Unique morphology of the human eye and its adaptive meaning: Comparative studies on external morphology of the primate eye

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Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye

In order to clarify the morphological uniqueness of the human eye and to obtain cues to understanding its adaptive significance, we compared the external morphology of the primate eye by measuring nearly half of all extant primate species. The results clearly showed exceptional features of the human eye: (1) the exposed white sclera is void of any pigmentation, (2) humans possess the largest ratio of exposed sclera in the eye outline, and (3) the eye outline is extraordinarily elongated in the horizontal direction. The close correlation of the parameters reflecting (2) and (3) with habitat type or body size of the species examined suggested that these two features are adaptations for extending the visual field by eyeball movement, especially in the horizontal direction. Comparison of eye coloration and facial coloration around the eye suggested that the dark coloration of exposed sclera of nonhuman primates is an adaptation to camouflage the gaze direction against other individuals and/or predators, and that the white sclera of the human eye is an adaptation to enhance the gaze signal. The uniqueness of human eye morphology among primates illustrates the remarkable difference between human and other primates in the ability to communicate using gaze signals.

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Introduction

Recognizing others' gaze direction is one of the important cognitive bases for communication in humans (Gibson & Pick, 1963; Kendon, 1967). To clarify the biological basis of this ability, especially in relation to the evolution of social intelligence, researchers have experimentally examined the cognitive ability to detect gaze direction of others in nonhuman primates (Gomez, 1991; Itakura & Anderson, 1996; Tomasello *et al.*, 1998). However, little attention has been given to external morphology of the eye, although this ability of humans might be supported by a unique morphology of

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the human eye. For example, in humans, the widely exposed white sclera (the white of the eye) surrounding the darker coloured iris makes it easy for others to discern the gaze direction and has been said to be a characteristic of humans not found in other primate species (Morris, 1985). However, this has not been examined in detail, partly because of the difficulty in measuring the soft parts of living animals.

In this study, we measured the external eye morphologies of nearly half of all extant primate species with video camera and computer-aided image analysing techniques to clarify the morphological uniqueness of the human eye and to understand adaptive meanings of external eye morphology in primates. The results clearly showed exceptional features of the human eye in both

shape and coloration. In our preceding paper (Kobayashi & Kohshima, 1997), we briefly reported the morphological uniqueness of the human eye and discussed its adaptive meanings. In the present paper we fully analysed the results and examined the following hypotheses on adaptive meanings of primate eye morphology.

We measured width/height ratio of the eye outline (WHR) and an index of exposed sclera size in the eye outline (SSI) to analyse eye shape. These eye-shape parameters closely correlated with habitat type or body size of the species examined. To explain the correlation, we postulated a hypothesis that these two features are adaptations for extending the visual field by eyeball movement, especially in the horizontal direction. This hypothesis was examined and supported by analysing the eye movement of video-recorded primates and comparing the way that gaze direction changes among species with various body sizes and habitat types.

To explain the unique coloration of the human eye with its exposed white sclera void of any pigmentation, we postulated a hypothesis that only coloration of the human eye is adapted to enhance the gaze signal while eye coloration of other primates is adapted to camouflage the gaze direction against other individuals and/or predators. This hypothesis was examined and supported by analysing relationships among iris coloration, sclera coloration and facial coloration around the eye. Our results suggested that unique features of the human eye started to evolve as adaptations to large body size and terrestrial life and were completed as a device for communication using gaze signal.

Method

Eye shape measurements
A total of 874 adult animals (88 species: Prosimii; 10, Ceboidea; 26, Cercopithe-

coidea; 43, Hominoidea; 9) were studied (Table 1). Facial images of 80 species were recorded by video camera at the Japan Monkey Centre. Facial images of eight species (*Microcebus* (1), *Loris tardigradus* (2), *Perodicticus potto* (1), *Tarsius* (1), *Saguinus imperator* (1), *Pithecia monachus* (1), *Cacajao rubicundus* (1), *Cercopithecus hamlyni* (1)) were collected from books (Itani & Uehara, 1986; Yoshino, 1994). For humans, facial images of 244 Japanese, 347 Caucasian and 68 Afro-Caribbean adults were studied. 244 Japanese, 280 Caucasian and 2 Afro-Caribbean images were recorded by video camera, and 67 Caucasian and 66 Afro-Caribbean images were collected from books (Ohara, 1970; Gomi, 1994).

Two parameters were measured for each species: the width/height ratio of the eye outline (WHR) and an index of exposed sclera size in the eye outline (SSI). Frontal full-face images without obvious facial expression of subjects were recorded by video camera. These images were processed and analysed on a Macintosh Quadra 840AV computer using the public domain *NIH Image* program. For each image, (A) the distance between the corners of the eye, (B) the longest perpendicular line between the upper and lower eyelid, (C) width of the exposed eyeball, and (D) diameter of the iris were measured (Figure 1). WHR means (A)/(B) and SSI means (C)/(D). Data of weight, crown–rump length and habitat type of primates were collected from books (Itani & Uehara, 1986; Napier & Napier, 1985) since we could not get permission for physical contact with primates. Walking-height and sitting-height of primates were measured in the Japan Monkey Centre using marks on the wall of the cages.

Eye-coloration measurements
Coloration of the exposed sclera (including the conjunctiva to be precise), iris and face around the eye was recorded for each of 91 species by direct observation of living

animals (82 species) and of eyeball speci-mens (55 species, 124 animals) kept in the Japan Monkey Centre (Table 1). The sclera colour included in the term "Pale brown" was a paler one than yellow ochre: 10YR 6/7·5 of Munsell Colour System (see Figure 9).

Eye coloration of 82 primate species were classified into 4 types (see Type 1–4, Figure 11) by the differences of colour or contrast between sclera and iris/face. This classifica-tion was carried out by one person observing living animals. To check reliability of this classification, another person independently classified the face pictures of 76 primate species (see Figure 11). The results agreed in 70 species (92%). Disagreement was only observed between Type 1 and Type 2 in 6 species (8%).

Eyeball specimens of the Japanese macaque (1 subject) and crab-eating macaque (2 subjects) were supplied from a co-operative program of the Primate Research Institute, Kyoto University, Inuyama, Aichi, Japan. Eyeballs were fixed with 4% paraformaldehyde in 0·1 M phos-phate buffer (pH 7·2) at 4°C overnight. The tissue including the conjunctiva and cornea separated from eyeballs was washed several times in cold phosphate-buffered saline (PBS), dehydrated in an ethanolic series finishing xylene and embedded in paraffin. Serial sections with a 4 μm thickness were cut with disposable blades, floated on water and placed on slides. These sections were deparaffinized in xylene, washed in ethanol and PBS and studied by light microscopy (see Figure 10).

Eye movement analysis
To analyse the movement of the eye and the head when the animals change the direction of their look, eating food by hand in cages various primates were video-recorded. As for humans, persons eating alone in a hamburger shop with a hamburger in their hands were video-recorded.

To calculate the ratio of scanning per-formed only by eyeball movement, move-ments of the eyeball and the head scanning were counted (total observation time: 10,037 sec) for 29 individuals of 18 species (Table 1).

To calculate the ratio of horizontal scan-ning to vertical scanning frequency and time duration of horizontal and vertical scanning were measured (total observation time=12,579 sec) for 40 individuals of 26 species (Table 1): arboreal species: *Lemur catta*, *Cebus apella*, *C. albifrons*★, *Pithecia pithecia*★, *Ateles belzebuth*★, *A. geoffroyi*, *A. paniscus*, *Cercocebus galeritus*, *Cercopithecus cephus*★, *Colobus angolensis*, *Presbytis cristata*, *P. vetulus*, *P. francoisi*★, *Nasalis larvatus*, *Hylobates lar* and *H. pileatus*; semi-arboreal species: *Macaca fuscata*★, *Cercocebus torqua-tus*, *Mandrillus sphinx*★, *M. leucophaeus*★, *Cercopithecus ascanius*, *Presbytis entellus* and *Pan troglodytes*; terrestrial species: *Papio hamadryas*, *Erythrocebus patas* and *Homo sapiens* (★: duration time only) (Table 1).

All these videotape analyses were carried out by one person. To check reliability of the analyses, a second person scored every 0·5 sec randomly sampled 20% of the video-tapes independently. Agreement between the persons was 82% on average. The Cohen's kappa (Bakeman & Gobbman, 1997) was 0·63 on average.

Results and discussion

Unique shape of the human eye
Figure 2(a) shows that human eyes have the largest exposed sclera area and show extraordinary horizontal elongation of the eye outline among primates. SSI increased in the following order: Prosimii (prim-itive type) <Ceboidea<Cercopithecoidea< Hominoidea. WHR increased in the follow-ing order: Prosimii (primitive type) <Ceboidea<Cercopithecoidea and Homi-noidea [the difference between phylogenic groups was significant with analysis of

Table 1A

| | Eye shape [Figure 2(a)] | Eye colour (Figure 9) | | Eye movement | | |
		Living animals (Figure 11)	Eyeball specimens	(Figure 5)	(Figure 7—time)	(Figure 7—frequency)
Prosimii						
Microcebus	1		3			
Lemur catta	3	3		1	1	1
L. macaco	2	2	2			
L. fulvus	2	2				
Varecia variegata	3	6	1			
Loris tardigradus	2		5			
Perodicticus potto	1		2			
Galago senegalensis	3	2	1			
Otolemur crassicaudatus	1	2	2			
Tarsius	1		2			
Ceboidea						
Callimico goeldii	1	2	1			
Callithrix jacchus	3	3	2			
C. argentata	2	2				
C. humeralifer	2	2				
G. geoffroyi	3	3	2			
C. penicillata		2	1			
Cebuella pygmaea	3	4	6			
Saguinus midas	1	2	2			
S. weddelli	1	1				
S. imperator	1	1	1			
S. labiatus	1	1	3			
S. mystax	2	2	2			
S. oedipus	1	4	3			
Cebus capucinus	3	3	3			
C. albifrons	1	4	1	2		
C. apella	2	3		1	1	1
C. nigrivittatus			1			
Aotus trivirgatus	3	4	2			
Callicebus moloch	2	5	2			
Saimiri sciureus	2	10	2			
Pithecia pithecia	2	2	1	1		
P. monachus	1					
Cacajao rubicundus	1					
Alouatta caraya	1	1	6			
Ateles paniscus	1	2		1	1	1
A. belzebuth	2	4			1	
A. geoffroyi	3	5	2	2	2	2
Lagothrix lagothricha	2	4				
Cercopithecoidea						
Macaca sylvanus	3	3				
M. silenus	2	3	1			
M. maurus	1	1				
M. nemestrina	3	3	2			
M. nigra	1	1				
M. fascicularis	3	3	5			
M. fuscata	6	7	1		1	
M. fuscata yakui	3	3	2			
M. mulatta	4	18	17			

Table 1B

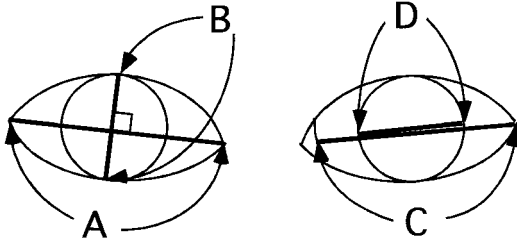| | Eye shape [Figure 2(a)] | Eye colour (Figure 9) | | Eye movement | | |
		Living animals (Figure 11)	Eyeball specimens	(Figure 5)	(Figure 7—time)	(Figure 7—frequency)
M. cyclopis	5	10				
M. sinica	3	4	1			
M. assamensis	1	1	1			
M. radiata	2	9	1			
M. thibetana	3	4				
M. arctoides	1	2				
Cercocebus torquatus	2	2		2	2	2
C. torquatus lunulatus	2	3				
C. atys	1	1	1			
C. galeritus agilis	1	1	1	1	1	1
C. galeritus chrysogaster	2	3				
C. albigena			1			
Papio papio	3	3	2			
P. anubis	12	50	2			
P. cynocephalus	1	3				
P. hamadryas	3	9	1	1	1	1
Mandrillus sphinx	3	4			1	
M. leucophaeus	2	4	1		2	
Theropithecus gelada	1	1	1			
Cercopithecus hamlyni	1		1			
C. neglectus	3	3				
C. mitis	2	5				
C. ascanius schmidti	2	2				
C. cephus	2	2			2	
C. ascanius	2	3		2	2	2
C. mona	2	2	1			
C. petaurista	1	1	1			
C. aethiops	2	5				
Miopithecus talapoin	2	2				
Allenopithecus nigroviridis	1	3				
Erythrocebus patas	4	4		2	2	2
Colobus angolensis	5	6		1	1	1
C. guereza	2	2				
Presbytis cristata	2	8	7	4	4	4
P. francoisi	2	4	1		1	
P. pileata	1	1	1			
P. vetulus	2	2		1	1	1
P. entellus	4	7	2	1	1	1
P. obscura			2			
Nasalis larvatus	2	2		2	2	2
Hominoidea						
Hylobates lar	2	2		1	1	1
H. agilis	1	1	2			
H. pileatus	2	2		1	1	1
H. syndactylus	2	2				
H. klossii			1			
Pongo pygmaeus	2	3	1			
Pan troglodytes	9	13	2	3	3	3
P. paniscus	1	1				
Gorilla gorilla	4	6				
Homo sapiens	659	247		2	2	2

Figure 1. (A): the distinace between the corners of the eye, (B): the longest perpendicular line to (A) between the upper eyelid and lower eyelid, (C): width of the exposed eyeball, and (D): diameter of the iris were measured. WHR means (A)/(B) and SSI means (C)/(D).

variance (ANOVA) (SSI: F $(3,90)=14\cdot68$, $P<0\cdot01$, WHR: F $(3,90)=32\cdot77$, $P<0\cdot01$). In multiple comparison (LSD), the difference between phylogenic groups, except WHR between Cercopithecoidea and Hominoidea, was significant (SSI: MSe= $0\cdot02$, $P<0\cdot01$, WHR: MSe=$0\cdot04$, $P<0\cdot01$)]. Even in Hominoidea species, SSI and WHR of human were exceptionally high [Figure 2(b): the difference between phylogenic groups was significant with ANOVA (SSI: F $(4,675)=79\cdot82$, $P<0\cdot01$, WHR: F $(4,676)=33\cdot92$, $P<0\cdot01$). In multiple comparison (LSD), the SSI difference between species of Hominoidea, except between orang-utan and gorilla and between orang-utan and chimpanzee, was significant (MSe=$0\cdot02$, $P<0\cdot01$). The WHR difference between human and others was significant (MSe= $0\cdot19$, $P<0\cdot01$). We measured both sexes of three human races: Mongoloid, Caucasian and Afro-Caribbean, and sexual and racial difference were slight in these parameters relative to interspecies difference.

It is possible that the difference in these eye shape parameters 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. Thus, we analysed relationships between the eye shape parameters and these factors.

Relationship between eye shape and visual function

Primates are mammals with well developed visual function. Many primate species have (1) cone cells for colour vision, (2) the fovea (a dense concentration of cones in the retina focused on the centre of gaze) for a high resolution visual image, (3) forward-facing eyes for wide stereoscopic vision by both eyes, and (4) a well developed postorbital plate behind the eyes. It is possible that the difference in eye shape parameters among phylogenic groups has some relationship with these anatomical structures for well developed visual functions. However, since most primate groups except the prosimians have all these anatomical structures, the difference in eye shape parameters among phylogenic groups cannot be explained by the difference in these visual functions. For example, some nocturnal prosimian species are the only primates which lack both cone cell and a fovea in their eyes (Wolin & Massopust, 1970; Alfieri et al., 1976; Webb & Kass, 1976; Debruyn et al., 1980; Castenholtz, 1984). Figure 3 shows the relationship of eye shape parameters with orbital axis angle measured from the cranium (Shigehara, 1996) which reflects the ability of stereoscopic vision. In this figure Prosimians with high values of orbital axis angle showed low values of SSI and WHR. However, among simians with more forward-facing eyes and developed postorbital closure, SSI and WHR spread over various values and no significant correlation is observed. These facts suggest that the variation in the eye shape parameters of each phylogenic group does not reflect evolutionary trends in these visual functions.

Relationship between body size and SSI

SSI correlates well with various body size parameters (weight: $r=0\cdot59$, $P<0\cdot001$, crown–rump length: $r=0\cdot59$, $P<0\cdot001$, sitting height: $r=0\cdot65$, $P<0\cdot001$, walking height: $r=0\cdot72$, $P<0\cdot001$). The best

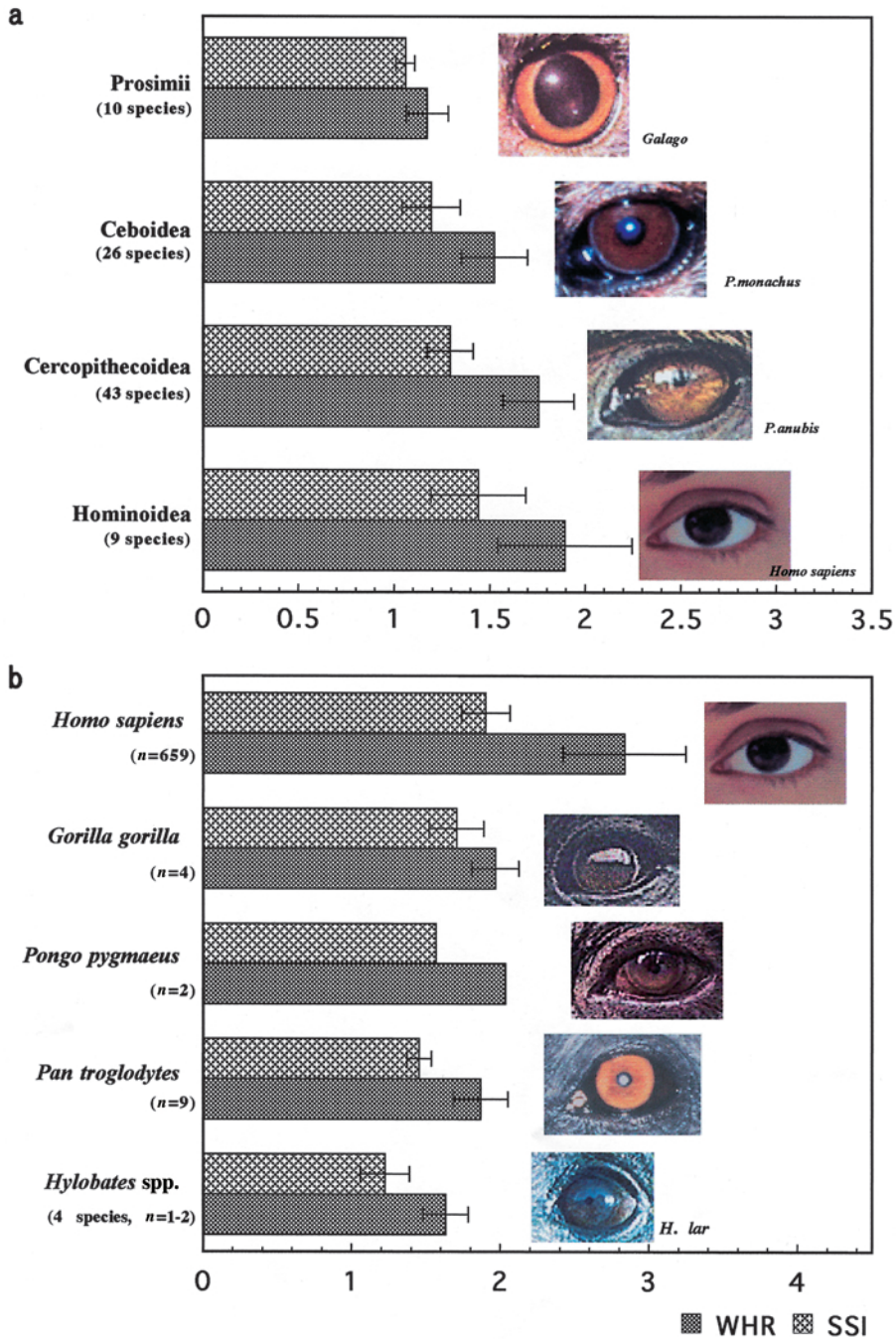Figure 2. Variation of WHR (width/height ratio of the eye outline) and SSI (index of exposed sclera size in the eye outline) among the phylogenic groups of primates (a), and in Hominoidea (b).
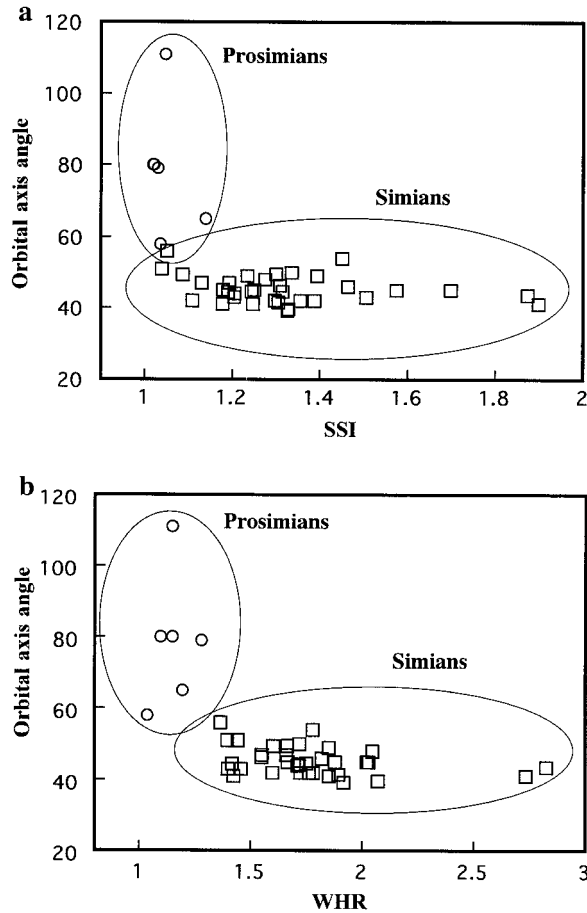
Figure 3. Orbital axis angle and WHR/SSI. Orbital axis angle is the angle formed when right and left orbital axes meet. Orbital axis is the line between the lowest point of the optic canal and the centre of the orbital width (Shigehara, 1996). Circles, prosimians; squares, simians.

correlation was observed with walking height (Figure 4). This means that species with larger body size have a larger exposed scleral area.

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. In mammalian animals, only primates have central foveae necessary for fine vision. Therefore, eyeball and/or head movement are important, especially for

primates, to adjust the images to the central fovea.

If we suppose that a larger exposed sclera is an adaptation for extending the visual field by eyeball movement, the correlation between SSI and body size can be explained by the theory of scaling. This is because, as body size becomes larger, visual field extension by eyeball movement becomes more effective than that by head or body movement. This is so because as body height becomes greater, the weight of the head and body increases proportionally to the cube of
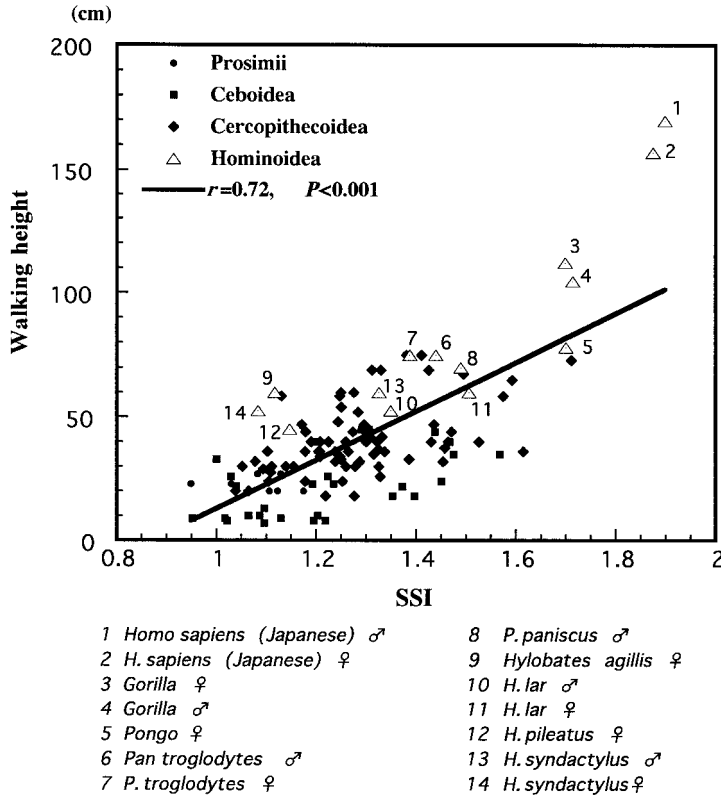
Figure 4. SSI and walking height.

body height. In contrast, the force required for movement increases only with the square of body height as it depends on the size of the muscle cross-section. Moreover, since the relative growth of the eyes to body height is smaller than that of head and body size, comparative eyeball size becomes smaller in larger animals (Schultz, 1940). Thus, to save energy when changing the direction of gaze, a large-sized species would move the eyeball more often than a small-sized species, and have a larger exposed scleral area. Besides, in small species with comparatively large eyeballs in a small skull, space for muscles moving the eyeball may be seriously limited.

To examine this hypothesis, we video-recorded various primates (18 species, 29 individuals) eating food by hand in cages, and counted the movements of head and eyeball when they changed the direction in which they were looking. The results showed that the proportion of scanning performed only by eyeball movement was correlated with SSI (Figure 5, $r=0.73$, $P<0.001$). It was exceptionally high in humans ($61 \pm 28\%$ of horizontal scan, $n=5$) compared with other primates (4·3–24·4%, mean=10·6%). The highest proportion in nonhuman primates was observed in chimpanzees (20–35%, $n=3$), the largest nonhuman species examined. These results agreed with our hypothesis.

Relationship between habitat type and WHR
The mean value of WHR is greatest in terrestrial species, moderate in semi-arboreal species and lowest in arboreal
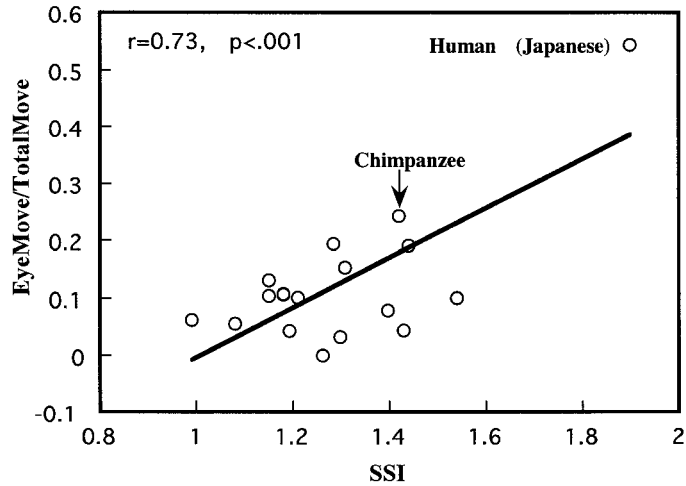
Figure 5. SSI and eye movement. EyeMove/TotalMove=frequency of gaze direction change only by eye movement/frequency of all gaze direction change by head movement or/and eye movement.
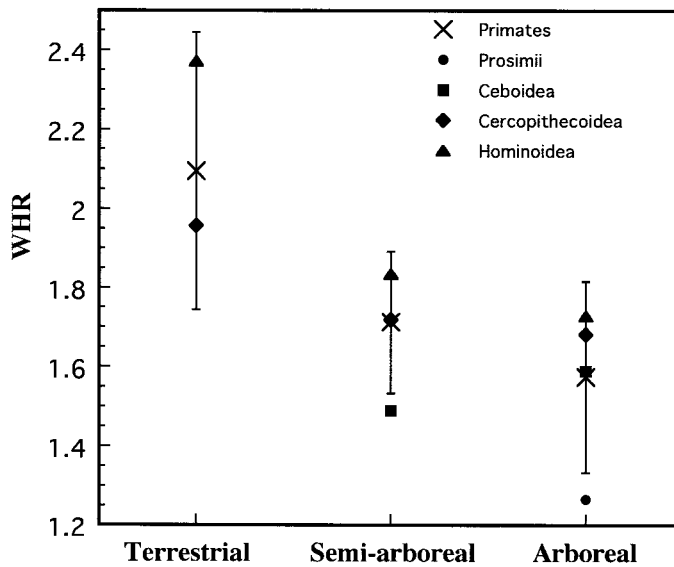
Figure 6. WHR and habitat type.

species [Figure 6: Difference among habitat types was significant with ANOVA and with multiple comparison (ANOVA: F $(2,127)$= $24 \cdot 63$, P<$0 \cdot 01$, LSD: MSe=$0 \cdot 052$, P<$0 \cdot 01$)]. This result suggests that a horizontally elongated eye outline is adaptive to terrestrial life in some way. We speculated that horizontal elongation of the eye outline

is adaptive in extending the visual field horizontally by eyeball movement, and terrestrial life needs more horizontal scanning than vertical scanning.

To examine this hypothesis, we observed various primates eating food by hand in cages and measured the time and frequency of horizontal scanning and vertical scanning.

a

b
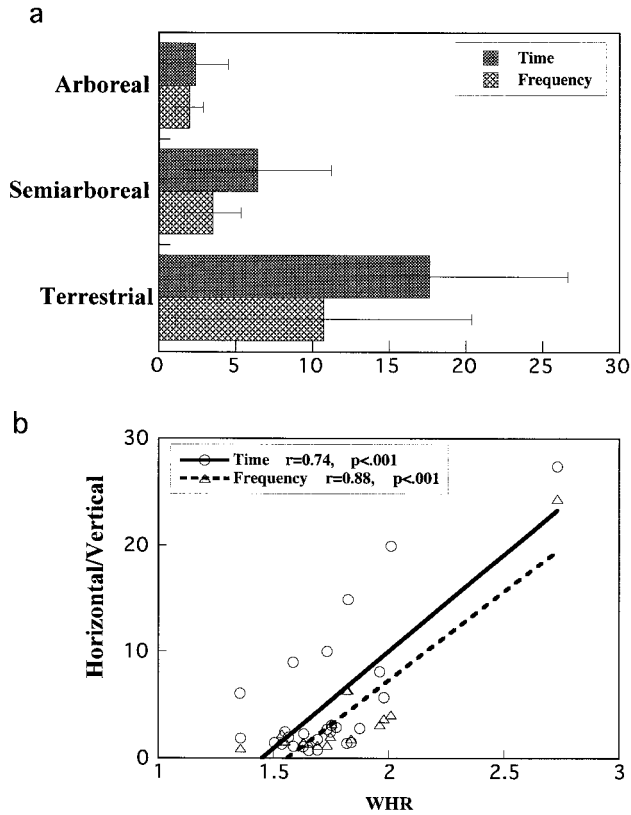
Figure 7. (a) Habitat type and the ratio of horizontal scanning to vertical scanning. (b) Ratio of horizontal scanning to vertical scanning and WHR.

The result shows that the ratio of horizontal scanning to vertical scanning is higher in terrestrial species than in arboreal species [Figure 7(a): the difference among habitat types was significant with ANOVA (time: $F_{(2,23)}=14.5$, $P<0.01$, frequency: $F_{(2,15)}=4.53$, $P<0.05$). The difference between terrestrial species and arboreal ones was significant in multiple comparison (LSD) (time: MSe=20.76, $P<0.01$, frequency: MSe=20.05, $P<0.01$)]. These ratios were also correlated with WHR [Figure 7(b), time: $r=0.74$, $P<0.001$, frequency: $r=0.88$, $P<0.001$]. The results support our hypothesis. These investigations suggest that the shape of the eye outline and relative size of the exposed scleral area are the result of an adaptation for visual field extension by eyeball movement.

Unique coloration of the human eye

The colour of exposed sclera. The following four colorations of exposed sclera were observed (Figures 8 and 9); (a) in almost all nonhuman primates (85 species out of 92 species, or 92%) the exposed part of the sclera is uniformly brown or dark brown, (b) *Macaca sylvanus* and *M. nemestrina* with a pale brown body colour had sclera coloured pale brown, (c) *Saguinus midas*, *S. labiatus*, *Callithrix argentata* and *Callimico goeldii* had brown sclera with a white part in corner of the eye, (d) humans were the only primates
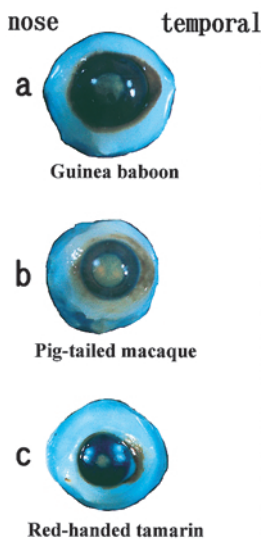
Figure 8. Three types of sclera coloration in nonhuman primates.
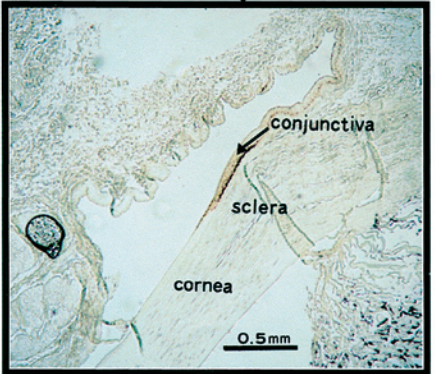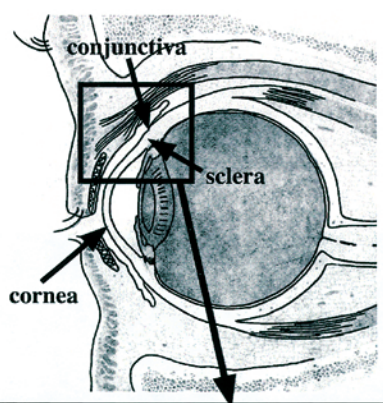
Figure 10. Eyeball section of crab-eating macaque.

having white sclera without any pigmentation. Microscopic analysis of the eyeball section specimens from the Japanese macaque and crab-eating macaque revealed
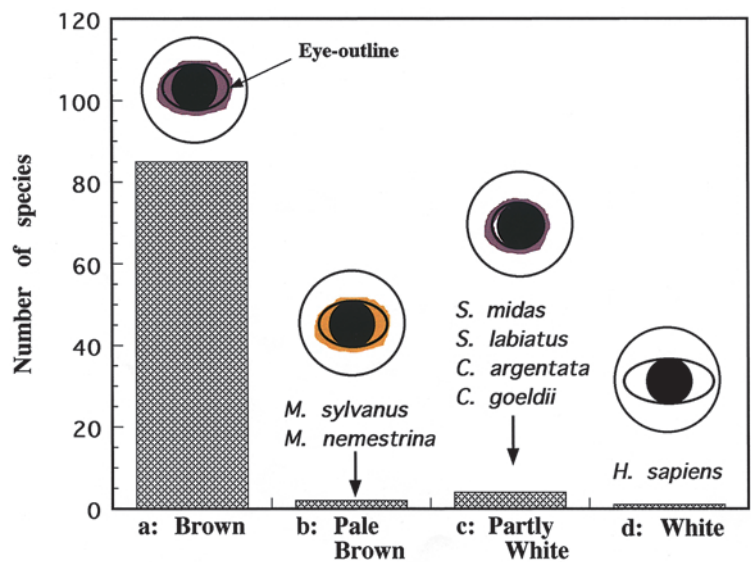

Figure 9. Variation of scleral colour. The shaded portion of the nonhuman primate eyeballs shows the general area where colour was noted. The solid line surrounding the cornea represents the eye outline.

that the brown coloration of the exposed sclera was due to pigmentation in the epithelium cornea, conjunctiva and sclera (Figure 10). External observations of other nonhuman primate eyes suggest that their dark coloration is also due to similar pigmentation. Humans have transparent conjunctiva and white sclera without pigmentation. The inner part of the sclera in nonhuman primates was also white like that of humans.

Adaptive meaning of dark-coloured sclera. Nonhuman primates have sclera coloured brown. As pigmentation costs some energy, the dark coloration of the exposed sclera probably has some adaptive function. Brown coloration of the exposed sclera was observed in many other mammal species too, and the following two hypotheses have been proposed on the adaptive meanings of sclera colour. (1) Anti-glare theory: it was pointed out that the pigmentation may be an anti-glare device because it seemed to be absent in nocturnal or crepuscular species (Duke-Elder, 1985). However, our results on primate species were contrary to this expectation: nocturnal species (*Galago senegalensis*, *Tarsius syrichta*, *Perodicticus potto*, *Nycticebus coucang* and *Aotus trivirgatus*) also had coloured sclera and diurnal humans had no pigmentation. Therefore, our results cannot be explained by the "anti-glare theory". (2) Gaze camouflage theory: in many nonhuman primates, gaze direction is important in intraspecific communication (Chance, 1962; van Hooff, 1962; Andrew, 1964). For example, direct eye contact is associated with gestures predominantly showing a tendency to attack in many monkeys. In macaques, it is reported that sclera pigmentation obscures gaze direction and may be adaptive for escaping the attacks of other individuals (Perrett & Mistlin, 1990). Coloured sclera obscuring gaze direction may serve to deceive natural predators too, by making it difficult

for predators to know if the prey has them in their gaze. If prey animals can make it known to the predator that they already know of its presence, their chances of survival may increase (Sherman, 1977).

To examine the gaze camouflage theory, we analysed the relationship between sclera colour, iris colour and face colour around the eye. If the dark coloration of exposed sclera is adaptation for gaze camouflage, the colour of exposed sclera should be similar to the colour of iris and/or face around the eyes, to make it difficult to detect the position of iris in the eye outline and/or the eye outline in the face.

Relationship between sclera colour, iris colour and face colour
Figure 11 shows the relationship between sclera colour, iris colour and face colour around the eye. 82 primate species observed were classified into the following four types by the difference of colour or contrast between sclera and iris/face.

Type (1) face $\simeq$ sclera $\simeq$ iris (43 species): darkness of sclera colour is similar to that of face and iris; both eye outline in the face and iris position in the eye outline are unclear.
Type (2) face < sclera $\simeq$ iris (37 species): sclera colour is darker than face colour but sclera colour is similar to iris colour; eye outline in the face is clear but iris position in the eye outline is unclear.
Type (3) face $\simeq$ sclera > iris (1 species, ruffed lemur): sclera colour is darker than iris colour but sclera colour is similar to face colour; eye outline in the face is unclear but iris position in the eye outline is clear.
Type (4) face > sclera < iris (1 species, Homo sapiens): sclera colour is paler than face colour and iris colour; both eye outline in the face and iris position in the eye outline are clear.
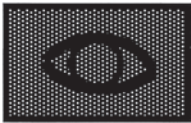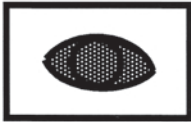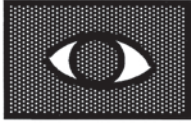
Figure 11. Colour patterns of sclera, iris and face skin around the eye.
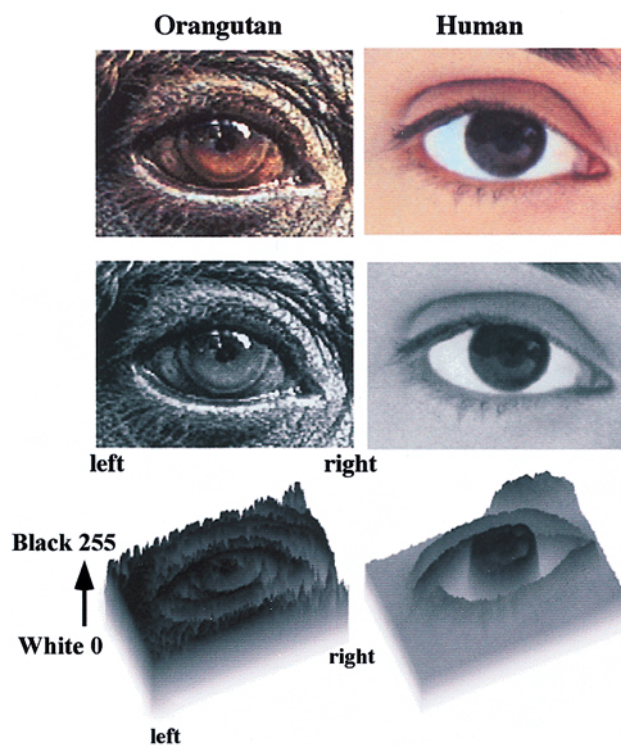

Figure 12. Difference of gaze stimulus between human and orang-utan.

Almost all nonhuman primate species observed (80 out of 81 species) belonged to Type 1 or Type 2 coloration. In these coloration types, the position of the iris in the eye outline was unclear because of similarity between sclera colour and iris colour (''Gaze camouflage type''). In Type 1 coloration (43 species), the position of the eye outline in the face was also unclear because of similarity between sclera colour and face colour around the eyes. In addition, the ruffed lemur (*Varecia variegata*), the only species that had Type 3 coloration, has a very small exposed sclera area (SSI=1·08) and almost all the area of its eye outline is occupied by the iris. Thus, the ruffed lemur's eye also can be seen as a ''gaze camouflage type''. The results thus support the ''gaze camouflage theory''.

In contrast, humans were the only species that had Type 4 coloration, in which both eye outline in the face and iris position in the eye outline were very clear because the colour of the exposed sclera is paler than that of the facial skin and iris (''gaze signalling type''). The human was the only species with sclera much paler than the facial skin. Because of this coloration, it is very easy to discern the gaze direction in human, in contrast to the gaze-camouflaging eyes of the other primates. Figure 12 shows the contrast between sclera colour and face/iris colour of human and orang-utan (*Pongo pygmaeus*). In this figure, darkness of colours was shown by 256 steps grey scale number (white=0, black=255, Figure 12). Even great apes that have SSI and WHR near that of humans [Figure 2(b)] had ''gaze camouflage eye'' type with brown sclera, brown facial skin and brown iris, in which the eye position and iris position is unclear. In contrast to the gaze-camouflaging eyes of orang-utan, the human sclera is remarkably paler than the facial skin and the iris, and it is very easy to discern the gaze direction.

Evolution of unique morphology of the human eye

Our results suggest that the unique shape of human eye (largest SSI and WHR in primates) is a result of adaptations to extend the visual field by eyeball movement, especially in the horizontal direction. In human evolution, the ratio of exposed sclera in the eye outline might increase because the visual field extension by eyeball movement became more effective as body size increased. And the eye outline might be horizontally elongated because the terrestrial life of humans needed more horizontal scanning than vertical scanning by eyeball movement.

Why have only humans discarded sclera pigmentation? It may be because the necessity for gaze camouflage decreased and that of gaze-signal enhancement increased in human evolution. The predation risk might decrease because of the enlarged body size and the use of tools and fire. Gaze-signal enhancement might aid the conspecific communication required for increased co-operative and mutualistic behaviours to allow group hunting and scavenging. Co-operative and mutualistic behaviours might need refined communication systems, such as language, to inform one's intention to other members of the group. The human eye, with a large scleral area surrounding the iris and a great ability of eyeball movement, would have provided a chance for a drastic change from ''the gaze-camouflaging eyes'' into ''the gaze-signalling eyes'' through a small change in scleral coloration. The SSI and WHR of human eyes are even greater than those of gorillas, the largest primate, which suggests adaptation for gaze-signal enhancement.

Eye morphology and gaze-signal communication

Baron-Cohen (1995) postulated a neural mechanism (eye direction detector) in human brains specialized to detect others'

eye direction, and discussed the possibility that such a mechanism might be related with the evolution of a ''theory of mind''. In recent years, many studies have been carried out to examine the cognitive ability to detect others' gaze direction in various nonhuman primates. The studies have suggested the limited ability to detect others' gaze direction in nonhuman primates (Itakura & Anderson, 1996; Tomasello et al., 1998). However, there seems to be some confusion in defining ''gaze direction'' in these studies. Since gaze direction can be changed by eyeball movement, by head movement and by body movement, it should be defined by considering all those factors: eyeball direction, head direction and body direction. Most of these studies, however, defined ''gaze direction'' mainly by eyeball direction. Our results (Figure 5) suggest that the contribution of eyeball movement to the change in gaze direction is extremely high in humans compared with other primate species. The gaze signalling eye coloration of humans also suggests that the contribution of eyeball direction to the gaze signal is exceptionally high in humans. Therefore, for nonhuman primates, head direction and body direction might be more important to detect others' gaze direction than eyeball direction. We should pay more attention to head direction and body direction in future analyses of gaze-signals in nonhuman primates.

Summary

Comparative analysis of the external morphology of the primate eye revealed exceptional features of the human eye: (1) the exposed white sclera is void of any pigmentation, (2) humans possess the largest ratio of exposed sclera in the eye outline, and (3) the eye outline is extraordinarily elongated in the horizontal direction. The close correlation of the parameters reflecting (2) and (3) with habitat type or body size of the species examined suggested that these two features are adaptations for extending the visual field by eyeball movement, especially in the horizontal direction. Comparison of eye coloration and facial coloration around the eye suggested that the dark coloration of exposed sclera of nonhuman primates is an adaptation to camouflage the gaze direction against other individuals and/or predators, and that the white sclera of humans is an adaptation to enhance the gaze signal.

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