Adaptation & Visual Experience

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(*Above*) How sharp or blurred an image appears is a relative judgment that is influenced by adaptation over time to the blur we have been exposed to and by comparisons over space to the surrounding context.

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Visual perception is continuously regulated by processes of adaptation that adjust visual coding to match the scenes we are exposed to. These adjustments are important both for optimizing sensitivity and for maintaining perceptual constancy. Adaptation strongly influences subjective judgments about image quality and perceptual norms, such as whether an image appears focused, and may strongly influence what we notice when we look around us.

As many despairing photographers will attest, whether or not a picture is in focus is a conspicuous property of images. The human visual system is highly sensitive to blur, and is constantly adjusting the power of the eye's lens to optimize the focus of the image falling on the retina. Some degree of blur is inherent in the retinal image, because of a host of factors including the limited depth of focus and the aberrations characteristic of normal eyes. With refractive errors, obviously, this blur becomes more pronounced. What is less obvious is that this intrinsic blur normally goes unnoticed. That is, even individuals with very poor acuity typically report that the world appears "in focus," and are only reminded of their acuity limit when confronted with a high resolution task like reading that suddenly taxes their abilities. How is it that we can be so sensitive to blur in the world yet seemingly so insensitive to the built-in blur in our eyes? One answer is that the point of perception is to see the object and not the retinal image. If the world before us has a characteristic spatial structure, that structure defines what appears normal, but may be corrupted by the limits of our vision. This matching of visual coding to the world is aided by an active calibration of visual sensitivity. If the world changes—or the eye changes—neural responses are recalibrated through processes of adaptation in order to maintain a stable perception.

Adaptation is a ubiquitous property of sensory systems.[1] Adaptive response changes in vision can occur as early as the receptors, which in the course of the day must operate over an enormous range of

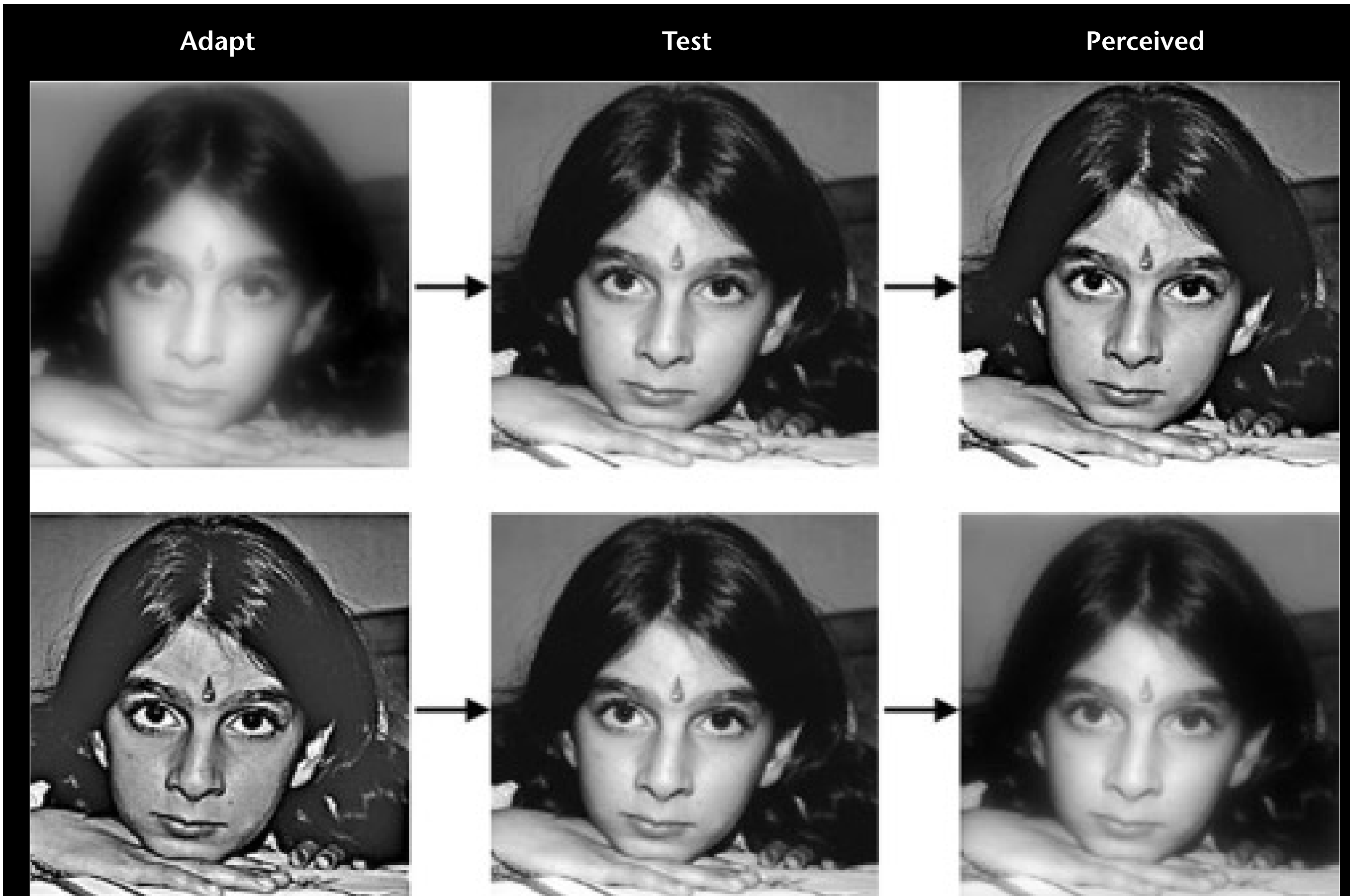

Figure 1. Blur adaptation. Viewing a blurred image (*top left*) causes the correctly focused image (*middle*) to appear too sharp (*top right*). After adaptation, the image that looks best focused is thus one that is moderately blurred. Viewing a sharpened image (*bottom left*) leads to the opposite after-effect.

light levels while preserving sensitivity to the small lightness variations that define most scenes. This is accomplished by matching sensitivity to the average light level (much as a camera must adjust for the overall light level to keep the scene within the limited dynamic range of the film).

Many classic visual illusions show that adaptation also occurs at higher stages of the visual system and adjusts to complex image properties. For instance, if you stare for a moment at water flowing down a fall, the static rocks to the side will appear to ooze upward, and this motion after-effect is thought to reflect sensitivity changes in cortical regions specialized for motion processing.

In addition to sensitivity regulation, such adjustments may play an important role in setting up and maintaining visual coding, mitigating the need for precise genetic specifications. If, for example, you are *always* seeing downward motion, it is more likely to reflect properties of your brain than properties of the world (e.g., because the neurons that signal downward motion are more responsive than neurons tuned to other directions). Adaptation could correct for this error by rebalancing the sensitivity across the motion mechanisms, removing the perceptual bias. In the same way, adaptation can maintain perceptual constancy by recalibrating the visual system whenever the observer changes (e.g., during development or aging). If, on the other hand, it is the world that changes, the same processes will track these changes, thus altering the way in which the same physical stimulus is perceived.

In a recent study we examined how the visual system adapts to changes in blur.[2] Subjects viewed pictures on a monitor that were filtered to reduce or increase the relative amplitude of high spatial frequencies or fine detail, causing the image to appear either too blurred or too sharp. Afterward the subjects adjusted the amplitude spectrum of a test image until it appeared properly focused. Even a few seconds of adaptation were sufficient to induce dramatic changes (Fig. 1). After

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looking at a blurry image, a physically focused image appeared too sharp, thus subjects chose a physically blurred image as the one that appeared focused. Viewing a sharpened adapting image caused the opposite after-effects. Both after-effects are consistent with a renormalization of spatial sensitivity so that the spatial structure we are exposed to defines what a focused image is. It remains, however, to be determined to what extent the adapting images themselves come to look better focused, as this putative renormalization process would predict.

There are good reasons to believe that the site at which blur adaptation alters sensitivity is the visual cortex. Cells there are tuned to different frequency ranges and their sensitivity is scaled to match the amplitude spectra of natural images, which characteristically vary inversely with frequency, or as 1/f (Ref. 3). Optical blur disproportionately reduces contrast at the higher frequencies and thus would disrupt this match by stimulating high frequency cells less. Yet adaptation could restore the balance because the low frequency cells will be desensitized to a greater extent. This is, however, an overly simplistic account, in that the after-effects of blur cannot be predicted from the adapting amplitude spectrum alone, and in that surprisingly, we still have a poor understanding of what aspects of the stimulus the perception of blur corresponds to.

Figure 2 shows that these neural adjustments operate not only across time but also across space. The centers of the three bars are composed of focused square-wave edges. When the surrounding edges are blurred, however, the center edges appear distinctly too sharp, while to a lesser extent the sharpened edges cause the center edges to seem blurred. This is not simply an interaction between local edges, for the same effects can be seen in arrays of pictures, as in Fig. 3. Here the two center eyes are the same and are both physically focused, but the eye that is surrounded by blur appears sharper (especially if you compare the center eyes while fixating between the two arrays).

As in the case of adaptation, there are numerous other examples of these "spatial contrast" effects in visual coding. It is interesting to note that with regard to blur, a stimulus of this sort often arises because of the limited depth of focus of the eye, which means that when we are focused for an object, the more distant background will often be blurred. It is not yet known how these contrast effects might alter the perceived sharpness of objects in real viewing situations of this kind. Another interesting case is that of portrait photography, where a common technique is to reduce the depth of focus to strongly blur the background. It is tempting to think that this trick might serve to perceptually sharpen the subject by introducing a contrast effect from the blurred surround.

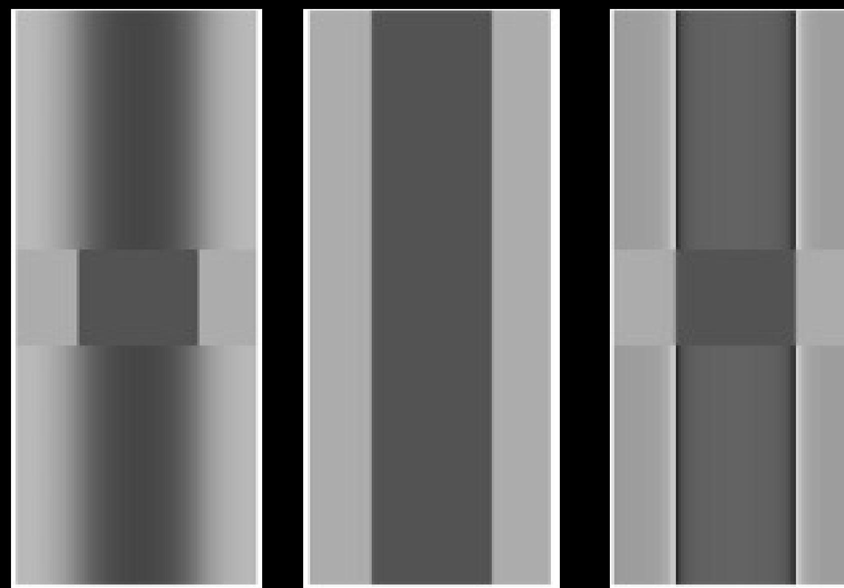

Figure 2. Blur induction. The center sections of all three bars are square-wave edges, yet the center of bar (a) appears sharpened because of the blurred surround, while the center of bar (c) appears blurred by the sharpened surrounds.

Subjects favored the images consistent with their own idiosyncratic aberrations, suggesting that they were adapted to the intrinsic blur in their eyes.

In our experiments the pictures themselves were blurred, but in most cases the primary source of retinal image blur is the optics of the eye. What are the implications for refractive errors of these adaptation effects? One is that adaptation may adjust the visual system to compensate for the aberrations specific to our own eyes. This idea has recently been tested by Artal and colleagues.[4] They used adaptive optics (see the article in this issue by Joe Carroll, p. 36) to measure the higher-order aberrations of an individual's eye. They then used the same system to form an image on the observer's retina that had the same, or a rotated version, of the point-spread function. Subjects favored the images consistent with their own idiosyncratic aberrations, suggesting that they were adapted to the intrinsic blur in their eyes. Such results may partly explain why individuals need time to adjust to a spectacle correction. Understanding the limits and time course of these adjustments may prove important for assessing whether the quality of vision is ultimately improved by removing all aberrations. A second implication of adaptation as far as refractive errors are concerned is that

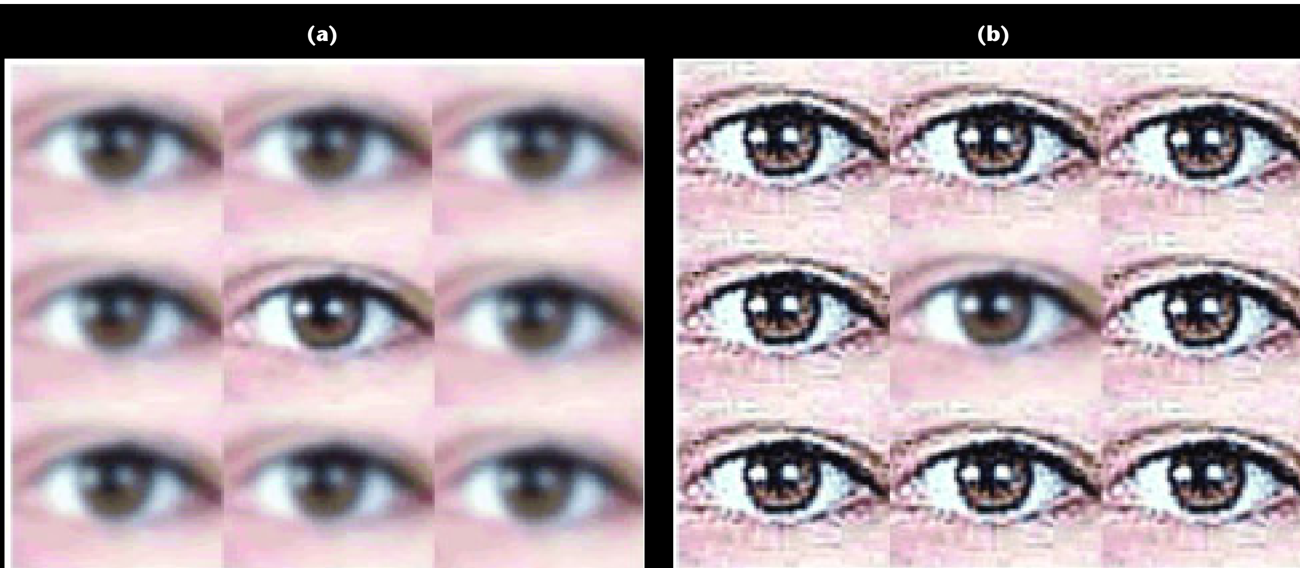

Figure 3. Blur induction. The eyes in the centers of panels (a) and (b) are the same, but the eye surrounded by sharper images appears blurrier. The effect is strongest if one fixates between the two panels.

adaptation might not only make the world look better, but could allow one to see better. Again, adapting to blurry images causes the world to appear sharper. Can visual acuity be improved by this enhanced salience of the fine detail in images? Our own efforts to find these effects in filtered images have so far proven unsuccessful. Yet a number of different groups have shown that if observers are given time to adjust to optically induced defocus, there are significant gains in acuity.[5] Whether these gains in acuity depend on the same processes that are revealed by adaptation to physically blurred images remains to be explored.

As noted, one important function of adaptation is to maintain perception even though the processes of perception are changing. Dramatic optical changes occur with aging. For example, the lens steadily loses its elasticity, which leads to a loss of accommodation. It is unknown how perceptual adaptation might adjust to conditions like presbyopia or myopia, yet notably, recent work has found that adaptation can be selective for different depths, so that the perception of focus might be contingent on perceived distance.[6]

Another profound optical change with aging is the progressive yellowing of the lens, which selectively filters short-wavelength light and thus strongly biases the spectrum of the light reaching the retina. If the mechanisms of color vision did not adjust for this change, what appeared white to us in our youth would become vividly yellow in old age. Yet this does not happen. J. S. Werner and his colleagues have carried out a number of studies characterizing color vision and aging, and have shown instead that color perception remains remarkably stable.[7] Recently they have also explored the changes that occur in color vision following cataract surgery. After a cataract is removed, the world appears very blue, and it can take months for the perception of white to drift back to the pre-surgery settings.[8] Such results suggest that some kinds of visual adaptation may operate over very long time scales.

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The foregoing suggests that two observers might describe the same stimulus as white even though their eyes might filter the spectrum very differently. This is because the adaptation is compensating for the filtering and thus for the differences between them. In the same way, two observers who differed in visual acuity might both perceive the world as focused because they are both adapted to the same world (though clearly one will still be able to resolve finer detail than the other). What does this imply when two observers view different worlds? In this case, even if the two observers are initially the same, adaptation should adjust them to the properties specific to their environments, and their perceptions might then diverge. In many respects, the world does vary in ways that would be expected to vary the states of adaptation. For example, it is likely that color perception would be different depending on whether one lives in a forest or a desert.

We have been examining how perception might be influenced by visual differences in one's "social" environment by asking how the appearance of a face depends on the faces a person has recently been exposed to.[9] These experiments are very similar to the studies of blur perception, but in this case we asked observers to choose the face that looked normal after adapting to a face that was distorted. Viewing faces with the features pinched together causes a normal face to appear too expanded. Moreover, these after-effects are large when observers adapt to the natural "distortions" that define individual faces (Fig. 4). For example, after adapting to female faces, a gender-neutral face (formed by morphing between a male and female image) looks distinctly masculine, and adapting to a sad or angry face can make a neutral countenance appear happy. These adjustments may provide a purely sensory explanation for many aspects of face perception that might otherwise seem a question of attitudes. For example, the anthropologist Malinowski observed that the longer he lived in the Trobriand Islands, the more his judgments of beauty began to agree with the Trobrianders' judgments. While this might sound like a change of heart, it is possible that it was instead simply a change of eye. Studies of attractiveness have found that average faces tend to be rated as more attractive, and Malinowski may simply have been adapting to the average facial characteristics of his new visual environment.

Face recognition is considered one of the most sensitive capacities of visual perception, akin to splitting hairs, because it requires exaggerating the fine distinctions between stimuli that are all physically very similar. It is still debated whether this ability depends on specialized "face-specific" processes in the brain, yet whatever its basis, these very high level perceptual judgments again appear to be strongly regulated by adaptation. Indeed, it may prove difficult to find a perceptual judgment that is not.

The states of adaptation may be particularly important for understanding subjective image quality, and whether these subjective judgments are the same or different from others. Notably, because adaptation is adjusting your perception to match the world, this suggests that some important aspects of visual experience (e.g., what surface looks white, or what face looks average) can be predicted from the properties of the observer's environment.[10] Understanding what it actually "feels like" to see has remained particularly problematic because visual awareness remains a private and subjective phenomenon, and thus we have access only to our own experiences.

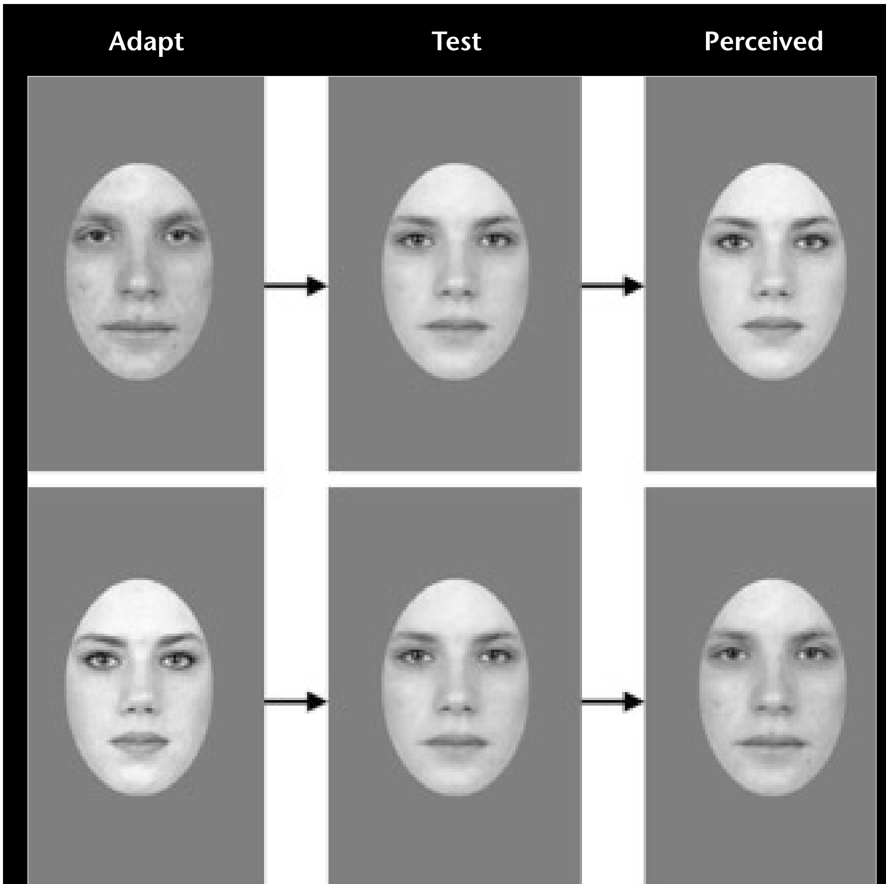

Figure 4. Face adaptation. Viewing a male face (*top left*) causes a gender-neutral face (*top center*) to appear more feminine (*top right*). Viewing the female face (*bottom left*) produces the opposite after-effect.

Yet if these are shaped by adaptation, then to answer whether you and I experience the world in similar ways we may not always have to probe our perceptions, for we can instead ask whether our vision has been molded by the same or different environments.

Adaptation also makes another prediction about visual experience. As we adapt to stimuli we are often unaware of the profound sensitivity changes that are occurring, yet these become strikingly obvious when we see the after-effect, and what we notice is how the stimulus deviates from the images we are currently adapted to. It is as if the visual system is building a predictive code for the environment, discounting properties that fit with expectations while highlighting the errors. This suggests that in everyday viewing, adaptation strongly influences what we notice as we look around us, and that much of what we notice is in fact a visual after-effect.

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