

Conservation of Absolute Foveal Area in New World Monkeys

A Constraint on Eye Size and Conformation

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Key Words

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Abstract

The foveal specializations of five New World monkeys, the marmoset, *Callithrix jacchus*; the golden-handed tamarin, *Saguinus midas niger*; the squirrel monkey, *Saimiri ustius*; the capuchin monkey, *Cebus apella*; and the howler monkey, *Alouatta caraya* were compared. Although retinal area varies by over a factor of two in these monkeys, the area of the fovea does not covary with retinal area and remains approximately the same absolute size, as measured by the dimensions of the high density region of cones, or the rod-free region. This constancy in foveal size also holds for rhesus monkeys and humans, bringing the variation in retinal area to a factor of five. *Alouatta caraya* is unusual, distinguished by a very high central cone density and a small rod-free zone. Physiological constraints that might limit foveal area over a wide range of eye sizes are considered.

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Introduction

The word ‘fovea’ specifically refers to a declivity or pit. A pit in the retinal surface appears in a number of forms in birds, mammals and reptiles and can have several functions [Walls, 1942]. In anthropoid primates, the retinal fovea is produced by the deflection of cell bodies away from photoreceptors, and maximizes acuity in high light conditions. The displacement of the cell bodies from the inner and outer segments of the photoreceptors to the edges of the foveal pit is allowed by drawn out processes, the fibers of Henle, connecting the photoreceptive elements to the cell bodies. The caliber of these fibers must be balanced to minimize volume but maintain signal transfer and rapid intracellular transport [Hsu et al., 1998]. The foveal region also has a number of other anatomical specializations relevant to maximization of diurnal acuity, including an extremely high density of cones, a near absence of rods, and an absence of retinal vasculature [Perry and Cowey, 1985; Curcio et al., 1987, 1990; Packer et al., 1989; Wikler et al., 1990; Curcio and Hendrickson, 1992]. All of these features maximize the density of transducing elements and hence acuity, and minimize scatter and undesired absorption of photons by supporting elements [Barlow, 1981; Snodderly and Weinhaus, 1990].

These same features also put this region of the retina at physiological risk, and macular degeneration in some form in humans is common in the aging human population

[Bressler et al., 1988]. The presence of a structure optimized for sensory processing, but perhaps suboptimal for lifetime physiological function, raises interesting questions for its evolution. More generally, evolution of a fovea is an example of a fundamental question of all biological systems: how are the functional requirements of a system balanced against physiological, biomechanical, and developmental constraints? A fovea in some form is characteristic of all diurnal Old and New World primates (excluding prosimians; further references to 'primate fovea' excludes prosimians) that have been studied [von Rohen and Castenholz, 1967]. Which features of the fovea and eye conformation generally are dictated by visual function, and which by physiological constraint?

In the present study, we compare features of the foveas of five New World platyrrhine monkeys representing three of the six subfamilies [note that the relationships of the New World primates have recently undergone fairly substantial revision; Schneider et al., 1996; Horowitz et al., 1998]. Four are from the family Cebidae, two Callitrichinae, the marmoset, *Callithrix jacchus*, and golden-handed tamarin, *Saguinus midas niger*, and two Cebinae, the squirrel monkey, *Saimiri ustius*, and the capuchin monkey, *Cebus apella*. We describe just one member of the family Atelidae, the howler monkey, *Alouatta caraya*. These are all diurnal canopy-dwelling animals, subsisting variously on insects, seeds, tree gum, fruits, and leaves. They vary over an order of magnitude in body size – from as little as 200 g in marmosets and squirrel monkeys to the 2,000–5,000 g range of the sexually dimorphic howler monkey. In the Callitrichinae and Cebinae, males are dichromats and females may be trichromats, whereas in the howler monkey (other Atelines have not yet been examined), both sexes have full trichromacy [Jacobs et al., 1996; Jacobs, 1998].

We have measured cone density and the dimensions of the cone-dense region of the fovea, and the area that is relatively devoid of rods, considering these in the context of absolute retinal area. We then further compare these data to published work on similar parameters to other anthropoids, including humans. A preliminary report of these results has been made [Snow et al., 1997].

Materials and Methods

Subjects

Sample sizes varied due to the availability of the primate species from animals bred or housed in the Centro Nacional de Primatas (CENP) in Pará, Brazil. All animal housing and procedures were in compliance with the principles defined in the NIH *Guide for the Care and Use of Animals*.

Retinas from *Cebus apella* were the most available. For this species we have both the left and right retinas counted from three individuals, all male, allowing comparison of interocular variability of foveal conformation, and counts of parafoveal cone density for another individual animal. Three complete samples from three individual *Saimiri ustius* were made (two males, one female; all right retinas), with additional information on parafoveal cone density in another animal (female). One additional flat-mounted retina stained with cresyl violet, mounted ganglion cell layer up, was made to photograph the gross foveal dimensions for both *Saimiri* and *Cebus*. Three *Saguinus midas niger* (all right retinas; two males, one female) were counted, with information on parafoveal cone density from a fourth male.

Because *Callithrix jacchus* had already been the subject of two studies of cone distribution [Troilo et al., 1993; Wilder et al., 1996], we obtained one full and one partial retinal assessment from two individuals (one male, one female) to calibrate our cone topography assessment against these papers. Unlike the other primates listed, which were bred in the primate facility, *Alouatta caraya* were wild-caught, and we were able to obtain both retinas from only one individual (female), with partial data on parafoveal cone and rod density in two other individuals (both male). One additional flat-mounted retina stained with cresyl violet, mounted ganglion cell layer up, was made for the photography of gross foveal dimensions. Details of all individuals are listed in table 1.

Preparation of Retinas

Animals were dark adapted for one half hour while lightly anesthetized with an intramuscular injection of a 1:4 mixture of 2% xylazine hydrochloride (Rompun, Bayer, Porto Alegre, Brazil) and 5% ketamine hydrochloride (Ketalar, Parke-Davis, São Paulo, Brazil). They were then deeply anesthetized with the same mixture, and perfused by a phosphate buffered saline solution (PBS). One or both unfixed eyes were then removed for the project described here, and further tissue samples were taken for use in other procedures. Body and brain weights were recorded for each animal.

The cornea and vitreous humor were removed and the eye was postfixed for 10–15 min in formol saline and then dissected as rapidly as possible away from the choroid layer. The retina was then postfixed for two hours in 10% formol saline. At this point the retina was rinsed in PBS, flat-mounted and drawn to calibrate for further shrinkage. The retina was then remounted on a nongelatinized slide in distilled water, and then cleared with dimethylsulfoxide overnight, rinsed, covered with glycerol and coverslipped. The retina was redrawn at the time of counting for calibration of shrinkage, considering principally the distance between the fovea and optic disc, the area examined in this study.

Quantification Procedures

Retinal area, and the retinal hemi-circumference from the nasal to the temporal ora serrata that intersected both the fovea and optic disc was measured from the flat-mounted retinas (drawn before and after slide mounting) using a digitizing tablet. In order to assess shrinkage, one of two measures was used, depending on the species. For *Cebus* and *Callithrix*, normative data was available on the fovea-papilla (optic nerve head) distance, the area of direct interest in this study, and correction for shrinkage was applied when the distance measured fell a standard deviation or more below the mean [*Cebus* papilla-fovea distance = 3.1 ± 0.1 mm ($n = 9$); Silveira et al., 1989; *Callithrix* 2.2 ± 0.2 mm ($n = 5$), Gomes et al., unpubl.]. This was the case for one *Callithrix*. For the remainder, length along the nasotemporal meridian was measured before and after remounting, and none of these retinas

Table 1. Information of individual animals

	Sex	Weight (g)	L/R	Retinal area (mm ²)	Nasotemporal extent (mm)	Peak cone density (cells/mm ² × 1,000)
<i>Cebus apella</i>						
Edgar	M	–	L	460	28	–
Stuart	M	–	L	455	27	168
			R	454	23.4	–
Ca880425	M	–	L	541	28.6	–
			R	575	30.4	164
Ca951227	M	–	L	637	28	176
			R	576	26.4	141
<i>Saguinus midas niger</i>						
Smn960110	M	484	R	258	20.2	129
Smn970108b	M	438	R	193	18.2	–
Smn960111	F	396	R	245	19.8	135
Smn970108a	M	370	L	196	28.6	–
<i>Saimiri ustius</i>						
Su960109a	M	–	R	293	22.2	–
Su970109b	M	–	R	365	24	–
Su960109c	F	–	R	408	24.6	140
Su970119	M	328	L	341	22.4	90
<i>Callithrix jacchus</i>						
Cj960518	F	–	R	184	16.6	152
Cj960304	M	–	R	204	18.6	–
<i>Alouatta caraya</i>						
Ac980115	F	2,280	R	502	27	430
		–	L	580	27.9	359

required correction, with variability under 6%. Retinal area and perimeter were also measured.

The magnification at which the photoreceptors were counted was constant (1,500×), but the sampling area varied with retinal location. For cones, a 256 μm² sampling area was used for the foveal center (to 0.1 mm), a 1,024 μm² sampling area for additional locations up to 2 mm from the fovea and a 6,400 μm² area for regions outside 2 mm of the fovea. For rods, the sampling area was always 1,024 μm². Cells were counted at 0.05 intervals up to 0.1 mm from the foveal center, up to 2 mm at 0.25 mm intervals (0.08 mm intervals in *Saguinus*) and at 1 mm intervals more peripherally. For assessment of cone and rod diameters in *Alouatta*, all of the rods and cones in the designated sampling area for each eccentricity were drawn and diameters measured on a digitizing tablet.

Sampling cell densities along the nasotemporal meridian generated the distributions of cone and rod densities shown in figure 4. To produce a measurement of the size of the cone-dense region, the length of the retina in mm at half the peak density was computed. This measurement was then regressed against nasotemporal length or retinal area to reveal the scaling of the size of the cone-dense region versus retinal size.

Results

Appearance of the Fovea in Flat Mounts Stained for Cell Bodies

The fovea has several aspects that can be quantified and in this paper we have formally quantified the distribution of cells of the cone-dense and rod-free zones. For the feature of the fovea that gives rise to its name, the displacement of the cell bodies of retinal neurons away from the high density cone region, we present three samples of retinal flatmounts from three individual monkeys to demonstrate this aspect of foveal appearance (fig. 1). Figure 1A is the left retina of *Saimiri ustius*, an intermediate-sized retina; B and C are larger retinas (B, retina of *Cebus apella* and C is a left retina of *Alouatta caraya*).

Individual Variability of Cone Density in the Fovea in Cebus apella

Because Curcio et al. [1990] demonstrated variability in peak cone density in the human retina by a factor of three (in a sample of seven individuals), it is interesting to examine whether high variability is a feature of foveas in general or humans in particular. In a sample of 3 *Macaca*

nemestrina, the variability was much less, the largest peak density just 17% larger than the smallest [Packer et al., 1989]; and in a sample of 6 *Callithrix jacchus*, again a smaller range of 25% was found [Troilo et al., 1993]. For the three *Cebus apella* plotted in figure 2, the range is also 25%, and the similarity of the curves of cone densities in the fellow eyes is quite striking.

Intraspecies Comparisons of Cone Density

Photomicrographs of the region of peak cone density in *Callithrix*, *Cebus* and *Alouatta* are shown in figure 3. The foveal depression in *Alouatta* appears deeper than in the other primates, which can be appreciated in the relative defocus of the parafoveal area. A plot of cone density along the horizontal meridian for the five species examined, centered on the peak of cone density, is shown in figure 4, left panel. All of the Y axes for the cone plots in figure 4 are identical, except for the axis of *Alouatta caraya*, which is doubled. The graphs are arranged from top to bottom in order of decreasing retinal area. Retinal nasotemporal length predicts neither the diameter of the region of peak density nor peak density itself.

Among the cebids, there is no obvious relationship of foveal structure to the subfamily to which the monkeys belong. Of the four Cebidae, there are two Cebinae, the capuchin and squirrel monkey, and two Callitrichinae, the marmoset and golden-handed tamarin. The capuchin *Cebus apella* has the highest peak cone density (162,000/mm²) and the largest nasotemporal retinal length (27.9 mm). The second highest density is in the marmoset *Callithrix jacchus* (152,000/mm²) which has the smallest nasotemporal retinal length (18.5 mm). Third is the tamarin, *Saguinus midas niger* with a peak of 134,000 cells/mm² and a retinal nasotemporal length of 19.0 mm, and last, the squirrel monkey, *Saimiri ustius*, with the lowest peak density at 110,000 cells/mm² and a retinal nasotemporal length of 21.7 mm. The data from *Saimiri* is noticeably more variable than the data from the other monkeys, showing nearly a twofold range in peak cell density.

The howler monkey (*Alouatta caraya*) for which we were able to examine only one individual (both retinas) is distinguished by an extremely high cone density, 429,000 cones/mm² for the right eye and 357,000 for its left eye (fig. 3C). The area of this monkey's retina is very close to *Cebus* (fig. 4). This density is higher than any other primate ever described, including humans, for which the highest reported individual value is 324,000 cones/mm² [Curcio et al., 1990]. Because the fovea in this retina appears atypical of New World primates in a number of ways, we considered the possibility that the center of the *Alouatta* fovea was not

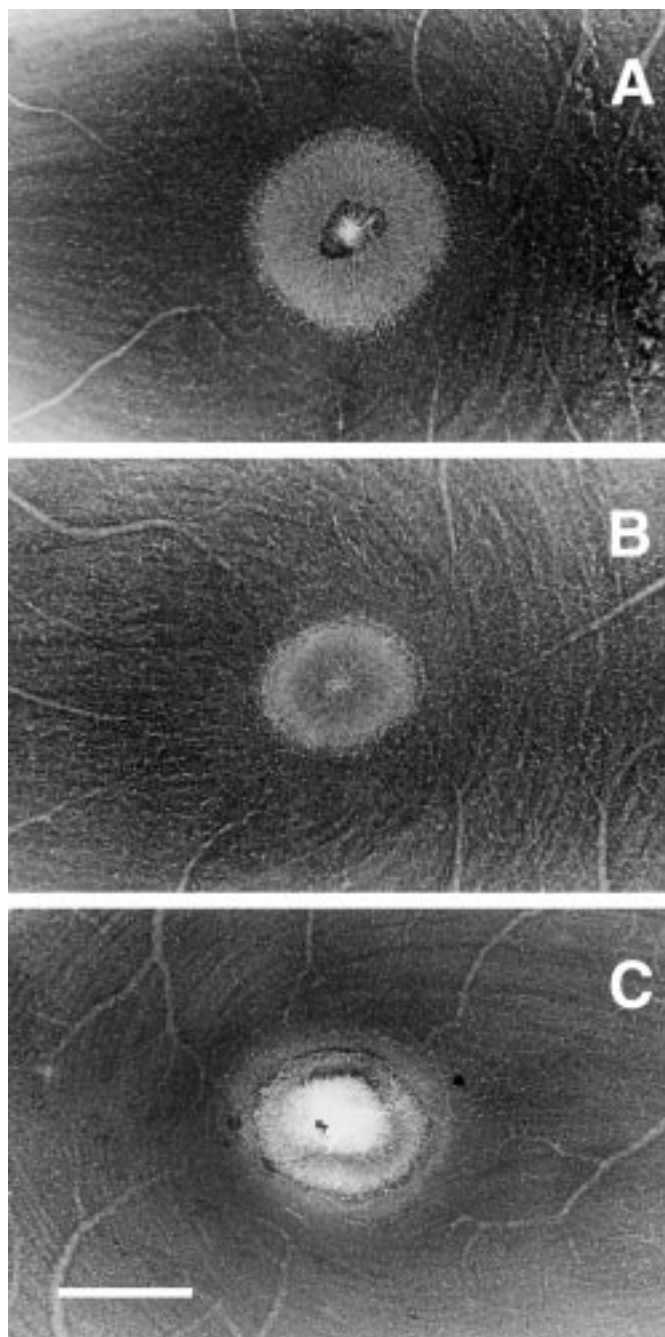


Fig. 1. Photomicrographs of the foveal region of flat mounts of three primate retinas stained with cresyl violet. Scale bar = 0.5 mm. **A** *Saimiri sciureus*, male, left retina. **B** *Cebus apella*, female, left retina. **C** *Alouatta caraya*, female, right retina.

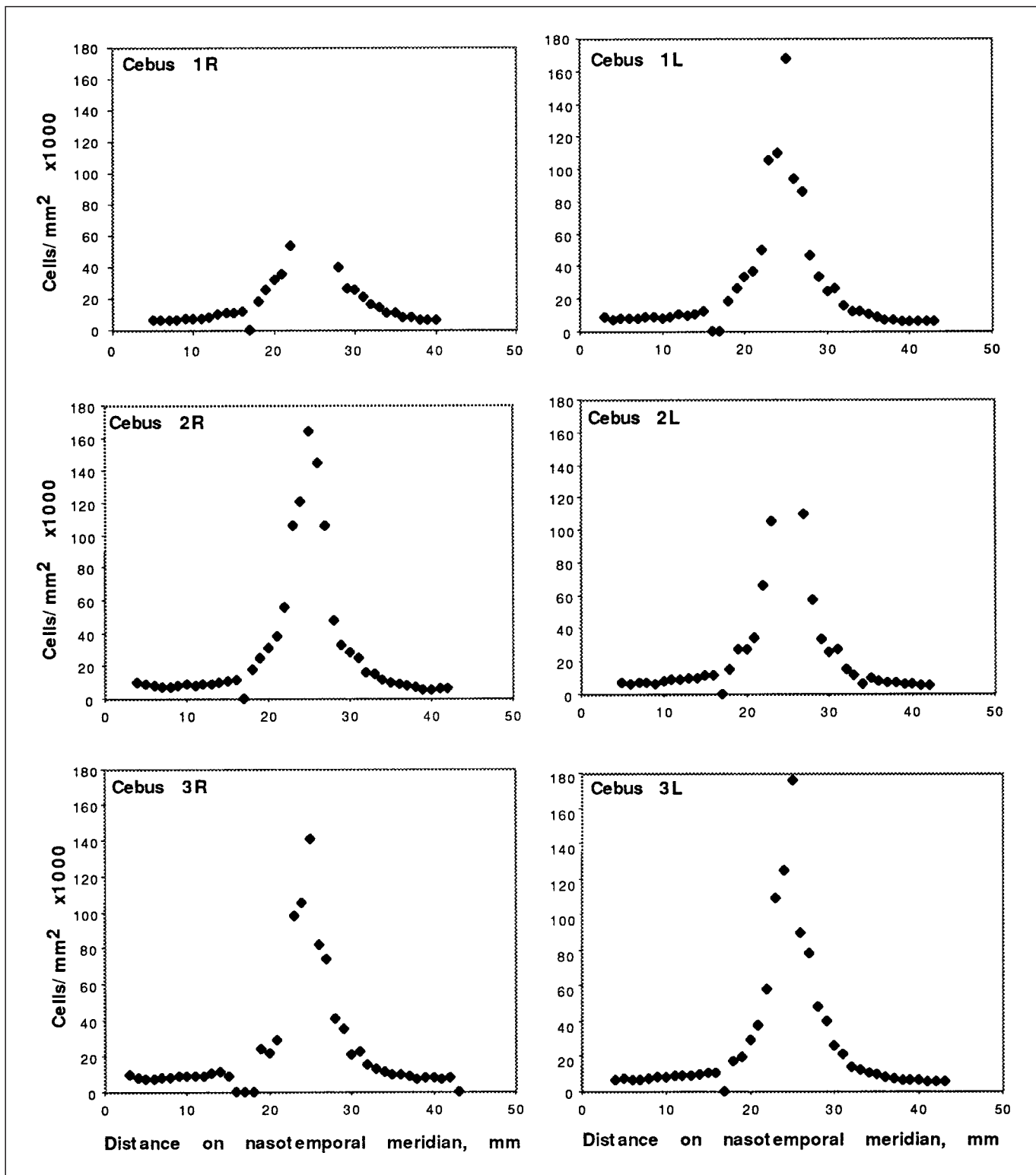


Fig. 2. Cone densities of the right and left retinas of three *Cebus apella* monkeys, for comparison of interocular and individual differences.

rod free, and some rods might have been mistaken for cones. Although immunohistochemical labeling of rod and cone opsins will eventually provide the definitive answer, we think that bimodality in size at the first appearance of distinct rods makes this unlikely. In the center of the fovea, the mean diameter of the photoreceptors is $1.95 \pm 0.16 \mu\text{m}$, quite uniform ($n = 91$). At 0.1 mm eccentricity, the mean diameter of cones is $3.3 \pm 0.29 \mu\text{m}$ ($n = 41$), and the first few rod-like processes are seen with a mean diameter of $1.7 \mu\text{m}$ ($n = 2$), smaller than the photoreceptor diameter in the foveal center. At 0.5 mm eccentricity, cone diameter is $5.46 \pm 0.22 \mu\text{m}$ ($n = 30$) and rod diameter is $2.9 \pm 0.26 \mu\text{m}$ ($n = 96$), maintaining the approximately 2/1 difference seen in the rest of the parafoveal region.

The Rod-Sparse Zone

Shown in figure 4, right panel, is a similar series of rod densities in the foveal and parafoveal region along the horizontal meridian for the five monkey species. In all the Cebid monkeys, the length of the essentially rod-free zone (less than 5 rods/mm²) along the nasotemporal meridian is the same, about one half mm. There is no suggestion of a relationship between retinal area and the dimensions of the rod-free zone. The density of rods rises with differential steepness, with higher parafoveal rod densities found in the larger retinas.

Alouatta caraya has a different rod distribution (note the larger magnitude on the Y axis in this plot as well), as was also true for its cone distribution. The area of the rod-free zone is smaller than in the other 4 monkey species, 0.25 mm, and the density of rods outside this area rises more steeply to a much higher value.

No Relation between Overall Retina Size and the Size of the Cone Dense Region

From the graphs in figure 4, we measured the diameter of the cone-dense region at the point that was one-half of the highest density. We also made similar measurements from the published literature for the human and macaque retina [Curcio et al., 1990; *Macaca nemestrina*, Packer et al., 1989]. A regression of the absolute dimensions of the cone-rich region against the retinal area for these seven primate species is shown in figure 5. The regression equation describing these points is negative in slope ($y = -0.0002 \times + 0.4499$; $R^2 = 0.1008$; $n = 7$) though not significantly so – that is, the length of the high density cone area slightly decreases, while the retina increases in area by approximately a factor of 5 (or in nasotemporal length by a factor of 2).

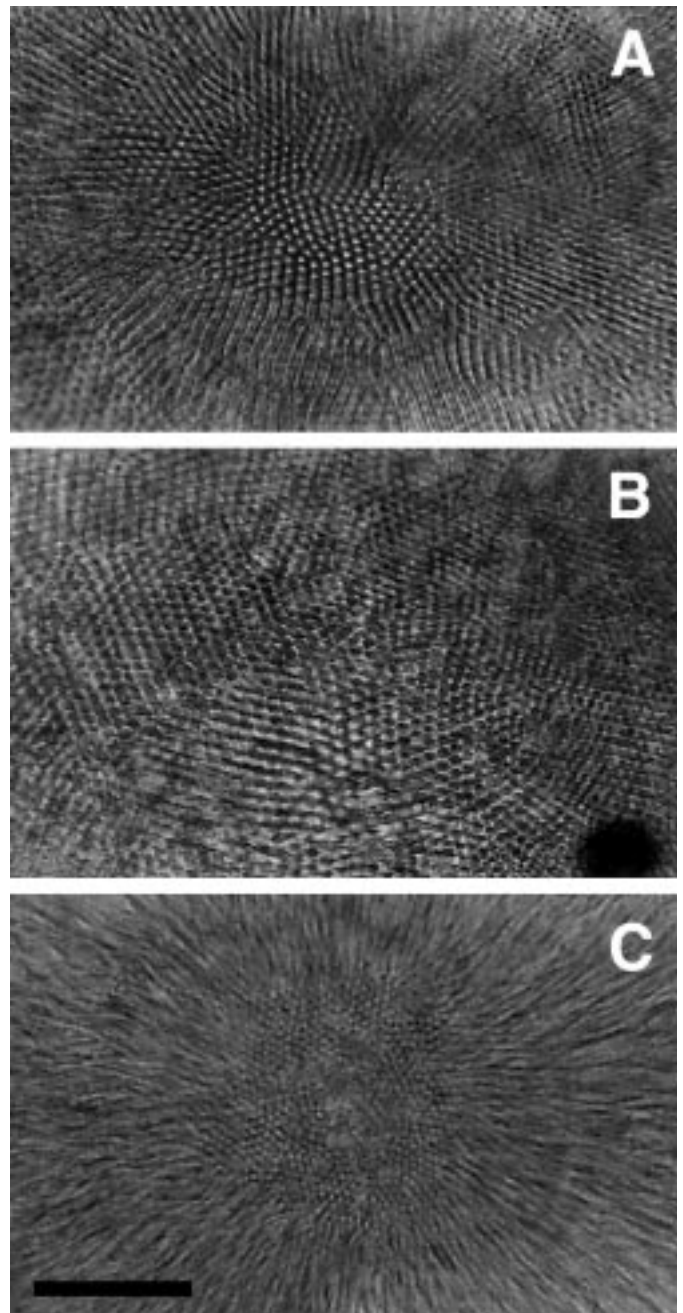
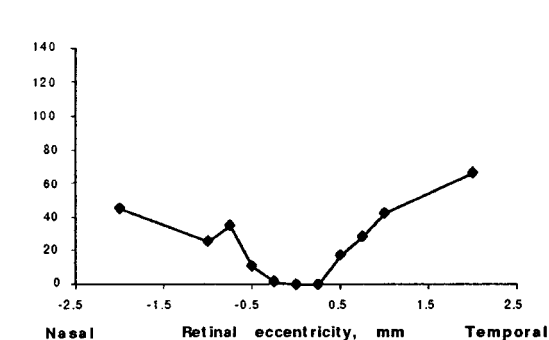
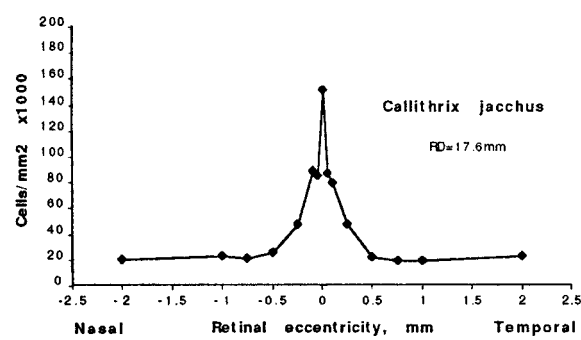
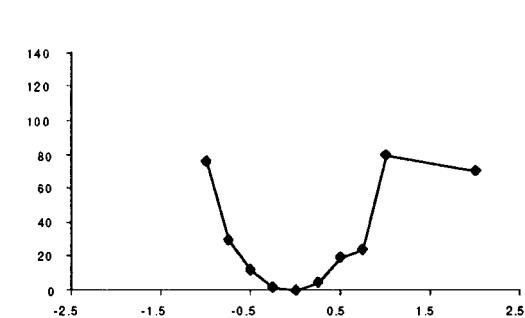
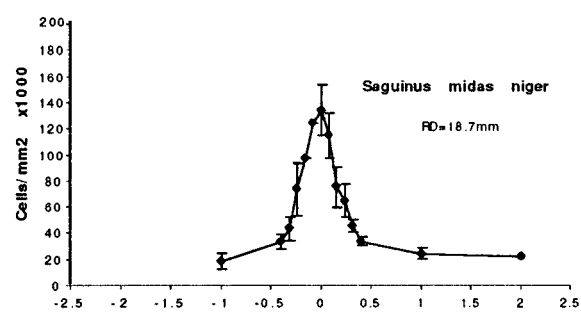
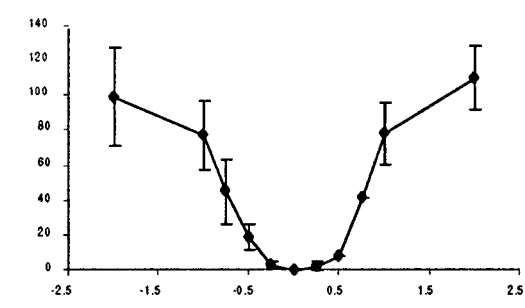
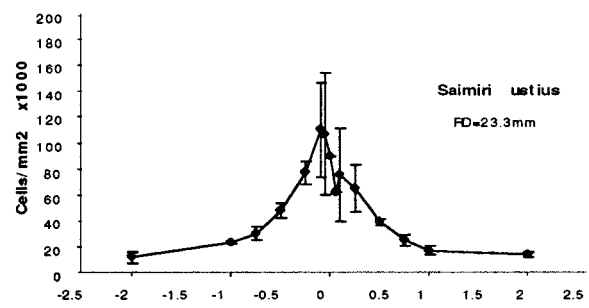
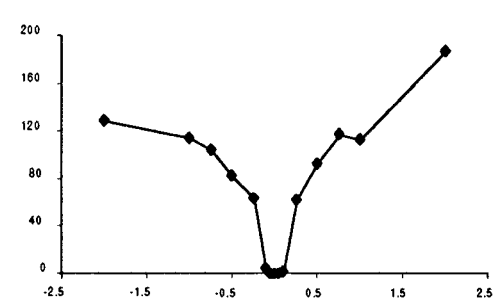
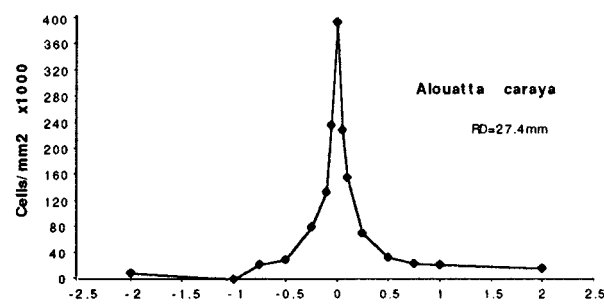
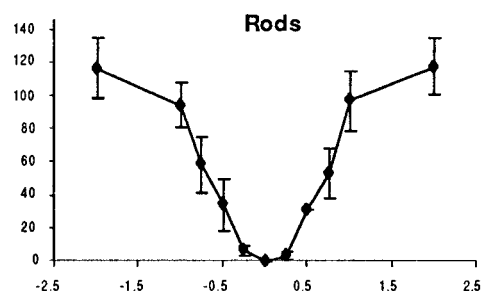
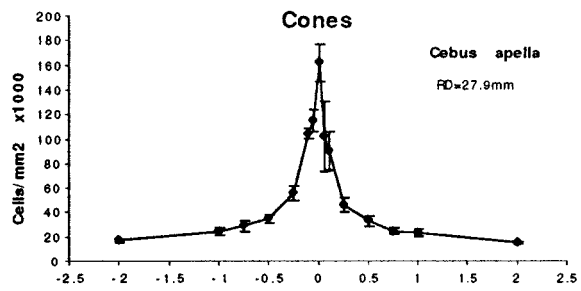


Fig. 3. Photomicrograph of region of peak cone density in *Callithrix jacchus* (A), *Cebus apella* (B) and *Alouatta caraya* (C). Scale bar = 40 μm .



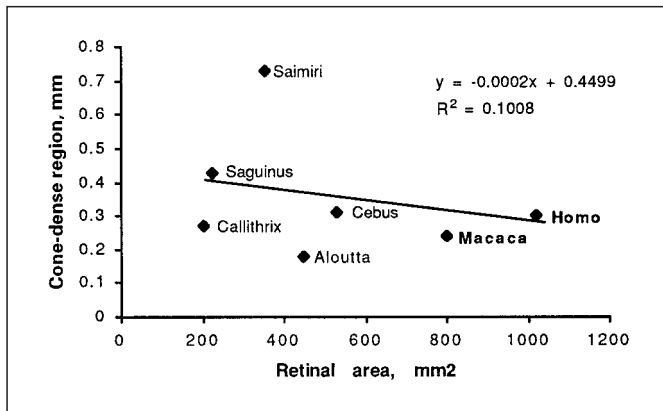


Fig. 5. Scatterplot of the relationship of the diameter of the peak cone density to retinal area for the five new World Primates examined in this study, and two other reported values for Old World primates (keyed in bold) [*Macaca nemestrina*, Packer et al., 1989; *Homo sapiens*, Curcio and Hendrickson, 1992].

Discussion

Summary and Methodological Concerns

We have presented data on cone and rod densities in five species of New World monkeys, concentrating on the foveal specialization as measured along the horizontal meridian of the eye. We describe a surprising conservation of the absolute dimensions of the foveal specialization, even as total retinal nasotemporal length increases by approximately a factor of 2.

Our results on peak cone densities of New World monkeys, with the exception of the Ateline monkey, *Alouatta caraya*, lie in the range of values previously reported for Old World monkeys and humans, and prior reports of New World monkeys. There has been a great deal of variability in the literature in the reported peak of the curve of cone densities in *Macaca sp.* [discussed at length in Packer et al., 1989]. Methodological concerns that account for the variation are tissue shrinkage, inappropriately large sampling areas, and difficulties aligning or locating the foveal center when reporting means across individuals. When these are appropriately corrected, however, a significant variation remains, at least a factor of 2, for individuals within a

Fig. 4. Left panel: Cone density along the horizontal meridian for five New World monkey species, arranged from top to bottom in decreasing retinal nasotemporal length (this value, called 'RD' is inset on each cone plot). **Right panel:** Rod density along the horizontal meridian for the same animals. Standard deviations are plotted when the number of observations per point were three or greater.

macaque species [*M. nemestrina*, 150,000 to 300,000 mm², mean 210,000 cones/mm²; Packer et al., 1989]. The two other reported macaque species have lower peaks [*M. mulatta*, 140,500 cones/mm²; *M. fascicularis*, 100,400 cones/mm²; Perry and Cowey, 1985]. In humans, peak cone density ranges from 98,000 to 324,000 cones/mm² with a mean of 199,000 cones/mm². In our comparison of the right and left retinas of three Cebus monkeys, we found a mean of 162,000 cones/mm² ± 15,000 without much striking variability, which corresponds well to the values reported recently by da Costa and Hokoç [2000], of 173,909 ± 74,139 cells/mm² whose observed variability was higher. Our counts of *Saimiri ustius* are the most variable of the data we report (fig. 3), as they contain an individual monkey with the low peak density of 89,000 cones/mm². Because such occasional low values are reported in other studies, it seems likely that this is natural variability and not error. For *Callithrix jacchus*, the study of Troilo et al. [1993] reported a peak cone density of 190,600 ± 15,600 cones/mm² (n = 6); our single individual is 25% lower in peak density. Wilder et al. [1996] report a higher mean of 211,000 cones/mm² (n = 3).

The Unusual Retinal Topography of *Alouatta caraya*

Interest has recently been focused on the howler monkey because it has full trichromacy in both sexes, unlike the sex-linked polymorphism found in various other cebid monkeys [Jacobs et al., 1996; Jacobs, 1998]. Because we have only one individual, and many reports of large variation among individual primates in peak cone density exist, obviously more data will be necessary before we can view this individual animal as typical of its species. However, the peak cone density in this single animal is higher than that ever reported for any other single primate species, including humans. Because all of our other observations fall in the ranges reported for identical or related species, this suggests that our observation is probably not due to methodological inconsistency. In addition, the diameter of the rod-free zone (fig. 4) is also distinctly different in *Alouatta* from the other species – one might guess that the extremely high cone density might exclude rods over a larger region, but instead the rod-free area is about half of what we found in *Cebus*, *Saimiri*, *Saguinus* and *Callithrix*. Perhaps due to the high cell density in the foveal region, the depth of the foveal depression appears distinctly greater in this animal.

At such high densities, the problem of matching the size of photoreceptors to the wavelength to be transduced [Snyder and Miller, 1977] and the problem of aliasing [Mollon and Bowmaker, 1992; Williams et al., 1993] become critical. It will be interesting to see if this high density requires us to rethink the nature of the limits on photoreceptor configura-

tion, or if, on the other hand, the howler monkey faces problems in the analysis of spatial and chromatic information in the fovea that the prior literature would suggest.

A convincing case has been made that the separate spectral tuning of the L and M photopigments would be of direct benefit for detecting and distinguishing the variety of fruits and leaves consumed in the tropical environment [Lucas et al., 1997; Regan et al., 1998; Kremers et al., 1999]. One account of the mechanism of the repeated evolution of trichromacy in tropical primates that possess a fovea is that the one-to-one convergence ratio of cones to cone bipolars to ganglion cells permits the faithful transmission to the brain of wavelength discriminations made possible by separate populations of M and L cones [Shapley and Perry, 1986; Mollon and Jordan, 1988]. In animals without a fovea, and in the retinal periphery, multiple L and M cones normally converge on single bipolar cells, and the expression of these slightly different photopigments does not appear to constrain their connectivity (unlike the case for S cones that are morphologically distinct and have unique connectivity). The large numbers of cones in *Alouatta*, if all photopigments were expressed in the fovea, would require similar increases in the numbers of bipolar and retinal ganglion cells if one-to-one convergence is to be maintained as the substrate for foveal trichromacy.

Conservation of the Absolute Dimensions of the Fovea and Its General Morphology

When scaling the eye, some features are naturally constrained by the properties of optics, such that the optical features of 'schematic eyes' of mammals of different sizes are virtually superimposable when appropriately scaled [for example, Remtulla and Hallet, 1985; Troilo et al., 1993] and some features are naturally constrained by the physiological constraints arising from what the eye is made of – cells that require oxygen and nutrient delivery, that cannot be arbitrarily large or small. For example, the thickness of the retina does not increase in scale with overall eye size. It is interesting to see that the size of the optical specialization of the fovea appears to fall in the category of features constrained by physiology. The fovea, across primates, is about 0.5 mm or less. The fovea thus subtends a decreasing visual angle in larger eyes (though we will argue below, diurnal primate eyes may be prevented from becoming very large by this specific feature).

Consider first two ways that eyes could scale. If the eye simply became larger without the addition of new photoreceptors and neurons, it would keep the same 'acuity' as represented by number of photoreceptors per visual angle (larger eyes are somewhat better optical instruments, how-

ever, and resolution would improve to some extent). Alternatively, the absolute density of photoreceptors could be maintained, which will increase acuity in terms of receptors per visual angle proportional to the increase in eye size. The primate fovea adopts the latter strategy, but also keeps the size of the high density area roughly constant so that the fovea becomes a smaller visual angle. For example, the marmoset fovea measures $7.8 \pm 0.2^\circ$ and has a calculated Nyquist frequency (maximum resolution) from cone receptor density of about 30 cycles per degree [Troilo et al., 1993] whereas the human fovea measures less than 5° of visual angle and has a calculated Nyquist frequency of 66 cycles per degree [Curcio et al., 1990].

It is easy to guess why the fovea cannot be larger than it is – the absence of direct vasculature, the possibility of the failure of information transmission through further-extended fibers of Henle, make it quite likely that further enlargement might result in physiological compromise. It seems unlikely that the fovea could be much smaller than it is without compromising the spatial sample available to each saccade. In addition, the precision of eye movements could be a factor in setting a lower limit on foveal size. However, the size of cones in the fovea could be adjusted (as *Alouatta* appears to have done, but the rest of the New and Old World anthropoids have not), maintaining the fovea at a constant angular rather than constant absolute dimension.

Implications for the Evolution of Primate Eyes

The monkeys described here each belong to separate subfamilies of the family Cebidae, superfamily Ceboidea. According to the most recent molecular phylogenies, this family includes all the marmoset, tamarin, and capuchin monkeys (and owl monkey), and is distinct from the Atelidae family, that includes the spider and howler monkeys; altogether these make up the Platyrrhine infraorder [Schneider et al., 1996; Horovitz et al., 1998] which is used interchangeably with the name 'New World primate'. It is important to recall that these groups are closely related, and are both about the same phylogenetic distance from current apes and hominids. Though prosimians existed in both the New and Old world, the New World primates are not derived from primitive New World prosimians, but are thought to have rafted or migrated at some time in the Oligocene from Africa to South America. The anthropoid primates extant in Africa at the time appear to be principally arboreal fruit and seed-eaters, ranging in size from the tamarin to *Cebus* range, sharing many of the characteristics of current New World primates. New World and Old World monkeys both appear to have diverged from this common stock approximately 35 million years ago, and

apes and hominids later, about 25 million years ago [Fleagle, 1988].

Because every anthropoid primate studied to date, with the exception of the owl monkey, possesses a fovea, it is likely that the common ancestor also possessed a similar adaptation. Perhaps, however, the fovea first arose at its present size in a monkey of comparatively small body and eye size. If so, this would account for a peculiar feature of scaling of anthropoid eyes with body size. Although these animals depend heavily on vision, and have in fact reduced the size of their olfactory systems [Jerison, 1973; Clancy et al., 2000], large primates have small eyes for their size [Hughes, 1977; Samy and Hirsch, 1989; Howland and Merola, 1993]. In a reanalysis and expansion of data originally gathered by Hughes [1977], Howland and Merola [1993] calculated the regression of the (log of) axial length of the eye on body mass to be $1.0258 \pm 0.19598 \cdot \log \text{ wt}$ for all vertebrates overall, and for primates, $1.13986 \pm 0.1261 \cdot \log \text{ weight}$. This signifies that primates have larger eyes overall for their body size compared to all vertebrates, but the scaling of axial length against body size is flatter – the regression lines for primates versus all vertebrates cross

at about 15 kg of body weight [Howland and Merola, 1993]. Nocturnal primates vary from this generalization – for example, owl monkeys (lacking a fovea) have an eye size characteristic of a diurnal monkey three times their body mass, evidence against any external physiological limit on eye size in monkeys [Snow et al., 1997]. Perhaps the presence of a fovea of conserved absolute dimensions has reduced the possibility for much further eye growth, so that the fovea might not become a uselessly small angular dimension. Further understanding of how foveas develop will illuminate which features of ocular development vary and which are constrained in primate evolution.

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