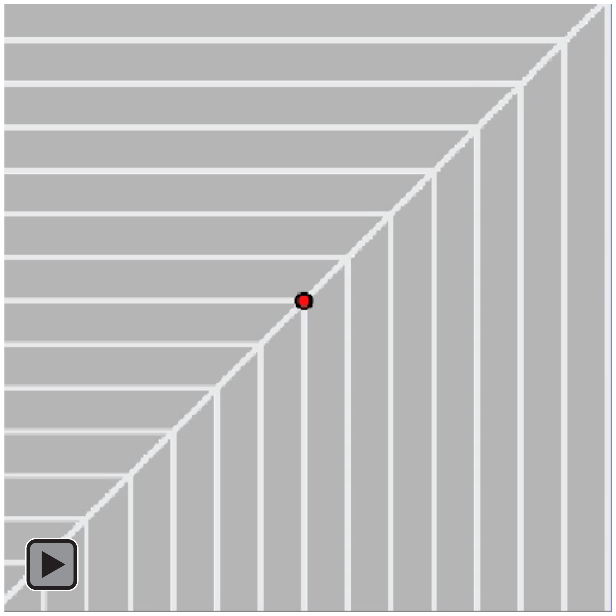
only as a vertical grating. The opposite is true for the bottom-right part of the plaid.

Selective adaptation can change a disk from light to dark

Movie 6 shows two identical mid-gray disks side by side, each embedded in a light gray annulus. The adapting stimuli on both sides are thin outline circles flickering between black and white. But notice that the adapting circle on the left of fixation is slightly larger than the one on the right, because they are congruent with the outside and inside edges of the test annuli respectively. Now adapt to the flickering circles. When the test pattern comes up, it now looks like two unequally light disks. The test disk on the left looks small, and darker than the surround, while the test disk



Movie 4. Adapt to the red spot in each star in turn. The adapting external outlines in the two top stars leaves only disembodied quadrants visible. The adapting internal crosses in the two bottom stars obliterate the internal quadrants, making each star look a uniform gray.



Movie 5. The horizontal adapting lines in the top-left half obliterate the horizontal edges in the test plaid, which now looks like a vertical grating. The opposite is true in the bottom-right half. So the test plaid looks like a set of capital Ls.

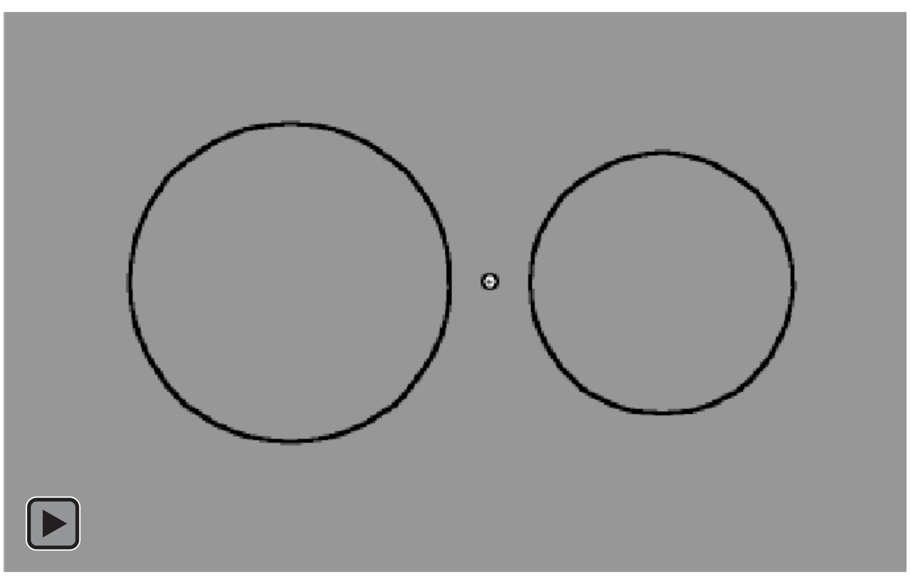
on the right looks large, and lighter than the surround. In fact, of course, both these test disks are identical in size and luminance.

On the left: The larger flickering circle erodes the *outer* edge of the annulus, so that the surround gray fills in the annulus, which becomes indistinguishable from the surround. However, the disk forms an intact dark-to-light edge with the inner edge of the annulus, so the inner disk looks small, and darker than the surround.

On the right: Conversely, the smaller flickering circle erodes the *inner* edge of the annulus, so that the gray of the interior disk fills in the annulus, making the annulus indistinguishable from the interior. However, the disk plus annulus forms an intact light-to-dark edge with the mid-gray surround, making the disk look large, and lighter than the surround. Corresponding effects (not shown) can be produced if the annulus is slightly darker than the surround. The annulus needs only to be thick enough to counteract the effects of eye tremors during fixation.

This display achieves the same effects as a Craik-O'Brien-Cornsweet edge (COBCE; O'Brien, 1958; Cornsweet, 1970, pp. 272–275; Laming, 1986, p. 64; Masuda et al., 2011), but by different means. Two mid-gray panels that meet at a COBCE look respectively lighter and darker, because two edges of opposite polarity are superimposed. Thus, a visible, sharp light-to-dark edge is superimposed on a below-threshold blurred dark-to-light edge, giving the net effect of a light-to-dark edge. In the present display, the edges are adjacent instead of superimposed, and one edge is driven below threshold, not by being blurred but by being adapted.

The COBCE has sometimes been taken as evidence for poor sensitivity to the low-spatial frequencies (SF) in the blurred edge, followed by a low-level "filling-in" mechanism subserving lightness perception. However, Dakin and Bex (2003) present evidence that the mechanism responsible for the COBCE effect operates not via propagation of a neural signal across space, but



Movie 6. Adapting to outline circles produces pseudo-Cornsweet edges. On the left, the large flickering circle erodes the outer edge of the test annulus, giving an apparently small, dark test disk. On the right, the smaller flickering circle erodes the inner edge of the test annulus, giving an apparently large, light test disk. See text.

by amplification of the low SF structure of the image. They propose a model that relies on the statistics of natural scenes actively to reconstruct the image that is most likely to have caused an observed series of responses across SF channels. Our "pseudo-COBCE," however, is compatible with a simple erosion of one edge by adaptation, followed by low-level filling-in across the eroded edge.

Erasing and reversing a Cornsweet edge

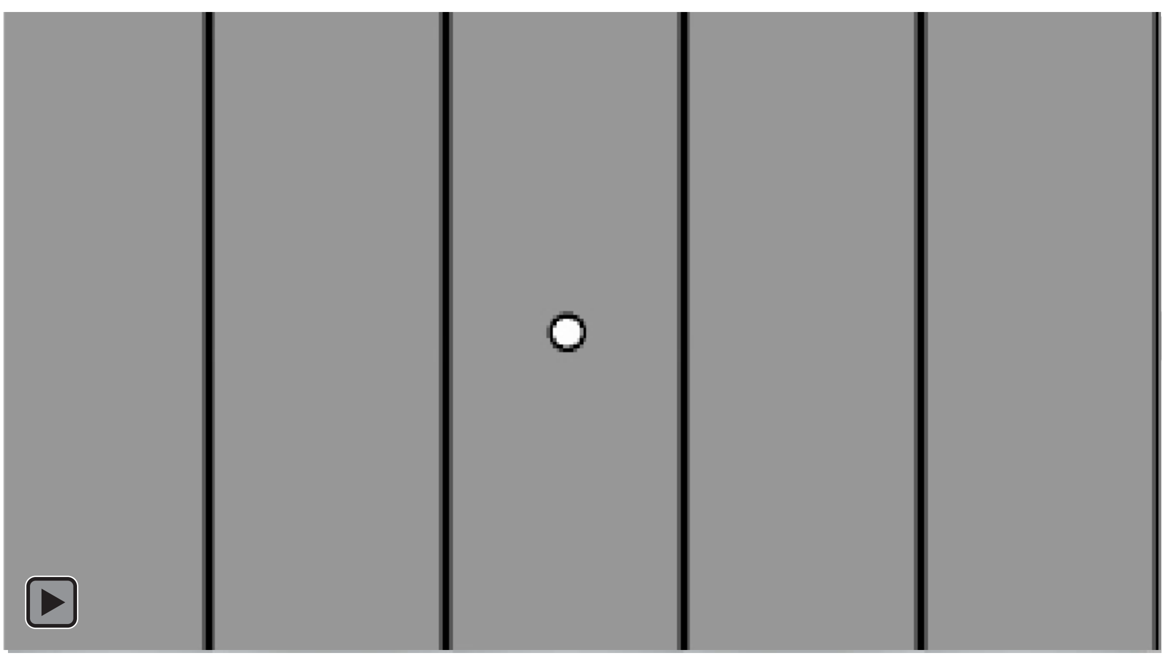
Movie 7 shows a set of vertical COBCE's—a "fluted square-wave grating" made by superimposing a sharp-edged square wave grating on top of its own sinusoidal fundamental which is in spatial counterphase. It is best to view this from close enough that each vertical bar subtends at least 1° of visual angle (0.5 cpd). Examine the central vertical bar on which the fixation point is placed. This bar looks dark, owing to the dark bar of the square-wave grating, and despite the light bar of the sinusoidal grating. This is because the sharp edges defining the dark central bar are more salient than the blurred edges defining the light central bar. Now run the adapting flickering lines, which lie along the edges of the square-wave grating. After several adapting cycles with strict fixation, these edges will gradually fade out and the central bar will appear to change from dark to light. When the movie is stopped, the dark central bar will gradually fade back into view. The bottom half of Movie 7 remains unadapted as a comparison.

Objective contours adapt; subjective contours do not

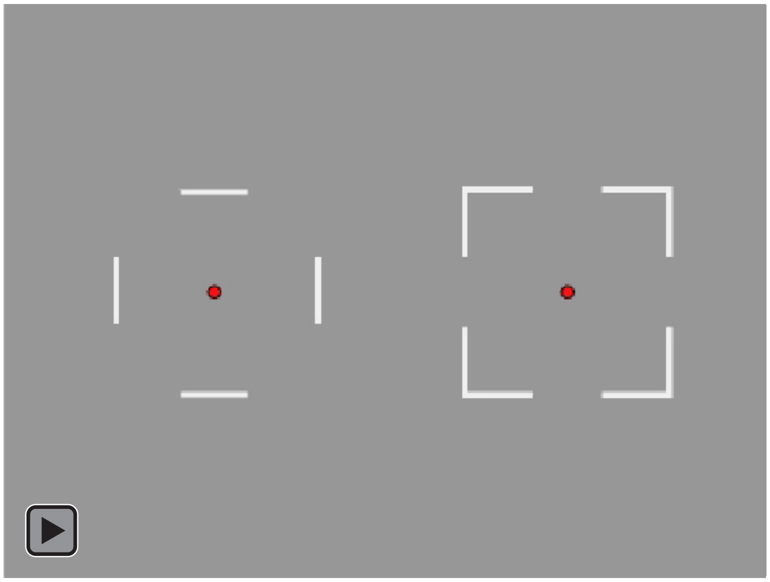
Movie 8 shows two low-contrast Kanizsa squares side by side (Kanizsa, 1976). Each figure comprises four pacmen with a right-angled bite taken out of each one. Observers perceive a subjective square, mentally filling-in imaginary vertical and horizontal sides to link up the pacmen.

Cortical area V2 contains neurons that explicitly and unambiguously signal the orientation of purely subjective contours, i.e., contours with no Fourier components at the orientation of the perceived edge (von der Heydt & Peterhans, 1989; Peterhans & von der Heydt, 1989, 1991). In Movie 8a the adapting, flickering lines lie on the putative site of such subjective contours, lying in the blank spaces between the pacmen. Result: Adapting to these made no discernible difference to the perception of the Kanizsa square. In Movie 8b the flickering lines coincide with the physical contours that lie within the pacmen and define the corners of the square. Result: These edges looked very blurred following adaptation and they degraded the subjective square, which no longer looked square but resembled a rounded foggy blob or luminous haze. For one observer the degradation was so complete that the pacmen looked like complete disks with no bites taken out of them.

We conclude that contour adaptation had no effect upon subjective edges, which are presumably signaled by cortical area V2 (von der Heydt & Peterhans, 1989;



Movie 7. Cornsweet edges, made by superimposing a square-wave grating on its own sinusoidal fundamental. The dark central square-wave bar dominates over the light central sinusoidal bar. But adapt to the flickering lines that lie along the edges of the square-wave grating. Result: The square-wave grating erodes and the central bar looks light.



Movie 8. (a) Adapting to the regions of subjective contours in the blank spaces between the pacmen does not destroy the subjective Kanizsa square. (b) But adapting the corners of the square defined within the pacmen turns the subjective square into a formless fog or luminous haze.

Peterhans & von der Heydt, 1989, 1991), but it did considerably blur and degrade the physical contours, which might be signaled by V1. This makes it likely that contour adaptation occurs in area V1.

Colors do not adapt

Movie 9 contains four test squares: light gray, dark gray, blue, and yellow. All the squares have low contrast or low saturation and approximately equal salience. With strict fixation on the central spot, three observers (one naive, two experienced) adapted to a repetitive "topping-up" regime of flickering outline squares for 3.6 s, alternating with the static test squares for 1.2 s. Observers called out when the gray and/or the colored test squares disappeared from view, and these times were recorded with a stopwatch. Trials were terminated after 2 min. Results: The gray squares adapted rapidly, disappearing from view after a mean time of 14 s. On the other hand, although the colored squares looked progressively more blurred as time went on, they retained their colors for the full 120 s duration of the trials. So the colors resisted adaptation, remaining visible for almost 10 times as long as the gray squares. We noticed (not shown) that adapting to outlines that flickered, not between black and white but between a saturated dark blue and light yellow, also made the gray, but not the colored, test squares disappear.

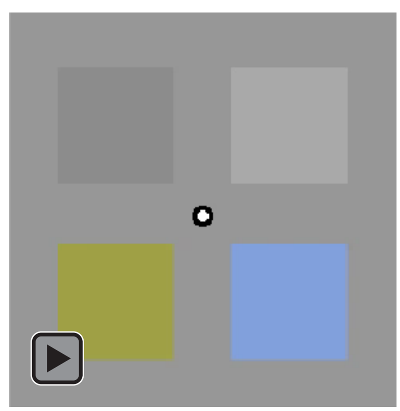
We conclude that colors are coded differently from luminance. Whereas luminance seems to be coded primarily at edges (luminance boundaries), colors seem to act more like a wash that fills in areas and stops only when it reaches a luminance boundary (Grossberg, 2003; Anstis, Vergeer & Van Lier, 2012a, 2012b).

Quantitative results

Experiment 1: Measuring contour adaptation

Method

We measured contour adaptation with a display similar to Movie 1, viewed by five observers, including



Movie 9. Adapt to the four flickering outline squares. The upper gray test squares vanish within 15 s, but the lower colored squares resist adaptation and remain visible for at least 2 min. Conclusion: Luminance fills in from edges, and if these edges are weakened by adaptation, the luminance fails to fill in. Color is different and does not depend upon filling-in from edges.

four naive and one experienced psychophysical observer. The two lateral stars were removed. A "topping-up" procedure was used that continuously alternated 5 s of adaptation with 1 s of test period. The two upper test stars alternated over time with flickering adapting patterns that were either solid stars or flickering outlines on different blocks of trials. The two lower test stars, unlike in Movie 1, were not exposed to any adaptation, and indeed were hidden during the adapting periods and were visible only during the test periods as matching stimuli. During the test periods all four stars were briefly shown, including the two upper stars, one light and one dark, and also the two lower stars, one light and one dark. The adapting and test periods cycled continuously. The observer adjusted the luminance of each (unadapted) lower star independently, by striking keys on a keyboard, until satisfied that they provided a subjective match to the upper (adapted) stars. The observer then struck the space bar, which automatically recorded the settings for later analysis and set up the next trial, with Michelson contrasts of the two upper test stars randomly chosen from the set ±1.2%, 3%, 6%, 12%, 18%, or 24%.

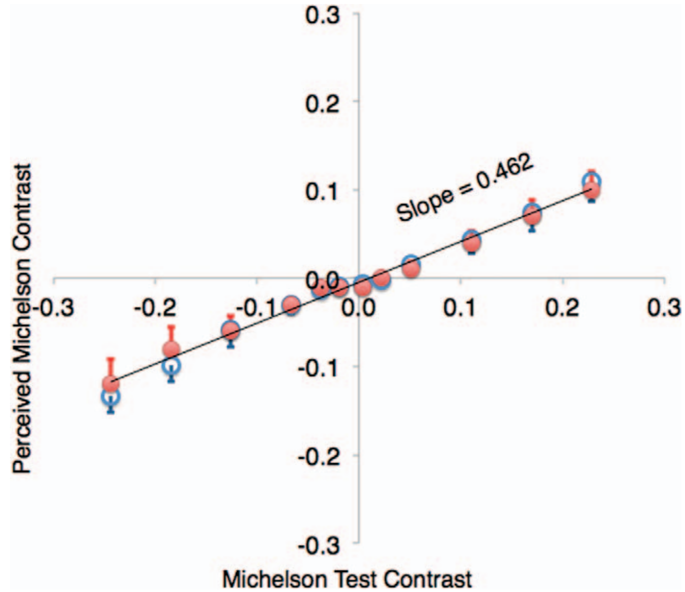


Figure 1. Adapting to solid flickering stars (solid symbols) or outline stars (outline symbols), similar to Movie 1, reduced the perceived contrasts of test stars to about 46% of their true values. Vertical lines show +1 *SE*. Results were about the same for both adaptors, showing that flickering outlines were just as effective adaptors as flickering solid stars.

Results

Results are shown in Figure 1 (mean of 5 subjects × 8 readings). Figure 1 shows that adapting to the outlines was just as effective as adapting to the solid stars. Both approximately halved the subjective contrast of the test stars. A single line with a slope of 0.46 has been fitted to all the data points following adaptation both to solid stars and to outline stars. The R^2 value was 0.987. This high correlation would seem to leave little room for any nonlinearities, yet such nonlinearities can be clearly seen if the same data are replotted in Figure 2 with y = perceived/actual contrast. In other words, instead of plotting the raw subjective test contrast, we plot the percentage reduction in perceived contrast (In both graphs, increasing y represents increasing contrast). This plot does show that solid stars were slightly more effective as adaptors than outline stars. Veridical perception would give a line of unit slope in Figure 1, and a horizontal line with y always equal to 1 in Figure 2. Reducing all test contrasts to 46% would have given a horizontal line of height $y = 0.46$ in Figure 2. In fact Figure 2 shows that for test contrasts below 0.1, the adaptation depressed the perceived contrast precipitously.

Experiment 2: Contour adaptation is monocular

Movie 10 shows a contour-adaptation stereogram that was binocularly fused via a prism stereoscope and was viewed by six observers (two experienced, four naive). Four squares were arranged around a central fixation point and enclosed in a textured picture-frame to maintain good fixation and fusion. The test field consisted of four faint gray squares, presented to the right eye only. On each trial, all four of these test squares were set to the same physical Michelson contrast, which was selected at random from a range of ten values lying between −0.15 to +0.15. Positive and negative Michelson contrast values refer to test squares that were lighter and darker than the surround. During adaptation, two outline squares flickering at 5 Hz were presented for 4 s, one to each eye. The left eye's adapting square was congruent with the upper left test square, and the right eye's adapting square was congruent with the upper right test square. Thus the upper left and right test squares were exposed to dichoptic and monocular adaptation, respectively. The lower left and right squares were adjustable matching stimuli, which the observer adjusted during the 1 s test periods to match the appearance of the upper, adapted squares, by striking four designated keys on the keyboard. When the observer pressed the spacebar, the settings were automatically recorded for later analysis and new contrast settings were randomly selected for the next trial. Data were collected over a series of randomly selected ten runs, one for each test contrast, during which three readings were taken for each datum point and averaged together during analysis.

Results (for 6 Ss × 3 trials) are shown in Figure 3. The horizontal axis shows the physical Michelson

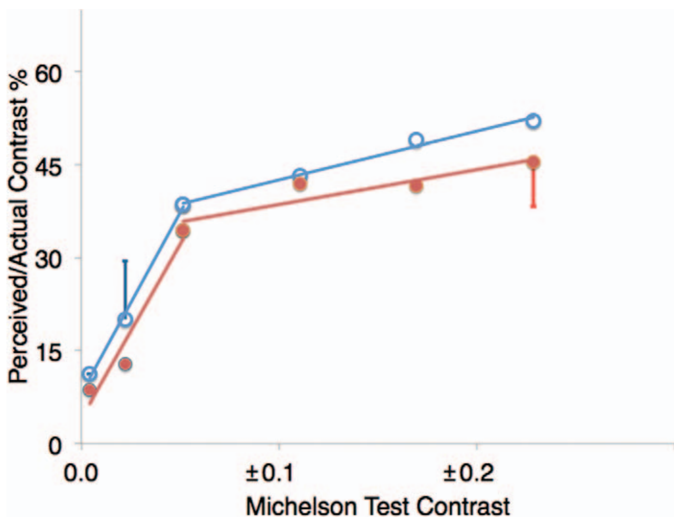


Figure 2. Same data as Figure 1, replotted to show perceived/actual contrast as a percentage. Adaptation disproportionately affected low test contrasts. Michelson test contrasts greater than 0.1 appeared to retain 35%–50% of their actual value. But test contrasts below 0.1 declined precipitously to only 10%–15% of their actual value. Solid stars were slightly more effective adaptors than outline stars. Vertical bars show median *SE* for each data set.

contrast of the test squares, and the vertical axis shows the Michelson contrasts that the Ss selected as subjective matches. The blue points show data for dichoptic adaptation, in which the left eye saw the flickering adapting outline and the right eye saw the test square. A 45° line has been drawn on the graph, for which $y = x$. It will be seen that the dichoptic data points lie close to this line. This shows that the observer was making veridical matches, so the dichoptic adaptation was totally ineffective. The red points show the data for monocular adaptation, where the flickering outline and the test square were both seen by the right eye. This monocular contour adaptation reduced the perceived test contrasts to about 45% of their true values, showing strong contour adaptation. Vertical bars show standard errors.

These results show that contour adaptation is a monocular process, with no detectable transfer between the two eyes. This is consistent with the evidence from Movie 8 that assigns contour adaptation to cortical area V1.

Experiment 3: Effectiveness of different adaptors

Method

Five observers (four naive, one experienced), viewed a version of Movie 3. In a paired-comparison design, they viewed two identical Webster test faces of Michelson contrast 10.9%, side by side, after adapting to different regimens, each of which flickered between black and white for 5 s. The flickering adaptors were either Webster faces congruent with the test stimuli, outline faces, checkerboards with 9 × 13 squares, blurred Webster faces, or spatially uniform fields. On each trial, two different adapting stimuli were randomly selected and presented on the left and right of fixation for 5 s. Each adapting and test stimulus was 16° high × 12° wide, and their inner edges were 0.5° from the fixation point.

Following the 5 s adapting period, the test portraits were presented for 2 s, and the observer pressed a left or right key to indicate which test portrait looked fainter, in other words, which adapting stimulus was more effective. Each of the five observers made a total of 50 comparative judgments, which were collected and stored for later analysis offline.

Results

These adapting stimuli were, in order of effectiveness:

	% of trials chosen as best adaptor (Mean + *SE*)
(1) A congruent flickering portrait, same as test faces except in contrast.	40.0% ± 4.0%
(2) A flickering outline, as shown in Movie 2.	29.5% ± 4.4%
(3) A contour-rich 9 × 13 checkerboard.	11.2% ± 2.9%
(4) A blurred version of the portrait.	10.4% ± 3.0%
(5) A blank rectangle bounding the area of a portrait.	0.4% ± 0.4%

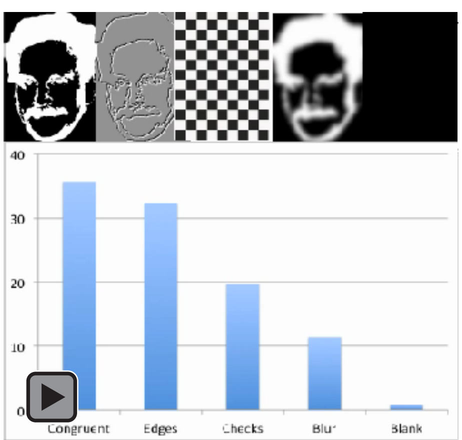
These results are shown graphically in Movie 10. Movie 10 shows, not surprisingly, that a congruent flickering face was the most effective adaptor. But a flickering outline was nearly as good, while a flickering blurred face was a very poor adaptor. Clearly the relevant brightness information in the adaptor is concentrated at the edges, not the middle, of the gray areas.

Discussion

We now compare our contour adaptation with the various published forms of contrast adaptation that were reviewed in the Introduction (Webster & Mollon, 1993; Webster & Wilson, 2000).

Movie 10. Fuse this stereo pair to show that contrast adaptation does not transfer across the eyes. Results are plotted in Figure 3. See text.

1. Contour adaptation is produced by flickering outlines that have the same mean luminance as a mid-gray background, and therefore leave no afterimage. Instead, they do leave a region of reduced sensitivity to low-contrast test stimuli within the area bounded by the flickering contour. This shows, of course, that contour adaptation is a form of contrast adaptation, which adjusts to the variations in target luminance, and is not simply luminance adaptation responding to the mean target luminance.



Movie 11. Experiment 3 used a paired-comparison design to show that congruent faces, identical to the test faces (but higher in contrast) were the best adaptors. But outlines were nearly as good, followed by checkerboards, whilst blurred faces were very poor adaptors, and uniform flickering fields produced no detectable adaptation at all. Vertical lines show $+1$ *SE*. Conclusion: Brightness and contrast information are concentrated at edges, and adaptation selectively weakens these edges.

2. Contour adaptation shows no interocular transfer (Experiment 2 and Movie 10), so it is probably confined to monocular pathways. This is consistent with the evidence from Movie 8 that the adaptation is confined to cortical area V1. On the other hand, Paradiso and Nakayama's (1991) filling-in effect is decidedly not monocular—it is actually greater when the disk and mask are presented dichoptically than when they are presented to the same eye. Also, the adaptation to gratings (Blakemore & Campbell, 1969; Kelly, 1972) that causes threshold elevation does transfer interocularly, and since it is selective for both orientation and spatial frequency, it cannot be retinal. Quite probably it arises in cortical area V1. So contour adaptation is not to be identified either with Paradiso and Nakayama's (1991) filling-in, or with Blakemore and Campbell's (1969) grating adaptation.
3. Movie 2 showed that if one adapts to a flickering outline circle, a gray disk of the same size can vanish. This is reminiscent of Krauskopf's (1963) finding that when a red disk in a green surround is stabilized on the retina, its borders gradually disappear and the disk fades out until the whole field looks green. But we found, as shown in Movie 9, that colored patches resist adaptation from flickering contours. Thus the two ways of weakening a contour—by contour adaptation, and by retinal

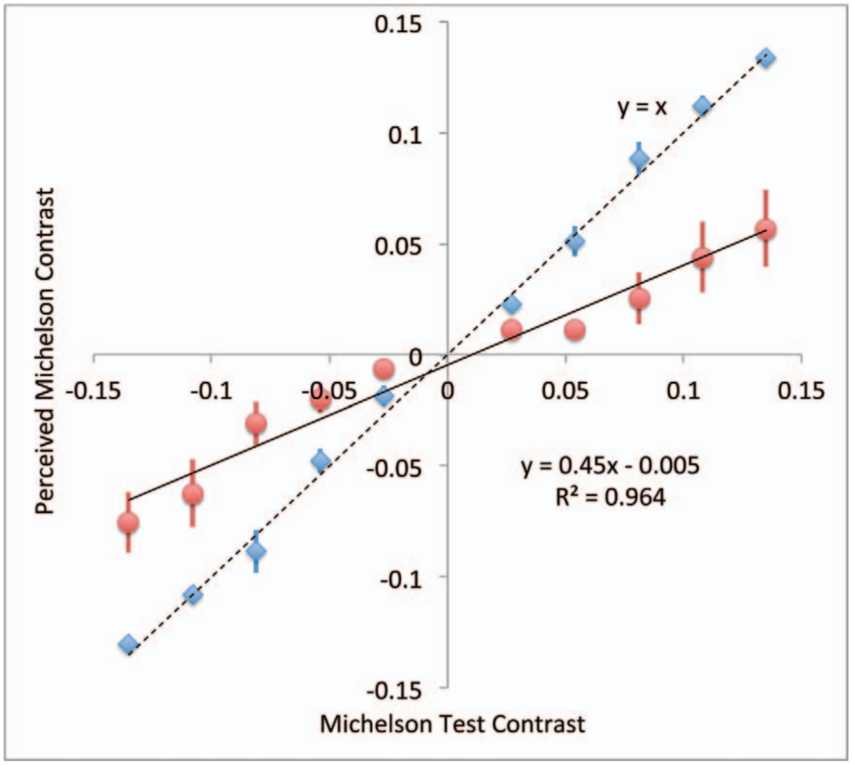


Figure 3. Contrast adaptation does not transfer interocularly. Adapting one eye to a flickering outline square reduced the perceived contrast of test squares seen by the same eye to 45% of their actual value (red data points). But it had no effect on test squares seen by the other eye, which were seen veridically ($y = x$) (blue data points). Vertical bars show +1 *SE*.

stabilization—are not equivalent. They probably have different mechanisms, with retinal stabilization causing stimulus failure by suppressing any jiggles of the retinal image caused by small eye movements. Contour adaptation leaves the test stimulus unchanged but presumably desensitizes the neural channels that respond to edges and brightness differences. Since contour adaptation strongly affects apparent luminance but barely affects perceived hue (Movie 9), it must be confined to the luminance pathways and has no effect on chrominance pathways. This makes it quite different from Webster and Wilson (2000).

4. In addition, Movie 9's demonstration that contour adaptation does not affect hues suggests that color and luminance are coded differently. Whereas luminance information may spread outwards from luminance edges, there is evidence that color spreads out, in a process analogous to physical diffusion, until it encounters luminance contours that halt its spread. Grossberg (2003) has modeled this process, and Van Lier, Vergeer, and Anstis (2009) and Anstis et al. (2012a, 2012b) have presented independent evidence that both real colors and afterimage colors do spread out in this way until the colors reach a luminance boundary.
5. We were surprised to find in Movie 8 that the objective contours inside the pacmen that define the corners of a Kanisza square could be adapted, blurring out the square, but that the subjective contours, which the pacmen induced into the white spaces between, showed no signs of being adaptable. We had expected that subjective contours would be weaker and more adaptable than the real ones, but that is not what we found. We tentatively locate contour adaptation in area V1, which responds to real contours, rather than in V2, which responds to apparent contours.
6. The production of pseudo-Cornsweet edges in Movie 6 and the erasure of Cornsweet edges in Movie 8 were caused by a position-specific edge adaptation that erased the sharp edges of a square-wave grating while, in Movie 7 having little effect upon a sinusoidal grating of the same fundamental spatial frequency. This is quite different from conventional grating adaptation (Blakemore & Campbell, 1969), which is specific to spatial frequency but is not sharply tuned for position, since continuous phase-shifts in an adapting grating do not perceptibly reduce the amount of adaptation. In fact observers are often encouraged to move their eyes back and forth while adapting to static gratings in order to reduce any unwanted afterimages. Any

attempt to modify Movie 7 to test for grating adaptation would require an entirely different adaptor based upon the harmonics of a square wave, which take the form f, 3f/3, 5f/5, 7f/7... To adapt out the square wave in Movie 7 while leaving the fundamental sine wave relatively intact, one might adapt to superimposed gratings of values 3f/3, 5f/5, 7f/7..., all vertical but jumping around in random phases. We have not attempted this.

7. In Experiment 3, the high spatial frequencies in flickering outlines produced strong adaptation, whereas the low spatial frequencies in a blurred picture produced very little. This rather surprising finding appears to be new, since previous studies on contrast adaptation have not used such stimuli.
8. The fact that adapting to, say, a thin outline flickering circle can obliterate the percept of a complete low-contrast test disk, as in Movies 1–4, shows a strong spatial spread of contrast adaptation within the bounded area and suggests that brightness information is concentrated at luminance edges and fills in from them to create perceived surfaces. It is consistent with a two-stage process for visual filling-in: a slow process, accelerated by contour adaptation, in which boundaries fade out, followed by a much faster process in which the properties of the surround fill into the bounded area (Spillmann & de Weerd, 2003). So a luminance boundary is like a dam that can be eroded rather gradually by Troxler et al. (1804) fading, or now much more rapidly and controllably by contour adaptation. Once the dam is breached, the surround luminance can rapidly flood like water into the central area.
9. We conclude that contour adaptation may prove to be a useful new technique for studying the roles played by boundaries, adaptation, and filling-in in the creation of perceptual surfaces.

Keywords: filling-in, adaptation, contrast, luminance, contour

Acknowledgments

Supported by a grant from the UCSD Psychology Department. I am grateful to Pembroke College, Oxford, for a Visiting Fellowship, and to the Humboldt Foundation for a Fellowship. Thanks to my students Sean Deering, Doreen Hsu, Katherine Hsueh, Alexis Pammit, Esther Strom, and especially Neal Dykmans for their assistance in collecting and analyzing the data. John Mollon suggested the title of this paper.

Commercial relationships: none.
Corresponding author: Stuart Anstis.
Email: sanstis@ucsd.edu.
Address: Department of Psychology, University of California–San Diego, La Jolla, CA, USA.

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