1 **TITLE:**

2 Visualizing Visual Adaptation

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18 19 **KEYWORDS**:

- 20 Neuroscience, Vision, Perception, Adaptation, Color, Image processing, Psychophysics, Modeling,
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- 22

23 SHORT ABSTRACT:

This article describes a novel method for simulating and studying adaptation in the visual system.

26 LONG ABSTRACT:

27 Many techniques have been developed to visualize how an image would appear to an individual 28 with a different visual sensitivity: e.g. because of optical or age differences, or a color deficiency 29 or disease. This protocol describes a technique for incorporating sensory adaptation into the 30 simulations. The protocol is illustrated with the example of color vision, but is generally applicable 31 to any form of visual adaptation. The protocol uses a simple model of human color vision based 32 on standard and plausible assumptions about the retinal and cortical mechanisms encoding color 33 and how these adjust their sensitivity to both the average color and range of color in the 34 prevailing stimulus. The gains of the mechanisms are adapted so that their mean response under 35 one context is equated for a different context. The simulations help reveal the theoretical limits 36 of adaptation and generate "adapted images" that are optimally matched to a specific 37 environment or observer. They also provide a common metric for exploring the effects of 38 adaptation within different observers or different environments. Characterizing visual perception 39 and performance with these images provides a novel tool for studying the functions and 40 consequences of long-term adaptation in vision or other sensory systems.

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45 **INTRODUCTION:**

46 What might the world look like to others, or to ourselves as we change? Answers to these 47 questions are fundamentally important for understanding the nature and mechanisms of 48 perception and the consequences of both normal and clinical variations in sensory coding. A wide 49 variety of techniques and approaches have been developed to simulate how images might 50 appear to individuals with different visual sensitivities. For example, these include simulations of the colors that can be discriminated by different types of color deficiencies¹⁻⁴, the spatial and 51 chromatic differences that can be resolved by infants or older observers⁵⁻⁹, how images appear 52 in peripheral vision¹⁰, and the consequences of optical errors or disease¹¹⁻¹⁴. They have also been 53 applied to visualize the discriminations that are possible for other species¹⁵⁻¹⁷. Typically such 54 55 simulations use measurements of the sensitivity losses in different populations to filter an image 56 and thus reduce or remove the structure they have difficulty seeing. For instance, common forms 57 of color blindness reflect a loss of one of the two photoreceptors sensitive to medium or long 58 wavelengths, and images filtered to remove their signals typically appear devoid of "reddish-59 greenish" hues¹. Similarly, infants have poorer acuity, and thus the images processed for their 60 reduced spatial sensitivity appear blurry⁵. These techniques provide invaluable illustrations of 61 what one person can see that another may not. However, they do not - and often are not 62 intended to – portray the actual perceptual experience of the observer, and in some cases may 63 misrepresent the amount and types of information available to the observer.

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65 This article describes a novel technique developed to simulate differences in visual experience which incorporates a fundamental characteristic of visual coding – adaptation^{18,19}. All sensory 66 67 and motor systems continuously adjust to the context they are exposed to. A pungent odor in a 68 room quickly fades, while vision accommodates to how bright or dim the room is. Importantly, 69 these adjustments occur for almost any stimulus attribute, including "high-level" perceptions such as the characteristics of someone's face^{20,21} or their voice^{22,23}, as well as calibrating the 70 71 motor commands made when moving the eyes or reaching for an object^{24,25}. In fact, adaptation 72 is likely an essential property of almost all neural processing. This paper illustrates how to 73 incorporate these adaptation effects into simulations of the appearance of images, by basically 74 "adapting the image" to predict how it would appear to a specific observer under a specific state 75 of adaptation²⁶⁻²⁹. Many factors can alter the sensitivity of an observer, but adaptation can often 76 compensate for important aspects of these changes, so that the sensitivity losses are less 77 conspicuous than would be predicted without assuming that the system adapts. Conversely, 78 because adaptation adjusts sensitivity according to the current stimulus context, these 79 adjustments are also important to incorporate for predicting how much perception might vary 80 when the environment varies.

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The following protocol illustrates the technique by adapting the color content of images. Color vision has the advantage that the initial neural stages of color coding are relatively well understood, as are the patterns of adaptation³⁰. The actual mechanisms and adjustments are complex and varied, but the main consequences of adaptation can be captured using a simple and conventional two-stage model (Figure 1a). In the first stage, color signals are initially encoded by three types of cone photoreceptors that are maximally sensitive to short, medium or long wavelengths (S, M, and L cones). In the second stage, the signals from different cones are 89 combined within post-receptoral cells to form "color-opponent" channels that receive 90 antagonistic inputs from the different cones (and thus convey "color" information), and "non-91 opponent" channels that sum together the cone inputs (thus coding "brightness" information). 92 Adaptation occurs at both stages, and adjusts to two different aspects of the color – the mean (in the cones) and the variance (in post-receptoral channels)^{30,31}. The goal of the simulations is to 93

- 94 apply these adjustments to the model mechanisms and then render the image from their 95 adapted outputs.
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97 The process of adapting images involves six primary components. These are 1) choosing the 98 images and 2) the format for the image spectra; 3) defining the change in color of the 99 environment or 4) in the sensitivity of the observer; 5) using the program to create the adapted 100 images; and 6) using the images to evaluate the consequences of the adaptation. The following 101 considers each of these steps in detail. The basic model and mechanism responses are illustrated in Figure 1, while Figures 2-5 show examples of images rendered with the model.

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104 **PROTOCOL:**

- 105 NOTE: The protocol illustrated uses a program that allows one to select images and then adapt 106 them using options selected by different drop-down menus.
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108 1. Select the image to adapt.

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110 1.1 Click on the image and browse for the filename of the image to work with. Observe the 111 original image in the upper left pane.

112

113 2. Specify the stimulus and the observer.

- 114 2.1 Click the "format" menu to choose how to represent the image and the observer.
- 115 2.2 Click on the "standard observer" option to model a standard or average observer adapting to 116 a specific color distribution.
- 117 NOTE: In this case standard equations are used to convert the RGB values of the image to the cone sensitivities³². 118
- 119 2.3 Click on "individual observer" option to model the spectral sensitivities of a specific observer.
- 120 NOTE: Because these sensitivities are wavelength-dependent, the program converts the RGB
- 121 values of the image into gun spectra by using the standard or measured emission spectra for the 122 display.
- 123 2.4 Click on "natural spectra" option to approximate actual spectra in the world.

124 NOTE: This option converts the RGB values to spectra, for example by using standard basis functions³³ or Gaussian spectra³⁴ to approximate the corresponding spectrum for the image 125 126 color.

127 **3. Select the adaptation condition.**

3.1 Adapt either the same observer to different environments (e.g. to the colors of a forest vs.
urban landscape), or different observers to the same environment (e.g. a normal vs. color
deficient observer).

- NOTE: In the former case, use the menus to select the environments. In the latter, use the menusto define the sensitivity of the observer.
- 3.2 To set the environments, select the "reference" and "test" environments from the dropdownmenus.
- NOTE: These control the two different states of adaptation by loading the mechanism responsesfor different environments.
- 137 3.2.1 Choose the "reference" menu to control the starting environment.
- 138 NOTE: This is the environment the subject is adapted to while viewing the original image.
- 139 NOTE: The choices shown have been precalculated for different environments. These were
- 140 derived from measurements of the color gamuts for different collections of images. For example,
- 141 one application examined how color perception might vary with changes in the seasons, by using
- 142 calibrated images taken from the same location at different times²⁷. Another study, exploring
- 143 how adaptation might affect color percepts across different locations, represented the locations
- 144 by sampling images of different scene categories²⁹.

3.2.2 Select the "user defined" environment to load the values for a custom environment.
Observe a window to browse and select a particular file. To create these files for independent
images, display each image to be included (as in step 1) and then click the "save image responses"
button.

- NOTE: This will display a window where one can create or append to an excel file storing the
 responses to each image. To create a new file enter the filename, or browse for an existing file.
 For existing files the responses to the current image are added and the responses to all images
 automatically averaged. These averages are input for the reference environment when the file
- 153 with the "user defined" option is selected.
- 3.2.3 Select the "test" menu to access a list of environments for the image to be adjusted for.Select the "current image" option to use the mechanism responses for the displayed image.
- NOTE: This option assumes the subjects are adapting to the colors in the image that is currently
 being viewed. Otherwise select one of the precalculated environments or the "user defined"
 option to load the test environment.

159 **4. Select the spectral sensitivity of the observer.**

160 NOTE: For the adaptation effects of different environments, the observer will usually remain 161 constant, and is set to the default "standard observer" with average spectral sensitivity.

- 4.1 There are three menus for setting an individual spectral sensitivity, which control the amountof screening pigment or the spectral sensitivities of the observer.
- 4.1.1 Click on the "lens" menu to select the density of the lens pigment. The different optionsallow you to choose the density characteristic of different ages.
- 4.1.2 Click on the "macular" menu to similarly select the density of the macular pigment. Observethese options in terms of the peak density of the pigment.
- 4.1.3 Click on the "cones" menu to choose between observers with normal trichromacy ordifferent types of anomalous trichromacy.
- NOTE: Based on the choices the program defines the cone spectral sensitivities of the observer
 and a set of 26 post-receptoral channels that linearly combine the cone signals to roughly
 uniformly sample different color and luminance combinations.

173 **5. Adapt the image.**

- 174 5.1 Click the "adapt" button.
- NOTE: This executes the code for calculating the responses of the cones and post-receptoral mechanisms to each pixel in the image. The response is scaled so that the mean response to the adapting color distribution equals the mean responses to the reference distribution, or so that the average response is the same for an individual or reference observer. The scaling is multiplicative to simulate von Kries adaptation³⁵. The new image is then rendered by summing the mechanism responses and converting back to RGB values for display. Details of the algorithm are given in ²⁶⁻²⁹.
- 182 5.2 Observe three new images on the screen.
- NOTE: These are labeled as 1) "unadapted" how the test image should appear to someone fully
 adapted to the reference environment; 2) "cone adaptation" this shows the image adjusted
 only for adaptation in the receptors; and 3) "full adaptation" this shows the image predicted by
 complete adaptation to the change in the environment or the observer.
- 187 5.3 Click the "save images" button to save the three calculated-images. Observe a new window188 on the screen to browse for the folder and select the filename.

189 **6. Evaluate the consequences of the adaptation.**

- 190 NOTE: The original reference and adapted images simulate how the same image should appear 191 under the two states of modeled adaptation, and importantly, differ only because of the 192 adaptation state. The differences in the images thus provide insight into consequences of the 193 adaptation.
- 194 6.1. Visually look at the differences between the images.

- 195 NOTE: Simple inspection of the images can help show how much our color vision might vary when
- 196 we live in different color environments, or how much adaptation might compensate for a 197 sensitivity change in the observer.
- 198 6.2. Quantify these adaptation effects by using analyses or behavioral measurements with the
 199 images to empirically evaluate the consequences of the adaptation²⁹.
- 6.2.1 One application is to measure how color appearance changes. For example, the colors in the two images can be compared to measure how color categories or perceptual salience shift across different environments or observers. For example, analyses of the changes in color with adaptation were used to calculate how much the unique hues (e.g. pure yellow or blue) could theoretically vary because of variations in the observer's color environment²⁹.
- 6.2.2 A second application would be to ask how the adaptation affects visual sensitivity or performance. For example, one study used the adapted images to compare whether visual search for a novel color is faster when observers are first adapted to the colors of the background. The experiment was conducted by superimposing on the images an array of targets and differentlycolored distractors that were adapted along with the images, with the reaction times measured for locating the odd target²⁹.

211 **REPRESENTATIVE RESULTS:**

- 212 Figures 2-4 illustrate the adaptation simulations for changes in the observer or the environment. Figure 2 compares the predicted appearance of Cezanne's Still Life with Apples for a younger and 213 214 older observer who differ only in the density of the lens pigment²⁸. The original image as seen 215 through the younger eye (2a) appears much yellower and dimmer through the more densely 216 pigmented lens (2b). (The corresponding shifts in the mean color and chromatic responses is 217 illustrated in Figure 1c.) However, adaptation to the average spectral change discounts almost all 218 of the color appearance change (2c). The original color response is almost completely recovered 219 by the adaptation in the cones, so that subsequent contrast changes have negligible effect.
- 220
- 221 Figure 3 shows van Gogh's Irises filtered to simulate color appearance in a deuteranomalous 222 observer, whose normal M photopigment is shifted in peak sensitivity to within 6 nm of the L 223 photopigment²⁸. Adaptation in the cones again adjusts for the mean stimulus chromaticity, but 224 the L vs M contrasts from the anomalous pigments are weak (3b), compressing the mechanism 225 responses along this axis (Figure 1d). It has been suggested that van Gogh might have 226 exaggerated the use of color to compensate for a color deficiency, since the colors he portrayed 227 may appear more natural when filtered for a deficiency. However, contrast adaptation to the 228 reduced contrasts predicts that the image should again "appear" very similar to the normal and 229 anomalous trichromat (3c), even if the latter has much weaker intrinsic sensitivity to the L vs M 230 dimension. Many anomalous trichromats in fact report reddish-greenish contrasts as more conspicuous than would be predicted by their photopigment sensitivities^{36,37}. 231
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- 233 Figure 4 shows the simulations for an environmental change, by simulating how the hazy image
- 234 portrayed by Monet's Sunrise (Marine) might appear to an observer fully adapted to the haze (or
- to an artist fully adapted to his painting). Before adaptation the image appears murky and largely

monochrome (4a), and correspondingly the mechanism responses to the image contrast are
weak (Figure 1e). However, adaptation to both the mean chromatic bias and the reduced
chromatic contrast (in this case to match the mechanism responses for typical outdoor scenes)
normalizes and expands the perceived color gamut so that it is comparable to the range of color
percepts experienced for well-lit outdoor scene (4b).

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242 Finally, Figure 5 illustrates the two examples noted in section 6.2 of the protocol for using the 243 model to study color vision. Figure 5a shows the Munsell Palette under adaptation to a lush or 244 arid environment, while Figure 5b plots the shifts in the palette stimuli required to appear pure red, green, blue, or yellow, when the same observer is adapted to a range of different simulated 245 246 environments. This range is comparable to measurements of the actual stimulus range of these focal colors as measured empirically in the World Color Survey²⁹. Figure 5c instead shows how a 247 248 set of embedded colors appear before or after adaptation to a Martian landscape. Adapting the 249 set for the image led to significantly shorter reaction times for finding the unique colors in a visual

- 250 search task²⁹.
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252 **FIGURES and LEGENDS**:



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Figure 1: The model. a) Responses are modeled for mechanisms with the sensitivities of the cones (which adapt to the stimulus mean) or post-receptoral combinations of the cones (which adapt to the stimulus variance. b) Each post-receptoral mechanism is tuned to a different

257 direction in the color-luminance space, as indicated by the vectors. For the simulations 26 258 mechanisms are computed, which sample the space in 45 deg intervals (shown for the L vs M and 259 S vs LM plane, and the L vs M and luminance plane). c) Responses of the mechanisms in the 260 equiluminant (L vs M and S vs LM) plane to the images in the top and middle panel of Figure 2. 261 Mean contrast responses are shown at 22.5 deg intervals to more fully portray the response 262 distribution, though the model is based on channels at 45 deg intervals. In the original image (2a) 263 the mean chromaticity is close to gray (0,0) and colors are biased along a bluish-yellowish axis. 264 Increasing the lens density of the observer produces a large shift in the mean toward yellow (2b). 265 d) Contrast responses for the images shown in Figure 3a and 3b. The cone contrasts in the original (3a) are compressed along the L vs M axis for the color deficient observer (3b). e) Contrast 266 267 responses for the images shown in Figure 4a and 4b. The low contrast responses for the original 268 image (4a) are expanded following adaptation, which matches the mean responses to the 269 painting to the responses for a color distribution typical of outdoor natural scenes (4b). 270

a) b) c)

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Figure 2: Simulating the consequences of lens aging. Cezanne's *Still Life with Apples (a)* processed to simulate an aging lens (b) and adaptation to the lens (c). Digital image courtesy of the Getty's Open Content Program.

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Figure 3: Simulating anomalous trichromacy. van Gogh's *Irises (a)* simulating the reduced color contrasts in a color-deficient observer (b), and the predicted appearance in observers fully

adapted to the reduced contrast (c). Digital image courtesy of the Getty's Open Content Program.

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Figure 4: Simulating adaptation to a low contrast environment. Monet's *Sunrise (Marine)*. The original image (a) is processed to simulate the color appearance for an observer adapted to the

low contrasts in the scene (b). This was done by adjusting the sensitivity of each mechanism's
 sensitivity so that the average response to the colors in the paintings is equal to the average
 response to colors measured for a collection of natural outdoor scenes. Digital image courtesy of
 the Getty's Open Content Program.



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289 Figure 5. Using the model to examine visual performance. a) The Munsell palette rendered 290 under adaptation to the colors of a lush or arid environment. b) Chips in the palette that should 291 appear pure red, green, blue, or yellow after adaptation to a range of different color 292 environments. Light-shaded symbols plot the range of average chip selections from the languages 293 of the World Color Survey. c) Images of the surface of Mars as they might appear to an observer 294 adapted to Earth or to Mars. Superimposed patches show examples of the stimuli added for the 295 visual search task, and include a set of uniformly colored distractors and one differently-colored 296 target. d) In the experiment search times were measured for locating the odd target, and were 297 substantially shorter within the adapted Mars-adapted images.

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299 **DISCUSSION:**

300 Critical steps within the protocol

301 The illustrated protocol demonstrates how the effects of adaptation to a change in the 302 environment or the observer can be portrayed in images. The form this portrayal takes will 303 depend on the assumptions made for the model – for example, how color is encoded, and how 304 the encoding mechanisms respond and adapt. Thus the most important step is deciding on the 305 model for color vision – for example what the properties of the hypothesized channels are, and how they are assumed to adapt. The other important steps are to set appropriate parameters for 306 307 the properties of the two environments, or two observer sensitivities, that you are adapting 308 between.

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310 Modifications and Limitations of the technique

311 The model illustrated is very simple, and there are many ways in which it is incomplete and could 312 be expanded depending on the application. For example, color information is not encoded 313 independently of form, and the illustrated simulations take no account of the spatial structure of 314 the images or of neural receptive fields, or of known interactions across mechanisms such as 315 contrast normalization³⁸. Similarly, all pixels in the images are given equal weight, and thus the 316 simulations do not incorporate spatial factors such as how scenes are sampled with eye 317 movements. Adaptation in the model is also assumed to represent simple multiplicative scaling. 318 This is appropriate for some forms of chromatic adaptation but may not correctly describe the 319 response changes at post-receptoral levels. Similarly, the contrast response functions in the 320 model are linear and thus do not simulate the actual response functions of neurons. A further 321 important limitation is that the illustrated simulations do not incorporate noise. If this noise 322 occurs at or prior to the sites of the adaptation, then adaptation may adjust both signal and noise and consequently may have very different effects on appearance and visual performance³⁹. One 323 way to simulate the effects of noise is to introduce random perturbations in the stimulus²⁸. 324 325 However this will not mimic what this noise "looks like" to an observer.

326 Significance of the technique with respect to alternative methods

As suggested by the illustrated examples, the simulations can capture many properties of color experience that are not evident when considering only the spectral and contrast sensitivity of the observer, and in particular function to highlight the importance of adaptation in normalizing color perception and compensating for the sensitivity limits of the observer. In this regard, the technique provides a number of advantages and applications for visualizing or predicting visual percepts. These include:

Better simulations of variant vision. As noted, filtering an image for a different sensitivity reveals what one experiences when information in the image is altered, but does less well at predicting what an observer with that sensitivity would experience. As an example, a gray patch filtered to simulate the yellowing lens of an older observer's eye looks yellower⁹. But older observers who are accustomed to their aged lenses instead describe and probably literally see the stimulus as gray⁴⁰. As shown here, this is a natural consequence of adaptation in the visual system²⁸, and thus incorporating this adaptation is important for better visualizing an individual's percepts.

340

341 A common mechanism predicting differences between observers and between environments. 342 Most simulation techniques are focused on predicting changes in the observer. Yet adaptation is also routinely driven by changes in the world^{18,19}. Individuals immersed in different visual 343 344 environments (e.g. urban vs. rural, or arid vs. lush) are exposed to very different patterns of stimulation which may lead to very different states of adaptation^{41,42}. Moreover, these 345 differences are accentuated among individuals occupying different niches in an increasingly 346 347 specialized and technical society (e.g. an artist, radiologist, video game player, or scuba diver). 348 Perceptual learning and expertise have been widely studied and depend on many factors⁴³⁻⁴⁵. But one of these may be simple exposure^{46,47}. For example, one account of the "other race" effect, 349 350 in which observers are better at distinguishing faces with our own ethnicity, is because they are adapted to the faces they commonly encounter^{48,49}. Adaptation provides a common metric for 351 352 evaluating the impact of a sensitivity change vs. stimulus change on perception, and thus for

predicting how two different observers might experience the same world vs. placing the sameobserver in two different worlds.

355 Evaluating the long-term consequences of adaptation. Actually adapting observers and then 356 measuring how their sensitivity and perception change is a well-established and extensively 357 investigated psychophysical technique. However, these measurements are typically restricted to 358 short term exposures lasting minutes or hours. Increasing evidence suggests that adaptation also 359 operates over much longer timescales that are much more difficult to test empirically⁵⁰⁻⁵⁴. 360 Simulating adaptation has the advantage of pushing adaptation states to their theoretical long-361 term limits and thus exploring timescales that are not practical experimentally. It also allows for 362 testing the perceptual consequences of gradual changes such as aging or a progressive disease.

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Evaluating the potential benefits of adaptation. A related problem is that while many functions have been proposed for adaptation, performance improvements are often not evident in studies of short-term adaptation, and this may in part be because these improvements arise only over longer timescales. Testing how well observers can perform different visual tasks with images adapted to simulate these timescales provides a novel method for exploring the perceptual benefits and costs of adaptation²⁹.

370

Testing mechanisms of visual coding and adaptation. The simulations can help to visualize and
 compare both different models of visual mechanisms and different models of how these
 mechanisms adjust their sensitivity. Such comparisons can help reveal the relative importance of
 different aspects of visual coding for visual performance and perception.

375

376 Adapting images to observers. To the extent that adaptation helps one to see better, such simulations provide a potentially powerful tool for developing models of image processing that 377 378 can better highlight information for observers. Such image enhancement techniques are 379 widespread, but the present approach is designed to adjust an image in ways in which the actual 380 brain adjusts, and thus to simulate the actual coding strategies that the visual system evolved to 381 exploit. Pre-processing images in this way could in principle remove the need for observers to 382 visually acclimate to a novel environment, by instead adjusting images to match the adaptation states that observers are currently in^{26,29}. 383

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385 Future directions

386 It may seem unrealistic to suggest that adaptation could in practice discount nearly fully a 387 sensitivity change from our percepts, yet there are many examples where percepts do appear unaffected by dramatic sensitivity differences⁵⁵, and it is an empirical question how complete the 388 389 adaptation is for any given case - one that adapted images could also be used to address. In any 390 case, if the goal is to visualize the perceptual experience of an observer, then these simulations 391 arguably come much closer to characterizing that experience than traditional simulations based 392 only on filtering the image. Moreover, they provide a novel tool for predicting and testing the consequences and functions of sensory adaptation²⁹. Again this adaptation is ubiquitous in 393 394 sensory processing, and similar models could be exploited to explore the impact of adaptation 395 on other visual attributes and other senses.

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399 **DISCLOSURES**:

- 400 The authors have nothing to disclose.
- 401

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