Visual Adaptation

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Abstract

Sensory systems continuously mold themselves to the widely varying con-
texts in which they must operate. Studies of these adaptations have played a
long and central role in vision science, partly because the specific adaptations
remain a powerful tool for dissecting vision by exposing the mechanisms that
are adapting. That is, "if it adapts, it's there." Many insights about vision have
come from this use of adaptation, as a method. A second important trend has
been the realization that the processes of adaptation are themselves essen-
tial to how vision works and thus likely operate at all levels. That is, "if it's
there, it adapts." This observation has focused interest on the mechanisms of
adaptation as the target rather than the probe. Together, these approaches
have led to an emerging view of adaptation as a fundamental and ubiquitous
coding strategy impacting all aspects of how we see.

INTRODUCTION

The visual system adapts to change in many ways, over timescales ranging from milliseconds to millennia, and each adjustment may recruit a diverse array of mechanisms or subserve multiple functions. This diversity makes it difficult to disentangle different forms of plasticity, such as adaptation versus learning (e.g., McGovern et al. 2012, Harris et al. 2012). Visual adaptation is typically defined operationally, as a brief and temporary change in sensitivity or perception when exposed to a new stimulus, as well as the lingering aftereffects when the stimulus is removed (Webster 2011) (see **Supplemental Video 1**; follow the **Supplemental Materials link** in the online version of this article or at **http://www.annualreviews.org**). A hallmark of these changes is that they are selective, reducing sensitivity for stimuli similar to the adaptor but not for sufficiently different patterns. Characterization of these selective changes reveals the coding strategies in the visual system and, equally importantly, how these codes are calibrated. A central insight from adaptation is that these codes appear to operate in functionally similar ways across diverse stimulus domains (**Figure 1**), pointing to a common repeating principle that is itself not selective and instead reaches the status of a universal law (Helson 1964). This review emphasizes the pervasiveness of adaptation in perception and neural coding, how adaptation-related adjustments operate within normal viewing, and what these adjustments suggest about visual representations and visual experience.

THE SCOPE OF VISUAL AFTEREFFECTS

If adaptation is an intrinsic feature of neural processing, then we should expect to see signs of it throughout the visual stream, reflecting at each stage a plasticity for the kinds of information the neural circuits are designed to represent. That is, the types and patterns of visual aftereffects should be nearly as rich and complex as the gamut of our perceptions. This does not seem far from the truth. Aftereffects were originally described for seemingly low-level features of form, color, and motion. However, as these effects have been probed with more diverse stimuli, it has become increasingly evident that each feature engages and adapts multiple processes and levels of the visual system. Adaptation to color includes a variety of distinct adjustments, including sensitivity changes in the cones, "second-site" calibrations in postreceptoral pathways, and adjustments not only to the mean chromaticity but also to the variance or contrast of the stimulus (Webster 1996). These contrast adjustments are more selective for some axes of color space than for others, but they can be tuned to any arbitrary direction, and this finding led to the discovery of both cardinal and higher-order color mechanisms (Krauskopf et al. 1986). Adaptation to color can also be contingent on the form or motion of the pattern, as in the McCollough effect (in which different color aftereffects are generated for different orientations of the adapting pattern) (McCollough Howard & Webster 2011). Some of these adaptations contribute to color constancy (Foster 2011), whereas others may reflect postconstancy stages, after surface color has been disambiguated from the illuminant (Goddard et al. 2010b).

Spatial adaptations such as tilt aftereffects can be induced with both real and subjective contours, and asymmetries between the effects suggest adaptation at different cortical sites (Paradiso et al. 1989). The aftereffects also depend on whether the same edges appear to belong to the same or different objects (von der Heydt et al. 2005), and they show varying dependence on whether the edges occupy the same position in space or on the retina (e.g., Knapen et al. 2010). Distinct shape aftereffects have also been found by briefly flashing adaptation and test stimuli (Suzuki & Cavanagh 1998). These effects are more susceptible to attention and less susceptible to low-level features compared with conventional tilt aftereffects, a finding that is again consistent with
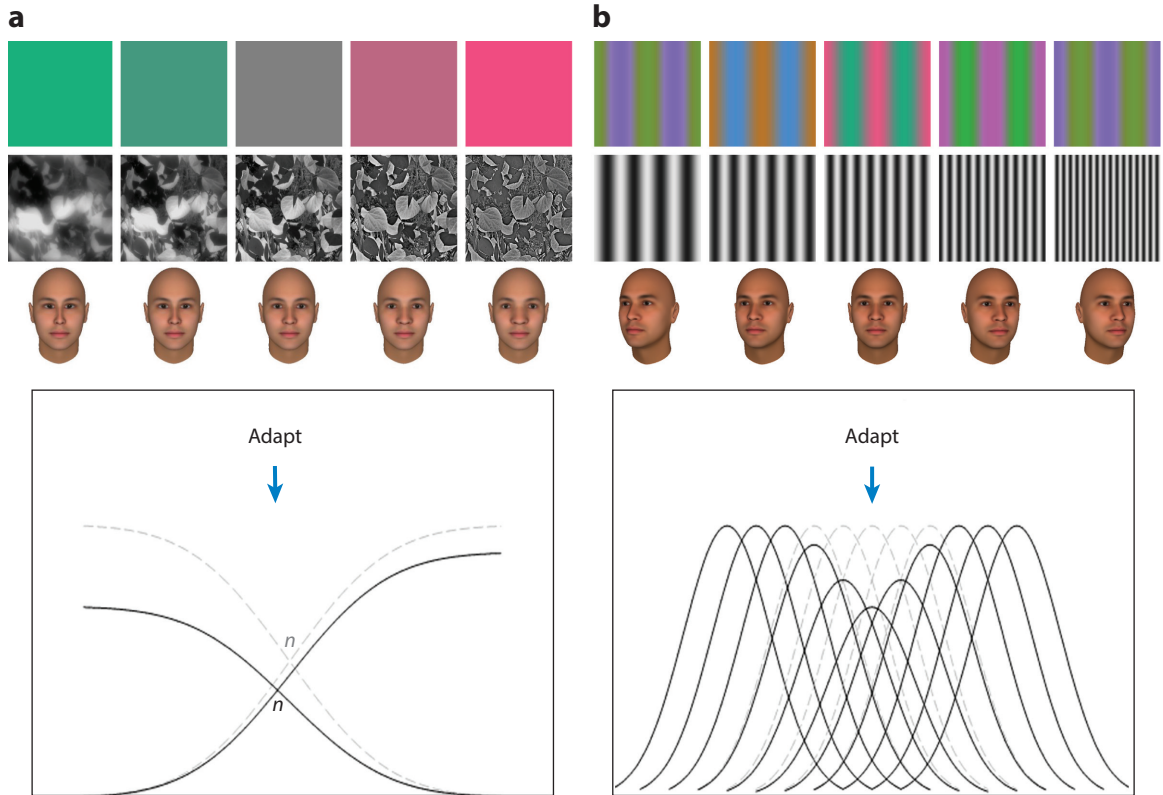
Figure 1

Examples of similar perceptual aftereffects across different stimulus domains. (*a*) Adaptation to a mean color, blur, or face produces roughly global shifts in the appearance of stimuli relative to a norm (e.g., gray, focused, undistorted), resulting in a more neutral appearance of the adapting stimulus, with no aftereffect when adapting to the norm (*n*). This type of adaptation is associated with a norm-based coding pattern and can arise if the underlying mechanisms are broadly tuned to the stimulus dimension or if the stimulus itself is broad rather than punctate (e.g., representing a bias in the stimulus spectrum). (*b*) Adaptation to stimulus domains including color contrast, spatial frequency, or viewpoint instead biases the appearance of other stimuli away from the adapting level, with no change in the perceived level (e.g., size) of the adapted stimulus. This type of adaptation produces similar aftereffects after adapting to any stimulus level across the dimension and implicates a coding pattern involving multiple more narrowly tuned channels.

response changes at higher visual levels. High- and low-level shape aftereffects are also affected in different ways by perceptual grouping (He et al. 2012). Similarly, different motion aftereffects occur for static versus dynamic test stimuli, for patterns defined by first-order (luminance) versus second-order (e.g., contrast) motion, or for global motion patterns such as expansion or rotation (Mather et al. 2008). They can also be induced by adapting to static images that imply motion (Winawer et al. 2008), and both motion and tilt aftereffects can be generated by mental imagery (Mohr et al. 2011, Winawer et al. 2010). These aftereffects again point to adaptation at multiple levels, tied to processing different aspects and representations of movement.

Adaptation is also increasingly being used to probe high-level percepts based on relatively abstract and complex stimulus attributes. For example, observers adapt not only to surface color but also to material properties, such as glossy versus matte (Motoyoshi et al. 2007); to the perceived affordances of scenes, such as how open or navigable the scenes seem to be (Greene & Oliva 2010); to the specific gaits implied by biological motion (Troje et al. 2006, Jordan et al. 2006); and to

the causal structure (Rolfs et al. 2013) and synchrony (Roseboom et al. 2015) of events. Strong aftereffects are also induced in the perceived three-dimensional orientation or viewpoint of objects (Fang & He 2005) or bodies (Lawson et al. 2009) and in the direction of gaze (Jenkins et al. 2006). Adaptation to faces is among the most widely studied classes of high-level aftereffects (Webster & MacLeod 2011). The perceived characteristics of a face can be strongly biased by the types of faces seen previously. These adaptations occur for most of the dimensions along which we classify faces, including identity, gender, expression, or ethnicity (Leopold et al. 2001, Webster et al. 2004). As with the different examples of form and motion aftereffects, many of these adaptations are assumed to reflect higher levels of visual coding, partly because they exhibit properties that cannot be accounted for by adaptation to low-level features, an issue we return to below. Regardless of their neural locus, however, such aftereffects reveal the pervasiveness of adaptation in affecting how we perceive nearly all aspects of the world.

Can we adapt to anything? Despite the rich varieties of visual aftereffects, there are also limits to how the visual system can adapt. One obvious limit is set by the selectivity of the adaptation. If different patterns produce the same net activity within the sites controlling the adaptation, then they will not induce different states of adaptation, even if the stimuli are distinguishable. In other cases, the visual system may not directly encode information in a way that can be adapted. For example, McCollough effects cannot be induced for any arbitrary pairing of color and form, even when the contingencies are readily apparent (McCollough-Howard & Webster 2011). These limits are important because they suggest that the response changes that occur with adaptation do in fact depend on, and thus can help reveal, the nature of the neural representations, implying that adaptation is probably manifest not only in every way we see, but also in ways strongly constrained by how we see.

NEURAL MECHANISMS

Paralleling the spread of perceptual aftereffects, physiological studies have revealed that adaptation is more extensive than previously expected. Originally, the retina was thought to adapt only to the average light level or color. An array of sophisticated mechanisms combine to control these adjustments: switching between different classes of photoreceptors, gain changes in the receptors, and adaptation to the pooled receptor signals within retinal circuits (Rieke & Rudd 2009). However, the retinas of many species also adapt to stimulus contrast (Demb 2008). This adaptation includes both a rapid contrast gain control and slower adjustments over many seconds. In the primate retina and lateral geniculate nucleus (LGN), this slow component is restricted to the magnocellular pathway (Solomon et al. 2004). A common principle underlying these different forms of adaptation might be gain changes driven by the mean level of the adapting stimulus (Kastner & Baccus 2014). For stimulus contrast, this mechanism could be implemented by altering the input (e.g., rectifying the contrast) so that variations around the mean are converted into a signal that varies in its mean level. Instead of simply filtering the image, the retina may also be built to detect complex features of the stimulus (Gollisch & Meister 2010), and consistent with this, ganglion cells can also adapt to surprising properties such as differential motion or orientation. A potential site of these pattern-selective adjustments may be the synaptic inputs from bipolar cells (Gollisch & Meister 2010).

Pattern-selective and contrast adaptation have been studied extensively in cortical cells (Kohn 2007, Solomon & Kohn 2014). Adaptation affects both the response gain of the cell and its tuning (Ohzawa et al. 1982, Movshon & Lennie 1979), and its effects depend on both intrinsic activity (Sanchez-Vives et al. 2000) and synaptic changes (Abbott et al. 1997). These selective aftereffects emphasize that for understanding the consequences of adaptation, the cell itself cannot be treated

as an isolated functional unit. An important development of this idea is to consider how adaptation alters the network of interactions within the cortex (Solomon & Kohn 2014). The response of cells depends on both the direct input the cells receive and on a divisive scaling drawn from a broad pool of cells that provides a suppressive surround beyond the classical receptive field and that functions to normalize the neural responses (Carandini & Heeger 2011). Adaptation that primarily targets this pool (e.g., adaptation to features to which the receptive field of the cell is not sensitive) can reduce the normalization signal and thus lead to disinhibition and enhanced responses. The interplay of these two components can predict many of the complex characteristics of adaptation measured in individual cells in the retina and cortex (Solomon & Kohn 2014).

Neural adaptation has also been probed at higher cortical levels along both the dorsal and ventral streams. For example, several studies have examined the consequences of motion-selective adaptation in the middle temporal cortex (MT), as well as those of adaptation to objects in the inferior temporal cortex (IT) (Kohn 2007, Solomon & Kohn 2014). These studies have revealed potentially strong parallels between perceptual aftereffects and the mechanism by which adaptation alters neural responses. For example, a recent study found that the effects of adaptation on the responses of face-selective cells in the human medial temporal lobe corresponded closely with the perceptual biases that adaptation induced in the observer (Quian Quiroga et al. 2014).

A further powerful approach for exploring the neural correlates of perceptual adaptation has been the technique of fMR-adaptation (fMR-A) (Grill-Spector & Malach 2001). The repeated presentation of a stimulus results in a decline in neural responses as measured by functional magnetic resonance imaging (fMRI). If a change in the stimulus leads to a release from this suppression, then this result implies that the underlying neural mechanisms are selective for the stimulus change and thus that the stimuli are encoded by distinct neural populations. These adaptation effects have now been widely applied to examine the nature of visual representations (Malach 2012, Weigelt et al. 2008), and they have been especially important in overcoming the spatial sampling limits of traditional fMRI. How the response changes indexed by fMR-A are related to changes in the actual neural activity remains uncertain (Krekelberg et al. 2006, Grill-Spector et al. 2006). Moreover, whether these changes are specifically a signature of perceptual adaptation is also unresolved, as they have also been interpreted as a correlate of priming or expectation (e.g., Larsson & Smith 2012). The logic of this approach closely parallels the rationale behind perceptual adaptation, however, and the neural tuning properties it has revealed at progressive stages of cortical processing are in many ways in line with the visual representations inferred from behavioral studies.

PROPAGATION OF ADAPTATION THROUGH THE VISUAL STREAM

Because adaptation affects neural processing at multiple levels, the signals available at any given level will depend on how responses are adapted at other levels. Thus, later stages inherit sensitivity changes arising at earlier levels. For example, the contrasts available to retinal and cortical mechanisms—and how these mechanisms adapt to them—depend on how the visual system is adjusted to the average light and color. The visual stream flows in many directions, and it includes reciprocal connections and feedback throughout the hierarchy. Thus, the potential also exists for earlier stages to inherit response changes arising at higher levels. Consequently, the effects of a sensitivity change at one site can be manifest and manipulated at many sites.

Consider the fate of color afterimages, which begin with the first steps of seeing but then percolate through the system to reach our awareness. After viewing a red patch, a gray patch appears greenish. The sensitivity changes that generate this aftereffect originate in the cone receptors. However, the afterimage lasts several seconds, a time period that is too long to depend on the cones and that instead parallels the sluggish after-discharge that occurs in ganglion cells (Zaidi

et al. 2012). On a uniform field, the color of the afterimage appears labile and diluted. Yet, when an outline is added, the hue becomes strikingly vivid and stable (van Lier et al. 2009). This spatial context triggers cortical filling-in processes that spread the perceived color between the delineated image regions, even to retinal locations that were not originally adapted. The strength of the afterimage can also be modulated by attention (Suzuki & Grabowecky 2003) or interocular suppression (Tsuchiya & Koch 2005) during adaptation, and the context affects its perceived size (Sperandio et al. 2012).

Successive stages of adaptation can account for several aspects of how adaptation alters neural responses at different levels. As noted, these response changes can include both changes in gain and changes in tuning. Gain changes can arise from adaptation at both the level of the cell and in the inputs it inherits, whereas biases in selectivity can arise from changes in the distribution of inputs (both types of changes are also affected by the network of normalizing interactions within each stage) (Solomon & Kohn 2014). For example, contrast adaptation alters sensitivity in the LGN but alters receptive field position in primary visual cortex (V1) because of the bias in the geniculate inputs to the receptive fields of V1 neurons (Dhruv & Carandini 2014). Contrast adaptation in the LGN may in turn be partly inherited from the retina (Solomon et al. 2004). Motion-sensitive cells in MT show changes in motion tuning and localized adaptation in different regions of the receptive field, consistent with both inheriting inputs adapted in V1 and adaptation arising directly in MT (Kohn 2007). In contrast, MT and V1 appear to adapt in similar ways when probed with similar stimuli (Patterson et al. 2014). Such results suggest that sensitivity changes are both generated and passed on to subsequent levels at each stage.

These serial effects have important implications for designing and interpreting perceptual experiments. For example, how can we know whether aftereffects for the abstract attributes of a face reflect adaptation within mechanisms that directly represent those attributes, rather than the low-level features of the stimulus? The appearance of a face can be biased by adaptation to nonface stimulus properties such as local curvature (Xu et al. 2008) or orientation gradients (Dickinson et al. 2010). Again, such effects are not unexpected, because the response changes they directly generate are likely to be carried forward in the processing stream to alter the subsequent codes from which they are assembled. However, several strategies have been devised to circumvent these feedforward effects. One is to create what are called "adaptation metamers": stimuli that should induce the same response changes at a given stage of the visual system. This technique is routinely used to study pattern aftereffects, for example by moving the stimulus during adaptation so that the aftereffect is not simply a result of the pattern of local light adaptation in the retina. The time-averaged light level can also be controlled by counterphasing the pattern contrast. However, this manipulation has recently been shown to generate powerful, contour-specific aftereffects (Anstis 2013). In a striking counterexample to the border-enhancement of color afterimages, adapting these contours out reduces the spatial context for filling-in and can render the grayscales (but not the color) of an actual image invisible.

A further strategy for isolating different levels of adaptation is to take advantage of known differences in neural representations at different stages. For example, interocular transfer was important in establishing a cortical locus of pattern aftereffects. Many of these effects show partial transfer that is consistent with adaptation in both monocular and binocular mechanisms (Blake et al. 1981). Eye specificity is progressively lost at higher levels of the visual hierarchy, and some aftereffects exhibit complete transfer, implicating later sites (Raymond 1993, Nishida et al. 1994). Higher visual levels are also characterized by greater invariance. We can recognize a face regardless of size, position or viewpoint, or global distortions such as stretching the image, and adaptation to faces partially transfers across both these lower-order image changes and higher-order attributes such as how faces are categorized (Webster & MacLeod 2011). These results suggest that high-level

aftereffects do depend at least in part on adaptation at the levels at which the attributes become explicitly encoded.

A fundamental issue for understanding the consequences of inheritance in adaptation and perception is whether the visual system is aware of its current state of adaptation (Series et al. 2009). In some cases, the signals generated by adaptation can be actively suppressed as if they are recognized as illusory. For example, the same contour processes that exaggerate color afterimages can reduce or hide them when the spatial context is misaligned, and these processes may explain why one normally must look closely to see the afterimage signals our eyes are constantly generating (Powell et al. 2012). For most aftereffects, however, the perceptual consequences appear equivalent to attributing the adaptation-induced biases to changes in the stimulus rather than in the observer. That is, subsequent levels process the inputs without accounting for the states of adaptation that generated them, giving rise to the "coding catastrophe" that underlies the perceptual biases in visual aftereffects (Schwartz et al. 2007).

TIMESCALES

Just as the sites and types of visual aftereffects have expanded, so too have their timescales. These dynamics are critically important for understanding the kinds of information the visual system is tracking and to which it is calibrating, yet, to a large extent, they remain poorly understood. Several factors influence the rates at which adaptation should adjust. One is the timescales over which visual coding must operate. Light levels drift not only from day to night but vary dramatically even within individual scenes, which can contain a 1,000-fold range of luminance and contrast. The ability to see within areas in both shadow and sun requires rapid and local adjustments each time we change fixation (Rieke & Rudd 2009). If adaptation is too rapid, however, then scenes would quickly fade, and information about the broader context would be lost. For example, adapting to the average illumination in the scene is important for lightness and color constancy. For spatially local mechanisms, this average requires pooling information over time across multiple surfaces and fixations, and thus it requires a longer memory.

A second factor is that adaptation should adjust sensitivity quickly when the world actually changes but respond slowly enough to maintain sensitivity when the changes are noise. Light adaptation is faster at higher light levels for which less pooling is needed to estimate the signal. The rate of adaptation in retinal ganglion cells also adjusts depending on the time required to estimate a change in the mean luminance or contrast; faster recalibrations occur in response to better evidence for a change (Wark et al. 2009).

Finally, both the world and the observer change over many different timescales, and the adaptation dynamics should be matched to appropriately track these changes (Kording et al. 2007). Fleeting changes in the world or observer should be compensated by more rapid but transient response changes than gradual but persistent ones. These multiplexed timescales have been most clearly revealed in analyses of visuomotor adaptation (Shadmehr et al. 2010, Wolpert et al. 2011). For example, the timescales of muscle fatigue differ markedly from those of muscle damage or development. An optimal observer should estimate the source of the error to set the timescale of the adaptation, and these estimates depend on the temporal pattern of the errors. Models of this kind predict several properties of the dynamics of visuomotor and saccadic adaptation, and similar strategies are likely involved in calibrating many aspects of visual coding.

Traditional studies of adaptation have focused on brief intervals ranging from seconds to minutes. Over this range, the strength and duration of aftereffects increase as a power law of the adapting duration (Greenlee et al. 1991). These dynamics appear to be similar for stimuli as different as gratings and faces, again suggesting common mechanisms (Leopold et al. 2005).

Rather than passively decaying, the duration of visual aftereffects depends in part on re-exposure to stimuli. Interposing an interval between the adaptation and test stimuli can result in storage of the adaptation such that stronger aftereffects persist at longer durations. In some cases, this type of storage can result in effectively permanent changes if an appropriate de-adapting stimulus is not experienced (Vul et al. 2008).

Recent work has extended adaptation to both shorter and longer timescales. Motion aftereffects can be elicited by exposures as brief as 25 ms, paralleling the rapid adjustments seen in single cells (Glasser et al. 2011). Results of this kind are important in showing that pattern adaptation is not merely a consequence of overstimulation; rather it is a process reactivated by each glance. Several recent studies have also explored adaptation to longer durations spanning hours or days. These studies have revealed longer-term aftereffects that may emerge only after sustained periods of adaptation. For example, long-term exposure to a bias in the average spectrum an observer is exposed to induces aftereffects that are much more persistent than those associated with short-term chromatic adaptation (Neitz et al. 2002, Belmore & Shevell 2011, Eisner & Enoch 1982), and color vision in cataract patients requires months to readapt after surgery (Delahunt et al. 2004). Similarly, although brief adaptation to blur or contrast is sufficient to induce a strong perceptual aftereffect, hours of exposure are required to see increases in acuity and sensitivity (Mon-Williams et al. 1998, Kwon et al. 2009, Zhang et al. 2009).

An important question is whether these longer-term changes are merely stronger adaptation or whether they tap into mechanisms tuned to different timescales. This has been tested by pitting long- and short-term adaptation against each other. The aftereffect of adapting to a prolonged stimulus (e.g., a clockwise tilt) can be extinguised by brief adaptation to its opposite (e.g., a counterclockwise tilt). This brief de-adaptation is itself short-lived, however; as it decays, the aftereffect of adaptation to the longer-term stimulus reemerges. This so-called spontaneous recovery indicates that at least two distinct mechanisms exist and are adapting at different rates (Shadmehr et al. 2010). These effects have now been demonstrated for a wide range of stimuli (Mesik et al. 2013, Vul et al. 2008). Distinct components of adaptation have also been inferred from the nonmonotonic effects of continuous adaptation over days (Haak et al. 2014) or even minutes (Chopin & Mamassian 2012), although adaptation in the latter case has also been accounted for by a single adjustment (Maus et al. 2013).

A further important issue is whether mechanisms tuned to different timescales induce the same response changes but track different rates or whether they adjust visual coding in qualitatively different ways. Kwon et al. (2009) adapted observers for four hours by asking them to wear goggles that reduced contrast. After this period, contrast sensitivity improved, and the pattern of adaptation shifted from resembling the contrast gain typical of short timescales to resembling a change in response gain. That shift could reflect a shift in strategy of contrast coding from one driven by the current mean contrast at short timescales to the overall range of contrast at longer durations. It is also possible that these differences reflect different time courses and consequences of adaptation within cortical cells and their suppressive surrounds. Over much briefer durations, the pattern of adaptation in single cells varies in qualitatively different ways as adaptation rebalances the relative responsivities of the cells and their gain control (Patterson et al. 2013).

ADAPTING TO THE ENVIRONMENT

Traditionally, the effects of adaptation have been studied by exposing observers to highly artificial stimuli and viewing contexts. J.J. Gibson (1986), who first documented the tilt aftereffect, in later years dismissed such aftereffects as irrelevant to natural vision, arguing that they arose only when observers were engaged in unnatural tasks. Yet, this dismissal missed the point that the processes

of adaptation are always engaged. Many now consider it evident that adaptation is an essential part of natural viewing and that adaptation itself can be understood only within the context of the visual worlds within which we normally see. This realization has been driven by the growing understanding of the importance of natural image statistics for all aspects of perception (Simoncelli & Olshausen 2001, Geisler 2008).

The characteristics of the environment constrain the mechanisms and consequences of adaptation in many ways. First, how the world varies shapes how vision is designed to cope with those variations. One of the greatest natural challenges is that of seeing over the enormous range of light levels one experiences during the course of a day. The magnitude and dynamics of these changes have shaped many design features of the retina (Rieke & Rudd 2009). Large changes in mean luminance and contrast occur even within different parts of the same scene. Analyses show that these image statistics vary independently and predict light and contrast adjustments that operate independently (Mante et al. 2005). Natural image statistics also point to the most efficient representations of images and how they vary, and, again, predict how neural responses should vary to encode them (Wainwright 1999, Wark et al. 2007).

How vision is adapted to the natural world also determines the natural operating states of the visual system. It is common to use a model of a standard observer to characterize spatial or spectral sensitivity. This observer is relevant only to the stimulus context in which it is embedded, however, and is often based on states of adaptation that we rarely encounter outside the lab. For example, natural images have a characteristic $1/f$ amplitude spectrum. Adaptation to this structure selectively reduces sensitivity at lower frequencies, resulting in a contrast sensitivity function that is effectively more band pass (Webster & Miyahara 1997, Bex et al. 2009), even for chromatic contrast (which is normally taken to be low pass) (Webster et al. 2006). The relative sensitivity to luminance and chromatic contrast also reflects adaptation to the world. Because the cones have overlapping spectral sensitivities, the cone contrasts for color are much smaller than for luminance. Yet postreceptoral gains are scaled to offset this imbalance (MacLeod 2003), such that the relative salience of luminance and color is matched to the range of luminance and chromatic variations in natural scenes (McDermott & Webster 2012). The distribution of color signals in the environment also predicts the relative scaling for different color dimensions. Many natural scenes have a blue–yellow bias, and adaptation to the natural color gamut leaves us less sensitive to this blue–yellow variation (Webster & Mollon 1997, Goddard et al. 2010a).

Substantial visual differences also exist within and between different environments, and these differences are important for understanding how much the states of adaptation and, thus, perception might vary between individuals or within the same person over time. For example, colors cycle with the seasons and vary widely across ecosystems, so color perception itself should vary with time or location (Webster & Mollon 1997, Welbourne et al. 2015) (**Figure 2**). Similarly, social environments vary systematically in facial attributes such as ethnicity or age. We are better at discriminating small differences in color around the mean color to which we are adapted, and a plausible account of the "other race effect" is that we are similarly tuned through adaptation to the average faces to which we are exposed (Webster & MacLeod 2011).

Although the natural world shaped the evolutionary design of our visual system, in many ways, the natural environment no longer corresponds to the carpentered visual worlds many people now occupy. This raises intriguing questions about how processes of adaptation that were built to operate within natural scenes might function within the new and sometimes arbitrary visual environments to which we are increasingly exposed. Cultural practices vary widely and thus expose individuals to very different visual diets. Thus, the so-called cultural relativity of some perceptual judgments could actually reflect universal processes of adaptation operating within different contexts (Webster et al. 2005). Within a culture, styles and aesthetics evolve continuously,
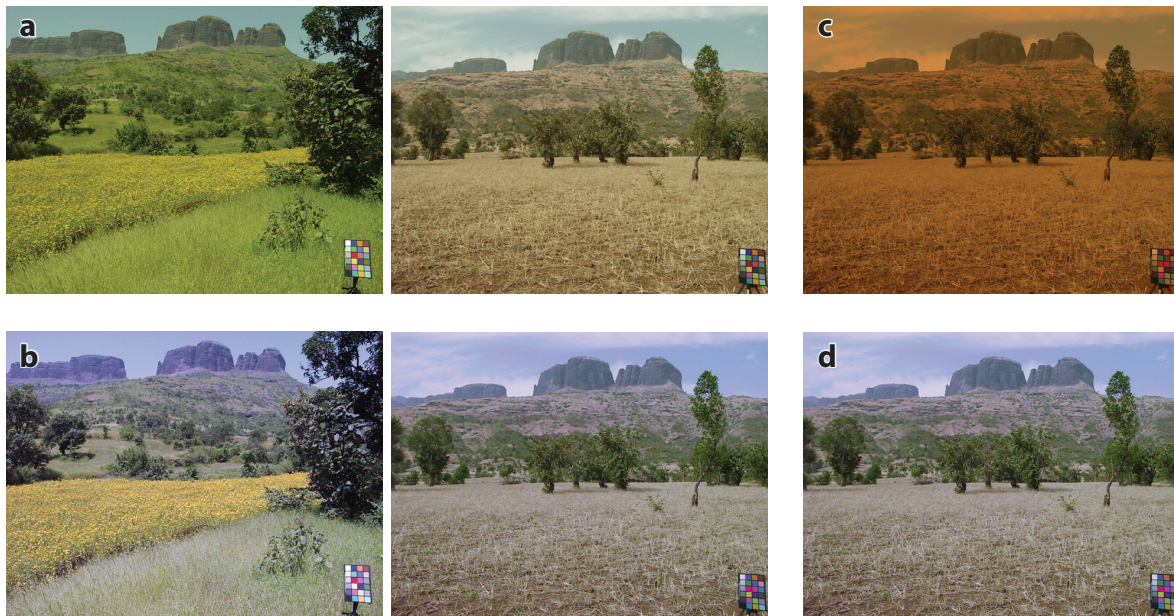
Figure 2

Simulations of color adaptation to a change in environment or change in observer. (*a*) Roughly the same scene in two seasons. (*b*) Adaptation to the color statistics in each season biases color appearance by toning down the dominant hues and increasing the salience of novel hues (e.g., increasing the perceived saturation of greens in the arid scene). Thus the same observer codes color differently in the two environments. (*c*) The middle, arid scene viewed through the lens of an older observer. (*d*) Adaptation to the spectral changes introduced by the lens removes most of the color bias. Thus, the two different observers code color similarly when adapted to the same environment.

and similarly, the dynamics of how these become incorporated into a society may depend in part on how members visually adapt to these changes (Carbon 2011). Individuals also increasingly occupy specialized and unique visual niches, and technology has created or made possible exploration of a diverse array of new visual worlds. For example, radiologists spend hours at a time inspecting medical images that have their own characteristic statistics, and adaptation to these statistics may influence how these images are perceived or interpreted (Kompaniez et al. 2013). Full adaptation to new environments may require long periods of time. To the extent that the effects of adaptation can be predicted, however, algorithms could be developed to adapt the images rather than the observer so that they are optimized for the calibration the observer walks in with (Webster 2014).

ADAPTATION AND COMPENSATION

If the states of adaptation vary as the same observer moves among different worlds, what of different observers immersed in the same world? In this case, the same processes should adjust each observer to the common prevailing environment in spite of possible inherent differences in their visual systems. This side of the calibration—adjusting to variations in the observer rather than in the environment—highlights the role of adaptation in compensating or error-correcting vision for the vagaries of the visual system of each individual. In many instances this may also be the more important side of calibration, as the visual system may often vary more than the properties of the world. For example, most of the blur in the retinal image arises from the optics of the eye rather than from the scene itself.

There are many examples of these compensatory adjustments. Sensorimotor control is constantly recalibrated to maintain the coordination of visual and proprioceptive signals and to adjust to physiological changes such as injury or fatigue (Shadmehr et al. 2010, Wolpert et al. 2011). In color vision, individuals vary widely in their spectral sensitivities because of differences in screening pigment density or in the sensitivity and relative numbers of cones. Yet, for the most part, these differences fail to predict individual differences in color percepts. Thus, a stimulus that appears white shows little change with age despite the steady yellowing of the lens (Werner & Schefrin 1993) (**Figure 2**), and what looks yellow is unaffected by the enormous interobserver differences in L:M (long-wavelength:medium-wavelength) cone ratios (Brainard et al. 2000). Similarly, many aspects of spatial vision are adjusted to discount variations in spatial sensitivity. Adaptation to a blurred or sharpened image recalibrates what stimulus appears to be in focus (Webster et al. 2002). Individuals vary widely in the magnitude and pattern of optical aberrations and thus in the amount and type of blur to which they are routinely exposed. Yet, they tend to agree on the physical stimulus that appears to be in focus. This occurs because each observer is adapted to discount their own native blur from their perception (Artal et al. 2004, Sawides et al. 2011, Radhakrishnan et al. 2015).

These adjustments are also critical for calibrating for sensitivity differences within the observer. Sensitivity varies markedly across the visual field, yet the appearance of the world degrades much more gracefully. Color percepts between the fovea and near periphery remain very similar despite large changes in factors such as macular pigment screening (Webster et al. 2010), and perceived focus is adjusted for the declines in spatial resolution with increasing eccentricity (Galvin et al. 1997). Processes such as adaptation also correct for sensitivity differences at a common locus. For example, the band-pass tuning of spatial contrast sensitivity at threshold gives way at visible contrast levels to a scaling that is instead independent of spatial frequency (Georgeson & Sullivan 1975).

How far can these processes go to compensate perception for the idiosyncrasies of the observer, or the environment? We can partly answer this for ourselves by asking how gray or focused the world appears through our own eyes, or when we compare these judgments across the visual field. Formal tests suggest that adaptation provides nearly complete compensation for some properties but is limited for others. One constraint is that, as noted, adaptation is less able to overcome sensitivity limits than appearance, because thresholds depend on less malleable constraints such as sampling and noise. For appearances, adaptation can factor out many, but not all, sensitivity variations. Perceived focus is largely corrected for the optical aberrations of the eye, but, for higher-order aberrations, this focus is more effectively adjusted to the magnitude than to the specific blur pattern (Sawides et al. 2012). Compensation of color appearance for the lens and macular pigment is better than predicted by adapting to the average color alone—suggesting that it goes beyond independent gain changes in the cones—but residual errors remain (Bompas et al. 2013, O'Neil & Webster 2014). An interesting example of the limits of adaptation for color perception is that of anomalous trichromats. Their longer-wave cones have very similar spectral sensitivities, so the differences they convey are much weaker. Yet, many seem to experience stronger color percepts than would be predicted by their reduced sensitivity (Neitz et al. 2002, Regan & Mollon 1997, Boehm et al. 2014). Again this phenomenon could occur if postreceptoral mechanisms amplify their gain to match the weakened inputs. However, color salience remains weaker and hue loci are altered relative to normal trichromats, suggesting that this compensation is incomplete.

The extent to which adaptation normalizes visual coding also depends on how much the processes of adaptation themselves vary. Little is known about individual differences in adaptation, although observers consistently differ in the magnitude and pattern of aftereffects (Elliott et al. 2012, Vera-Diaz et al. 2010), and some of these differences may reflect polymorphisms in the genes coding neurotrophins (Barton et al. 2014). Adaptation also varies over the life span. The kinetics of light adaptation varies with development and aging (Brown & Lindsey 2009, Owsley 2011). Less is

known about cortical adaptation. Pattern-selective adaptation can be seen with evoked potentials as early as three weeks of age (Suter et al. 1994), but whether this adaptation shows developmental changes has not been well documented, and distinguishing changes in plasticity from changes in other factors such as stimulus selectivity is difficult. In aging, declines in neural tuning linked to decreased inhibition have been associated with senescent changes in some cortical aftereffects (Wilson et al. 2011). Yet, the strength of adaptation to blur or chromatic contrast remains similar or even stronger in older observers (Elliott et al. 2007, 2012). This finding suggests that many aspects of adaptation remain stable across the life span, and this stability might be essential to stabilizing visual perception for the many optical and neural changes that do occur.

ADAPTATION, CHANNELS, AND NORMS

As noted, the popularity of adaptation studies continues to be driven primarily by the use of adaptation as a tool for probing vision. New examples are constantly reported in which a mechanism is inferred by demonstrating selective adaptation to the stimulus it is presumed to encode. Such measurements have played a central role in defining the number and tuning of visual channels encoding different stimulus dimensions (Graham 1989). Because of its role in defining these channels, adaptation is repeatedly described as "the psychologist's electrode."

But, at what level of the system is this electrode recording? This issue is a murky one because the relationship between psychophysically defined channels and single cells is poorly understood. If an adaptation effect is selective, then clearly the stimulus differences must be represented in the underlying neural code. Yet, the selectivity of an aftereffect places little constraint on how or whether the neural code is tuned for those differences. In some cases, there is striking agreement between the tuning functions derived from adaptation and individual neurons. How color appearance is adapted to uniform fields corresponds closely to the spectral sensitivities of the cones, and the bandwidths of aftereffects for orientation, spatial frequency, or color contrast approximate the average spatial tuning of V1 cells. In such cases, adaptation may hold promise for tapping deep into the neural architecture. However, it remains challenging to reconcile visual aftereffects with the enormous heterogeneity of cell responses found at many levels of the system (Tailby et al. 2008, Webster & Mollon 1994). Moreover, many studies have pointed out that this problem is inherently ill posed, in that the same aftereffects could arise from very different channel structures (Hegdé 2009, Mur et al. 2010, Ross et al. 2014). Drawing inferences about the underlying representation is further complicated by the fact that it is sometimes difficult to disentangle properties of channels from properties of the stimulus. For example, whether the channels appear to be broadly or narrowly tuned depends partly on whether the stimulus itself is best conceived as broad or punctate (Elliott et al. 2011). This difference may seem evident for a single wavelength versus a light spectrum, but it is less certain for many of the complex attributes now probed with adaptation. For example, it remains unclear whether blur or a face is represented as an explicit feature or as the envelope of many.

Problems of this kind suggest that we cannot use adaptation to unambiguously decipher the architecture of the visual code. Yet, in other ways, the channel structure it reveals is profoundly important and simple, because it directly measures the tuning characteristics of the mechanisms mediating how the visual system responds to and recalibrates for changes in the stimulus context. That is, the channels that adaptation measures are by definition the functional ways in which vision can selectively adapt. What do these indicate about visual representations? An important distinction has been made between two general classes of visual codes in which a stimulus dimension is represented either by its absolute or relative value (Valentine et al. 2015). In the former case, known as exemplar-based or multichannel coding, different levels of the stimulus dimension are

represented by different channels, each of which is tuned to and labeled for a narrow range. Thus the stimulus is encoded by the identities of the most responsive channels. In the latter case, termed a norm-based code, the stimulus is encoded by the relative activity of broadly tuned mechanisms, and thus the stimulus level is conveyed by the responsiveness of the channels. The differences between these models therefore amount to whether the channels themselves are narrowly or broadly tuned (as well as how the outputs are labeled), but the two models make very different predictions about the pattern of visual aftereffects (Webster 2011, Webster & MacLeod 2011).

In multichannel codes, adaptation has more localized effects by reducing sensitivity in the channels tuned to the adapting stimulus, thus pushing away the appearance of nearby stimuli. In norm-based codes, the response changes are more global, and they tend to recenter the appearance of all stimulus levels so that the adapting stimulus appears to be more neutral (**Figure 1**). Both types of aftereffects are prevalent, and, for many stimuli, both patterns may occur (Storrs & Arnold 2012). For example, the tilt aftereffect includes both a repulsion and renormalization of perceived orientation that intriguingly unfold at different rates (Muller et al. 2009). In both models, an important consequence of adaptation is normalization of the responses across mechanisms. In multichannel models, normalization amounts to equating sensitivity across channels so that their average responses are similar within the current context. This is seen in the recalibration of cone sensitivities so that the response to the mean color is equivalent to gray, as well as in how populations of cortical cells adjust to compensate for a bias in the distribution of orientations (Benucci et al. 2013). In norm-based codes, normalization reflects the rebalancing of sensitivities to neutralize the intensity of the response. This could occur within a pair of mechanisms that signal opposing levels of the stimulus, in which the norm is represented implicitly by equal responses within the mechanisms, or alternatively, it could reflect an actual opponent mechanism in which the norm is represented by an explicit null point (e.g., the null in a color-opponent cell). These norms are important because they reflect the response states that the visual system is constantly readjusting to achieve. As a consequence, visual coding is always relative because the response is always contingent on the current norm.

The norms established by adaptation have further significance because they represent unique and special states in the neural code—states in which the neural responses are unbiased. Do these states have perceptual correlates? The subjective experience of many stimulus dimensions varies relative to a point that itself appears to be psychologically neutral. Thus, colors become more saturated as they differ more from gray, and the identity of a face becomes better articulated the more it differs from the prototype, which itself appears indistinct. The stimuli that define these perceptual norms likely correspond to the stimuli to which the visual system is currently adapted, and evidence for this hypothesis is that the stimulus that appears subjectively neutral to an observer is the same as the stimulus that does not produce a visual aftereffect (Webster & Leonard 2008, Sawides et al. 2011, Radhakrishnan et al. 2015). This finding argues against the possibility that perceptual norms are arbitrarily shaped by criterion (e.g., norms correspond simply to how we label what we are used to seeing) and that they are instead direct manifestations of how sensitivity is calibrated. The problem of whether special percepts reflect special neural states is unresolved, and it continues to plague fields such as color vision, in which a neural basis for pure hue sensations has yet to be found. In the case of pure gray, or of norms more generally, however, there may be a simple and direct link between our subjective experience of what appears to be neutral and what is objectively neutral in the underlying neural code, both of which are set by the state of adaptation. Moreover, this adaptation is again inherently asymmetric—the mind is fit to the world. Thus, the norms in our percepts and neural coding are both set by the norms in the environment, and all of these components are linked through the fact that we are adapted to the environment. We still have no way of revealing the subjective mental experience of another individual, but at least

some aspects of the problem of other minds can arguably be traced via adaptation to objective properties of the physical world. Whether two individuals experience the same stimulus as being phenomenologically neutral—as a "gray" percept—may depend on the extent to which they are adapted to the same or different worlds (Webster et al. 2005).

THE FUNCTIONS OF ADAPTATION

The presence of adaptation throughout visual processing provides both insights into and challenges for understanding the potential roles it plays. On the one hand, its prevalence highlights the degree to which adaptation is fundamental to neural computations at all stages, pointing to a common purpose. On the other hand, the nature and demands of visual coding change at different stages, suggesting that the reason the code adapts may also change across levels or tasks.

Many disparate roles have been posited for adaptation. One set of roles emphasizes efficient coding and information optimization (Wainwright 1999, Stocker & Simoncelli 2006, Clifford et al. 2007, Wark et al. 2007, Rieke & Rudd 2009). Neurons have limited dynamic range but must potentially encode an enormous range of stimulus levels. By adjusting this range to the ambient level, adaptation prevents response saturation and balances sensitivity across mechanisms, maximizing the information they can carry. Efficiency might also be enhanced by reallocating resources (Gepshtein et al. 2013) or by removing redundancies between mechanisms (Barlow 1990a). These information theoretic approaches have been highly successful in predicting the properties of both visual coding and adaptation at early levels of the visual system, where initially both the range of stimulus levels and the need for compact codes are especially important. They also account well for the marked effects of adaptation on visual sensitivity—without light adaptation, we would literally be blind most of the time. The same principles likely are necessary to understand how higher-level representations are calibrated, especially for first establishing the sensitivities. That is, adaptation may be essential for initial adjustment of the operating curve of each mechanism for the range of stimuli it is likely to receive. It is less clear, however, why higher-level visual codes require continuous readjustments. Few visual attributes vary over the range that light levels do, and demonstrating impressive improvements in sensitivity or discrimination following pattern adaptation has proven difficult.

A second set of functional accounts focuses on the changes that adaptation produces in appearance rather than performance. The fact that very strong visual aftereffects occur even when there is no sign of a change in sensitivity is an important and striking one. What role might these effects play? One account is that they reflect error correction (Andrews 1967). If the world looks tilted or too yellow, then a possible cause is that the neural code is biased, and this bias can be corrected by adaptation. This function is implied by how adaptation compensates for properties of the observer or enables constancy when the stimulus (e.g., the lighting) changes (Foster 2011). In such cases, adaptation acts to filter out uninteresting variations in the context (e.g., the sensitivity of the observer), in order to provide stable percepts of the informative properties.

A final putative set of roles involves building predictions about the world (Srinivasan et al. 1982, Chopin & Mamassian 2012). Adaptation tends to null out the stimuli to which we are exposed. These stimuli represent our current expectations about the world, and an efficient representation of the world is to encode these expectations implicitly, as a null response. As noted, these null responses also correspond to norms. Predictive coding saves metabolic resources and allows the system to use its full capacity to signal only the errors or unexpected stimuli, and it may help us make these errors more conspicuous (Barlow 1990b, Gardner et al. 2005, Ranganath & Rainer 2003, Boehnke et al. 2011). In support of this idea, adaptation has been shown to enhance salience and visual search for novel stimuli (McDermott et al. 2010, Wissig et al. 2013), suggesting that,

in building the current prediction, adaptation plays a central role in determining what captures our attention. Much of what we notice about the world may be a visual aftereffect, driven by the world to which we are currently adapted (Barlow 1990b, Webster et al. 2005).

In some cases, these functions may be incompatible. For example, different adjustments may be required to optimize detection versus identification (Hillis & Brainard 2007) or to promote constancy versus efficiency (Webster & Mollon 1995) or salience (McDermott et al. 2010). But, a definitive test between different functional accounts remains lacking, and trying to choose between functional accounts is probably a futile exercise. All of them make sense, and all of them seem necessary. Moreover, for most, if not all, accounts, there is good evidence that these goals are in fact achieved. Instead, a more fruitful approach for understanding the universality of adaptation may be to note that most if not all of these benefits can be realized by a single shared adjustment—normalization of neural responses for the mean stimulus level (Webster 2014). Similar to other canonical computations (Carandini & Heeger 2011), this adjustment probably represents a universal principle that is woven into the fabric of the response of any neuron and thus affects everything we see.

SUMMARY POINTS

1. Adaptation operates throughout most, if not all, levels of sensory coding and thus impacts all aspects of perception. Aftereffects that were traditionally studied with simple stimulus features are increasingly being found and characterized for more abstract and naturalistic stimuli.

2. The visual system may adapt in very similar ways to very different stimulus attributes, pointing to common representations that are calibrated in similar ways.

3. These adaptation effects may also occur over a wide range of timescales and thus track different rates and patterns of change in the stimulus.

4. Adaptation remains an important and widely used psychophysical and physiological paradigm for characterizing visual coding and the properties of visual channels.

5. The natural visual environment provides potent stimuli for driving adaptation. These natural states of adaptation play an important role in setting the natural operating characteristics of the visual system.

6. Adaptation also adjusts to properties of the observer such as the sensitivity limits imposed by optical or neural factors. Adaptation tends to compensate visual coding for these limits, contributing to perceptual constancy.

7. Adaptation probably serves a variety of related functions, ranging from increasing coding efficiency to supporting perceptual constancy and highlighting novel information. Many of these functional benefits may result from the same underlying response changes.

FUTURE ISSUES

1. How does adaptation differ functionally and mechanistically from other operationalized types of plasticity and learning, and how do these different phenomena interact?

2. How are behavioral measures of adaptation related to adaptation effects observed in neuroimaging or single cells?

3. Are the properties and consequences of adaptation best understood at the level of neurons or networks?

4. To what extent do different adaptation phenomena reflect common computational strategies and mechanisms?

5. What are the limits of what we can adapt to, and what sets these limits?

6. How are observers adapted to the actual visual worlds they live in? How different are real visual environments in terms of the adaptation states they induce and the consequences of these states for an observer's visual experience?

7. To what extent can we predict and thus simulate or compensate for how an observer might adapt to a new environment or a change in their sensitivity (e.g., with aging or disease)?

8. What can we realistically conclude about neural representations from specific patterns of visual adaptation?

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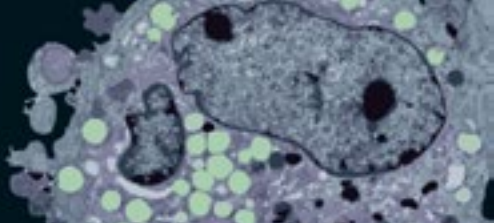
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