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Forum

Evolution of the uniformly white sclera in humans: critical updates

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The human eye characteristically has exposed and uniformly white sclera, which is hypothesized to have evolved to enhance eye-gaze signaling for conspecific communication. Although recent studies have put this hypothesis into question, current morphological and experimental evidence supports its key premise, albeit with recommendations for critical updates.

Although it is commonly held that the white sclera is unique to humans among primates, this feature *per se* is not uncommon in non-human primates. As Figure 1 illustrates, many species of primates have whiteness in at least some parts of the sclera, and there are substantial individual differences in the degree of pigmentation within a given species. What is, then, unique about the human eye?

Kobayashi and Kohshima [1] were the first to perform a comparative study on the external eye morphologies of 88 primate species. They claimed that one unique aspect of the human eye is that 'the exposed white sclera is void of any pigmentation' ([1] p. 419), namely that the human sclera is both widely exposed and uniformly white (from the iris edge to the eye corner) due to the loss of pigmentation on the surface structures of eyes (including epithelium cornea, conjunctiva, and sclera). Based on this key finding, Kobayashi and Kohshima proposed the 'gaze-signaling hypothesis', that humans have evolved these unique eye features to increase the visibility of eye-gaze to enhance conspecific communication. This hypothesis was extended by Tomasello *et al*. [2] as the 'cooperative-eye hypothesis', proposing that humans have evolved unique eye features as well as a special sensitivity to conspecific eye-gaze to enforce close-range joint attentional and communicative interactions, key interactive components to human cooperation.

Kobayashi and Kohshima [1] evaluated the colors of surface eye features using qualitative categorization methods and did not particularly consider individual variation within each species. Consequently, recent quantitative studies have questioned the key premise of their hypothesis by demonstrating that human eyes are not necessarily unique compared with non-human primate eyes in terms of color features [3–7]. Critically, these studies used large image samples of humans and non-human apes and found that the color contrasts/differences between the iris and sclera are similar between humans and non-human apes. Interestingly, some primate species, such as chimpanzees and mountain gorillas, typically have a dark sclera and a brighter iris (Figure 1) and this color contrast is similar to the one between the uniformly white sclera and the darker iris of the human eye [4–6]. This finding clarified that non-human ape eyes are as conspicuous as human eyes, at least in the sense that their eye positions on their face are visible due to high iris–sclera color contrast (thus partly against Kobayashi and Kohshima's 'gaze-camouflaging hypothesis', which proposed that non-human primates' pigmented sclera camouflages their gaze directions).

One important distinction, however, is the visibility of eye position and eye-gaze. It should be emphasized that the visibility of eye position on the face only clarifies where an individual's head is directed (head-gaze), but not where the individual's eye-gaze is directed. Notably, although visible iris–sclera color contrast is sufficient for the eye position (on the face) to be visible, for the eye-gaze to be visible, both eye position and iris position need to be visible with respect to the eye outline (the perimeter of the eye-opening) [1] because the visible eye outline functions as the reference frame for the iris position. A recent study [6] therefore directly quantified the conspicuousness of all these features in seven great ape species, including humans, using the color-difference analysis similar to [4,7] and also the edge-detection analysis that identified edges of images (discontinuities of image brightness) on both eye and iris outlines. They found that while the iris position is equally conspicuous across species, the eye outline is generally more conspicuous in human faces as compared with non-human ape faces. Critically, although both features are sufficiently conspicuous when there is minimal visual noise on the facial images, the eye outline becomes increasingly less conspicuous in non-human ape faces as compared with human faces when the facial images are darker and blurrier (i.e., simulating longer viewing distances and less lighting). This is mainly because the uniform whiteness of the human sclera creates a thick eye outline (mainly consisting of local shades around the eyelashes), which is robust to visual noise, while darker or more patchy colors of non-human ape sclera more easily blend into the color of the adjacent skin in the presence of visual noise.

Therefore, the gaze-signaling hypothesis needs to be critically updated as follows: human eyes may have a signaling advantage over non-human eyes: (i) in terms of the visibility of the eye-gaze [6], but not necessarily the eye position on the face (also not necessarily the head-gaze) [3–6]; and (ii) only under visually challenging conditions (e.g., longer visual distances and less lighting) [6].

There is new evidence that supports this updated gaze-signaling hypothesis. In a recent experimental study [8] researchers

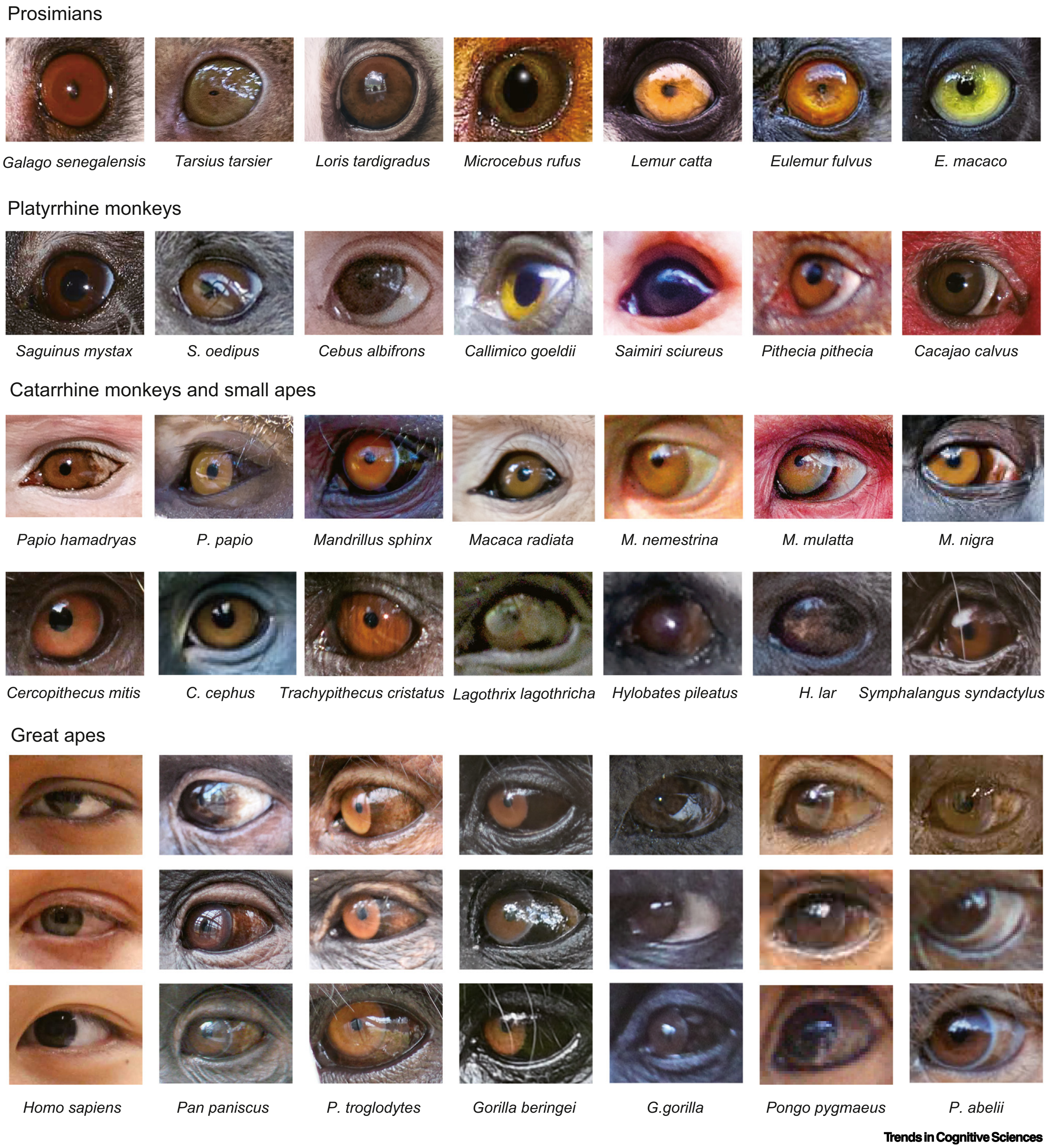

Figure 1. Examples of eye colors in primates. Within-species individual variation in eye color and prominence of a white sclera is also indicated in great ape species.

tested the discrimination performance of human participants in visual search tasks of eye direction in facial images with manipulated eye colors. They found that darkening the sclera colors of human facial images deteriorated the participants' performance and that the eye-gaze with white sclera remained visible to the participants even when the facial images were downsized and darkened, suggesting the role of the uniformly white sclera in supporting gaze perception under visually challenging conditions.

What about the evidence from non-human primate subjects? Testing non-human primates is particularly important to distinguish between the two possibilities; whether human eyes *per se* have a perceptual advantage to enhance the eye-gaze cues or whether humans have special perceptual expertise to read subtle eye-gaze cues from conspecifics' eyes. These two possibilities were explored in a study [9] that adopted a fully crossed species comparative design where both human and chimpanzee participants discriminated the eye directions of both human and chimpanzee facial images in computerized screen-based tasks. Chimpanzees were trained with a touch screen until they learned to reliably discriminate the eye directions of both species' images. Although this training was demanding for them, three chimpanzees mastered this task. In the critical test conditions, the contrast polarities of eyes were either kept normal or reversed in both chimpanzee and human faces, so that both chimpanzee and human faces have both uniformly white and dark sclera across conditions. In both chimpanzee and human participants, faces with uniformly white sclera had critical advantages over faces with darker sclera for their gaze discrimination performances, but only when the facial images had simulated visual noise, again supporting the updated gaze-signaling hypothesis.

One interesting implication of these recent updates in the gaze-signaling hypothesis is that human eyes seem to have a signaling advantage over non-human ape eyes under very specific communicative situations; specifically, where an individual needs to exchange information about their own and another's precise points of visual attention, from both head and eye directions, even across various viewing distances and lighting conditions. This is likely not necessarily a situation where a dyad is interacting face-to-face, in close range. Rather, it may be a situation where multiple individuals communicate with one another in a large group, of which members are distributed over space: thus they cannot always optimize the visibility of others' faces and eyes. Although the cooperative-eye hypothesis [2] suggested that humans evolved the special morphological eye features mainly for close-range social interactions 'involving two or a few individuals' ([2] p. 315), it may have been larger-scale interactions that provided selective pressures for the unique appearance of the human eye (also see Box 1 for alternative potential evolutionary drivers). Thus, these recent updates in the gaze-signaling/cooperative-eye hypothesis may underscore the importance of considering the scale of social interactions in uncovering the evolution of human communication.

Box 1. Evolutionary drivers of white sclera

Although the gaze-signaling/cooperative-eye hypothesis presumes that the major function of humans' uniformly white sclera is aiding individuals to convey eye-gaze directional cues during joint attentional and communicative interactions, alternative functions can be suggested in distinctive contexts/behaviors. For example, the features that are clarified by the uniformly white sclera (i.e., the eye outline and the iris position in the eye outline) should also aid individuals to signal nuanced emotional expressions via both degrees of eye-opening and directions of eye-gaze. Recent experimental studies have shown that agents having uniformly white sclera, compared with those having darker sclera, are perceived as more cooperative by human children [10] and healthier, younger, more attractive and trustworthy, and less aggressive by human adults [11] ([10,11] as the most recent examples of this line of research); thus, a uniformly white sclera may also serve as a cue for partner choice in humans, which may partly explain why nearly all individuals of humans have this trait across different populations. Thus, humans' uniformly white sclera may have evolved under multiple selective pressures (also see a recent phylogenetic comparative study [12] that suggests self-domestication as another driver of sclera whiteness in primate species).

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Declaration of interests

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