

# Quantifying ocular morphologies in extant primates for reliable interspecific comparisons

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## Abstract

Cross-examining evidence from comparative morphology has become a way to support specific hypotheses in social cognition. In particular, ocular morphology has been compared across extant primate species in order to argue that humans present a unique morphology that enables also an uniquely human array of socio-cognitive functions—including a crucial role in the acquisition and practice of linguistic abilities. Even though some of these comparisons have relied on quantifiable dimensions of ocular morphology, other aspects of the comparison have been established qualitatively, based on subjective ratings. In this article, I present a new method that intends to restrain the focus of attention to one specific perceptual aspect of ocular morphology—namely, the contrast between scleral and iridal colors, as it is thought to enable (or ease) gaze following from other individuals. The method also allows for more reliable comparisons across extant primate species, as it relies on quantifiable measurements. I exemplify the potential of this method with a three-fold comparison of three great ape species (*Pongo pygmaeus*, *Pongo abelii*, and *Homo sapiens*).

## 1. Introduction

The field of comparative psychology provides a convoluted picture of eye-gaze following in monkeys, apes, and humans. Findings from the field of comparative morphology (Kobayashi and Koshima 1997, 2001) have supported the view that eye-gaze following is a distinctly human behavior that does not occur even in other great apes (Tomasello 2007). Namely, Kobayashi and Koshima (1997, 2001) have held that the occurrence in humans of a high contrast between the iris and the sclera (resulting from a total depigmentation of the sclera) is an adaptation that facilitates gaze following by contributing to a hyper-conspicuous gaze. It has been proposed in parallel that this adaptation cannot be found outside our genus (Kobayashi and Koshima 1997, 2001).

The presence of this depigmented sclera in a member of a nonhuman primate species would have an important impact on gaze-following abilities because, as Kaplan and Rogers (2002) put it, '[g]azing can attain signal function only if the message delivered by gazing alone can be seen and interpreted by a receiver'. Both the binary character of the trait (i.e. totally apparent in human, and not apparent at all in other primates) and the alleged one-to-one mapping with a socio-cognitive function (i.e. gaze following) have been recently contested (Mayhew and Gómez 2015). Given the attentional aspect of gaze following (Povinelli 2001), this morphological adaptation has thus been directly associated with high-order cognitive skills. Some authors have gone so far as to establish a correlation between neural proxies of sociality like degree of encephalization

(Jerison and Barlow 1985; Herculano-Houzel 2009) and the occurrence of a depigmented sclera, suggesting that social factors influenced the evolution of eye morphology (Kobayashi and Hashiya 2011).

But how can a better understanding of ocular morphology inform the study of language in general, and the study of language evolution in particular? It is a pervasive view in the relevant literature that gaze following is capital in the acquisition of language, especially with regard to the association between lexical items, such as words, and the referents they denote (Tomasello and Farrar 1986; Dunham et al. 1993; Mundy et al. 2007; Tomasello, 2009; cf. Baldwin 1993, 1995). This is because following the gaze of others affords the establishment of joint attention, whereby two (or more) organisms can direct their attention to an entity outside the communicative dyad. As such, exploring how—and to what degree—different ocular morphologies afford gaze following behaviors can inform us about the degree to which referentiality can be instantiated as a mere by-product of visually attending to a referent outside the communicative dyad. This dependence on a depigmented sclera for the normal development of linguistic-referential communication in humans would seem congruent with the assumption that only humans present this trait (Kobayashi and Koshima 1997, 2001).

But to begin with, does the available evidence suggest that a depigmented sclera is uniquely human, or could it be said to be more generally characteristic of great apes as a clade? In his review, Emery (2000) points out that, relative to prosimians and monkeys, great apes show a much more reduced protrusion of the face (as a result of a smaller jaw size and length of the snout). Emery (2000) speculates that this reduction in facial protrusion could have resulted in a shift of salience whereby hominoids would attend to the eyes when inferring direction of attention (as a function of perceived gaze). He goes on to remark that, whereas

*[d]etermining the direction of another individual's attention is easier to establish from larger visual cues, such as the head, [f]lattening the face of the great apes (for example, as a result of a reduction in olfactory processing and an increased reliance on binocular vision) could have reduced the amount of information that could be transmitted by the head alone. The eyes are much smaller than the head, but they present a more precise indicator of where another is looking. (Emery 2000)*

This could be further enhanced by the overall loss of facial hair also observed in great apes, which facilitates the perception of components of facial expressions such

as movements of the eyebrows (Sadr et al. 2003) or the lips (Kuze et al. 2005).

However, the most widespread view is that humans are the only primate species whose morphology has shifted morphology to one that affords eyes being taken as reliable visual cues of attention. This is the case even though, as pointed above, the morphological adaptations that ‘force’ the shift from head to eyes as cues of attention (e.g. loss of facial protrusion) are a characteristic of great apes as a clade, and not only humans.

Here, I will review the literature in order to trace the origins of the idea that only humans have developed an ocular morphology that ‘makes up’ for the loss of facial protrusion as a cue of attention. I will argue that new comparative evidence indicates the occurrence of this trait to some degree in other great apes, forcing us to reconsider its involvement in instantiating referential information. This new evidence will be used as a case study to present a more reliable method for the comparison of ocular morphology across great ape species than that has been heretofore used.

### 1.1 Morphological adaptations that facilitate the inference of attentional states

Even though information inferred from the eyeball itself has been the focus of previous research, it is worth pointing out that this is far from being the only body part that great apes might look at when building inferences about the attentional states of others. Body and head directions are often taken as attentional cues by great apes (Tomasello 2007). Emery (2000) points to bipedalism as partly responsible for the adaptations that facilitate the inference of attentional states from facial information (including the eyes):

*It would appear to be relatively simple to determine the direction in which a body is pointed if a quadrupedal stance is adopted. Humans rarely adopt this posture, remaining in a more upright bipedal stance. Monkeys and apes, being characteristically quadrupedal in posture, may not require a more accurate method for interpreting direction of attention than head direction or body posture, because the information provided from posture may be sufficient.*

However, apart from the eyeball, body or face orientation, some other morphological features have been pointed out at as possibly facilitating the perception of others’ attention in great apes. Kaplan and Rogers (2002), for example, consider a series of morphological features of the eye and surrounding areas that might not be as important in human intraspecific communication,

but could potentially be an integral part of intraspecific communication in other primate species. The authors mention the silvery or white color of eyelids that is typical of some baboon and macaque species, respectively (Napier and Napier 1994), raising the possibility that the high contrast with the color of the surrounding skin or hair could be used for social signaling. Kaplan and Rogers (2002) specifically assess the eye morphology of orangutans, pointing out that they have some unique surrounding features:

*Infant orangutans have light-colored circumocular skin that later darkens; their eyelids are pink to white. Adult Sumatran orangutans also have light pink eyelids, which are very conspicuous when the eyes are closed. [...] The eyelashes are a different color from that of the eyelids and surrounding area. In Sumatran orangutans, the eyelashes in the center of the eye are a silver color. When the orangutan looks down, the silver eyelashes are exposed and, from a distance, this may give the impression that the individual is alert and watching when, in fact, it is preoccupied with an object in the lower field of vision.*

It should be noted again that, as Kaplan and Rogers (2002) themselves remark, it is currently not known whether these morphological features are used in communication between primates, great apes, or, more specifically, orangutans. More naturalistic observations of orangutans interacting with conspecifics should shed light on these questions.

## 1.2 Depigmented sclera—an adaptation linked to socio-cognitive functions

Relatively few publications have investigated primate eye coloration (iris color in *Macaca fuscata*: Zhang and Watanabe, 2007; comparative study of the blue iris phenotype in humans and lemurs: Bradley et al. 2009; comparative gorilla eye pigmentation: Knapp et al. 2007) and even fewer have been conducted with regard to possible implications for attentional cues (Kobayashi and Koshima 1997, 2001; Kaplan and Rogers 2002; Mayhew 2013; Mayhew and Gómez 2015). Of these studies, it has been Kobayashi and Koshima's (1997) that undoubtedly had the biggest impact in the relevant literature.

The authors compared and classified the ocular morphology of eighty-eight primate species according to both quantitative and qualitative measures. The quantitative measures consisted first of a width/height ratio, determining the dimensions of the exposed area of eyeball from one corner of corner of the eye to the other



**Figure 1.** 'A' denotes the distance between the corners of the same eye. 'B' identifies the longest perpendicular line to 'A' (i.e. the distance from top to bottom of the eye). 'C' refers to the width of the exposed eyeball. 'D' is the diameter of the iris. Kobayashi and Koshima obtained WHR by dividing A/B. Likewise, they obtained the SSI by dividing C/D.

and from the upper eyelid to the lower—which Kobayashi and Koshima termed 'the width/height ratio of the eye outline (WHR)'. The second quantitative measure is defined as 'an index of exposed sclera size in the eye outline (SSI)', which is obtained by dividing the width of the exposed eyeball by the diameter of the iris (Fig. 1). They also qualitatively assessed patterns of coloration of the eye (sclera and iris) and surrounding facial skin, or hair, establishing a taxonomy in which humans are presented as presenting a unique pattern among all of the eighty-eight species included in the survey (Table 1).<sup>1</sup>





## 1.3 Is a depigmented sclera a uniquely human morphological feature?

The comprehensiveness of Kobayashi and Koshima's (1997) study is both its strength and its major caveat—in attempting to establish generalizations about morphological features in primates, they blur the finer commonalities among great apes. Thus, whereas the study boasts an impressive eighty-eight species of primates, it crucially fails to include two extant great ape species (*Gorilla beringei* and *Pongo abelii*). Mayhew (2013; see also Mayhew and Gómez 2015) already noted the occurrence of a human-like sclera in *G. beringei*, suggesting that this could also be true of other great ape species. Furthermore, the sample size in Kobayashi and Koshima's (1997) study is limited, in that it includes only an analysis of six gorillas (*G. gorilla*), and of three orangutans (*Pongo pygmaeus*). This is important because, as Mayhew and Gómez noted (2015), a depigmented sclera is only typical of certain individuals within a gorilla population. This also seems to be true of Sumatran orangutans (see 'Results' section below)—where this trait is clearly less conspicuous in fully mature males.

Additionally, as noted by Kaplan and Rogers (2002), Kobayashi and Koshima's study did not consider

<sup>1</sup> Both have been adapted from those by Kobayashi and Koshima (2001).

**Table 1.** An adaptation of Kobayashi and Koshima’s qualitatively assessed patterns of eye coloration and surrounding areas in primates. According to their criteria, the only species (*humans*) to fall in the ‘D’ category is *H. sapiens*

	Face~sclera~iris	Highly-visible eye outline	Highly visible iridal contour	
A	 Face~sclera~iris	✗	✗	Woolly monkey, mandrill...
B	 Face~sclera~iris	✓	✗	Japanese macaque, squirrel monkey...
C	 Face~sclera~iris	✗	✓	Ruffed lemur
D	 Face~sclera~iris	✓	✓	Phenotypically “Caucasian”, “Japanese”, and “African” humans

ethologically relevant constraints, assuming that all analyzed primates typically look at other conspecifics’ eyes while facing them. However, Kaplan and Rogers’ (2002) detailed analysis of video images strongly suggests that, at least in the case of *P. pygmaeus* (Bornean orangutan, included in Kobayashi and Koshima’s original study), the species-specific way to engage in eye contact involves what they termed *sideways gazing*:

[w]e observed that orangutans rarely engage in face-to-face direct viewing. Instead, they appear to view each other via sideways looking with the head turned away.

As such, the view of Kaplan and Rogers (2002) diverges from the view of Kobayashi and Koshima’s (1997) in comparing the area of exposed sclera of the eyes when facing forward, concluding that (emphasis added):

[o]ur findings disagree with the conclusion of Kobayashi and Koshima (1997) that humans are better able to communicate via gaze direction than are apes and other primates. Preferred direction of eye gaze needs to be taken into account. Sideways gazing by orangutans exposes the same proportion of sclera as does that of direct gazing in humans.

Interestingly enough, Kaplan and Rogers’ (2002) study reviews all the original measures by Kobayashi and Koshima (1997, 2001). Namely, they replicate the results in regards of the WHR and SSI (see above). Furthermore, they apply these measurements to check for differences between *P. pygmaeus* (Bornean) and *P. abelii* (Sumatran). Unfortunately, they make no mention of the pigmentation of the sclera, which is the key differentiating morphological feature at hand. This might have been due to yet another caveat of Kobayashi

and Koshima’s original comparative study—that measurements of pigmentation are subjective, making it difficult to establish species comparisons.

Kobayashi and Koshima’s assessments are embedded in an arbitrary set of four patterns (Table 1) that seems to be built on the assumption that humans are unique (alas, also disregarding any intraspecific variation within humans). Even though Mayhew (2013) refined these qualitative measurements by referring only to scleral pigmentation (disregarding iridal color or surrounding facial features), her measurements are still qualitative in nature. In analyzing the scleral pigmentation in *G. beringei*, she established a continuum of pigmentation in which she distinguished between seven degrees of pigmentation from completely dark to completely white (Table 2).

2. New method for the comparison of primate ocular morphologies

Previous methods for the comparison of ocular morphologies among extant primates relied on subjective ratings that hindered a consensus in the field. The method I present here has the potential to establish reliable comparisons in a crucial aspect of primate ocular morphology that has been linked to socio-cognitive functions (the contrast between iridal and scleral areas).

2.1 Methods

Photographs ( $n=6$  for each species—*P. pygmaeus*, *P. abelii*, and humans) were derived from the internet—only images with sufficient quality and resolution were considered for analyses, excluding those in which the species could not be determined with absolute certainty. These images were enough to conduct an illustrative

**Table 2.** Summary of the observed patterns of scleral pigmentation in *G. beringei* as categorized by Mayhew (2013). Adapted from Mayhew (2013)

Pattern	All-dark sclera	‘Patchy’ pattern	‘Banded’ pattern	‘Crescent’ pattern	‘Combination pattern’	All-white pattern
Description	‘the sclera of the individual is completely dark and there is no visible depigmentation’	‘various areas of variable sizes are lighter than others’	‘the lightened sclera appears as if it runs from the top eyelid to the bottom eyelid in a columnar shaped band and is typically (but not always) positioned between two darker bands or areas of sclera’	‘the lightened sclera forms a half moon shape where there is less depigmentation around the middle edge of the iris (darker region) and more depigmentation at the iris poles (lighter regions)’	‘two of the [previous] patterns are present’	‘the sclera of the individual is completely lightened’

study, but not to derive statistical inferences about the pervasiveness and distribution of the trait within and across great ape (sub-)species.

Two sets of images were compared, both including images of the eyes of *P. abelii*, *P. pygmaeus*, and *Homo sapiens*. The reason why I compare these three species is that they present different degrees of transition in the depigmentation of the sclera, showing that it is not an all-or-nothing feature of great ape ocular morphology that can only be found in humans, while remaining completely absent in other primate species, as proposed before (Kobayashi and Koshima 1997, 2001). Whereas Bornean orangutans (*P. pygmaeus*) present a very dark sclera, Sumatran orangutans display an intermediate form of this trait, between *P. pygmaeus* and *H. sapiens* (that clearly shows the lightest and most homogenous sclera of the three).

The first set of images (directed gaze) consisted of images of the eyes of members of these three great ape species looking in the same direction as their faces were oriented. The second set (averted gaze), consisted of images of the eyes of the same three great ape species while facing the camera, but directing their eye-gaze away from it, or vice-versa (thus exposing the highest area of sclera). The second set was included in order to consider the ethological constraints pointed out by Kaplan and Rogers (2002), regarding the orangutans’ typical ‘sideways gazing’ (see Section 1.3). Both sets included one comparison between infants of both species, and also one comparison with adults of each sex (one adult female and one adult male).

Since this analysis was illustrative of the new method, I selected the images that best represented completely human-like sclera in Sumatran orangutans—termed as ‘all-white pattern’ in Mayhew’s (2013) categorization. To make sure that the pictures were of

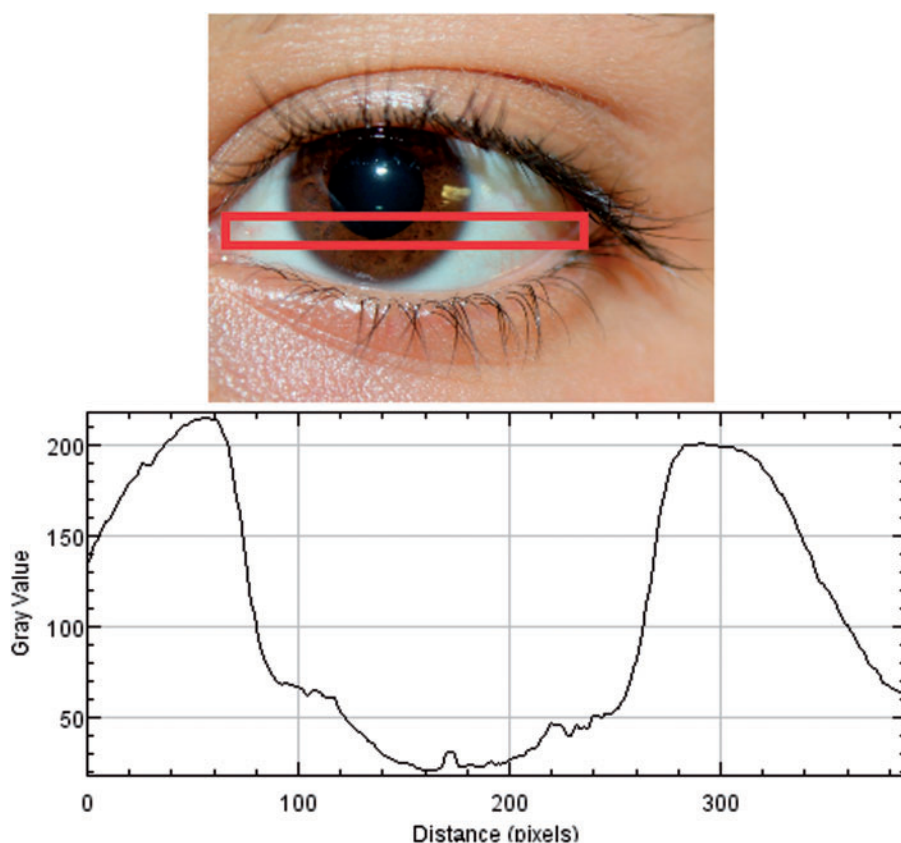
Sumatran or Bornean orangutans, I checked the source websites for such information.

In order to establish comparisons in a quantitative manner, I devised a method inspired by one of the graphs that Kobayashi and Koshima (2001) used in order to illustrate the ‘[d]ifference of gaze stimulus between human and orang-utan [(Pongo pygmaeus)]’. I used the ‘plot profile’ in the ImageJ<sup>2</sup> software. This tool allows us to analyze an image in terms of luminosity in a selected rectangular area of the image. For all pictures, the selected area was a rectangle extending from one corner to the other of the eye being analyzed (see the red rectangle in Fig. 2). This output can be used to quantify (1) the highest contrast (HC) values between inner and outer region of the eyeball, and; (2) the abruptness with which the (typically darker) pigmentation of the inner region of the eyeball transitions into the (typically lighter) pigmentation of the outer region of the eyeball (i.e. the slope of the transition from one high, to low luminosity). Figure 2 shows a sample plot profile, together with the source image as well as the precise section of the image that the plot profile represents.

In order to obtain the HC of a specific ocular morphology, the lowest gray value in the output plot profile is subtracted from the highest gray value. The abruptness with which the pigmentation in the inner region of the eye transitions into the outer, typically lighter area of the eye, is calculated by obtaining the slope of the line between the highest and lowest gray values in the output plot profile. This is done with the formula  $m = \frac{y_2 - y_1}{x_2 - x_1}$ .

2 I used the software ImageJ (Image Processing and Analysis for Java) version 1.49v for Windows 7, freely available at <<http://imagej.nih.gov/ij/>> accessed 25 March 2016.





**Figure 2.** Plot profile of a sample picture (human eye). The plot profile below represents the mean gray scale values (vertical axis, measured in a scale from 0, darkest, to 255, lightest) of the selected area of the image, from left to right (horizontal axis, measured in pixels). The HC in this case is of  $\sim 210$  (the lightest value being at pixel 60 in the horizontal axis, and the darkest value at pixel 160 in the horizontal axis).

In some cases, there were reflections in the cornea and/or retina that gave fake peaks in the gray values—these peaks can be easily identified as originating from such artifacts in the lighting conditions of the picture, so I omitted them in the analyses, focusing instead on the values originating from sclera and inner region of the eye.

### 3. Results

The output values (HC and slope) for the ocular morphology of each individual are summarized in Table 3. The average results of each species were compared for both HC and slope (combining the values from the samples with directed and averted gaze). This comparison is graphically represented in Fig. 3A and B.

These results indicate that, in terms of HC, the ocular morphology of *P. abelii* (mean of 179) strongly resembles that of humans (mean of 179), rather than that

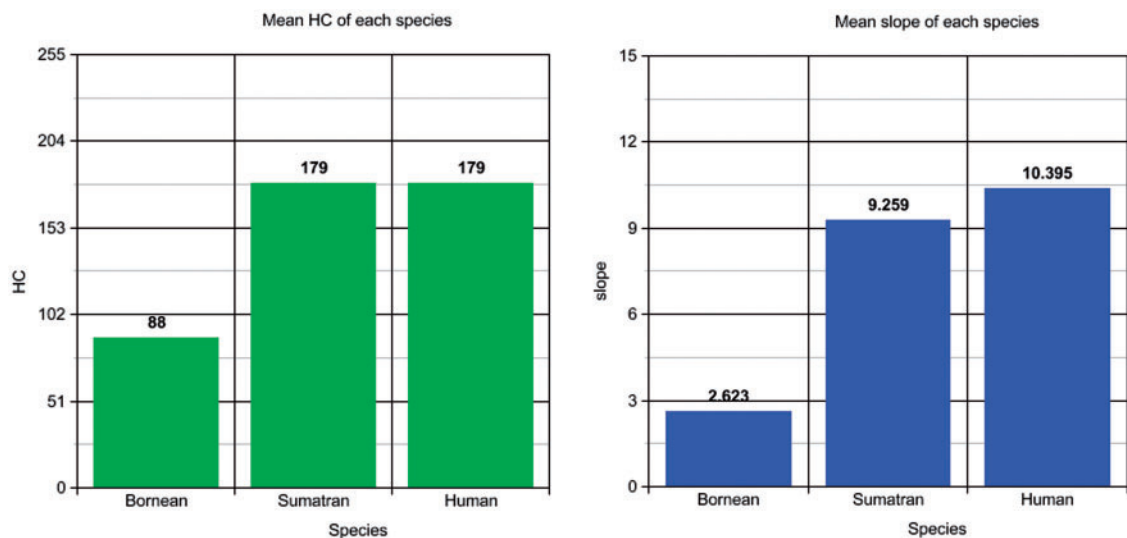
of *P. pygmaeus* (mean of 88). The same goes for the slope, with humans and Sumatran orangutans departing from the more gradual transition of luminosity values typical of *P. pygmaeus* ( $\sim 2.6$ ) even though there is some difference between *P. abelii* ( $\sim 9.3$ ) and humans ( $\sim 10.4$ ).

### 3. Discussion

The results obtained with this quantitative method for the interspecific comparison of ocular morphology point toward a direction that is very different from the most widespread view in the literature. The results suggest that eye coloration is not essentially different from, at least, one of our closest relatives, as traditionally presumed. Namely, great apes also present a white sclera—a morphological trait that was previously only reported in humans (Kobayashi and Koshima 1997; Tomasello 2007, but see also Mayhew 2013, and Mayhew and Gómez 2015) and was therefore linked to

**Table 3.** Summary of all data points in the study

Bornean orangutans ( <i>Pongo pygmaeus</i> )			Sumatran orangutans ( <i>Pongo abelii</i> )			Humans ( <i>Homo sapiens</i> )		
Av. Infant: HC: 55. Slope: 1.73	Av. Male: HC: 150. Slope: 2,469.	Av. Female: HC: 80. Slope: 4,867	Av. Infant: HC: 220. Slope: 20,27	Av. Male: HC: 200. Slope: 4,7.	Av. Female: HC: 220. Slope: 2,973	Av. Infant: HC: 220. Slope: 16.	Av. Male: HC: 190. Slope: 14,84	Av. Female: HC: 180. Slope: 15,41
Dir. Infant: HC: 48 Slope: 0,606	Dir. Male: HC: 120. Slope: 4,961.	Dir. Female: HC: 75. Slope: 1,11.	Dir. Infant: HC: 120. Slope: 11,27	Dir. Male: HC: 125. Slope: 1,5	Dir. Female: HC: 193. Slope: 14,846	Dir. Infant HC: 200. Slope: 8	Dir. Male: HC: 120. Slope: 1,165	Dir. Female: HC: 165. Slope: 6,956



**Figure 3.** (A) and (B) show the mean values of HC and slope values from the data points, sorted by species, respectively.

characteristically human behaviors (such as establishing joint attention). These human behaviors are thought to give structural support to the flexible referentiality that defines linguistic communication in humans.

The caveats of this study consist of the lack of available materials to conduct a statistical analysis that accounts for the variability of this trait within and across species. Additionally, the random conditions of lighting, etc. in which the pictures were taken should make us wary of taking these results beyond their condition of promising evidence until more detailed analyses have been conducted.

It is also worth noting that, in this study, I restrained my interest to only one of the aspects contributing to the conspicuity of gazing cues (the strength and abruptness of the contrast between inner and outer regions of the eyeball). Kobayashi and Koshima's 'width/height ratio of the eye outline' (WHR), for example, provides an objective measure that certainly has a role to play in the transmission of ocular cues. Regarding the exceptional horizontal extension of the exposed eyeball in humans,

Kobayashi and Koshima (2001) attribute it to the organisms' habitat. They propose that the trait facilitates the perception of a horizontally larger visual input in plains (as would have been the case for our hominin ancestors), allowing them to scan horizontally by doing eye-saccade movements instead of turning their heads. Even though this might have been one of the driving factors for the unusually elongated WHR in humans, it could also be worth testing the idea that the adaptation facilitates the behavioral pattern of 'sideways gazing' (Kaplan and Rogers 2002) a behavior whose rudiments might have been shared by our last common ancestors with orangutans.

#### 4. Implications for the study of language evolution

Understanding the relationship between eye coloration and linguistic communication, as well as the development of the morphological features themselves in the history of our genus, can help us reconstruct the

communicative practices of our ancestors. This exercise can be done by inferring the range of effectivity of specific communicative resources as afforded by the morphological constraints of the anatomical features (Tylén et al. 2013) that serve to instantiate them.

The extent to which ocular coloration facilitates the perception of eye-gaze (that is necessary for eye-gaze following) can then be used to demarcate the potential of eye-gaze as an effective tool to redirect attention to referents beyond the communicative dyad. This would enable triadic interactions, which have been observed regularly in wild-born orangutans (Gruber 2014), and have been pointed at as a prerequisite for linguistic-referential communication (Tomasello et al. 2005; Gómez 2007). Since the results of this study indicate that a depigmented sclera might have been shared by a much earlier common ancestor of extant great apes than has been presumed, our assumptions about referential communication in hominin ancestors should change accordingly.

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