



What is unique about the human eye? Comparative image analysis on the external eye morphology of human and nonhuman great apes

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ABSTRACT

The gaze-signaling hypothesis and the related cooperative-eye hypothesis posit that humans have evolved special external eye morphology, including exposed white sclera (the white of the eye), to enhance the visibility of eye-gaze direction and thereby facilitate conspecific communication through joint-attentional interaction and ostensive communication. However, recent quantitative studies questioned these hypotheses based on new findings that certain features of human eyes are not necessarily unique among great ape species. Accordingly, there is currently a heated debate over whether external eye features of humans are distinct from those of other apes and how such distinguishable features contribute to the visibility of eye-gaze direction. The present study leveraged updated image analysis techniques to test the uniqueness of human eye features in facial images of great apes. Although many eye features were similar between humans and other great apes, a key difference was that humans have uniformly white sclera which creates clear visibility of both the eye outline and iris—the two essential features contributing to the visibility of eye-gaze direction. We then tested the robustness of the visibility of these features against visual noise, such as shading and distancing, and found that both eye features remain detectable in the human eye, while eye outline becomes barely detectable in other species under these visually challenging conditions. Overall, we identified that humans have unique external eye morphology among other great apes, which ensures the robustness of eye-gaze signals in various visual conditions. Our results support and also critically update the central premises of the gaze-signaling hypothesis.

1. Introduction

The gaze-signaling hypothesis proposed by Kobayashi and Kohshima (1997, 2001) posits that the unpigmented exposed sclera of human eyes (i.e., the white of the eye) enhances the visibility of eye-gaze orientation, thereby enabling the eye-gaze signal to function as a powerful

communicative device in humans. Their complementary gaze-camouflaging hypothesis exploited the opposite logic, proposing that the pigmented exposed sclera of nonhuman primates conceals the visibility of their eye-gaze orientation, particularly direct gaze, to predators or dominant conspecifics. These hypotheses derive from Kobayashi and Kohshima's findings that 1) among 88 systematically studied primate

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species, exposed white sclera was a unique feature of the human eye, that 2) in humans, the sclera was more widely exposed than in other species, and that 3) human eyes were horizontally more elongated than those of other primates. The related cooperative-eye hypothesis (Tom- asello, Hare, Lehmann, & Call, 2007) extended the gaze-signaling hypothesis to propose that humans evolved such unique eye morphology as well as a special sensitivity to conspecific eye-gaze signals to facilitate joint attentional and communicative interactions among conspecifics in a cooperative context. Others also noted that such unique traits of humans may facilitate ostensive communication via eye-gaze signals during cultural and language learning (Csibra, 2010; Csibra & Gergely, 2009).

Despite the widespread popularity of the gaze-signaling hypotheses in the literature, this hypothesis has been severely challenged by recent quantitative morphological studies showing that the human eye is not necessarily unique compared to the eye morphology of other great ape species in terms of shape and color (Caspar, Biggemann, Geissmann, & Begall, 2021; Mayhew & Gómez, 2015; Perea-García, Kret, Monteiro, & Hobaiter, 2019). Using a larger sample of images of gorillas and humans than Kobayashi and Kohshima (2001), Mayhew and Gómez (2015) found that, although human eyes are more elongated than gorilla eyes, the sclera is exposed to a similar degree in both species, especially when eye gaze is averted. Caspar et al. (2021) recently replicated these results, further questioning the proposed uniqueness of sclera exposedness. However, these studies only measured sclera exposure in the horizontal dimension (called the Sclera Size Index in Kobayashi & Kohshima, 2001). Kaplan and Rogers (2002) pointed out that the degree of sclera exposedness in primates should be examined two-dimensionally, rather than only in the horizontal dimension. In fact, one of Kobayashi and

Kohshima’s (2001) findings showed that primates with more arboreal living styles move their eyes more vertically than those with more terrestrial living styles (e.g., nonhuman apes as compared to humans). Thus, it remains unclear whether the sclera is more widely exposed two-dimensionally (i.e., area-wise) in the human eye compared to the eyes of other ape species.

These previous studies also questioned the uniqueness of human eye colors. Mayhew and Gómez (2015) examined both individual and species differences in sclera pigmentation using a large sample of gorillas and humans and found that, while all of the examined human individuals had uniformly white sclera (depigmented all the way from the iris edge to the eye corners), there were substantial individual differences among western lowland gorillas in the extent to which the exposed sclera was depigmented. More recently, Perea-García et al. (2019) measured the contrast between the highest and lowest lightness values within an eye image using a large sample of bonobos, chimpanzees, and humans, and Caspar et al. (2021) extended this work to include all great and lesser ape species. In this measure, high iris-sclera contrast means either high lightness in the sclera and low lightness in the iris or the opposite, namely low lightness in the sclera and high lightness in the iris. Among great apes, the former pattern of eye color was observed in humans, lowland gorillas, and Sumatran orangutans, whereas the opposite pattern was observed in chimpanzees and mountain gorillas (Fig. 1). Overall, these previous studies found that the iris-sclera color contrast does not generally differ between humans and nonhuman apes, irrespective of the differences in iris and sclera colors between species.

These recent findings on the iris-sclera color contrast have cast doubt on the gaze-camouflaging hypothesis (concealment of direct gaze). However, it remains unclear how these findings relate to the gaze-

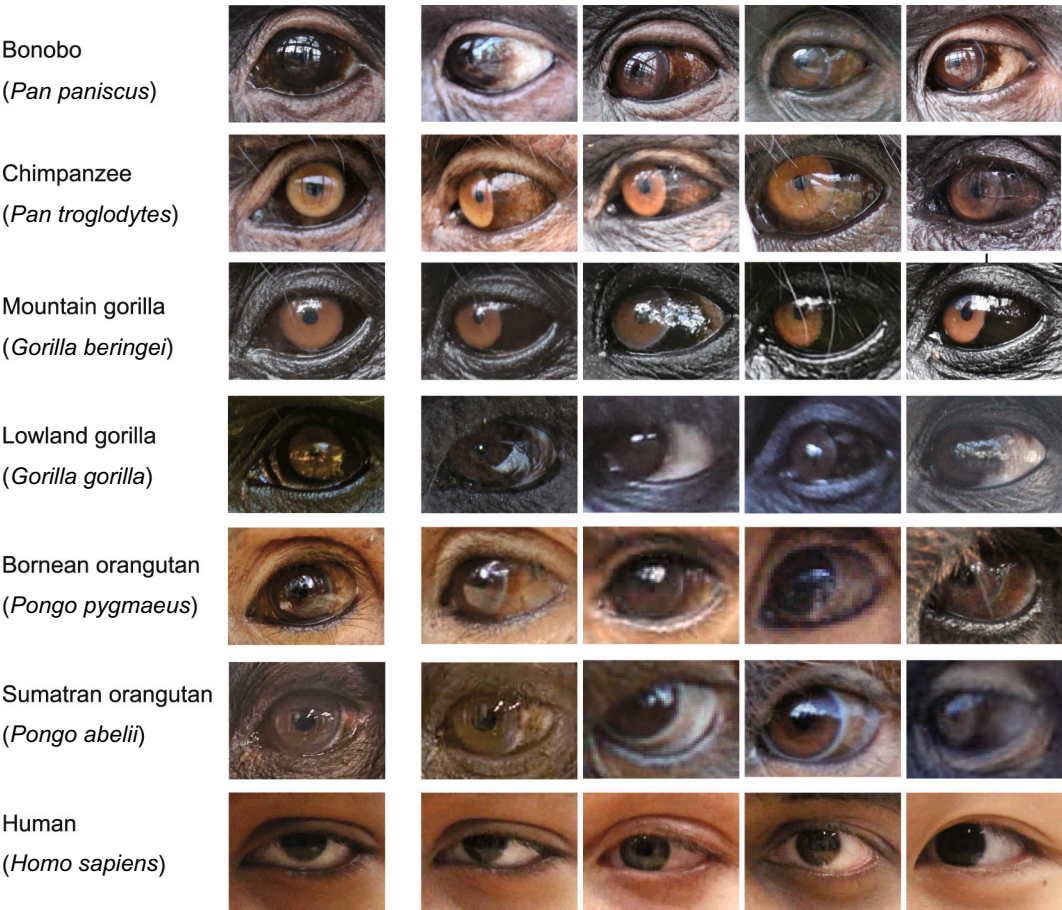


Fig. 1. Examples of eye images from great ape species. In the first and second columns, direct and averted eyes of the same individuals are presented. Permission was obtained for the publication of human images from the authors of the public database, The Columbia Gaze Data Set (Smith et al., 2013).

signaling hypothesis (advertisement of gaze directions) because, as Kobayashi and Kohshima (2001) pointed out, the visibility of eye-gaze orientation critically depends on the visibility of the iris as well as the eye outline. Namely, while a strong iris-sclera color contrast ensures the visibility of the eye in the face, clear visibility of both the eye outline and the iris is essential to ensure the visibility of eye-gaze direction (see Fig. 2). It thus remains unclear how humans and nonhuman apes compare in terms of the visibility of these two eye features. Moreover, the eye-color coding method employed by Perea-García et al. (2019) has been criticized by more recent studies (Caspar et al., 2021; Mearing & Koops, 2021). We also note that their method (measuring a ratio between the highest and lowest lightness values in the eye) may be too simplistic to capture the complex color patterns of great ape eyes, particularly graded and patchy patterns of the sclera and the colorfulness of the iris (see Fig. 1).

In this study, we leveraged updated image analysis techniques to test the uniqueness of external eye morphology in humans as compared to nonhuman great apes. Specifically, using the facial images of human and nonhuman great apes, we examined 1) the area-wise sclera exposedness by measuring the number of pixels in the iris and sclera, 2) the conspicuousness or saliency of eyes in the face using a visual saliency model, 3) the detectability of edges in the eye outline and iris outline using an edge-detection algorithm, and 4) the conspicuousness of the eye outline and iris using a color-difference analysis. We examined both direct and averted gaze faces because many nonhuman ape individuals have pale colors in peripheral sclera areas, which are revealed only when the gaze is averted (Fig. 1). Moreover, as the strength of a visual signal critically depends on natural noises such as shading and distancing, we manipulated the brightness and blurriness (correlating with distance) of eye images and tested the detectability/conspicuousness of both the eye outline and iris against these manipulations. Throughout these analyses, we assumed a fundamental similarity between the visual systems of humans and nonhuman catarrhine primates (Deeb, Jorgensen, Battisti, Iwasaki, & Motulsky, 1994; Dulai, Bowmaker, Mollon, & Hunt, 1994; Jacobs & Deegan, 1999; Jacobs, Deegan, & Moran, 1996; Matsuno, Kawai, & Matsuzawa, 2004). However, as some differences have been also reported between these species in their spectrum sensitivities (Jacobs et al., 1996; Waitt & Buchanan-Smith, 2006), we return to this issue in our discussion.

2. Material and methods

Samples: We collected high-resolution images of seven great ape species: bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*; mostly *verus*, also including one *elliotti* and two hybrids), mountain gorillas (*Gorilla beringei beringei*), western lowland gorillas (referred to as ‘lowland gorillas’ in this paper; *Gorilla gorilla gorilla*), Bornean orangutans (*Pongo pygmaeus*), Sumatran orangutans (*Pongo abelii*), and humans (*Homo sapiens*). Nonhuman ape images were obtained from researchers and keepers at zoos, research institutes, sanctuaries, and field sites (see Acknowledgements). Human images were obtained through The Columbia Gaze Data Set (Smith et al., 2013) which includes the faces of

diverse ethnicities with various iris and skin colors. See our online repository for the thumbnails of our images:

https://osf.io/z6753/?view_only=5f6f393077194fb789c7fe5c44bbe06e

From our collection of images, we selected 122 images of direct gaze faces (one image per individual) and 117 images of averted gaze faces (one image per individual), for a total of 160 individuals represented in the data set (Table 1). All images were of subadults or adults (> 10 years old), and the number of females and males was balanced for each species. We selected images based on the following criteria: all parts of the faces were focused, zoomed, and oriented toward the camera (we accepted deviations of ± 10 degrees for the direct gaze faces, and ± 45 degrees for the averted gaze faces), and also illuminated with bright light sources (natural daylight for nonhuman apes, and bright room lighting for humans) relatively uniformly projecting onto the faces. Emotional expression was either absent or minimal in the faces. Each image was then cropped to include central facial parts (eyes, nose, mouth, and eyebrow ridges). The background was masked with a neutral color and not included in our analyses. The nonhuman ape images and human images were then converted into 345×460 and 400×400 pixels, respectively (the difference in the width-height ratio was due to the difference in facial configurations). Finally, to standardize overall brightness and contrast in each facial image, each image was auto-leveled in Photoshop; that is, the means of RGB values (RGB/3 per pixel, ranging from 0 to 255) were adjusted so that they ranged between the darkest (0) and brightest pixels (255) in each image, and the intermediate level (128) became closer to the peak of the levels histogram in each image (i.e., gamma correction).

Shape analysis: In each image, we traced outlines of the eye-opening and iris with 2-pixel lines in Photoshop and then filled those traced lines to make binary masks for eye-opening and iris, respectively, using a custom program in MATLAB v. 2019–2021 (MathWorks, Natick). We then measured 1) the maximal horizontal length (pixel) of the eye-opening mask, 2) the number of pixels in the eye-opening mask, and 3) the number of pixels in the sclera mask (by subtracting the iris mask and its outline from the eye-opening mask). Analogous to the one-dimensional measures used in Kobayashi and Kohshima (2001), namely the Sclera Size Index and Width/Height Ratio, we created the following two-dimensional measures: 1) Sclera Area Index, defined as

Table 1

The number of images and individuals used in this study (number of females in parentheses).

Species	Direct gaze	Averted gaze	N of images	N of individuals
<i>Pan paniscus</i>	18 (13)	17 (11)	35 (24)	26 (17)
<i>Pan troglodytes</i>	28 (14)	29 (15)	57 (29)	49 (25)
<i>Gorilla beringei</i>	16 (9)	14 (9)	30 (18)	14 (8)
<i>Gorilla gorilla</i>	11 (6)	11 (8)	22 (14)	19 (10)
<i>Pongo pygmaeus</i>	10 (4)	10 (4)	20 (8)	13 (5)
<i>Pongo abelii</i>	5 (3)	2 (2)	7 (5)	5 (3)
<i>Homo sapiens</i>	34 (17)	34 (17)	68 (34)	34 (17)
Total	122 (66)	117 (66)	239 (132)	160 (85)



Fig. 2. Examples of human (left) and chimpanzee eye images (right) in original forms (a) and in binarized forms (b) at an arbitrary brightness (LAB ΔE from black = 40).

the number of pixels in the sclera mask divided by the number of pixels in the eye-opening mask, and 2) Horizontal Elongation Index, defined as the squared maximal horizontal length of the eye-opening mask divided by the number of pixels in the eye-opening mask.

Saliency analysis: To examine the conspicuousness of eyes in the images, we used a well-established saliency model (Itti & Koch, 2001) implemented in MATLAB (Walther & Koch, 2006) to calculate the pixel-level local saliency of the images (conspicuousness and saliency of color are exchangeable terms in this study). Although there are updated saliency models in the literature (see Sharma, 2015, for a review), we chose the Itti and Koch model mainly due to its simplicity and common use in literature. One previous study demonstrated close similarity between chimpanzees and humans in their responses to local saliency as measured by the Itti and Koch model (Kano & Tomonaga, 2011). This model simulates the early visual system of primates (with habitual trichromatic vision) and calculates local saliency within an image based on color (in the red-green and blue-yellow channels), intensity (lightness contrast), and orientation (the direction of edges/lines). The orientation information was discarded in this analysis because our purpose was to evaluate the saliency of eye colors and intensities. We combined color and intensity information in the combined map with a weight of 1:1. To determine the saliency of the eye regions within each image, we defined the eye region as the rectangular area surrounding each eye and eyelid and then calculated the sum of saliency values within the eye regions divided by the sum of saliency values within the whole image. We traced the background of each image and excluded them from the analysis. We also traced the pupils and any reflections of the light source in the eyes of each image and excluded them from the analysis.

Edge detection analysis: Stevens and Cuthill (2006) used edge-detection analysis to examine the crypsis (background pattern matching) of prey models to the eyes of avian predators. We used this approach to examine the visibility of the eye and iris outlines based on the same assumption that Stevens and Cuthill made; ‘edge detection, via sharp changes in light intensity or spectral composition (defined mathematically below), has a primary role in object/background segmentation because changes in light intensity and composition frequently occur where one object ends and another begins’ (p. 2142). Considering catarrhine primates (with habitual trichromatic vision) observing the eyes of conspecifics, we defined the brightness of each pixel in the CIE LAB color space as the primary stimulus intensity (see below for the definition of brightness). To do so, we first converted RGB values of all pixels into brightness values in each image and then ran an edge detection algorithm on those brightness-converted images using the ‘edge’ function with the ‘Sobel’ operator (default) in MATLAB (the ‘Sobel’ operator captures only thick edges as compared to other operators, such as ‘LoG’ and ‘Canny’). To simulate the visibility of detected edges at varying distances/blurriness, we blurred the original images (before the brightness conversion) using the ‘imgaussfilt’ function in MATLAB (the image processing toolbox) with a Gaussian of width, $\sigma = 1, 2, 4, 8$. The intensity of blur (σ) is known to correspond linearly to the visual distance at which the image is presented (Coppens & van den Berg, 2004). For example, the visual acuity measured on an image blurred with $\sigma = 2$ at 1 m is identical to that measured when the image is presented at 2 m. Furthermore, to quantify the edges detected in the iris and eye outlines (and both combined) in each image (with $\sigma = 1, 2, 4, 8$), we created iris-outline and eye-outline masks by dilating the traced 2-pixel lines for each feature to 8 pixels in width and then calculated the proportion of pixels in which the edge was detected in these outline masks.

Color analysis: To examine the color difference between eye features in each image, we used the CIE LAB color system. While this color system was created to simulate human color vision, it is also considered applicable for nonhuman primates with human-like trichromatic color vision (Stevens, Stoddard, & Higham, 2009). In this color system, the L dimension represents lightness (0 to 100) and the A and B dimensions represent red-green (–128 to 127) and blue-yellow (–128 to 127),

respectively. The color difference was described as LAB ΔE , defined as the Euclidean distance between the two LAB colors (i.e., the CIE 1976 style; although there are updated versions (e.g., CIE 2000), we used this older version for simplicity). Namely, LAB ΔE between color 1 and 2 was calculated as $\sqrt{(L1 - L2)^2 + (a1 - a2)^2 + (b1 - b2)^2}$. Throughout the paper, we refer to *lightness* as the lightness (or grayscale) component of a given color (i.e., L), *colorfulness* as the chromatic components of a given color (i.e., $\sqrt{a^2 + b^2}$), *brightness* as the color difference between a given color and black (L = 0, a = 0, b = 0; i.e., $\sqrt{L^2 + a^2 + b^2}$), and *conspicuousness* as the color difference between a given color and its adjacent color(s).

To examine the color differences between each eye feature, we created outlined and filled masks for the iris, sclera, eye outline, and eye region using the rectangular eye region and 8-pixel outline masks described above. These outlined and filled masks did not overlap with one another. That is, the filled masks did not include the 8-pixel outlines of the iris and sclera. The pupils and any reflections of the light source in the eye were also traced and excluded from the analysis. We then calculated the mean LAB of all pixels in each mask and the LAB ΔE between these means (thus, this color analysis was size-independent).

We also measured the mean LAB of all pixels in the face region (the area excluding the background) and covaried this value in the analysis to control for variation in the overall brightness of the whole face across individuals and species (note that the auto-leveling with Photoshop, described above, also adjusted the overall brightness of each facial image to some extent, but not fully). This variation was mainly due to different skin colors across individuals and species and also partly due to the variations in lighting conditions across images. This control led to a conservative (lower) estimation of color differences in our human samples (including diverse ethnicities) as their facial colors were generally brighter than those of other great apes.

To simulate the visibility of color differences between the masks at varying brightness (the color difference from black) levels of the images, we decreased the brightness of each image by dividing the RGB value of each pixel by a factor of 1, 2, 4, 8 (by definition, LAB ΔE decreases proportionally to this change). This manipulation is intended to simulate the conditions when the eyes are viewed in the shade. LAB ΔE around 1–3 is known as the ‘just noticeable difference’ (JND) in human perception (Stokes, Fairchild, & Berns, 1992). We assumed these same values for nonhuman apes, given the applicability of the CIE LAB color space to their visual system (Stevens et al., 2009); also see Osorio and Vorobyev (1996) for a related model of JND in nonhuman primates.

Statistical analysis: We analyzed the images of direct and averted gaze faces separately because we aimed to test the uniqueness of human eyes in both gaze directions. To test species differences in eye properties, we used an analysis of variance (ANOVA) with species as a between-subject factor in SPSS v. 23 (IBM Corp., 2015, Armonk). If the ANOVA included a within-subject factor (e.g., different eye parts) and the assumption of sphericity was violated, a Greenhouse-Geisser’s correction was applied to the degrees of freedom. To directly test the uniqueness of human eye properties, we conducted follow-up tests comparing humans with each nonhuman ape species with the alpha level corrected for the number of pairwise comparisons in the Bonferroni correction. We excluded Sumatran orangutans from our analyses due to an insufficient number of samples (Table 1) but present their results in all graphs. We visually inspected the results from each Sumatran orangutan and confirmed that all individuals fit well within the individual/species variations of other nonhuman apes (see graphs). For the color analysis, we covaried the brightness of the face mask in an analysis of covariance (ANCOVA).

3. Results

Shape analysis: We tested species differences in the Sclera Area Index (the number of pixels in the sclera mask divided by the number of pixels

in the eye-opening mask; Fig. 3a) for the direct and averted gaze faces (Fig. 3b). An ANOVA with species as a between-subject factor revealed significant main effects of species for both direct-gaze faces ($F[5, 111] = 17.65, p < 0.001, \eta_p^2 = 0.29$) and averted-gaze faces ($F[5, 109] = 8.92, p < 0.001, \eta_p^2 = 0.44$). Post-hoc pairwise comparisons between humans and the other species ($\alpha = 0.05/5$) revealed that the sclera of humans is significantly more widely exposed than that of bonobos and Bornean orangutans ($p < 0.001$), less exposed than that of chimpanzees ($p = 0.007$), but not significantly different from that of mountain and lowland gorillas ($ps > 0.3$) in the direct gaze faces. In the averted gaze faces, the sclera of humans is significantly less exposed than that of chimpanzees, mountain gorillas, and lowland gorillas ($ps < 0.001$) but not significantly different from that of bonobos and Bornean orangutans ($ps > 0.6$).

We then tested species differences in the Horizontal Elongation Index (the squared maximal horizontal length of the eye-opening divided by the number of pixels in the eye-opening mask; Fig. 3a) for the direct and averted gaze faces (Fig. 3c). An ANOVA with species as a between-subject factor revealed significant main effects of species for both direct-gaze faces ($F[5, 111] = 92.80, p < 0.001, \eta_p^2 = 0.81$) and averted-gaze faces ($F[5, 109] = 73.32, p < 0.001, \eta_p^2 = 0.77$). Post-hoc pairwise comparisons between humans and the other species ($\alpha = 0.05/5$) revealed that the eyes of humans are significantly more elongated than those of any other species in both direct ($ps < 0.001$) and averted gaze faces ($ps < 0.001$). These results indicate that the sclera of humans is not much more widely exposed than that of other apes, while human eyes are horizontally longer than the eyes of other apes.

Saliency analysis: We tested species differences in the eye saliency (the sum of saliency values within the eye region divided by the sum of all saliency values within the whole face; Fig. 4a) of the combined map respectively for the direct and averted gaze faces (Fig. 4d). An ANOVA

with species as a between-subject factor revealed significant main effects of species for both direct-gaze faces ($F[6, 109] = 3.99, p = 0.0021, \eta_p^2 = 0.16$) and averted-gaze faces ($F[6, 111] = 9.93, p < 0.0001, \eta_p^2 = 0.31$). Post-hoc pairwise comparisons between humans and the other species ($\alpha = 0.05/5$) revealed that the eyes of humans in direct-gaze faces are significantly more salient than those of Bornean orangutans ($p < 0.001$), but not significantly different from those of other ape species ($ps > 0.01$), and in averted-gaze faces, the eyes of humans are significantly more salient than those of Bornean orangutans ($p = 0.001$) but not significantly different from those of other ape species ($ps > 0.05$). Fig. 4b-c indicates that the saliency of chimpanzee and mountain gorilla eyes mainly depends on the colorfulness of their eyes (i.e., the color map), while that of human eyes mainly depends on the lightness contrast of their eyes (i.e., the intensity map). These results suggest that human eyes are not much more salient than other apes' eyes.

Edge detection analysis: We tested species differences in the detectability of edges on the combined mask for the iris and eye outlines (the proportion of pixels in which edges were detected on the combined mask) on the brightness-converted images. To simulate visual distances, we manipulated the original images using Gaussian blurs with four levels of blur intensities ($\sigma = 1, 2, 4, 8$; Fig. 5a). We then tested the robustness of detected edges on the combined outline mask against such blurs across species (Fig. 5d). A repeated-measures ANOVA with species as a between-subject factor and image blur as a within-subject factor revealed significant interaction effects between species and image blur for both direct-gaze faces ($F[8.8, 194.4] = 17.29, p < 0.001, \eta_p^2 = 0.44$) and averted-gaze faces ($F[8.9, 193.6] = 21.16, p < 0.001, \eta_p^2 = 0.49$). We then tested species differences for the images blurred with $\sigma = 8$ using an ANOVA with species as a between-subject factor. The main effects of species were significant for the images of both direct-gaze faces ($F[5, 111] = 18.96, p < 0.001, \eta_p^2 = 0.46$) and averted-gaze faces ($F[5, 109] = 25.38, p < 0.001, \eta_p^2 = 0.54$). Post-hoc pairwise comparisons between humans and the other ape species ($\alpha = 0.05/5$) revealed that more edges were detected in the combined masks of humans than those of other ape species in both direct-gaze ($ps < 0.001$) and averted-gaze faces ($ps < 0.001$). Similar patterns of results were observed respectively for the iris-outline and eye-outline masks (Fig. 5b-c). These results indicate that the iris and eye outlines are more visible in human eyes than nonhuman ape eyes, particularly when the faces are blurred (or in a distant location).

Color analysis: We tested species differences in the conspicuousness of the combined mask for the eye outline and iris (the color difference between the combined mask and elsewhere in the eye region; Fig. 6g). An ANCOVA with species as a between-species factor and face region brightness as a covariate revealed significant main effects in both direct-gaze ($F[5, 110] = 22.87, p < 0.001, \eta_p^2 = 0.51$) and averted-gaze faces ($F[5, 108] = 22.80, p < 0.001, \eta_p^2 = 0.51$). Post-hoc pairwise comparisons between humans and the other ape species ($\alpha = 0.05/5$) revealed that colors were more conspicuous in the combined mask of human eyes compared to that of any other ape species in both direct-gaze faces ($ps < 0.001$) and averted-gaze faces ($ps < 0.001$). Fig. 6a-f indicates that this result depends on the conspicuousness of both the eye outline and iris in the human eye.

Fig. 7 shows how eye color differences decrease as a function of image brightness (the color difference from black). We manipulated the image brightness by dividing the RGB value of each pixel by a factor of 1, 2, 4, 8. By definition, LAB ΔE decreased proportionally to this decrease in RGB. Given that LAB ΔE is barely noticeable around 1–3, the iris remains noticeable in the eyes of most great ape species (including humans) in shaded images, while the eye outline remains noticeable only in the eyes of humans in shaded images. Together, these results indicate that both the iris and eye outlines are visible in humans while eye outlines are particularly difficult to see in nonhuman apes, especially when the brightness of the face is low.

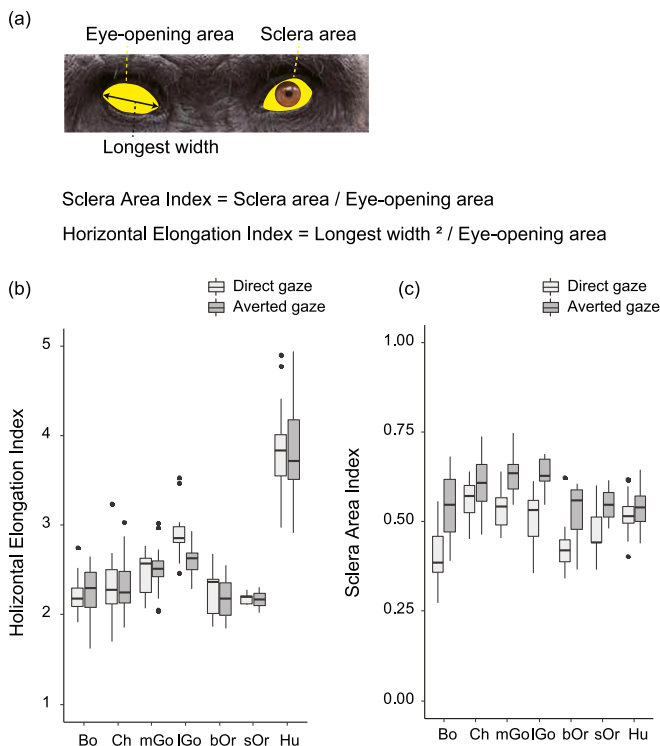


Fig. 3. Eye shape of the great apes evaluated using our unique measures (a); Horizontal Elongation Index (b) and Sclera Area Index (c). Box plots show the median, interquartile range (IQR), and $1.5 \times \text{IQR}$, with outliers plotted individually. Bo = bonobos; Ch = chimpanzees; mGo = mountain gorillas; lGo = lowland gorillas; bOr = Bornean orangutans; sOr = Sumatran orangutans; Hu = humans.

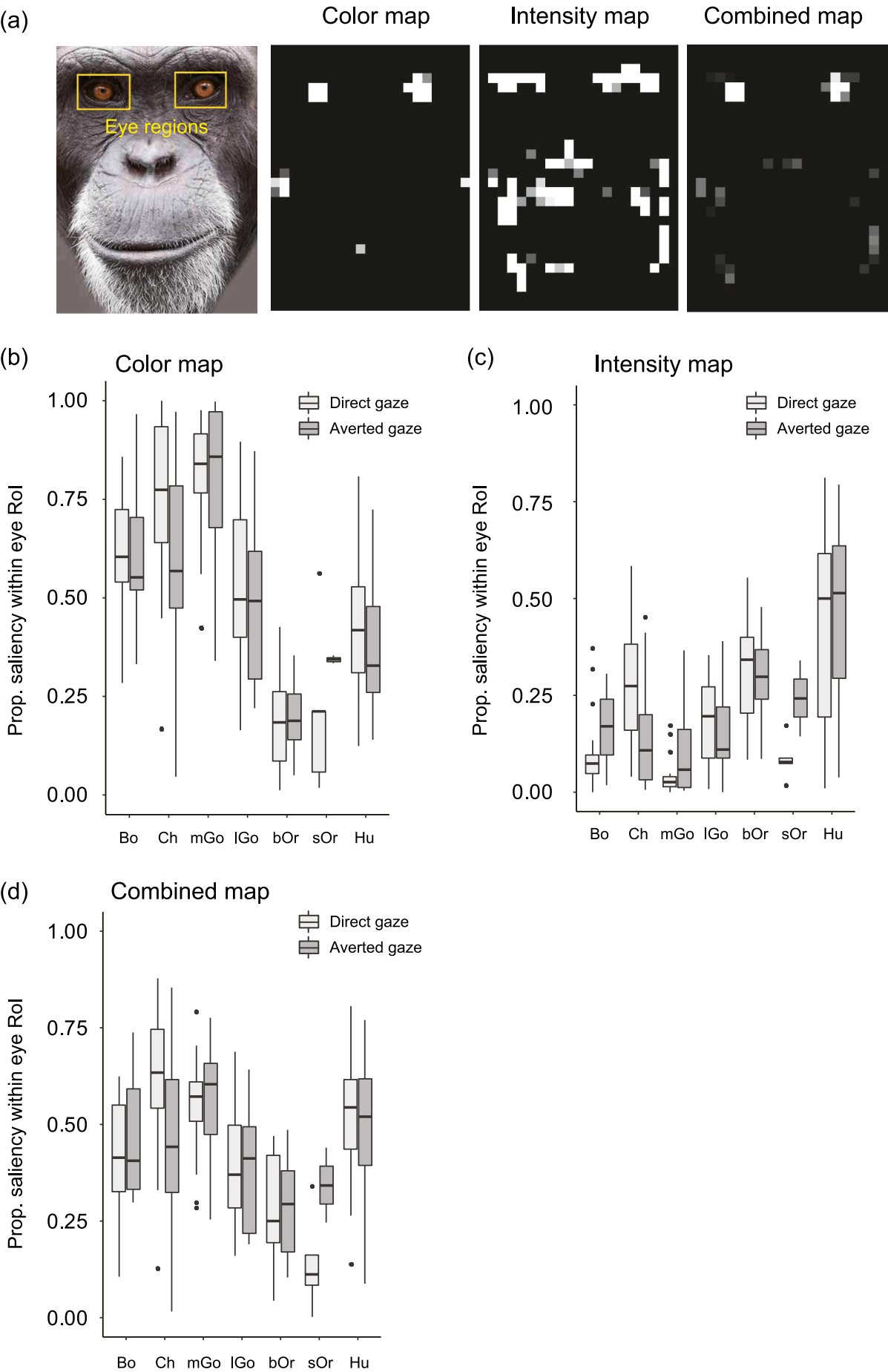


Fig. 4. Saliency analysis. (a) Examples of the eye region, the color, intensity, and combined map (in a chimpanzee face). (b) The proportion of pixels identified as salient in terms of colorfulness within the eye region, with respect to all pixels identified as salient within the whole image. (c) The proportion of pixels identified as salient in terms of intensity within the eye region, with respect to all pixels identified as salient within the whole image. (d) The proportion of pixels identified as salient in terms of both color and intensity within the eye region, with respect to all pixels identified as salient within the whole image. Box plots show the median, interquartile range (IQR), and $1.5 \times \text{IQR}$, with outliers plotted individually. Bo = bonobos; Ch = chimpanzees; mGo = mountain gorillas; lGo = lowland gorillas, bOr = Bornean orangutans; sOr = Sumatran orangutans; Hu = humans.

4. Discussion

We found that the uniqueness of human eyes is characterized by clear visibility of both the eye outline and the iris, two essential features that critically contribute to the visibility of eye-gaze direction. Clear visibility of these features is attributable to the uniform whiteness of the exposed sclera in human eyes because the uniformly white sclera characterizes clear edges on both iris outline and eye outline. Notably, the eye outline is distinguishable from adjacent features in humans irrespective of skin color because eyelashes and local shades create thick dark lines surrounding the eyes (see Figs. 1 and 2). Conversely, even though the iris is highly visible in all great ape species, the eye outline of nonhuman apes is less distinguishable from adjacent features than that of humans because their sclera color is darker or more graded/patchier (thus blending into adjacent features) compared to the uniformly white human sclera. Our results thus support a key premise of the gaze-signaling hypothesis proposed by Kobayashi and Kohshima (2001), namely that the eye-gaze directions of humans are more visible than those of nonhuman great apes. However, our results did not support two other claims by Kobayashi and Kohshima. Specifically, we found that, while the human eye is horizontally longer than the eye of other great ape species, the sclera of humans is not more widely exposed than that of other great apes. Furthermore, we found that, in both human and nonhuman apes, eyes are the most salient features of their faces and thus do not appear to conceal gaze direction. Additionally, we newly discovered that the visibility of eye outlines critically depends on visual noise, such as shading and distancing.

Consistent with Kobayashi and Kohshima (2001), our analyses identified that horizontal elongation is a distinguishing feature of the human eye. It could be argued that this feature may have evolved to signal eye-gaze direction, particularly in the horizontal dimension. However, and as Kobayashi and Kohshima discovered, a horizontally elongated eye shape may have evolved to allow more terrestrial primates to scan their environment more widely in the horizontal dimension (e.g., humans compared to other great apes). Thus, although it is possible that the horizontally elongated shape of human eyes enhances the visibility of eye-gaze direction at least in the horizontal dimension, it remains unclear whether this eye feature evolved for conspecific communication or other ecological reasons.

Consistent with Perea-García et al. (2019), our results showed that eyes are salient features in the faces of both humans and nonhuman apes, suggesting that great ape eyes are advertising rather than concealing their presence in the face. These results thus cast doubt on the gaze-camouflaging hypothesis proposed by Kobayashi and Kohshima (2001). One might argue that the gaze-camouflaging hypothesis can be updated by proposing that the eyes of nonhuman primates conceal eye-gaze direction rather than the presence of the eyes in the face. However, gaze direction can be inferred not only by eye orientation but also by head orientation (Emery, 2000), and nonhuman great apes typically rely on head-directional cues rather than eye-directional cues to follow another's gaze direction (Tomasello et al., 2007). Furthermore, our results showed that eye-gaze directions are reliably visible in both human and nonhuman great apes, at least under good visual conditions. Accordingly, if the gaze-camouflaging hypothesis remains true, one must consider a nuanced condition in which the concealment of eye-gaze but not head-gaze is functional. For example, consider the following situation: a dominant chimpanzee is looking roughly in the direction of a far away subordinate chimpanzee, and the subordinate chimpanzee is

watchful of the dominant's entire visual field. In this case, the unclear eye-gaze cues from the dominant individual may be functional in a competitive context because they effectively expand the area the subordinate perceives as being watched. However, it remains unclear whether such a social situation is sufficient for the evolution of pigmented sclera in nonhuman apes. Rather, given that pigmented sclera is widespread among nonhuman primates (Kobayashi & Kohshima, 2001), it may be more reasonable to postulate a more parsimonious selective force for its evolution (e.g., protection from UV; Perea-García, Danel, & Monteiro, 2021).

Our results suggest that the uniformly white sclera facilitates the visibility of eye-gaze directions in humans, supporting one of the key findings of Kobayashi and Kohshima (2001). However, we updated the findings of this and other previous studies mainly in two aspects. First, we clarified that it is the uniformly white sclera but not necessarily the other unique features, such as the sclera exposedness and the iris-sclera color contrast, that distinguishes the human eye from the eye of nonhuman apes, and we also clarified that it is this feature that critically contributes to the visibility of eye-gaze directions in the human eye. Second, the clear advantage of the human eye over the nonhuman ape eye is its visibility under visually challenging conditions (e.g., in the shade, from far away) but not necessarily under good visual conditions. Thus, although the gaze-signaling hypothesis should be updated at least in these two aspects, its key claim regarding the functionality of the uniformly white sclera seems to hold. Namely, humans may have evolved the uniformly white sclera (but not necessarily the other unique features) to enhance the visibility of eye-gaze in conspecific communication (more specifically the robustness of the visibility of eye-gaze across various visual conditions). Consequently, other related hypotheses deriving from the original Kobayashi and Kohshima's findings also seem to hold. Therefore, as the cooperative-eye hypothesis proposes, humans may effectively employ this unique eye feature to facilitate joint attentional and communicative interactions among conspecifics in a cooperative context (Tomasello et al., 2007). Relatedly, clear cues of 'being watched' by another individual in humans, compared to more ambiguous cues in nonhuman apes (i.e. reliant on head direction), may trigger reputational concerns and facilitate subsequent cooperative behaviors (Bateson, Nettle, & Roberts, 2006). Furthermore, humans' uniformly white sclera effectively articulates ostensive-communicative signals via eye-gaze during cultural and language learning (Csibra, 2010; Csibra & Gergely, 2009).

It should be mentioned that clear visibility of both the eye outline and iris in the human eye contributes not only to the visibility of eye-gaze directions but also to the visibility of nuanced facial expressions together with fine musculatures around the eyes (Whalen et al., 2004). Additionally, Provine and colleagues have pointed out that humans' uniformly white sclera can signal emotional and health status by its color variations; for example, people associate reddish sclera as sadder and yellowish sclera as less healthy (Provine, Cabrera, & Nave-Blodgett, 2013; Provine, Nave-Blodgett, & Cabrera, 2013). These findings suggest that this distinguished feature of humans may have evolved under multiple selective pressures related to communication. Given that humans are sensitive to cues from the uniformly white sclera from infancy (Farroni, Csibra, Simion, & Johnson, 2002; Farroni, Massaccesi, Pividori, & Johnson, 2004; Jessen & Grossmann, 2014; Tomasello et al., 2007), it is also possible that humans have co-evolved the uniformly white sclera as well as special sensitivities for the nuanced cues provided by this feature.

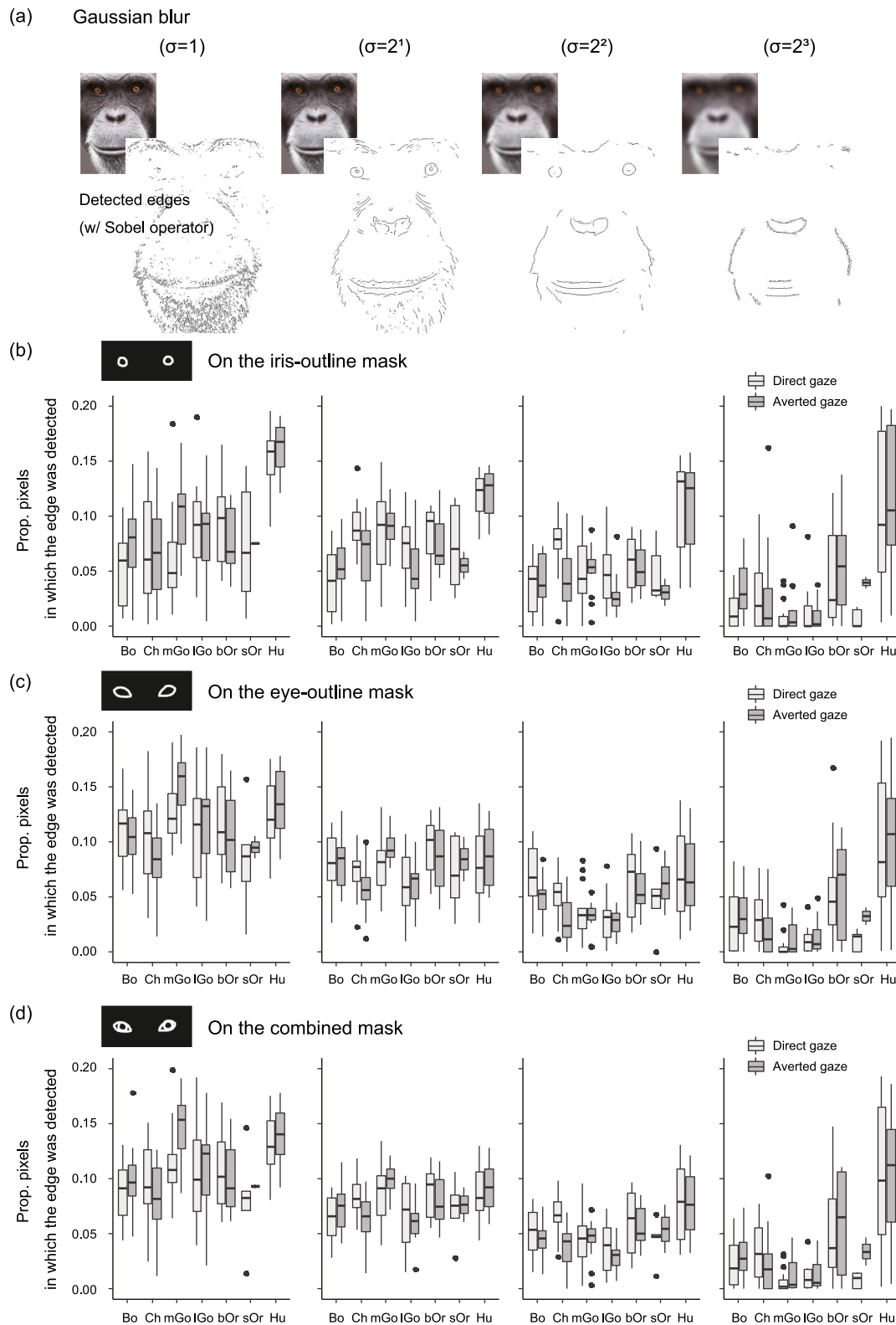


Fig. 5. Edge-detection analysis and blurriness (or distance) manipulation test. Facial images were blurred with a Gaussian of width $\sigma = 1, 2, 4, 8$. (a) Examples of face images (top-left) and edges detected using an edge-detection algorithm; b) Proportion of pixels in which the edge was detected on the iris-outline mask (with respect to all pixels on the iris-outline mask) as a function of image blur; c) Proportion of pixels in which the edge was detected on the eye-outline mask (with respect to all pixels on the eye-outline mask) as a function of image blur; d) Proportion of pixels in which the edge was detected on the combined mask (with respect to all pixels on the combined mask) as a function of image blur. Box plots show the median, interquartile range (IQR), and $1.5 \times \text{IQR}$, with outliers plotted individually. Bo = bonobos; Ch = chimpanzees; mGo = mountain gorillas; lGo = lowland gorillas; bOr = Bornean orangutans; sOr = Sumatran orangutans; Hu = humans.

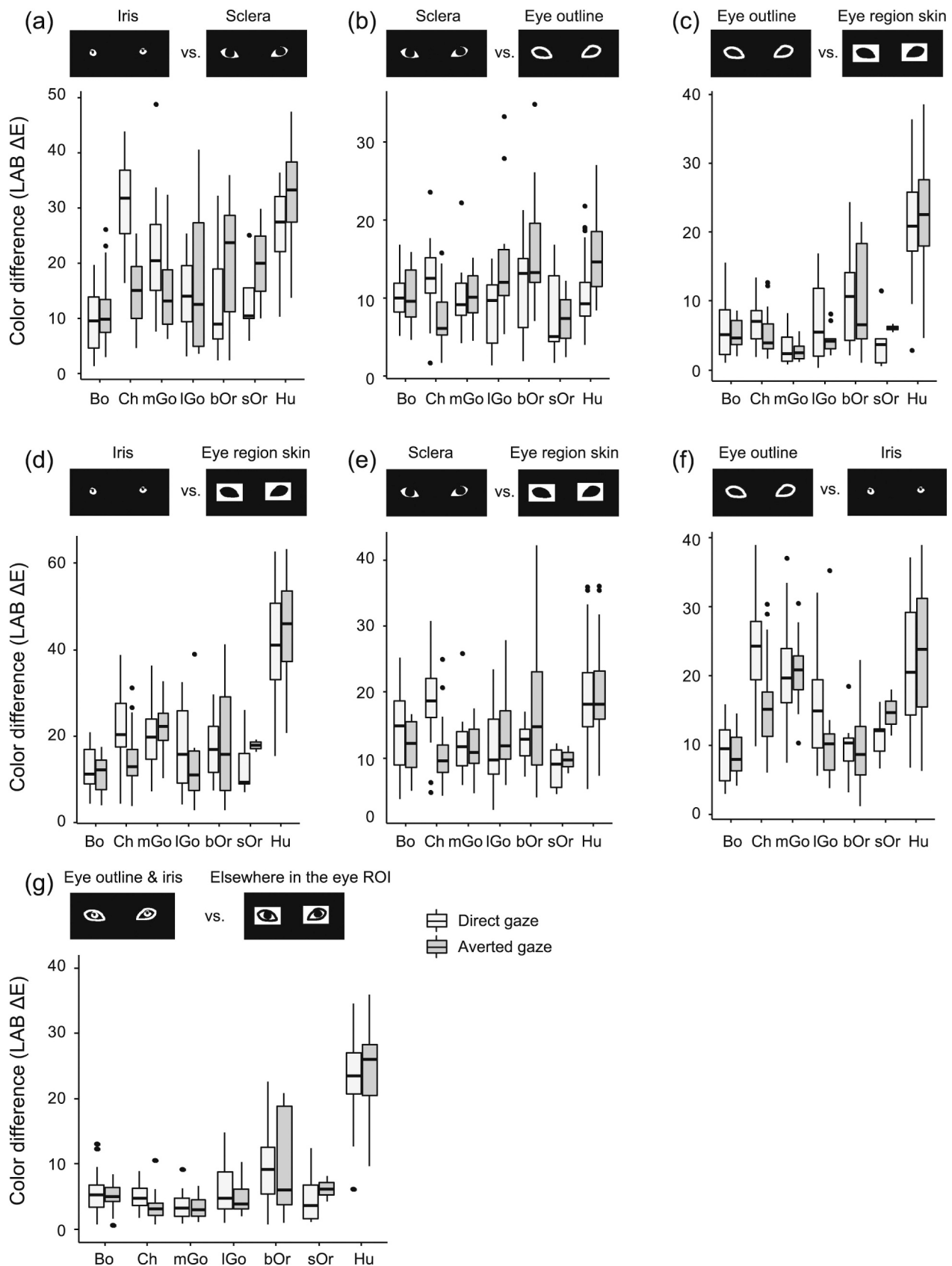


Fig. 6. Color-difference analysis. (a-f) Pairwise color differences (LAB ΔE) between the iris, sclera, eye outline, and eye region skin masks. (g) Color differences (LAB ΔE) between the combined masks (the eye-outline and iris masks) and elsewhere in the eye region. Box plots show the median, interquartile range (IQR), and $1.5 \times$ IQR, with outliers plotted individually. Bo = bonobos; Ch = chimpanzees; mGo = mountain gorillas; lGo = lowland gorillas; bOr = Bornean orangutans; sOr = Sumatran orangutans; Hu = humans.

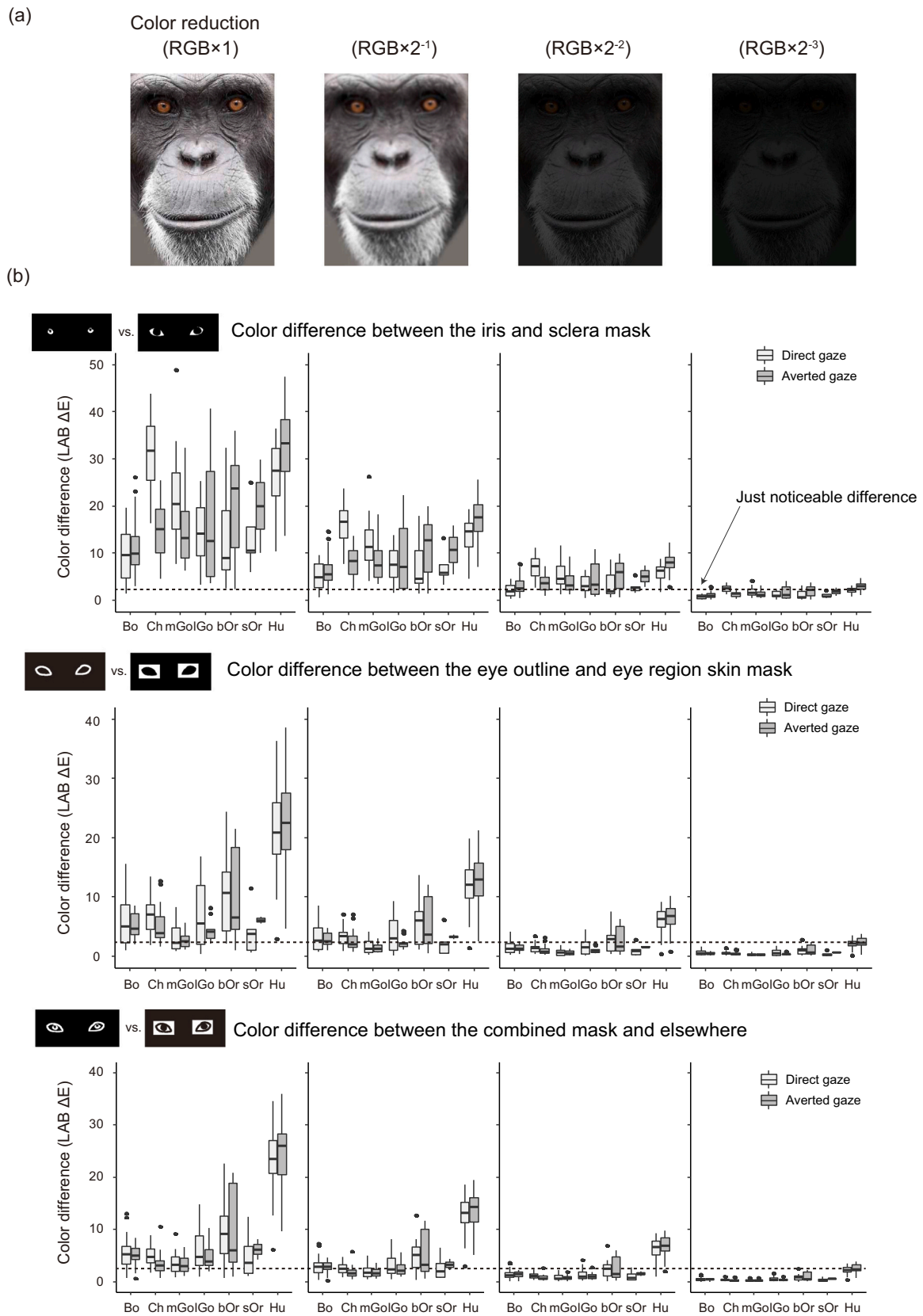


Fig. 7. Color manipulation test. (a) Examples of a face image of which brightness was reduced by a factor of 1, 2, 4, 8. (b) Color difference (LAB ΔE) between the iris and sclera masks, the eye outline and eye region skin masks, and the combined masks (the eye-outline and iris masks) and elsewhere in the eye region as a function of image brightness. The dotted line indicates the just noticeable difference ($\Delta E \approx 1\text{--}3$) in human perception. Box plots show the median, interquartile range (IQR), and $1.5 \times \text{IQR}$, with outliers plotted individually. Bo = bonobos; Ch = chimpanzees; mGo = mountain gorillas; lGo = lowland gorillas; bOr = Bornean orangutans; sOr = Sumatran orangutans; Hu = humans.

Finally, several limitations of our study should be discussed. First, while we only used high-quality images taken under good lighting conditions for our analysis and controlled for overall contrast and brightness of images *post-hoc*, we did not thoroughly control the absolute luminance and chromaticity of images using formal color-sampling methods, namely by photographing color standards in the same image/locations (Gerald, Bernstein, Hinkson, & Fosbury, 2001; Stevens, Párraga, Cuthill, Partridge, & Troscianko, 2007). Unfortunately, this is a limitation of all previous studies of primate eye color. Although it is generally challenging to collect such eye images from live nonhuman primates, such efforts are essential in the future to more thoroughly control for the differences in lighting conditions between images. Second, our image-processing techniques relied on the assumption that humans and nonhuman great apes have similar visual perceptions. We believe that this assumption is largely valid because previous electrophysiological, genetic, and behavioral evidence generally indicates minimal differences in visual perception between humans and other catarrhine primates with habitual trichromatic vision (Deeb et al., 1994; Dulai et al., 1994; Jacobs et al., 1996; Jacobs & Deegan, 1999; Matsuno et al., 2004). However, previous studies also indicate that slight differences exist between these species in their spectrum sensitivities (Jacobs et al., 1996; Waitt & Buchanan-Smith, 2006); in particular, macaques and chimpanzees may be slightly more sensitive to shorter wavelengths and slightly less sensitive to longer wavelengths than humans, which may lead to higher chromatic sensitivity in the former and higher luminance sensitivity in the latter. Moreover, although visual acuity and contrast sensitivity are largely similar, they may be slightly inferior in nonhuman apes compared to humans (Adams, Wilkinson, & MacDonald, 2017; Bard, Street, McCrary, & Boothe, 1995; Matsuno & Tomonaga, 2006; Matsuzawa, 1990). If these potential differences were taken into account in our study, we should modify our results as follows; compared to humans (i.e., compared to our current estimates), nonhuman apes may be slightly less sensitive to eye outlines (consisting of eyelashes and local shades), and some nonhuman species such as chimpanzees and mountain gorillas are slightly more sensitive to the color saliency of their orangish iris. In principle, therefore, such possible differences in spectrum sensitivity between species do not critically affect our main results demonstrating clear visibility of the eye outline in humans and clear visibility of the iris in both human and nonhuman apes (in their conspecific communication). However, to directly test the perceptual advantage of the white sclera, future experimental tests with both human and nonhuman ape subjects are necessary.

In conclusion, our results support, but also critically update, the gaze-signaling hypothesis. Specifically, we found that a key unique characteristic of the human eye is clear visibility of both the eye outline and iris, the two eye features that contribute to the visibility of eye-gaze direction, rather than the extent to which the sclera is exposed (area-wise) or the conspicuousness of eyes per se (in the face). Clear visibility of both the eye outline and iris is related to the uniformly white sclera in the human eye, which ensures the robustness of eye-gaze signals against various visual conditions. Humans may employ such robust eye-gaze signals as a powerful communicative tool to leverage their everyday social interactions by constantly updating and exchanging information about their own and others' attentional foci.

Declaration of Competing Interest

None.

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References

- Adams, L., Wilkinson, F., & MacDonald, S. (2017). Limits of spatial vision in sumatran orangutans (*Pongo abelii*). *Animal Behavior and Cognition*, 4, 204–222.
- Bard, K. A., Street, E. A., McCrary, C., & Boothe, R. G. (1995). Development of visual acuity in infant chimpanzees. *Infant Behavior and Development*, 18(2), 225–232.
- Bateson, M., Nettle, D., & Roberts, G. (2006). Cues of being watched enhance cooperation in a real-world setting. *Biology Letters*, 2(3), 412–414.
- Caspar, K. R., Biggemann, M., Geissmann, T., & Begall, S. (2021). Ocular pigmentation in humans, great apes, and gibbons is not suggestive of communicative functions. *Scientific Reports*, 11(1), 12994.
- Coppens, J. E., & van den Berg, T. J. T. P. (2004). A new source of variance in visual acuity. *Vision Research*, 44(9), 951–958.
- Csibra, G. (2010). Recognizing communicative intentions in infancy. *Mind & Language*, 25(2), 141–168.
- Csibra, G., & Gergely, G. (2009). Natural pedagogy. *Trends in Cognitive Sciences*, 13(4), 148–153.
- Deeb, S. S., Jorgensen, A. L., Battisti, L., Iwasaki, L., & Motulsky, A. G. (1994). Sequence divergence of the red and green visual pigments in great apes and humans. *Proceedings of the National Academy of Sciences*, 91(15), 7262–7266.
- Dulai, K. S., Bowmaker, J. K., Mollon, J. D., & Hunt, D. M. (1994). Sequence divergence, polymorphism and evolution of the middle-wave and long-wave visual pigment genes of great apes and old world monkeys. *Vision Research*, 34(19), 2483–2491.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, 24(6), 581–604.
- Farroni, T., Csibra, G., Simion, F., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proceedings of the National Academy of Sciences*, 99(14), 9602–9605.
- Farroni, T., Massaccesi, S., Pividori, D., & Johnson, M. H. (2004). Gaze following in newborns. *Infancy*, 5(1), 39–60.
- Gerald, M. S., Bernstein, J., Hinkson, R., & Fosbury, R. A. E. (2001). Formal method for objective assessment of primate color. *American Journal of Primatology*, 53(2), 79–85.
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, 2(3), 194–203.
- Jacobs, G. H., & Deegan, J. F. (1999). Uniformity of colour vision in Old World monkeys. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1432), 2023–2028.
- Jacobs, G. H., Deegan, J. F., & Moran, J. L. (1996). ERG measurements of the spectral sensitivity of common chimpanzee (*Pan troglodytes*). *Vision Research*, 36(16), 2587–2594.
- Jessen, S., & Grossmann, T. (2014). Unconscious discrimination of social cues from eye whites in infants. *Proceedings of the National Academy of Sciences*, 111(45), 16208.
- Kano, F., & Tomonaga, M. (2011). Perceptual mechanism underlying gaze guidance in chimpanzees and humans. *Animal Cognition*, 14(3), 377–386.
- Kaplan, G., & Rogers, L. J. (2002). Patterns of gazing in orangutans (*Pongo pygmaeus*). *International Journal of Primatology*, 23(3), 501–526.
- Kobayashi, H., & Kohshima, S. (1997). Unique morphology of the human eye. *Nature*, 387(6635), 767–768.
- Kobayashi, H., & Kohshima, S. (2001). Unique morphology of the human eye and its adaptive meaning: Comparative studies on external morphology of the primate eye. *Journal of Human Evolution*, 40(5), 419–435.
- Matsuno, T., Kawai, N., & Matsuzawa, T. (2004). Color classification by chimpanzees (*Pan troglodytes*) in a matching-to-sample task. *Behavioural Brain Research*, 148(1–2), 157–165.
- Matsuno, T., & Tomonaga, M. (2006). Measurement of contrast thresholds of chimpanzees using a parameter estimation by sequential testing (PEST) procedure (summary of awarded presentations at the 24th annual meeting). *The Japanese Journal of Psychonomic Science*, 25(1), 115–116.
- Matsuzawa, T. (1990). Form perception and visual acuity in a chimpanzee. *Folia Primatologica*, 55(1), 24–32.
- Mayhew, J. A., & Gómez, J.-C. (2015). Gorillas with white sclera: A naturally occurring variation in a morphological trait linked to social cognitive functions. *American Journal of Primatology*, 77(8), 869–877.

- Mearing, A. S., & Koops, K. (2021). Quantifying gaze conspicuousness: Are humans distinct from chimpanzees and bonobos? *Journal of Human Evolution*, 157, Article 103043.
- Osorio, D., & Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society B: Biological Sciences*, 263(1370), 593–599.
- Perea-García, J. O., Danel, D. P., & Monteiro, A. (2021). Diversity in primate external eye morphology: Previously undescribed traits and their potential adaptive value. *Symmetry*, 13(7).
- Perea-García, J. O., Kret, M. E., Monteiro, A., & Hobaiter, C. (2019). Scleral pigmentation leads to conspicuous, not cryptic, eye morphology in chimpanzees. *Proceedings of the National Academy of Sciences*, 116(39), 19248–19250.
- Provine, R. R., Cabrera, M. O., & Nave-Blodgett, J. (2013). Red, yellow, and super-white sclera. *Human Nature*, 24(2), 126–136.
- Provine, R. R., Nave-Blodgett, J., & Cabrera, M. O. (2013). The emotional eye: Red sclera as a uniquely human cue of emotion. *Ethology*, 119(11), 993–998.
- Sharma, P. (2015). Evaluating visual saliency algorithms: Past, present and future. *Journal of Imaging Science and Technology*, 59(5), 50501-1–50501-17. <https://doi.org/10.2352/J.ImagingSci.Technol.2015.59.5.050501>
- Smith, B. A., Yin, Q., Feiner, S. K., & Nayar, S. K. (2013). Gaze locking: passive eye contact detection for human-object interaction. *Andrews. Scotland, United Kingdom*. <https://doi.org/10.1145/2501988.2501994>
- Stevens, M., & Cuthill, I. C. (2006). Disruptive coloration, crypsis and edge detection in early visual processing. *Proceedings of the Royal Society B: Biological Sciences*, 273 (1598), 2141–2147.
- Stevens, M., Párraga, C. A., Cuthill, I. C., Partridge, J. C., & Troscianko, T. (2007). Using digital photography to study animal coloration. *Biological Journal of the Linnean Society*, 90(2), 211–237.
- Stevens, M., Stoddard, M. C., & Higham, J. P. (2009). Studying primate color: Towards visual system-dependent methods. *International Journal of Primatology*, 30(6), 893–917.
- Stokes, M., Fairchild, M. D., & Berns, R. S. (1992). Precision requirements for digital color reproduction. *ACM Transactions on Graphics*, 11(4), 406–422.
- Tomasello, M., Hare, B., Lehmann, H., & Call, J. (2007). Reliance on head versus eyes in the gaze following of great apes and human infants: The cooperative eye hypothesis. *Journal of Human Evolution*, 52(3), 314–320.
- Waitt, C., & Buchanan-Smith, H. M. (2006). Perceptual considerations in the use of colored photographic and video stimuli to study nonhuman primate behavior. *American Journal of Primatology*, 68(11), 1054–1067.
- Walther, D., & Koch, C. (2006). Modeling attention to salient proto-objects. *Neural Networks*, 19(9), 1395–1407.
- Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., & Johnstone, T. (2004). Human amygdala responsivity to masked fearful eye whites. *Science*, 306 (5704), 2061.