

Chapter 108

Adaptation to Brightness Change, Contours, Jogging, and Apparent Motion

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Frisby and Stone (2010) have dubbed adaptation the “psychophysicist’s electrode,” and John Mollon once (1974) famously said, “If it adapts, it’s there.” Psychologists piously hope that their many experiments on visual adaptation will tell physiologists where to look inside the brain. This chapter describes visual adaptation to temporal ramps, spatial edges, and apparent motion (AM) and touches on kinesthetic aftereffects from jogging.

Sawtooth Adaption

Sawtooth adaptation (or a ramp aftereffect) is produced by gazing at a spatially uniform patch whose luminance is temporally modulated by a repetitive sawtooth, either gradually dimming and turning sharply back on (rapid-on) or gradually brightening and turning sharply back off (rapid-off). This can lead to two different kinds of aftereffect: a shift aftereffect (ramp aftereffect), in which a steady test patch appears to be gradually brightening or dimming in the opposite direction to the adaptor, and a threshold-elevation aftereffect, in which a weak sawtooth of the same polarity as the adaptor becomes more difficult to see. I describe shift aftereffects (ramp aftereffects) first. It is well known that adapting to a static, dark (or light) square gives rise to a light (or dark) negative afterimage. I also discovered a dynamic version, namely adaptation to gradual change of luminance. This can be called a ramp aftereffect ([Video IX.108-1](#)).

[insert [Video IX.108-1](#)]

[insert Figure IX.108-1]

Following adaptation to a spatially uniform patch of light that is growing gradually brighter, a subsequently viewed static gray test patch appears to be growing gradually dimmer ([Video IX.108-1](#), upper panel). Conversely, following adaptation to a patch that is growing gradually dimmer, a gray test patch appears to be growing gradually brighter (lower panel; Anstis, 1967). A single rising or falling adapting ramp is usually sufficient to produce a detectable aftereffect, but it is convenient in practice to fold the ramp into a repetitive sawtooth. Typically, an adaptation period might consist of 30 sawteeth, each lasting 1 s during which the luminance would grow or shrink through 1 log unit. During the aftereffect, the test stimulus appears to brighten or darken monotonically for 3 to 8 s. In [Figure IX.108-1](#) the solid black lines show the luminance profile of a typical stimulus over time in (a) and (c) and the perceived aftereffect in (b) and (d). Aftereffects are more conspicuous if either the adapting or the test field—or both—are spatially shaded from light to dark (not shown), which produces an impression of motion when the adapting field changes in luminance or when an aftereffect changes the subjective brightness of the test field.

Effects can be measured by a matching method. The maximum aftereffects, equivalent to about ± 15 dB/s, can be obtained from a large adapting amplitude of ± 20 dB/s (=1 log unit/s), but they are fairly insensitive to the temporal rate of this sweep. The channels are present out to an eccentricity of at least 40° , but they almost disappear during dark adaptation. The ramp aftereffects were asymmetrical: the subjectively darkening aftereffect produced by a brightening adapting ramp were 30% stronger than vice versa (Arnold & Anstis, 1993), suggesting that units that detect gradually rising

luminance are more plentiful than units that detect gradually falling luminance.

Aftereffects also decline markedly at low (scotopic) luminance levels, falling from 12 to 3 dB/s when the luminance is reduced by 2.5 log units. The spatial resolution of the underlying temporal channels that create the aftereffects was very low, estimated to be equal to an acuity of only 20/400. Thus the “perceptive fields” underlying the aftereffect are extremely coarse, and they rapidly become even coarser with increasing eccentricity (Anstis & Harris, 1987). Bosten and Macleod (2013) report a surprising relationship between static and dynamic luminance. After adaptation to a brightening (rapid-off) sawtooth, the threshold is raised for detecting a static disk that is slightly lighter than its surround (spatial increment).

Sawtooth adaptation can coexist with simultaneous contrast; if a small grey spot of constant luminance is centered in a brightening field, it appears to be growing gradually dimmer by simultaneous contrast. This apparent (illusory) dimming leads to a brightening aftereffect in the spot (Anstis, 1979). Chromatic sawtooth aftereffects have been sought but not found. If a dimming red patch is superimposed on a brightening green patch, the result is an equiluminous patch that modulates from red through yellow to green, but adaptation to this yields no aftereffect of apparent color change. This lack of color response, plus the fact that sawtooth aftereffects show no interocular transfer (Anstis, 1967), suggest that the underlying ON and OFF channels lie early in the M pathways, which respond to flicker but are believed to be insensitive to colors, unlike P pathways. Ramp aftereffects imply that neural units exist selective for gradual brightening and for gradual dimming. In a simple model, a summation unit receives two inputs from a single retinal region: a direct input and a delayed input that signal,

respectively, the present and the immediately past luminance. Subtracting the delayed from the direct input gives zero signal for an unchanging luminance, a positive signal for a brightening field, or a negative signal for a dimming field. This model is equivalent to Reichardt's (1961) motion detector but with zero spatial shift. Reichardt's motion detector receives inputs from two adjacent retinal regions and detects motion from one region to the other, whereas the dimming/brightening model receives two inputs from the same retinal region and effectively yields the time derivative of the luminance.

There is a related effect of apparent brightening when gratings with an asymmetrical ramp (sawtooth) waveform move across the retina (Cavanagh & Anstis, 1986). If the grating moves in a direction that stimulates a given retinal area with a gradual brightening, interspersed with sudden darkening, the grating looks apparently lighter while it moves. When it moves in the opposite direction, it looks apparently darker (Fig. IX.108-2). Or we can move our finger across the figure and track that. Some people also report faint colors associated with the brightness changes.

[insert Figure IX.108-2]

The movement drifts the spatial sawtooth across retinal receptors, which therefore see a temporal sawtooth. The apparent brightness change bespeaks a nonlinearity in the visual system that under-reports the rapid phase and/or over-reports the slow phase of the sawtooth.

Adapting to a temporal sawtooth can also raise the threshold for test sawteeth of the same polarity. Exposure to a large uniform field modulated in luminance by a sawtooth function, repeating between one and five times per second, raised the threshold for detection of a test stimulus of similar waveform by a factor of 2 to 4.5. In comparison, the threshold elevation for a test stimulus of the inverse waveform was only half as great.

This polarity-sensitive adaptation indicates that separate visual channels signal “brightening” and “darkening” (Hanly & Mackay, 1979; Purkiss & DeMarco, 2002). It is assumed that rapid-on sawtooth and rapid-off sawtooth tests are detected differentially by temporal ON and OFF channels, respectively. The visual system is generally more sensitive to rapid-off sawtooths than to rapid-on sawtooths, which strengthens the evidence that the visual system is more sensitive to sudden decrements than increments in light level (Bowen, Pokorny, & Smith 1989). Kremers, Lee, Pokorny, and Smith (1993) explored the physiology of temporal ON- and OFF-center channels in macaque retinal ganglion cells. They concluded that human luminance sawtooth sensitivities measured by psychophysics are consistent with selective detection through M pathways in the macaque visual system.

Contrast Adaptation Is Pattern-Specific

It is well known that adapting to a white (or black) square gives rise to a negative afterimage that is black (or white). Adapting to a square that flickers between black and white on a grey surround gives no visible afterimage, provided that the time-integrated black and white are equal to the luminance of the grey surround. But it does leave a region of reduced sensitivity, so that a congruent low-contrast test square can become invisible. Webster and Mollon (1994) describe this as “contrast adaptation” and conclude that light adaptation adjusts sensitivity to mean luminance, while adaptation to contrast (i.e., to flicker) adjusts sensitivity to variations in luminance.

Note that contrast adaptation absolutely requires that the adapting and test regions must be congruent (Anstis, 2014). This is shown in [Video IX.108-2](#), in which the test stimulus consists two transparently superimposed, low-contrast grey-scale photos, one of

Albert Einstein and the other of Marilyn Monroe (Oliva & Schyns, 1997). Two identical Einstein+Marilyn photos are set up side by side with a fixation point between them; each looks like a confused jumble, and neither face can be seen clearly. The adapting stimuli are high-contrast flickering versions of the two single components: Einstein on the left and Marilyn Monroe on the right. The resulting adaptation makes Einstein fade out subjectively from the left-hand Einstein+Marilyn, which now looks like Marilyn Monroe. Conversely, Monroe subjectively fades out from the Einstein+Marilyn on the right, which now looks like Einstein. This adaptation selectively picks out (and degrades) the test photo with which it is congruent and has little effect on the other, superimposed but noncongruent test photo.

[insert [Video IX.108-2](#)]

Contour Adaptation

Contour adaptation is a process of reducing a shape's perceived contrast, or even making it invisible, by adapting to its flickering outline. [Video IX.108-3](#) shows four low-contrast stars on a grey background. Two stars are slightly lighter than the background and two are darker. This is the test stimulus. While playing the video, fixate on the central spot. What is seen during the adaptation phase is outline contours of the top and bottom stars that flicker between black and white. This gives "contour adaptation" that reduces contrast sensitivity. The result is when one views the four test stars again, after the flickering adapters, one will probably be able to see only two. So adaptation has made two of the test stars invisible. Thus adapting to just the outline of a star makes the whole area of the test star invisible. This suggests that brightness information may be stored in edges and normally fills inward from them.

[insert [Video IX.108-3](#)]

One can selectively adapt different contours within a stimulus. [Video IX.108-4](#) shows two identical stars that are divided into light and dark gray quadrants. Adapt separately to each star by gazing at each fixation spot on different trials. Adapting to the cross deletes the test star's internal structure so that it appears uniform gray. Adapting to the external star contour deletes the test star's external structure so that it looks like four disembodied quadrants.

[insert [Video IX.108-4](#)]

Contour adaptation suggests that a uniform light-colored shape is like a lake of brightness with a dam around its edge. Thus brightness information is stored in contours and normally fills-in from them. Adapting to a contour perceptually deletes it and breaches the dam, allowing the background brightness to fill-in like water, making the shape indistinguishable from the background. Filling always seems to work inward, from large surrounds into small enclosed objects, never outward (the same is true for simultaneous contrast). The reasons for this have not yet been studied.

[Video IX.108-5](#) shows that edges are more important than surfaces. There are two round adapting shapes. On the left is a flickering outline circle, and on the right is a flickering blurred disk, which contains virtually all of the information of a disk except for the outline. In other words, the left and right adapting circles specialize in high versus low spatial frequencies. Adaptation to the flickering outline circle makes its whole low-contrast grey test disk disappear perceptually, while adaptation to the blurred flickering disk does not. Thus the outline circle is a much more efficient adaptor than the blurred disk. The fact that adapting out the edges makes the whole disk disappear confirms that brightness is coded at the edges and fills into the center from there.

[insert [Video IX.108-5](#)]

[insert [Video IX.108-6](#)]

[Video IX.108-6](#) shows two identical light-grey test annuli, alternating over time with two flickering adapting outline circles that are of slightly different sizes. The adapting circle on the left is congruent with the outer edge of the test annulus and the circle on the right with the inner edge. Following adaptation, the two test annuli look very different. The annuli on the left and right look like a small dark disk and a larger light disk, respectively. This is because the adapting circles selectively erase the inner and outer edges of the test annulus, allowing the neighboring greys to fill-in. Contour adaptation is a useful technique for temporarily erasing contours to explore the effects of filling-in.

Aftereffects From Jogging

Running is not a clockwork reflex but an adaptive skill. Runners constantly adjust their running to the local terrain, shortening their stride uphill, picking their way over rough ground, and so on. These adaptive processes are multimodal and can manifest themselves as both kinesthetic and visual negative aftereffects (see reviews by Herman, Grillner, Stein, and Stuart, 1976, and Patla, 1991). A useful test activity to demonstrate kinesthetic aftereffects is jogging in place (running on the spot). Adaptive changes in gait, namely negative aftereffects, occur after running on an exercise treadmill, a conveyor belt device that carries the runner backward at the same speed as he or she runs forward (Anstis, 1995). A runner adapted to the treadmill by running on it for 60 s at a speed of 8 km/h, with eyes closed (to rule out visual components such as optic flow) and holding on to the handrail (to avoid being flung off backward). When he dismounted from the treadmill

and walked or ran forward on the ground, he had a subjective illusion of being apparently borne forward, as if on invisible wheels. More objectively, when asked to dismount from the treadmill and jog in place with eyes closed, a runner actually jogged forward through about 150 cm in 15 s without being aware of it. Running backward or sideways produced an aftereffect of an inadvertent backward or sideways drift. Running on a turntable that rotated clockwise about a vertical axis that ran through the middle of the runner's body required the runner to keep turning counterclockwise in order to keep facing north, and this led afterward to an inadvertent counterclockwise drift. The aftereffects dissipated gradually over time; if the runner stepped off the treadmill after 60 s and then jogged in place, either immediately or else after standing still for 15, 30, 60, or 120 s, with eyes closed throughout, the inadvertent forward motion was greatest for zero delay and decreased as the delay was progressively increased to 120 s. Thus the stored aftereffect gradually dissipated over the course of a minute or two.

A hopping technique helps to show the neural site of these aftereffects. The runner hopped on his preferred leg on the treadmill for 30 s at a speed of 5 km/hr. This slow speed was used because hopping is very fatiguing. The runner then dismounted and hopped in place on solid ground with eyes closed, using either the same (adapted) leg or the other (unadapted) leg on different trials. An aftereffect was found when the same leg was used (showing bipedal gait was not necessary) but *not* when the other leg was used. This failure of the aftereffect to transfer across legs suggests a peripheral rather than a central neural site. Thus the adaptation could not be visual or vestibular but must occur in those parts of the nervous system that control each leg separately. This aftereffect from jogging was purely kinesthetic with no visual component, since it was found when the

observer's eyes were kept closed throughout, and it was also found for three congenitally blind observers, who bravely ran on the treadmill and upon dismounting showed the same inadvertent forward drift as normal observers. Durgin and Pelah (1999) confirmed that the running-in-place aftereffect may result from a recalibration of visuomotor control systems that takes place even in the absence of visual input. However, running is a multimodal activity, and visual components may also adapt during running (Durgin et al., 2005). Simon Levay, a neurophysiologist and long-distance cyclist, has observed a pedaling-contingent visual aftereffect (personal communication). When he mounted a *stationary* exercise bike and started pedaling, he noticed that the visual world momentarily seemed to move forward, in the direction of his intended movement.

Visual feedback can also interfere with kinesthetic aftereffects: Durgin and Pelah (1999) reported that aftereffects were not limited to treadmill running but could also be strongly generated by running behind a golf cart when the eyes were closed but not when the eyes were open. Walking or running uphill can measurably affect judgments of slope. Walking up a slope of 8° gave an aftereffect that made a horizontal test path feel downhill and made an uphill test slope of 5° feel horizontal. What is the neural site of the kinesthetic aftereffects? Since the two legs adapted independently in hopping trials, we can rule out central components such as vestibular adaptation—the aftereffects occurred not necessarily within the leg itself but at least within the neural pathways that control each leg separately. Since running around the block was found to produce no significant aftereffects, the adaptation must specifically counteract the backward motion of the treadmill. We conclude that running on the treadmill adapts those neural pathways that compare the muscular effort of swinging each leg forward (or backward) with the

resulting postural position of each leg (Houk, Keifer, & Barto, 1993). The backward motion of the treadmill produces an artificial mismatch between motor output and normal postural feedback, for which the adaptation compensates or nulls out by adjusting internal gain parameters to bring output and feedback back into line. But once the runner steps on to solid ground, these newly adjusted parameters become inappropriate and manifest themselves as an aftereffect, which dissipates as the parameters automatically update to match the solid ground. Visual feedback also plays an important if not yet fully understood role. So these aftereffects, both kinesthetic and visual, reveal the continuous neural recalibration of the gait control system.

Adaptation to Apparent Motion

A spot alternating between two positions can produce AM or stroboscopic motion. [Video IX.108-7](#) shows that following prolonged inspection, the AM degenerates into flicker.

Blue fixation spots are provided.

[insert [Video IX.108-7](#)]

This adaptation effect depends on spacing and timing; the probability of seeing motion declines linearly with log spatial separation (over a range from 0.1° to 1°) and with log alternation rate (over a range from 2 to 4.5 Hz). So motion adapts out sooner in [Video IX.108-7](#) for spots that are further apart (left-hand column) and alternate faster (top row). Adaptation to real motion strongly suppresses AM (not shown), which suggests that AM must be stimulating the same neural pathways as real motion.

[insert [Video IX.108-8](#)]

[Video IX.108-8](#) shows that embedding the adapting spots in configurations of two vertically moving spot paths, a maneuver that alters the pattern of perceived adapting

motion without altering the local retinal stimulation, minimizes the adaptation and has little effect on the horizontal path of the test motion. So the adapting mechanism must be responding to the path of seen motion and may be occurring in cortical area MT. This adaptation can be used to measure the strength of AM and shows that AM is strongest for small separations, low alternation rates, and high luminance contrast (Anstis, Giaschi, & Cogan, 1985).

Adapting to Flicker Changes Apparent Spatial Frequency

The contrast required to detect a flickering grating results from an interaction between its spatial and temporal frequencies. Robson (1966) showed that at low temporal frequencies, spatial contrast sensitivity is bandpass, while at high temporal frequencies it is low pass. There is some evidence, though of a conflicting kind, that could attribute this performance to magnocellular pathways that are selectively sensitive to high temporal and low spatial frequencies (Goodbourn et al., 2012). Kaneko, Giaschi & Anstis (2015) reasoned that if such visual channels exist, then adapting to a patch of spatially uniform flicker would reduce the sensitivity of these channels, which would in turn affect their ability to code low spatial frequencies and therefore shift upward the apparent spatial frequency of a static coarse grating. And this is what we found. See [Video IX.108-9](#), in which the upper half flickers at ~8 Hz. The two static test gratings are identical, but the upper one will look finer following adaptation.

Carrasco (1990) did an opposite experiment. She adapted her observers to a sinusoidal grating and tested them on a blurred flickering patch. She found that adapting to a low-spatial frequency grating *reduces* sensitivity to low temporal frequencies, while

adapting to a high spatial frequency grating *increases* sensitivity to high temporal frequencies.

[insert [Video IX.108-9](#)]

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Figure [IX.108-1](#).

(a) Adaptation to a spatially uniform patch that repetitively brightens along a sawtooth luminance waveform shows an aftereffect, in which (b) a steady test patch of light appears to grow gradually dimmer. Conversely, adapting to a patch that (c) repetitively dims, yields an aftereffect in which (d) a test patch appears to grow gradually brighter.

Figure [IX.108-2](#).

Gratings with sawtooth luminance profiles. If this picture is moved sharply to the left, the upper grating appears briefly dimmer and the lower grating appears briefly brighter.

[Video IX.108-1.](#)

Ramp aftereffect. The upper adapting panel brightens repetitively while the lower adapting panel dims repetitively, both driven by sawtooth waveforms. When the panel luminances are briefly held constant, the upper panel appears subjectively to dim while the lower panel appears to brighten.

[Video IX.108-2.](#)

Two identical test stimuli show Einstein on top of Marilyn Monroe in low contrast. Following adaptation to a flickering Einstein on the left and Monroe on the right, the (identical) test stimuli look like Monroe on the left and Einstein on the right.

[Video IX.108-3.](#)

Contour adaptation. Adapting to the thin flickering outline contour of a star makes the entire low-contrast test star disappear. It makes no difference whether the test stars are lighter or darker than the surround. Not shown: A higher-contrast test star, say of Michelson contrast C , is perceptually reduced to a subjective contrast of $C/2$.

[Video IX.108-4.](#)

Contour adaptation. The test stimuli are two four-pointed stars, each divided into light and dark grey quadrants. Adapt first to the thin outline that defines the left-hand star's outer edge. Result: The grey test star looks like four disembodied quadrants. Next, adapt to the cross that defines the inner structure of the right-hand star. Result: This test star looks like a uniform grey.

[Video IX.108-5.](#)

Contour adaptation. Adapting to the thin circular contours on the left is much more effective than adapting to the flickering blurred surface on the right. Following adaptation, the left test disk disappears while the right test disk remains visible.

[Video IX.108-6](#).

Contour adaptation. Test stimuli are two identical light grey annuli. The small adapting circle on the right erases the inner edge of the test annulus, which fills in to look like a uniform light grey disk. The large adapting circle on the left erases the outer edge of the test annulus, which merges with the surround so that the round area enclosed by the annulus looks like a small, dark grey disk.

[Video IX.108-7](#).

Adaptation to apparent motion. During strict fixation, prolonged apparent motion of a spot that jumps back and forth between two positions degenerates into a percept of two spots flickering in place. Somehow, adaptation causes loss of temporal phase information. Jumps with rapid alternations over large distances provide weak motion signals show the quickest adaptation and degenerate soonest.

[Video IX.108-8](#).

Adaptation to apparent motion. The test spot jumps horizontally between two positions to the left and right of the fixation dot. The two adapting spots jump vertically. Although they land on the same two positions as the test spot, the vertical motions fail to adapt out the horizontal test motion. Thus the adapted motion signals are somewhat divorced from position.

[Video IX.108-9](#).

Flicker adaptation. Following adaptation to the upper flickering panel, the upper test grating looks slightly finer than the lower one. Conclusion: Spatial frequencies are coded by a balance between transient/magno channels that respond to low-spatial, high-temporal frequencies and sustained/parvo channels that respond to high-spatial, low-temporal frequencies. The flicker is thought to adapt out the transient channels, reducing their low spatial frequency signal.