

SSI and the outline shows extraordinary horizontal elongation. Humans are also the only species with white sclera. We failed to detect any significant sexual or racial differences in these parameters. Although a small number of primates had pale sclera (*Macaca sylvanus*, *M. nemestrina*) or brown sclera with small white regions to the side of the iris (*Saguinus midas*, *S. labiatus*, *Callithrix argentata*, *Callimico goeldii*), almost all other primates examined have similar coloration to that of the skin around the eyes (Fig. 1).

SSI correlates with weight and crown-rump length^{2,3} ($r = 0.59$, $P < 0.001$ in both cases), sitting height ($r = 0.65$, $P < 0.001$) and walking height ($r = 0.71$, $P < 0.001$) (Fig. 2). Larger SSIs allow the iris a wider range of movement and hence a larger visual field. This may be advantageous to larger species where eye movement becomes increasingly more efficient than head or body movement, especially as comparative eyeball size is smaller in larger animals⁴. In addition, in small species with comparatively large eyeballs in a small skull, muscle space may be seriously limited.

We video-recorded various primates eating (18 species, 29 individuals), and counted eye and head movements. The amount of scanning by eye movement alone was correlated with SSI ($r = 0.73$, $P < 0.005$) and was high in humans ($61 \pm 28\%$ of horizontal scanning, $n = 5$) compared with other primates (4.3–24.4%; mean, 10.6%). The highest rate in non-human primates was observed in the chimpanzee, *Pan troglodytes* (20–35%, $n = 3$).

WHR is largest in terrestrial species, smallest in arboreal species, with semi-arboreal species lying in-between (Fig. 1). There is a corresponding high ratio of horizontal to vertical scanning in terrestrial species, as might be expected to suit this lifestyle, and a low ratio in arboreal species. The ratio is correlated with WHR (scanning time ratio: $r = 0.74$, $P < 0.001$; frequency ratio: $r = 0.88$, $P < 0.001$).

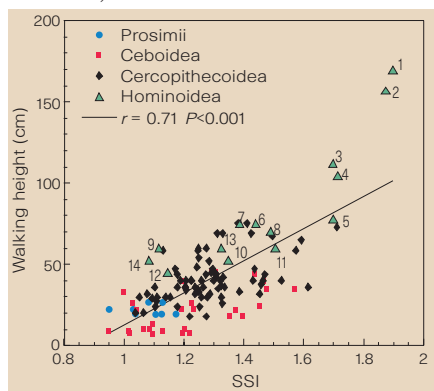


Figure 2 Relationship between SSI and walking height. 1, Human (Japanese) male; 2, female; 3, *G. gorilla* male; 4, female; 5, *P. pygmaeus* female; 6, *Pan troglodytes* male; 7, female; 8, *P. paniscus* male; 9, *H. agilis* female; 10, *H. lar* male; 11, female; 12, *H. pileatus* female; 13, *H. syndactylus* male; 14, female.

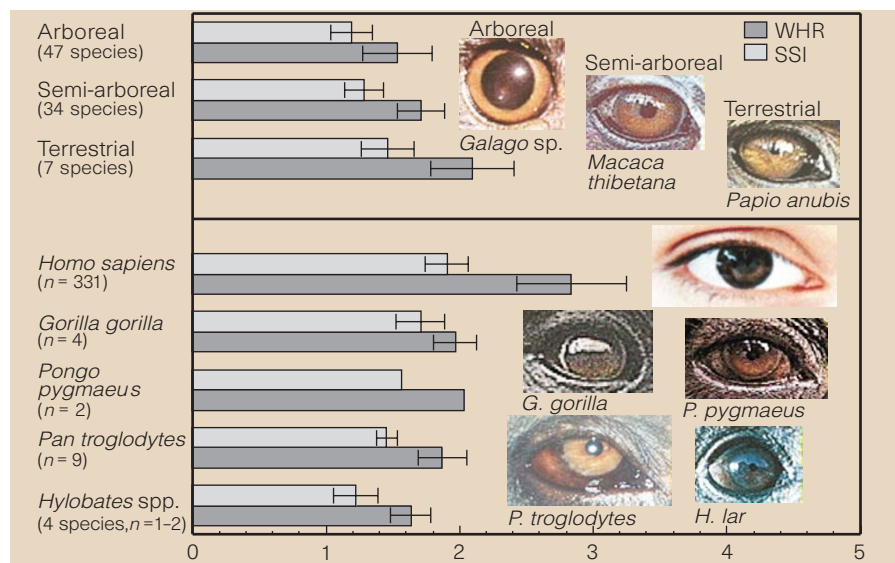


Figure 1 Variation of WHR and SSI (mean \pm s.d.). Difference between habitat types was significant (WHR: $F_{2,85} = 18.69$, $P < 0.01$, least significant difference, mean square of errors = 0.058, $P < 0.01$; SSI: $F_{2,85} = 10.86$, $P < 0.01$, least significant difference, mean square of errors = 0.024, $P < 0.01$). We studied frontal full-face images without obvious facial expression of 387 adult animals (88 species: Prosimii, 10; Ceboidea, 26; Cercopithecoidea, 43; Hominoidea, 9). Facial images of 80 species were recorded by video camera at the Japan Monkey Centre and those of 8 species (*Microcebus* sp., *Loris tardigradus*, *Perodicticus potto*, *Tarsius* sp., *Saguinus imperator*, *Pithecia monachus*, *Cacajao rubicundus*, *Cercopithecus hamlyni*) were collected from books. 182 Japanese, 80 Caucasian⁸ and 68 Afro-Caribbean^{8,9} adults were observed. Images were analysed using the NIH Image program. WHR = distance between the corners of the eye/longest perpendicular line between the upper and lower eyelid; SSI = width of exposed eyeball/diameter of iris.

Microscopic analysis of Japanese macaque (*Macaca fuscata*) eyes showed brown pigmentation of the sclera tissue around the cornea, apparently common in primates and other mammals. This pigmentation was thought to reduce glare as it is absent in many nocturnal and crepuscular species⁵, but nocturnal primates (*Gelago senegalensis*, *Tarsius syrichta*, *Perodicticus potto*, *Nycticebus coucang* and *Aotus trivirgatus*) also had coloured sclera and diurnal humans showed no pigmentation.

In many primates, gaze direction is important in communication, and direct eye contact often elicits attacks. Sclera pigmentation to obscure the gaze direction may thus be adaptive⁶. It may also serve to deceive natural predators, as if the predator believes that the prey animal is aware of its presence, it may be less likely to attack⁷. In some nonhuman primates (9 of 10 species examined), sclera coloration of newborns was paler than adults, indicating that infant gaze signals might have special meanings in these species. In all of 14 species examined, including humans, SSI and WHR of newborns were lower than those of adults.

The human sclera is much paler than the facial skin or iris so it is very easy to discern the gaze direction. Predation risk might have decreased with the evolution of enlarged body size and the use of tools and fire. In addition, gaze-signal enhancement might aid the communication required for increased cooperative and mutualistic behaviours to allow group hunting and

scavenging. A small change in sclera coloration may have altered 'gaze-camouflaged' to 'gaze-signalling' eyes. SSI and WHR of human eyes are even larger than those of gorillas, the largest primate, which suggests adaptation for gaze-signal enhancement. The uniqueness of human eye morphology among primates illustrates the difference between humans and other primates in the ability to communicate using gaze signals.

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erratum

In the Scientific Correspondence "Evidence for stone age cranial surgery" by Kurt W. Alt *et al.* (*Nature* **387**, 360; 1997), the carbon-14 estimate of the age of the human bones was printed incorrectly. It should have read 'Utrecht ¹⁴C laboratory sample UIC-5406: 6,155 \pm 39 radiocarbon years before present, ~5100 BC'.