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Evolution of the Human Eye as a Device for Communication

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1 Introduction

Recognizing the gaze-directions of others is one of the important cognitive bases for communication in humans (Gibson and 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 the gaze direction of others in nonhuman primates (Gomez 1991; Itakura and Anderson 1996; Tomasello et al. 1998). However, little attention has been given to the external morphology of the eye although this ability of humans might be supported by a unique morphology of the human eye. For example, in humans, the widely exposed white sclera (the white of the eye) surrounding the darker colored 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 analyzing techniques to clarify the morphological uniqueness of the human eye and to understand the adaptive meanings of external eye-morphology in primates. The results clearly showed exceptional features of the human eye in both shape and coloration.

In order to understand the adaptive meaning of these exceptional features of the human eye, we postulated some hypotheses and examined them. To explain the close correlation of eye-shape parameters (width/height-ratio of the eye-outline and the proportion of exposed sclera in the eye-outline) with habitat type or body size of the species examined, we postulated a hypothesis that these features are adaptations for extending the visual field by eyeball movement, especially in the horizontal direction. This hypothesis was examined and supported by analyzing the eye-movements of video-recorded primates and the developmental change of eye morphology in humans and olive baboons. To explain the unique coloration of

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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 analyzing the relationships among iris coloration, sclera coloration and facial coloration around 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.

2 Methods

2.1 Eye-Shape Measurements

A total of 874 adult animals (88 species: Prosimii; 10, Ceboidea; 26, Cercopithecoidea; 43, Hominoidea; 9) were studied. Facial images of 80 species were recorded by video camera at the Japan Monkey Centre. Facial images of 8 species (*Microcebus, Loris tardigradus, Perodicticus potto, Tarsius, Saguinus imperator, Pithecia monachus, Cacajao rubicundus, Cercopithecus hamlyni*) were collected from books (Itani and Uehara 1986; Yoshino 1994). For humans, facial images of 244 Japanese, 347 Caucasian and 68 Afro-Caribbean adults that were video recorded or collected from books (Ohara 1970; Gomi 1994) were studied. Frontal full-face images without obvious facial expression by subjects were recorded by video camera. These images were processed and analyzed 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 (Fig. 1).

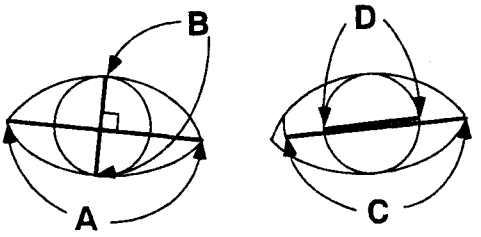

Fig. 1. The following parameters were measured: (*A*) the distance between the corners of the eye; (*B*) the longest perpendicular line to (*A*) between the upper eyelid and lower eyelid; (*C*) the width of the exposed eyeball, and (*D*) the diameter of the iris. Width/height ratio (WHR) is (A)/(B) and ratio of exposed sclera in the eye-outline (SSI) is (C)/(D)