

THE WHITES OF THEIR EYES: THE EVOLUTION OF THE DISTINCTIVE SCLERA IN HUMANS

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At some point in human evolution, hominins developed eyes that were morphologically unique in comparison with their close primate relatives. Specifically, the amount of exposed sclera increased and the tan or dark brown pigment found in the sclera of other primates was eliminated. Because visual cues and gaze detection are so important to human behavior, it follows that the unique morphology of the human eye conferred fitness upon those individuals. Several theories have been proposed to explain these changes as adaptations to particular environmental and social selective forces, but very few studies have directly tested these theories. Based on the available data, it seems most likely that the unique morphology of the human eye initially developed as a result of hominins becoming terrestrial predators and was completed by the need to communicate effectively with other hominins.

The theories surrounding research in this area of hominin evolution range from very simple—that the white sclera would have signaled health and thus conferred reproductive fitness in the same way that a peacock's brilliantly colored tail attracts a mate—to complex theories that integrate both biological and cultural phenomena (Tomasello et al. 2007). A commonly espoused idea in the scientific community is that the most parsimonious answer to a question is often correct, but no evidence corroborates the mate attraction theory (Tomasello et al. 2007). Two major studies which will be explored in this paper concern the comparative morphology of a wide range of primates, how these differences affect behavior, and what inferences one can make regarding the adaptive reasons behind those differences. Hiromi Kobayashi and Shiro Kohshima conducted a study in 1998 that measured the eyes of 88 species of primates using computer-aided image analysis to determine the differences between species and to examine how these differences correlate with biological and environmental variability (Kobayashi & Kohshima 2001). Michael Tomasello and associates have carried out numerous studies using apes, monkeys, and children that explore issues relating to cognition and communication; this body of work is integrated into the "cooperative eye hypothesis," which will be explored in the body of this paper (Tomasello et al. 2007:316).

Kobayashi and Kohshima measured the width/height ratio of the eye outline (WHR) and an index of exposed sclera size in the eye outline (SSI) to analyze and compare eye shape differences. A total of 874 individuals representing 88 species were recorded by video camera or analyzed from photographs to collect eye shape measurements. Information concerning weight, sitting height, crown-rump length, and habitat type was collected from published sources (Kobayashi & Kohshima 2001), and some walking-height and sitting-height information was collected in the Japan Monkey Center. Eye coloration measurements of 92 species were recorded by direct observation of living animals and of prepared eye specimens by two persons working independently. Disagreement between the two observers occurred only 8% of the time, concerning the distinction between the eye colors of 6 species. Sclera coloration was divided into four categories: brown, pale brown, partly white, and white. The researchers collected data on eye movement by directly observing primates eating in cages and humans eating alone in a restaurant and calculated ratios of horizontal scanning to vertical scanning by counting eyeball and head movements (Kobayashi & Kohshima 2001).

Kobayashi and Kohshima found that humans have the largest area of exposed sclera and have the most horizontal eye elongation among the primates studied. Both SSI and WHR ratios increased in an order similar to what one would observe by following the branching of a primate phylogenetic tree: Prosimii, Ceboidea, Cercopithecoidea, Hominoidea. That is, the most primitive primates had the smallest SSI and WHR ratios. In light of this preliminary evidence, the researchers postulated that these differences could “reflect some difference in visual function and/or adaptation to some environmental or physiological factor such as the habitat and body size of the species” (Kobayashi & Kohshima 2001:424). To test whether or not relationships between the eye differences and these factors exist, they compared their eye data to known data regarding eye function, body size, and ecology (Kobayashi & Kohshima 2001).

The researchers found that not enough difference exists between the eye functionality of the studied phylogenetic groups to explain the eye shape disparities, but correlations with body size and environment were marked. The researchers then ranked the subjects using the aforementioned body size measurements, finding that the amount of exposed sclera increased with body size. This correlation was especially noticeable in walking height comparisons; the species with the tallest walking height, in this case the humans, have the largest area of exposed sclera (SSI). In primates, eyeball and/or head movement are especially important for the adjustment of perceived images (Kobayashi & Kohshima 2001). “A larger SSI means a smaller iris relative to the eye outline and probably a greater ability for visual field extension by eyeball movement; in eyes with a large SSI the small iris has a wider space to move within the open eye

outline” (Kobayashi & Kohshima 2001:426). Kobayashi and Kohshima hypothesized that the correlation between SSI and body size is an adaptation for extending the visual field by eyeball movement, as opposed to head movement. Without digressing into an intensive explanation, suffice to say that larger animals save energy by using the eyeball to redirect gaze as opposed to turning the whole head (Shultz 1940). Kobayashi and Kohshima tested this hypothesis by observing 18 species and counting the number of head and eyeball movements involved in changing gaze direction (2001). The results supported their hypothesis.

Observing that the mean value of WHR is “greatest in terrestrial species, moderate in semi-arboreal species and lowest in arboreal species,” Kobayashi and Kohshima theorized that a “horizontally elongated eye outline is adaptive in extending the visual field horizontally by eye movement, and terrestrial life needs more horizontal scanning than vertical scanning” (2001:428). They tested this hypothesis by again observing primates eating in cages and measuring the time and frequency of horizontal and vertical scanning. They found that the ratio of horizontal to vertical scanning is significantly higher in terrestrial species than in arboreal species.

As stated previously, Kobayashi and Kohshima separated 92 species into four categories based on the color of the sclera. Most of the primates observed have a dark brown sclera, while a few had lighter brown sclera or a partially white sclera; humans were the only primates observed to have white sclera without any pigmentation. Since pigmentation requires some energy, it follows that if primates have this pigmentation, it must have some adaptive function. A theory advanced by S.S. Duke-Elder (1985), states that the pigmentation may be an anti-glare device. If this were true, then nocturnal species should have white sclera and humans should have colored sclera; neither case occurs. Other researchers have proposed that having dark sclera is adaptive in many nonhuman primates because gaze direction is so important in intraspecific communication (Chance 1962; van Hooff 1962; Andrew 1964; Tomasello et al. 2007).

Direct eye contact is construed as threatening behavior in many species of monkeys, thus the inability to perceive whether or not another individual is looking at a dominant individual would reduce violent intraspecific altercations (Kobayashi & Kohshima 2001; Perrett & Mistlin 1990). Kobayashi refers to the research of P.W. Sherman in stating that “colored sclera obscuring gaze direction may serve to deceive natural predators . . . by making it difficult for predators to know if the prey has them in their gaze” (Kobayashi & Kohshima 2001:431; Sherman 1977). Thus prey might gain a slight advantage in concealing their gaze direction from potential predators. Kobayashi and Kohshima realized that if this “gaze camouflage theory” is a factor, then the color of the exposed sclera should

be similar to the color of the iris and/or the face around the eye, making it difficult to “detect the position of [the] iris in the eye outline and/or the eye outline in the face” (Kobayashi & Kohshima 2001:431). Another examination of the sclera data becomes necessary.

Kobayashi and Kohshima separated 82 primate species into four categories based on the degree of contrast between the sclera and the iris/face. The four types are: (1) dark sclera and similarly dark face and iris, obscuring both eye outline and iris position; (2) sclera darker than iris but similar to face color, obscuring iris position while allowing eye outline in face to be discerned; (3) sclera darker than iris but similar to face color, obscuring eye outline while allowing iris position in face to be discerned; (4) sclera is paler than face/iris and both eye outline and iris position are clearly discernable (Kobayashi & Kohshima 2001). The researchers found that “almost all [of the] nonhuman primates species observed (80 out of 81 species) belonged to Type 1 or Type 2 coloration types” (Kobayashi & Kohshima 2001:433). In these types, the direction of gaze is effectively camouflaged by obfuscation of the position of the iris in the eye outline and/or the position of the eye outline in the face because of similarly colored features. The only nonhuman species that did not belong to Type 1 or Type 2 was the ruffed lemur, which has a clearly discernable iris position but an obscured eye outline; this morphology also effectively camouflages the direction in which the animal is gazing. The only species that had a clearly visible eye outline and iris position were *H. sapiens*; in all cases the sclera was much paler than the surrounding facial skin and the iris. Thus Kobayashi and Kohshima’s results support the “gaze camouflage theory”; the question then arises as to why humans are the only species to completely lose pigmentation of the sclera (Kobayashi & Kohshima 2001:431).

The researchers suggest that humans may have lost the pigmentation of the sclera because of an increase in terrestriality, an increase in body size, and the use of tools and fire which may have made humans less susceptible to predators. This, coupled with an increase in cooperative and mutualistic behaviors, may have necessitated gaze signal enhancement instead of obfuscation. These factors would have reduced or eliminated the necessity of the protective feature of the darkened sclera while selecting for improved communication via clearly visible gaze signaling (Kobayashi & Kohshima 2001). While research regarding the correlation between body size and use of tools (and how they affected predation) is largely impossible due to the lack of fossil evidence that might have significant bearing on these issues, it is possible to study the differences in gaze signaling and cooperative communicative behavior in present day primates and humans to gain some insight as to how and why modern human ancestors may have begun to utilize complex communicative signals. Michael Tomasello and colleagues address the differences in gaze following in human and nonhuman primates in a recent (2007) study conducted at the Max Planck Institute for Evolutionary Anthropology.

Before presenting the results of Tomasello's study on the differences in gaze following, it is helpful to examine previous experiments which bear upon this issue. It has been noted that humans and some nonhumans cooperate in "some unique ways in close-range social interactions involving two or a few individuals acting together toward a concrete goal" (Tomasello et al. 2007:314). While chimpanzees have been observed to hunt together in small groups (Boesch and Boesch 1989; Mitani and Watts 1999), humans seem much more likely to engage in cooperative activities that are not goal oriented (Warneken et al. 2006). Also, "humans seem especially inclined, as compared with other primates, to engage with one another in collaborative activities around objects- so called joint attentional interactions" (Tomasello et al. 2007:314; Bard and Vauclair 1984; Tomasello and Carpenter 2005). In a 2005 study, Tomasello and colleagues found that in joint attentional interactions, individuals monitored what other individuals were focused upon, including whether or not the other individual was monitoring their own activity.

In an example important for understanding the circumstances in which language evolves, two separate studies have found that joint attentional interactions between mothers and infants form the "referential context within which skills with language develop" (Tomasello et al. 2007:315; Bruner, 1983; Tomasello 2003). Joint attentional interactions between human infants and their caregivers average twice as long in duration as those of human-raised great apes with their caregivers and the duration of infants' looks to the face/eyes of their caregivers average twice as long as those between human-raised great apes and their caregivers (Carpenter et al. 1995). Thus it would seem that communication via gaze is more important in human interactions and more highly visible eyes might have evolved because they would be especially helpful in initiating and maintaining joint attentional communicative interactions. Tomasello recognizes that studies have been enacted that demonstrate gaze following in both human and nonhuman primates, but only one study makes a distinction between head following and eye following. That study concerns only human infants, finding that infants follow an adult's gaze direction more often when her eyes are visible and open than when they were closed or obstructed with a blindfold (Brooks and Meltzoff 2002). In his recent study, Tomasello hypothesizes that, "based on humans' greater propensity for object-centered cooperative/communicative interactions. . . and their especially visible eyes. . . human infants would be more influenced by the eyes than the head, whereas great apes would be more influenced by the head than the eyes" (Tomasello et al. 2007:316). He calls this theory the "cooperative eye hypothesis" (Tomasello et al. 2007:316).

Tomasello and his colleagues performed one experiment with 19 great apes, including 11 chimpanzees, 4 gorillas, and 4 bonobos (aging from 4 to 27 years); the experiment was replicated with 40 human infants (aging approximately 12 months and approximately 18 months). Each participant was tested individually in a test

room where the participant was separated from the experimenter (E) by plexiglass or wire mesh (Tomasello et al. 2007). Each participant was tested 5 separate times in each of the 6 experimental conditions (for the apes) or 4 separate times in each of the 5 experimental conditions (for the humans). The experimental conditions were as follows:

Head only. E closed his eyes and looked immediately to the ceiling.

Eyes only. E kept his head stationary and glanced with his eyes to the ceiling.

Both. E looked to the ceiling with head and eyes.

Neither. E stared straight ahead at the subject.

Back of Head. E sat with his back to the subject and looked up to the ceiling.

***Back Control.** E sat with his back to the subject and stared straight ahead.

*The “Back Control” condition was not used with the human infants because pilot testing revealed a tendency for infants to become upset when they were ignored (Tomasello et al. 2007).

The tests were videotaped and the tapes were reviewed by an independent scorer (not the experimenter). In the ape trial, the experimenters found that “apes followed E’s head direction up even if his eyes were closed, and they were more likely to follow his eyes to the ceiling if his head was also directed up” (Tomasello et al. 2007:317). From this, the experimenters concluded that head direction is more important in the gaze following of great apes, with the eyes playing a minor role (Tomasello et al. 2007). In the human trial, the experimenters found that the human infants followed both head and eyes movements, but, unlike the apes, “the most important factor for human infants was the eyes” (Tomasello et al. 2007:317-18).

Overall, the nonhuman apes and the human infants both responded similarly when E’s head and eyes were either oriented upward or downward, but in the conditions in which head and eye orientation were different, the two groups showed very different patterns. Apes looked up “approximately 2.5 times more often when only E’s head was oriented up (eyes closed) than when only E’s eyes were oriented up,” while the human infants looked up “approximately three times more often when only E’s eyes were oriented up (head down) than when only E’s head was oriented up (eyes closed)” (Tomasello et al. 2007:318). These results support Tomasello’s hypothesis and suggest that in gaze following situations, humans are much more attuned to eye movement than nonhuman apes.

Tomasello recognized that this area of research is new and thus the information gained from this study may be limited in certain respects. The age disparity between the test groups, for instance, could have affected the results, but other studies with younger apes—including a few concerning human raised apes—supported these results (Tomasello et al. 2001; Call and Tomasello 1994; Gomez 1996; Itakura and Tanaka, 1998). The fact that the experimenter was a human may also have affected the results; primates might more reliably follow the gaze of conspecifics. However, it is worth noting that in this experiment the overall level of gaze following was higher in the great apes than that in the human infants (Tomasello et al. 2007). In addition, only about half of all extant primate species were studied. It is both possible and probable that other species of primates could exhibit different gaze-following behavior. The lack of studies that differentiate between head and eye movement is also a problem. Future studies that also emphasize a qualitative distinction between eye oriented gaze following and head oriented gaze following would be instrumental in understanding this phenomenon.

Like Kobayashi and Kohshima, Tomasello discusses the possible reasons why nonhuman primates would have retained camouflaged eyes while humans have evolved high eye visibility. “In general, using head and/or face direction as the major cue makes sense for all animals, as head direction can be seen from a much larger distance” (Tomasello et al. 2007:318). As stated previously, subordinate animals living in a hierarchical social group would benefit from being able to hide the direction of their gaze, as perceived staring at a dominant male could have disastrous consequences. In terms of food acquisition, it would also be detrimental for an observer to be able to tell where an individual was looking; if the individual was looking at a potential food source, its visible gazing might introduce competition over that food source. Therefore, individuals in constant competition for food sources, even those that live in social groups, would not benefit from having highly visible eyes. From this standpoint, the evolution of highly visible eyes would “seem to imply cooperative group mates who will not exploit the gaze direction of others to the extent that the looker is disadvantaged” (Tomasello et al. 2007:318). In a related study, chimpanzees were more skillful in using a human communicative cue to find food when it was given in a competitive environment (Hare and Tomasello 2004); human two-year olds showed the opposite pattern (Hermann and Tomasello 2006). Tomasello’s body of work thus seems to support the “cooperative eye hypothesis.”

It may never be known when, and exactly why, hominins developed such unique eyes, but the current evidence lends itself to a theory that encompasses both environmental and social selective forces. Kobayashi and Kohshima found a strong correlation between body size and terrestriality; primates generally increase in body size as they become more terrestrial (Kobayashi & Kohshima 2001). Their

study found that terrestrial primates have larger and more visible eyes. While Kobayashi and Kohshima examined the difference between primates with dark colored sclera and those with white colored sclera, they neglected to examine the four species that exhibited a partially white sclera. If these species possess ecological and/or communicative characteristics that are intermediate between those of highly arboreal and highly terrestrial species, their morphologies would support the hypothesis that humans lost the pigmentation of the sclera when they moved into a highly terrestrial environment and began using more complex forms of communication. Michael Tomasello and colleagues tested nonhuman apes and human infants to detect what differences, if any, existed in their methods of gaze redirection. Their evidence, that humans are more attuned to eye-based gaze redirection, supports a theory that humans use their eyes more complexly in communicative interactions (Tomasello et al. 2007). In addition, human interactions are more likely to involve object-centered cooperative communication. Humans seem to use the direction of eye gaze more reliably than other primates and enjoy communicating for both the sake of communication and for mutual benefits.

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