Neural adjustments to image blur

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Blur is an intrinsic feature of retinal images that varies widely across images and observers, yet the world still typically appears 'in focus'. Here we examine the putative role of neural adaptation[1] in the human perception of image focus by measuring how blur judgments depended on the state of adaptation. Exposure to unfocused images has previously been shown to influence acuity[2,3] and contrast sensitivity[2,4], and here we show that adaptation can also profoundly affect the actual perception of image focus.

Whether an image appears blurry or sharp depends on the distribution of contrast across different spatial scales. Smoothing the sharp transitions in an image by low-pass spatial filtering makes it appear blurred, whereas accentuating them by high-pass filtering makes it appear too sharp. Natural images have a characteristic distribution of spatial contrasts, as captured by the $1/f$ amplitude spectra typical of natural scenes (in which amplitude falls in inverse proportion to increasing spatial frequency (f); this spectrum also describes simple intensity steps or edges[5,6]).

Cells in visual cortex are well-matched to this property: their frequency bandwidths increase with preferred frequency, such that the average signal encountered for $1/f$ spectra is roughly constant across cells from coarse to fine scales[6,7]. This way, information at different scales can be represented in mechanisms with the same limited dynamic range[8]. Variations in both the environment (such as reduced visibility) and the observer (such as refractive errors), however, often corrupt this match between the visual cortex and natural visual stimuli. Adaptive adjustments may be important in compensating for these variations so that perceptual constancy for the expected spatial profiles of objects[9] is maintained. Adaptation may also be essential for calibrating and maintaining this match during development.

We tested whether the perception of blur shows adaptive changes. To evaluate the role of neural adjustments (and to minimize the role of optical changes), we measured the perceived focus of images that were physically blurred or sharpened. Adaptation was assessed for a variety of stimuli, from simple edges to grayscale images of natural scenes. For each stimulus, we generated a large array of images that varied from blurred to sharpened. With a staircase procedure, we determined which image of the set appeared the best-focused to the observer. On each trial, observers reported whether the presented image was "too blurred" or "too sharp". Subsequent stimuli were then varied to find the null point at which the two responses occurred with equal probability. Measurements began after a 3-minute adaptation period of viewing a single blurred or sharpened image. Test images were presented for 0.5 s each, interleaved with 6-s periods of readaptation.

Does prior adaptation to blurred or sharpened versions of an image alter the perceived focus of the original image? We found that judgments of focus were strongly biased by adaptation (**Fig. 1c**), and these shifts were pronounced relative to observers' sensitivity to blur (given by the steepness of the functions). The aftereffects were similar for different images and observers (**Fig. 1d**). They were also similar for Gaussian blur and whether or not image contrasts were equated after filtering. In all cases, exposure to a blurred image caused the original image to appear too sharp, so that "in focus" judgments were shifted toward stimuli that were physically blurred. Adaptation to sharpened images induced the opposite aftereffect. These shifts were large and perceptually salient, despite the brief periods used for adaptation (**Fig. 1b**). Indeed, we found vivid aftereffects after only a few seconds of adaptation (see **Supplementary Movie** online).

These aftereffects are consistent with an adjustment that recalibrates the neural response to blur according to the prevailing image blur, such that the adapting image itself appears better focused. We confirmed this by asking observers to rate changes in the perceived focus of blurred (–0.25 slope change) or sharpened (+0.25) versions of the images in **Fig. 1a** after a 2-minute exposure to each image. Blurred images were consistently judged to become less blurred, and the sharpened images became less sharp; that is, the adapting images themselves were judged to be better focused with prolonged viewing. This renormalization of perceived focus is anal-

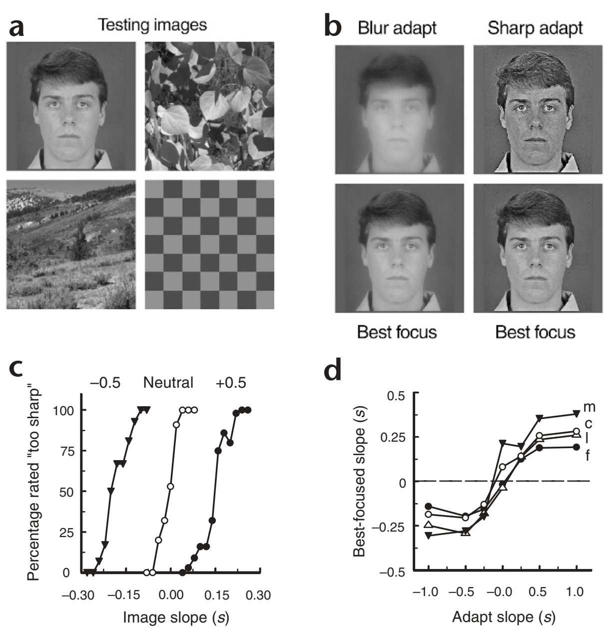

Fig. 1. Blur adaptation. (**a**) Grayscale images used to test the adaptation. For each image, the original amplitude spectrum was multiplied by f^{s}, with slope (s) varied from –1 to +1 in steps of 0.01 to create 101 images that varied from moderately blurred to moderately sharpened. Filtered images were scaled to have the same r.m.s. contrast and mean luminance (~10 cd/m^2) as the original. All images were 256 × 256 pixels presented in a 4° field on a monitor, and were viewed binocularly. Procedures were approved by the Institutional Review Board of the University of Nevada, and informed consent was obtained from all subjects. (**b**) Examples of face images selected as best-focused after adapting to a blurred (left, s = –0.5) or sharpened (right, s = +0.5) version of the image. (**c**) Percentage of "too sharp" responses as a function of the filter exponent, before or after adapting to the blurred (s = –0.5) or sharpened (s = +0.5) face image. (**d**) Slope that appeared "best-focused" as a function of the slope of the adapting image (f, face; l, leaves; m, meadow; c, checkerboard).

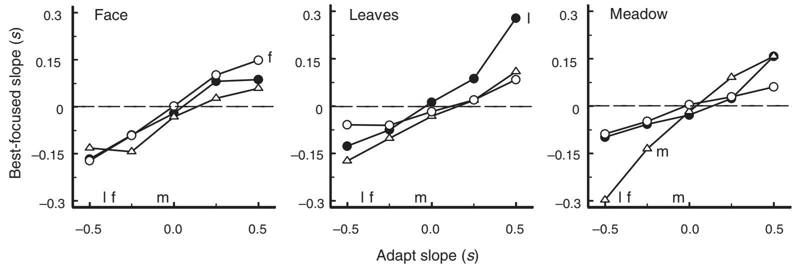

Fig. 2. Blur aftereffects between different test and adapting images. Each panel plots focus settings made for one image (labeled) after adapting to filtered versions of the same or different images for the face (f), meadow (m) or leaves (l). Letters along the adapt axis indicate the unfiltered slopes (relative to f^{-1}) of the images.

ogous to the renormalizations of the white point in chromatic adaptation[10], and suggests that the point of best focus has a special status in the neural representation of blur, which may reflect a 'prior expectation' about the spatial structure of scenes.

To further characterize which aspects of the images the visual system is adjusting to, we examined how adaptation to blur in one image altered the perceived focus of different images. For these runs, the spatial position of the adapt image was randomly jittered (every 250 ms by up to ±0.5 times the image width) to prevent spatially local adaptation. There was significant but incomplete transfer of the adaptation across different natural images (**Fig. 2**), indicating that the adjustments are not tied to the specific content of individual images. This suggests that the visual system need not readjust to blur in each fleeting image, but rather to the recent ensemble of images as different scenes are sampled in the course of natural viewing. These measurements also showed that perceived focus was not affected by adaptation to images that were in focus but had different intrinsic amplitude spectra (**Fig. 2**). For example, while the original images were all physically focused, the face and leaves had steeper spectral slopes than the meadow, presumably because they contain less structure at finer spatial scales[8]. These two images might therefore have been equivalent to blurry adapting images when aftereffects were tested with the meadow, but instead they had least influence on the meadow when they were physically focused during the adaptation stage. This suggests that, as in perceptual judgments of focus[8,11], the adaptation is controlled by the local blur of image features rather than by the global amplitude spectra of the images.

We also discovered a spatial analog of the blur adaptation. Simply embedding a focused image in a blurred or sharpened background caused it to appear sharpened or blurred, respectively (**Fig. 3a** and **b**). These induction effects were similar in both form and magnitude (**Fig. 3c**) to the successive aftereffects of adaptation, but imply adjustments to relative differences in focus across the visual field, and may reflect a spatially-selective manifestation of cortical contrast gain control[12].

Our results point to large and rapid changes in the perception of image focus when people view images with altered spatial statistics. Finer spatial scales are necessarily degraded in the retinal image, yet once above threshold, the perceived contrast of patterns is largely independent of spatial frequency. This supports the idea that visual responses are calibrated to compensate for variations in sensitivity with spatial scale[13,14]. This spatial calibration may be continuously updated by processes of cortical adaptation. The large adjustments seen here are likely to be important in tuning the match between cortical responses and the spatial structure of natural images, providing constancy for image structure despite short- or long-term variations in the observer. These adaptation effects are thus important for understanding both normal vision and how vision changes during development and with refractive errors.

Note: Supplementary information is available on the Nature Neuroscience website.

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Competing interests statement

The authors declare that they have no competing financial interests.

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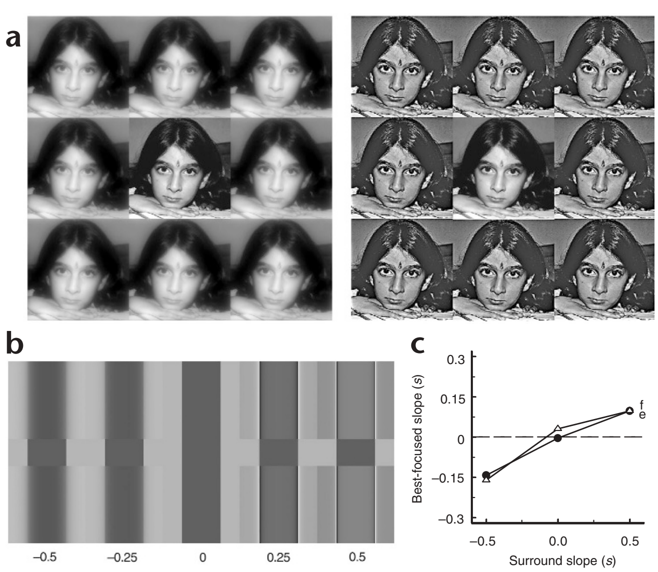

Fig. 3. Simultaneous blur contrast. (**a**) The two center faces are identical and physically focused, but the right image appears blurry in the sharpened surround, while the left image appears sharp in the blurry surround. (**b**) The central bars in each column are equivalent square-wave edges. However, the bars flanked by blurred edges appear sharpened, while the bars abutting sharpened edges appear blurred. (**c**) Changes in perceived focus when the face (f) or edge (e) test image was surrounded by blurred or sharpened images, as in the arrangement shown in (**a**).