Scleral pigmentation leads to conspicuous, not cryptic, eye morphology in chimpanzees

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Gaze following has been argued to be uniquely human, facilitated by our depigmented, white sclera [M. Tomasello, B. Hare, H. Lehmann, J. Call, *J. Hum. Evol.* 52, 314–320 (2007)]—the pale area around the colored iris—and to underpin human-specific behaviors such as language. Today, we know that great apes show diverse patterns of scleral coloration [J. A. Mayhew, J. C. Gómez, *Am. J. Primatol.* 77, 869–877 (2015); J. O. Perea García, T. Grenzner, G. Hešková, P. Mitkidis, *Commun. Integr. Biol.* 10, e1264545 (2016)]. We compare scleral coloration and its relative contrast with the iris in bonobos, chimpanzees, and humans. Like humans, bonobos' sclerae are lighter relative to the color of their irises; chimpanzee sclerae are darker than their irises. The relative contrast between the sclera and iris in all 3 species is comparable, suggesting a perceptual mechanism to explain recent evidence that nonhuman great apes also rely on gaze as a social cue.

sclera | iris | eye | coloration | comparative morphology

Nonhuman great ape sclerae are typically darker than humans', which has been suggested to render their gaze direction "cryptic," inhibiting conspecific gaze following (1). However, recent behavioral evidence suggests that nonhuman great apes share the human ability to follow conspecific gaze (e.g., refs. 2–4). We suggest that whether gaze is conspicuous or cryptic is driven not by absolute depigmentation of the sclera but by the relative contrast between sclera and iris. We compare chimpanzee, bonobo, and human eye morphology. We show that, like humans, bonobo sclerae are lighter relative to their irises. We also show that, despite darkened sclerae in chimpanzees, the relative contrast between the sclera and iris is similar across all 3 species: Chimpanzee, bonobo, and human eye coloration are similar in their conspicuity, facilitating gaze following by a conspecific. Depigmentation of the sclera relative to the iris offered one evolutionary route to conspicuous gaze; the proximity of a lighter iris to a darker sclera offered an alternative, similarly conspicuous, pattern of eye coloration.

Results

We compared grayscale values of sclerae across humans ($n = 52$), bonobos ($n = 51$), and chimpanzees ($n = 50$) (ANOVA: F = 221.82, degree of freedom = 2, $P < 0.001$; Tukey honestly significant difference [HSD] all species comparisons: $P < 0.0001$). Chimpanzees had the darkest sclerae ($\bar{x} = 36.38 \pm 20.3$, $n = 50$), humans had the lightest ($\bar{x} = 168.06$, $\pm$ 36.77, $n = 52$), and bonobos had an intermediate value ($\bar{x} = 107.86 \pm 56.47$, $n = 51$). The iris also differed across species (F = 11.341, $P < 0.001$), although these differences were less pronounced (bonobos: $\bar{x} = 54.43$, $\pm$ 22.47, $n = 51$; chimpanzees: $\bar{x} = 63.82$, $\pm$ 22.7, $n = 50$; humans: $\bar{x} = 82.13$, $\pm$ 29.8, $n = 52$). The contrast between the scleral and iridial areas (measured as relative iris luminance [RIL]; see *Methods*) showed that all species display a comparable relative difference in grayscale value between the sclera and iris (3-way general linear model including interactions between species [$P = 0.916$, z value = 0.105], age [$P = 0.536$, z value = −0.619], and sex [$P = 0.579$, z value = −0.554]) (Fig. 1).

Humans show the most-uniform depigmentation of the sclera, but as a difference of degree: Most bonobos also present a lighter sclera than iris (we term this type 1 coloration; bonobos $n = 42$ of 51 individuals). Chimpanzee sclerae are darker than their irises (we term this type 2 coloration; chimpanzees: $n = 48$ of 50). In both types, the eye morphology displays a clear contrast between the iris and sclera. We ran a series of Tukey HSD tests between age groups in *Pan* species. Scleral values decreased with maturity in chimpanzees (difference = 2.35; adjusted $P = 0.0443$) and bonobos (difference = 4.87; adjusted $P = 0.0005$). Iridial coloration did not (bonobos: difference = −0.15, adjusted $P = 0.9797$; chimpanzees: difference = 0.11, adjusted $P = 0.9828$). RIL decreased (indicating increased conspicuousness) in chimpanzees (difference = 25.86; adjusted $P < 0.0001$), but not bonobos (difference = −17.10; adjusted $P = 0.3955$).

Discussion

Our data suggest a perceptual mechanism to inform behavioral observations of conspecific gaze following in great apes (2–4). All 3 species present similarly conspicuous gaze as a function of the difference between iridial and scleral areas. Bonobos have a morphology like ours: reduced pigmentation in the sclerae and darker irises. Chimpanzees sclerae are darker than their irises. While equally conspicuous, the different patterning of species-typical coloration cues may partially explain the behavioral finding that bonobos (typically type 1) followed gaze in human targets (also type 1), while chimpanzees (typically type 2) did not (4).

The observation that all 3 species present conspicuous eye coloration suggests reliance on gaze cues was relevant to our last common ancestor (LCA), and may date to the LCA of all extant great apes, with differential patterns of scleral depigmentation reported in gorillas (5) and orangutans (6). We do not know the ancestral state of scleral pigmentation, so we can only speculate about why bonobos and humans take a different route to conspicuous eye color than chimpanzees. One possibility is that scleral depigmentation arose as a spandrel—a by-product of selection against aggression. It has been proposed that bonobo and human behavior and morphology are the result of a marked period of selection against aggression (7, 8), resulting in a suite of phenotypic traits similar to those observed in domesticated animals (9), where depigmentation is consistently observed across species (10). If scleral depigmentation beneficially enhanced individual ability to track attention through gaze following, selection could then act on it in species-specific ways.

The decrease of scleral lightness with age is similar to that observed in humans (11), suggesting shifts in heterochrony. Delays

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Data deposition: The data reported in this paper have been deposited in the Open Science Framework (https://osf.io/uk4b2/?view_only=07d1a6cfd5fe409ca7e49d4cad437beb).

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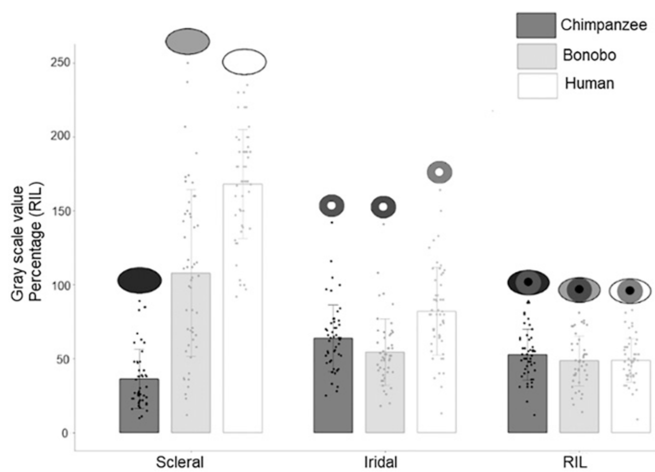

Fig. 1. RIL expressed as a percentage difference between how light the darkest part of the eye is relative to the lightest part. Each entry provides the mean, SD, and distribution of individual values across species.

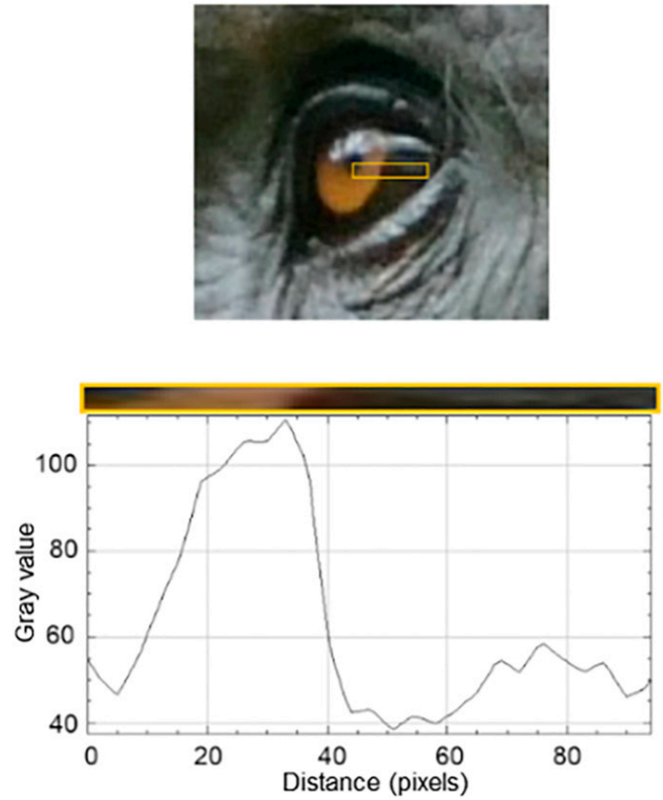

Fig. 2. Grayscale values of the sclera and iris, and the relative difference in luminance (RIL). The yellow rectangle is the selection area used to obtain grayscale values for iris and sclera. The graph shows the output from ImageJ's "plot profile" tool. Gray value is indicated on the *y* axis; distance is indicated on the *x* axis. The lightest area of the eye corresponds to the iris, and the darkest corresponds to the sclera.

in the migration of neural crest cells (NCC) in early embryogenesis have been proposed as the underlying cause for both reduced emotional reactivity and depigmentation in domesticates, as both adrenal glands and melanocytes derive from NCC (9). Whether scleral depigmentation arises from processes of selection against aggression is a testable hypothesis. Signatures of selection in the bonobo but not chimpanzee genome should resemble those of domestic animals relative to their wild ancestors (e.g., ref. 12). Similarly, if the genetic underpinnings of variation in scleral pigmentation are a by-product of selection against aggression, these should correspond to genes that affect migration of NCC in embryogenesis. These methods could be applied to test whether selection against aggression underlies speciation between extant species of apes: Lowland gorillas display lighter sclerae than mountain gorillas (5), and Sumatran display lighter sclerae than Bornean orangutans (6).

Our findings support behavioral evidence that chimpanzees follow conspecific gaze (13), contributing to mounting evidence (5) against the suggestion that darkened sclerae lead to inherently cryptic gaze (1, 14). Factors other than contrast (interplay between lighting and facial and ocular coloration and morphology, viewer contrast thresholds) may also affect gaze detectability in face-to-face interaction and should be further explored. Nevertheless, the relative coloration of scleral and iridial morphology within the eye provides a robust measure of potential gaze conspicuity and should be explored across a wide range of species, particularly where gaze following has been argued to be absent based on scleral coloration alone. Doing so may reveal further insight into the evolution of gaze-following behavior.

Methods

Samples. The study conformed to the legal requirements of the countries in which it was conducted, and the American Society of Primatologists' principles for the ethical treatment of primates. Photographs (*Pan troglodytes*, $n = 50$; *Pan paniscus*, $n = 51$; *Homo sapiens*, $n = 50$) were collected from various sources. We searched online for the terms "bonobo zoo." Photographs of wild chimpanzees were collected by C.H. at the Budongo Conservation Field Station, Uganda. For chimpanzees, all individuals could be identified and sexed; because exact information on bonobos' ages was sometimes absent, age was coded as "immature": 0 y to 12 y; or "mature": 13+ y (15, 16). M.E.K. collected photographs ($n = 50$) from adult human participants that were corrected for lighting differences using a color swatch, measured, and analyzed as a point of comparison with the *Pan spp.* The study protocol for the collection of the human sample was approved by the Psychology Research Ethics Committee (PREC) Internal Review Board (IRB) of the University of Leiden. Participants signed a consent form approved by the same IRB.

Scleral and Iridial Luminance. We used ImageJ (1.51j8, W. Rasband, National Institutes of Health, https://imagej.nih.gov/ij/). Following ref. 5, we focused on scleral coloration and its contrast with the iris, instead of including the surrounding skin as in ref. 14. We followed the procedure in ref. 6 but further specified our sampling area: The selection extended from the pupil and two-thirds the length of the iris radius into the sclera. The height was up to 10% of the total iris diameter. The selection finished if the rectangle reached potentially confounding factors, such as reflections or skin (Fig. 2). We noted whether the highest grayscale value was in the sclera (type 1) or the iris (type 2). Both eyes were measured, and a mean value per individual was calculated. RIL (17) was calculated; this is an index of the contrast between iridial and scleral areas, considering the context-sensitive nature of human brightness perception (18).

Analyses. Analyses were carried out in R 1.0.153. Data were examined for appropriateness for parametric statistics, and, where necessary, Tukey transformations were applied and data were retested.

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