

On the Relationship Between Orbit Orientation and Binocular Visual Field Overlap in Mammals

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ABSTRACT

The orbital apertures of Primates are among the most convergent (i.e., facing in the same direction) among mammals. It is often assumed that orbit convergence is associated with binocular visual field overlap and stereoscopic depth perception in primates. Likewise, it is also assumed that orbit orientation reflects the shape of the visual field across mammals. To date, however, no study has demonstrated that orbit and visual field orientation are correlated, much less comparable, across mammals. In this study, data on orbit convergence were collected for a representative sample of mammals for which data on the extent of the visual field are available. Both standard and phylogenetically controlled comparisons were made. The results demonstrate that orbit convergence and binocular visual field overlap are significantly correlated and display a linear relationship. Based on orbit convergence, Primates as a group have the largest binocular visual fields among mammals. © 2004 Wiley-Liss, Inc.

Key words: orbit orientation; binocular vision; stereopsis; visual field; mammals

Studies that have addressed the adaptive significance of primate orbit convergence (the degree to which the orbits face in the same direction) have implicitly or explicitly assumed that high convergence is associated with substantial binocular visual field overlap (Fig. 1) (Collins, 1921; Cartmill, 1972, 1974, 1992; Allman, 1977, 1999; Pettigrew, 1978, 1986; Heesy, 2003). Indeed, several of these studies have used orbit convergence as a proxy for binocular visual field overlap among mammals in general (Cartmill, 1974; Heesy, 2003). It is further assumed that the binocular field is synonymous with the zone of stereoscopic depth perception, the perception of solidity and three-dimensional structure (Howard and Rogers, 1995). Ross (2000) found that orbit and visual field orientation were correlated when *Tarsius*, *Galago*, *Saimiri*, and *Macaca* were compared. However, no study conducted to date has quantitatively compared orbit convergence with binocular visual field overlap across mammals.

There are several reasons to question the strength of association between orbit convergence and the maximum extent of binocular visual field overlap. Comparative research on avian visual adaptations has demonstrated that visual field shape cannot be predicted from orbit orientation. For example, owls and diurnal predatory raptors are predicted to have substantial binocular visual field overlap based on orbit and eye orientation. However, compar-

ative ophthalmoscopic investigations have demonstrated that these taxa exhibit considerably narrower binocular visual fields than expected (Martin, 1984, 1990; Martin and Katzir, 1999). Reorientation of the orbits in these animals is suggested to be a consequence of very large eye sizes to increase visual sensitivity in otherwise spatially constrained skulls and does not reflect adaptation to binocular vision (Martin, 1990). Another reason to question the association between orbit and visual field orientation is the high mobility of the optic globe in many mammals. This can presumably reorient the visual axes to adjust the relative overlap of the two monocular fields (within limits) virtually at will, thereby reducing the importance of re-

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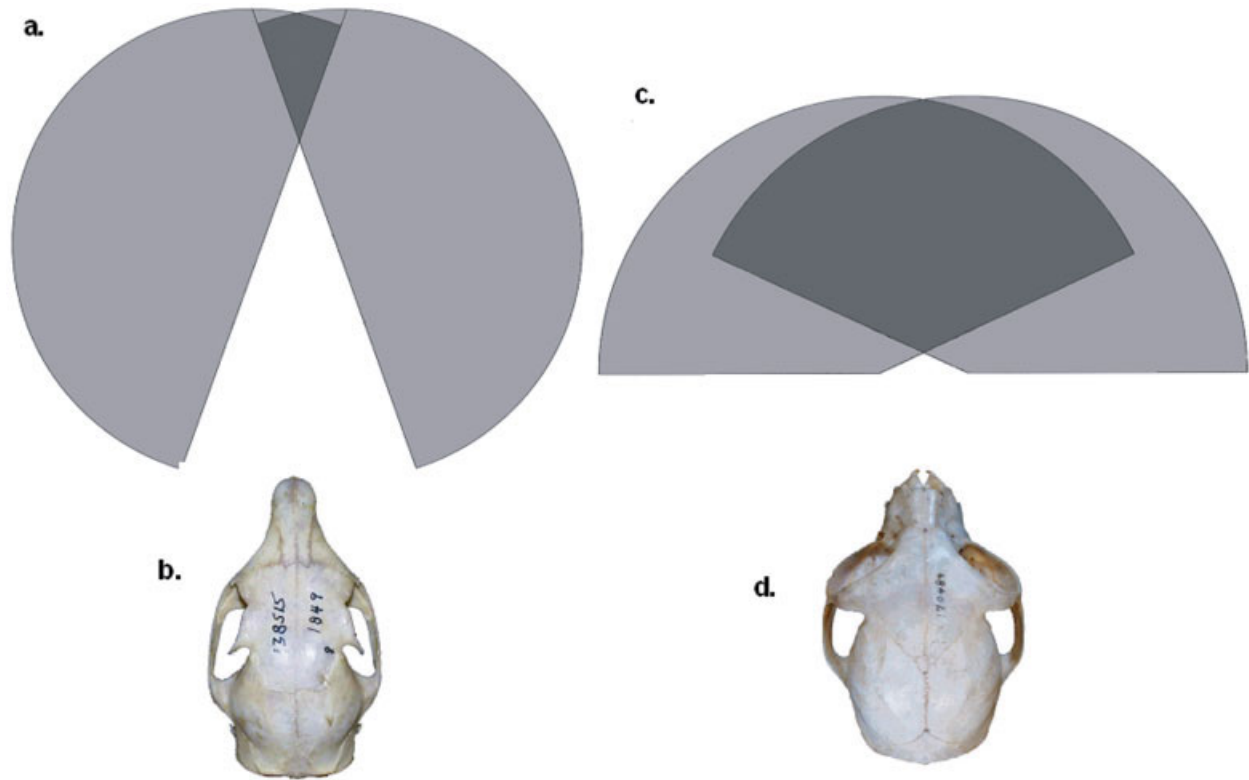


Fig. 1. Hypothesized relationship between orbit orientation and visual field overlap. **a:** Panoramic visual fields are associated with monocular visual fields (lighter-shaded regions) that are associated with small regions of binocular overlap (darker-shaded region). **b:** Skull of the squirrel *Sciurus carolinensis*, which has laterally facing orbits and a large panoramic visual field. **c:** Mammals with substantial binocular visual

fields are associated with relatively abbreviated monocular visual fields (lighter-shaded regions) compared with the regions of binocular overlap (darker-shaded region). **d:** Skull of the strepsirrhine primate *Propithecus verreauxi*, which has convergent (similarly facing) orbits and possibly a large binocular visual field. Skulls not to scale.

orienting the orbits to enhance binocular vision. Indeed, many taxa noted for their large panoramic fields with minimal binocular overlap, such as horses and large artiodactyls, are quite able to reorient the visual axes to greater overlap toward their forefeet despite their laterally facing orbits [personal observation; see also Hughes (1977)]. If mammals can reorient their visual fields and increase binocular overlap by ocular mobility with great variability, then the association with orbit convergence is unclear. This article evaluates the relationship between orbit convergence and the maximum horizontal extent of the binocular visual field in a representative sample of mammals.

MATERIALS AND METHODS

Morphometric data on orbit convergence were collected on 121 specimens of 27 taxa of eutherian and metatherian mammals (Table 1). The samples are housed in the Departments of Mammalogy of the American Museum of Natural History, Smithsonian Institution, Museum of Comparative Zoology (Harvard), Museum of Comparative Anatomy (Stony Brook University), and the comparative anatomy collection of Dr. Nikos Solounias of the New York College of Osteopathic Medicine.

Data on the maximum extent of binocular overlap of the monocular fields are derived from the literature (Table 1).

These data come from several sources and were originally collected using multiple methodologies. Most data on the size and shape of the monocular and binocular visual fields were collected using a projected reflex ophthalmoscopic technique in which the extents of each retina are reflected onto a globular calibrated ophthalmoscope and measured (Fite, 1973; Grobstein et al., 1980; Martin, 1984). Additional data were collected based on the retinotopic projections to cortical visual areas. The correspondence of ophthalmoscopic and the retinotopic organization of cell projection data has been explored elsewhere (Rodger et al., 1998; Arrese et al., 1999), but in general these provide similar estimates of the size of the binocular visual field.

Orbit Convergence

Eye position and orientation are often described as frontal- and lateral-eyed in the neurobiological literature (Hughes, 1977; Howard and Rogers, 1995). However, these frontal- and lateral-eyed descriptions do not directly translate to descriptions of orbit orientation in mammals (Cartmill, 1972). The main problem is that the term "frontal" often conflates orbit convergence, the degree to which the orbits face in the same direction, with the vertical orientation of the orbit relative to the braincase or face. This is problematic because the orientation of the orbits

TABLE 1. Orbit convergence and binocular visual field overlap

Species	Common name	n	Orbit convergence	Binocular visual field	Reference
<i>Equus caballus</i>	Horse	4	24.4° (2.5°)	57°	Walls (1942)
<i>Ovis aries/canadensis</i>	Sheep	2	28.8°	61.7°	Piggins and Phillips (1996)
<i>Bos taurus</i>	Cattle	4	32° (4.3°)	51°	Walls (1942)
<i>Capra hircus</i>	Goat	3	38.7° (2.6°)	63°	Walls (1942); Hughes and Whitteridge (1973)
<i>Rattus rattus</i>	Rat	2	32°	40–60°	Hughes (1979); Arrese et al. (1999)
<i>Mus musculus</i>	Mouse	6	38.3° (6.4°)	40°	Drager (1978); Arrese et al. (1999)
<i>Mesocricetus auratus</i>	Hamster	6	55.8° (3.5°)	80°	Finlay and Berian (1984); Arrese et al. (1999)
<i>Sciurus carolinensis</i>	Squirrel (E. Grey)	4	22.1° (2.0°)	60°	Hughes (1977)
<i>Lepus</i> sp.	Rabbit	2	20°	27–32°	Walls (1942)
<i>Canis lupus</i> /sp.	Dog	6	50.4° (5.6°)	78–116° ^{aa}	Walls (1942)
<i>Felis catus</i>	Cat	6	65.4° (5.8°)	120°	Illing and Wassle (1981); Dunlop et al. (1998)
<i>Mustela putorius (furo)</i>	Ferret	2	35.3°	80°	Morgan et al. (1987); Dunlop et al. (1998)
<i>Pteropus poliocephalus</i>	Gray-headed flying fox	3	50.9° (3.8°)	108°	Rosa and Schmid (1994)
<i>Dasyurus hallucatus</i>	Marsupial cat	6	41.6° (3.5°)	125°	Harman et al. (1986)
<i>Didelphis virginiana</i>	N.A. opossum	6	59.8° (8.3°)	125°	Rapaport et al. (1981)
<i>Didelphis marsupialis</i>	S.A. opossum	4	57.2° (4.9°)	125°	Oswaldo-Cruz et al. (1979)
<i>Trichosurus vulpecula</i>	Brush-tailed possum	5	59.7° (2.6°)	125°	Sousa et al. (1978); Arrese et al. (1999)
<i>Myrmecobius fasciatus</i>	Numbat	4	34.4° (4.5°)	80°	Arrese et al. (2000)
<i>Macropus eugenii</i>	Tammar wallaby	6	43.9° (1.9°)	60°	Wye-Dvorak et al. (1987)
<i>Sminthopsis crassicaudata</i>	Fat-tailed dunnart	2	40.8°	140°	Rodger et al. (1998)
<i>Tupaia glis</i>	Common treeshrew	6	32° (3.4°)	60°	Hughes (1977)
<i>Otolemur crassicaudatus</i>	Bushbaby	6	55.0° (3.8°)	136°	Ross (2000)
<i>Tarsius bancanus</i>	Tarsier	6	52.5° (2.8°)	127°	Ross (2000)
<i>Aotus trivirgatus</i>	Owl monkey	6	67.5° (2.0°)	138°	Allman and McGuinness (1988)
<i>Saimiri sciureus</i>	Squirrel monkey	6	69.9° (3.9°)	146°	Ross (2000)
<i>Macaca mulatta</i>	Rhesus macaque	6	73.9° (7.1°)	140°	Ross (2000)
<i>Homo sapiens</i>	Human	2	79.3°	140°	Vakkur and Bishop (1963); Bruce et al. (1996)

^{aa}Walls (1942) reports a multiple binocular visual field values for domestic dogs. A mean value was computed and used here.

relative to the long axis of the braincase or relative to the face can differ greatly among taxa that are otherwise convergent (Cartmill 1972, 1974; Heesy, 2003). For example, *Tarsius* and *Didelphis* have similar convergence values (127° and 125°, respectively), but the orbits face dorsally in *Didelphis* and rostrally in *Tarsius*. In addition, the vertical orientation of the orbits is not expected to be correlated with the maximum horizontal extent of overlap of the two monocular visual fields. For the purposes of this study, only orbit convergence, which measures the degree to which the bony orbital margins face in the same direction, is used.

Convergence is defined as the dihedral angle (an angle between two planes) between the orbital margin plane and the midsagittal plane (Fig. 2) (Cartmill, 1970). The sagittal plane is defined by prosthion, nasion, and inion. The orbital plane is defined by the points orbitale inferius (point on the orbital margin closest to the alveolar margin), orbitale anterius (point on the orbital margin most distant from inion), and orbitale superius (point on the orbital margin furthest from the alveolar margin).

These three-dimensional coordinate data were collected for the six landmark points on the skull with a Micro-Scribe-3DX coordinate data stylus (Immersion, San Jose, CA). Each specimen was mounted on an elevated clay base so that all coordinate data could be collected in a single series (Lockwood et al., 2002). Each specimen sits within its own three-dimensional coordinate data space with this arrangement. Orbit convergence was calculated from these coordinate data following a macro available in Heesy (2003).

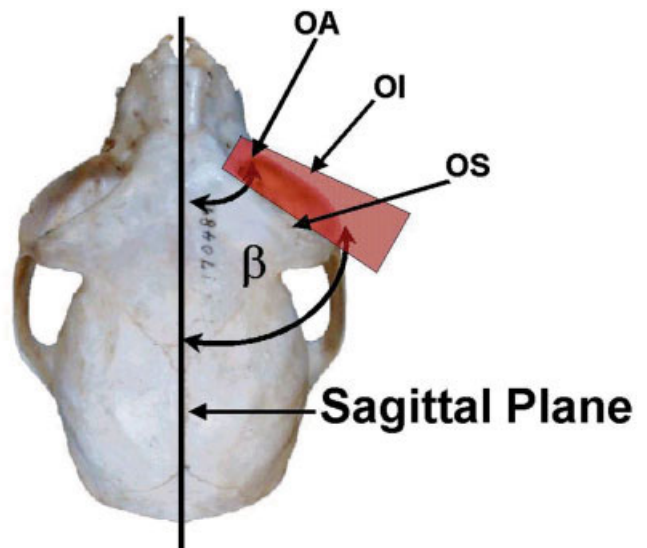


Fig. 2. Angular measurements. Convergence is the dihedral angle between the orbital and sagittal planes. The sagittal plane is defined by prosthion, nasion, and inion. The orbital plane is defined by the points OS, OI, OA. OS, orbitale superius, point on the orbital margin furthest from the tooth row; OI, orbitale inferius, point on the bony orbital margin closest to the tooth row; OA, orbitale anterius, point on the bony margin most distant from inion; β , convergence angle.

Data Analysis

An analysis of the regression slope between the variables was conducted in order to determine whether the relationship between convergence and binocular visual field overlap is isometric or allometric. Slope comparisons between orders were not possible due to small sample sizes. The reduced major axis regression was chosen because error variance is assumed to exist for both variables and the ratio of these variances is also assumed to be proportional to the population variances (Ricker, 1984; Rayner, 1985; Plotnick, 1989; Harvey and Krebs, 1990). The expected line of isometry between convergence and binocular visual field overlap has a slope of 2. This is a consequence of measuring convergence as the angle between only one orbital margin and midsagittal plane. For this reason, the angle of convergence is expected to be one-half of the angle of binocular visual field overlap because the latter is a measure of the orientation of the monocular visual fields of both eyes.

In order to investigate the correlation between variables, Spearman's rank correlation coefficients were calculated. Both nonphylogenetic and phylogenetic approaches were used for bivariate correlation analyses. Continuous biological data potentially violate standard statistical assumptions of independence due to phylogenetic relatedness (Felsenstein, 1985). Half of the taxa included in this study are either marsupials or primates and can possibly bias statistical analyses. Data were adjusted for phylogenetic similarity with the method of phylogenetic generalized least squares (PGLS) (Martins and Hansen, 1997; Rohlf, 2001) using COMPARE 4.4 (Martins, 2001). The PGLS method is based on normal least-squares regression but with a specialized error term that is a function of the covariance matrix and phylogenetic relationships of all included taxa. Rohlf (2001) has demonstrated that the more commonly used method of phylogenetic independent contrasts (Felsenstein, 1985) is a special case of PGLS, but that the generalized least-squares method is not limited to the assumption of the Brownian motion continuous random walk model of evolution.

In order to conduct the PGLS analyses, a composite phylogeny that included all taxa in this study was derived from a number of source trees as follows (Fig. 3): ordinal relationships among mammals (Murphy et al., 2001; Springer et al., 2003), artiodactyls (McKenna and Bell, 1997; Hassanin and Douzery, 2003), carnivorans (Bininda-Emonds et al., 1999), rodents (Huchon et al., 2002), primates (Purvis, 1995), and marsupials (Colgan, 1999; Wroe and Muirhead, 1999). Divergence dates were not available in all cases. For this reason, branch lengths were set equally to 1.

Angular data can potentially be nonnormally distributed due to the constraints of circular dimensions (Fisher, 1993). Departures from normality for angular and linear data were tested using the Kolmogorov-Smirnov test with Lilliefors modification (Sokal and Rohlf, 1995). Data on binocular visual field overlap deviated moderately from normality, but not to a degree that required a specialized statistical distribution (Fisher, 1993). Nonparametric alternatives were used instead.

RESULTS

The analysis of orbit convergence and the maximum extent of binocular visual field overlap was conducted

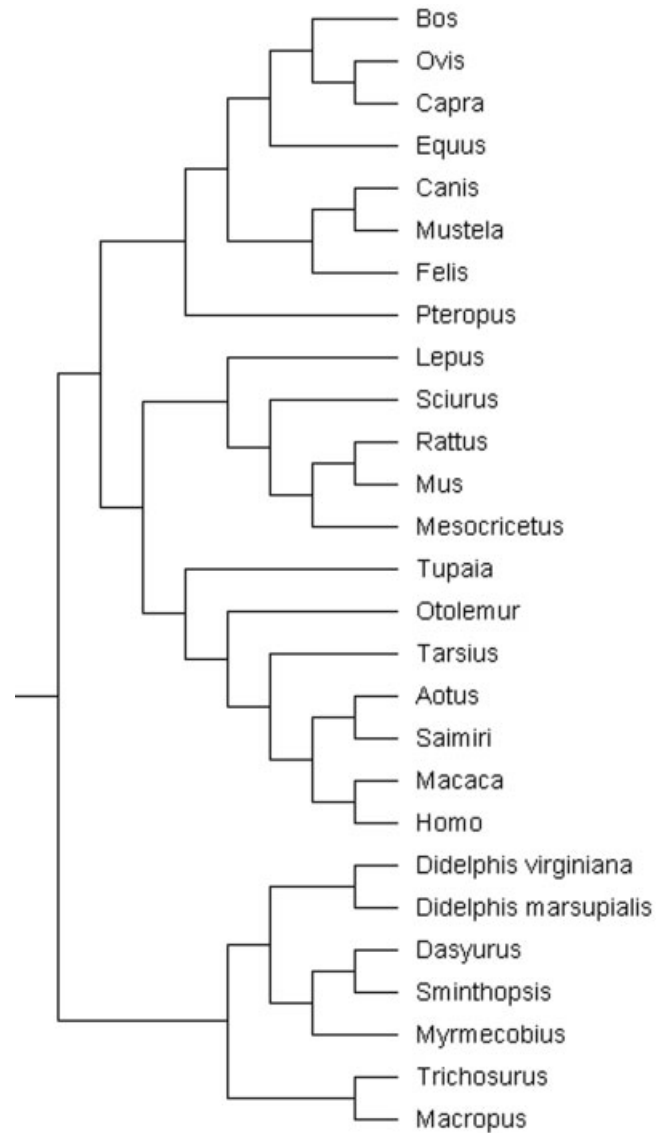


Fig. 3. Composite phylogeny used in the PGLS analysis. This phylogeny contains the 9 orders and 27 species that are included in this analysis. The source trees from which this comparative phylogeny was constructed are provided in text.

using the Spearman's rank correlation coefficient because the visual field data deviated moderately from normality. Orbit convergence and binocular visual field overlap are significantly correlated in the standard (i.e., nonphylogenetically corrected) analysis (Spearman's $\rho = 0.832$; $P < 0.01$; $n = 27$). The reduced major axis slope is 2.38, and the confidence intervals include isometry (1.86–2.9; see above for the justification of the slope of the isometric line). The relationship between convergence and visual field overlap is illustrated in Figure 4. Examination of this plot identifies two outliers, *Sminthopsis crassicaudata* and *Dasyurus hallucatus* (Fig. 4). These two marsupials have larger zones of binocular overlap than expected based on orbit convergence.

These data were reanalyzed adjusting for potential bias due to phylogenetic relatedness using PGLS in COM-

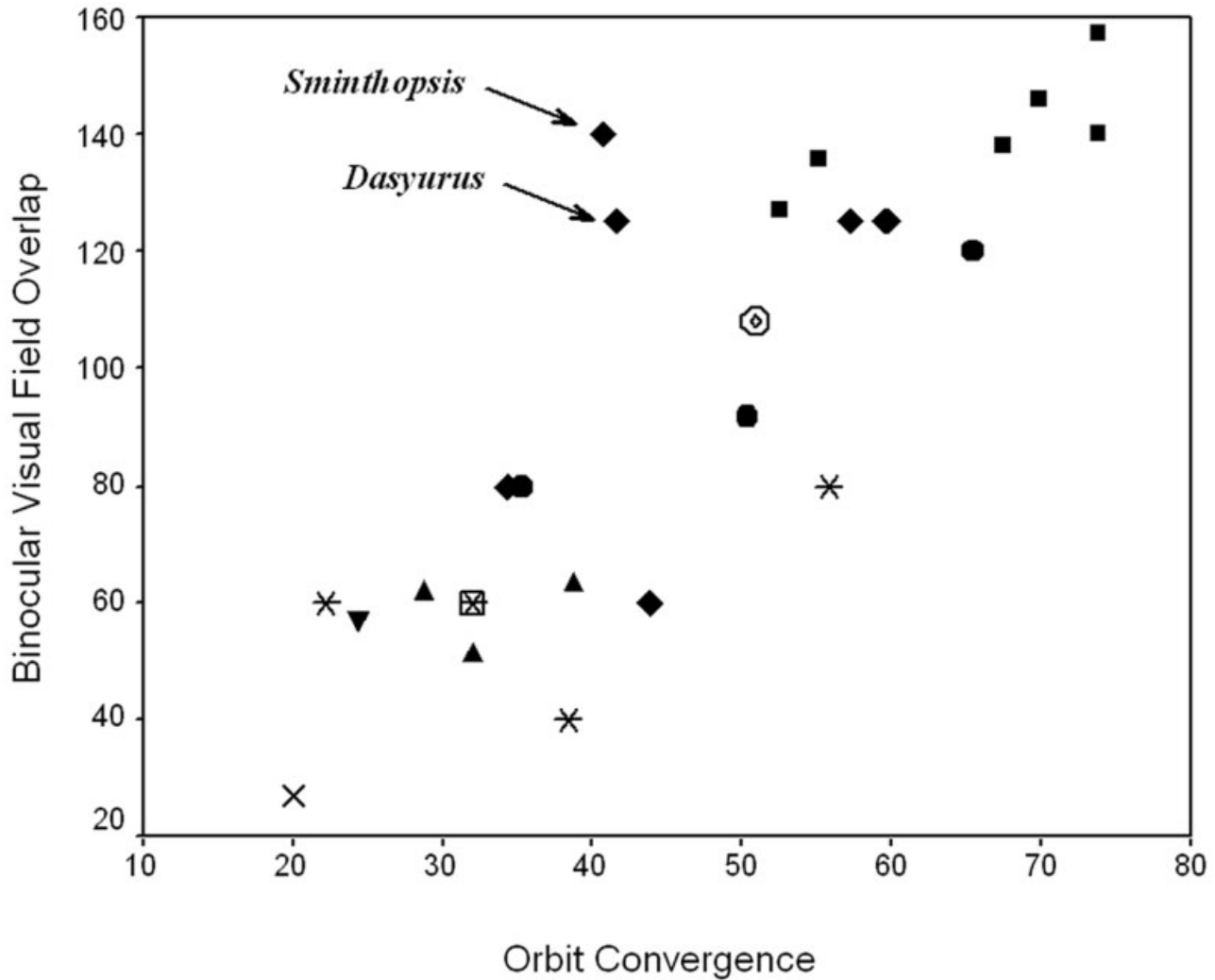


Fig. 4. Correlation between orbit convergence and binocular visual field overlap. Both variables are presented in degrees. The fitted line is the expected line of angular similarity between the variables. The outliers, *Sminthopsis crassicaudata* and *Dasyurus hallucata*, are illustrated. ▲, Artiodactyla; ●, Carnivora; ⊙, Chiroptera; ×, Lagomorpha; ◆, Metatheria; ▼, Perissodactyla; ■, Primates; ✱, Rodentia; □, Scandentia.

PARE 4.4. Just as with the standard statistical approach, orbit convergence and binocular visual field overlap are significantly correlated ($r = 0.82$; $P < 0.01$; $n = 27$).

The standard and phylogenetically controlled approaches are congruent in indicating that orbit convergence and binocular visual field overlap are positively correlated. The two approaches are also in agreement that convergence explains approximately 70% of the variance in the size of the binocular visual field in mammals. Orbit convergence is isometrically related to binocular visual field overlap across mammals. In general, these data indicate that reorientation of the bony orbit such that they face the same direction is highly correlated with expansion of the size of the binocular zone of the visual field.

DISCUSSION

The results of this study support the previous assumption that orbit convergence is a correlate of the degree of binocular visual field overlap in mammals. Taxa with

laterally facing orbital margins, such as horses and artiodactyls, have narrow fields of binocular overlap and presumably large panoramic visual fields. Taxa with high orbit convergence, such as primates, have comparatively very broad binocular visual fields. Importantly, isometry cannot be excluded as a description of the linear relationship between these two variables, suggesting that the functional relationship between eye and orbit orientation is virtually equivalent across mammals.

Among the taxa sampled in this study, only the marsupials *Sminthopsis crassicaudata* and *Dasyurus hallucatus*, which are phylogenetically closely related (Fig. 3) (Wroe and Muirhead, 1999), deviated from the overall general relationship illustrated in Figure 4. An explanation for why these two taxa deviate from the overall trend may be related to the fact that they are among the smallest in body size of those included in this study. Cartmill (1970, 1972) suggested that orbit convergence tends to be lower in small-sized taxa because their relatively larger

eyes may lead to lateral displacement of the lateral orbital margin, rostral displacement of the medial orbital margin, or both. That the binocular fields of these two taxa are larger than expected based on orbit convergence is interesting because it implies that, at least under experimental conditions, animals may expand binocular overlap by converging the visual axes. Two cited advantages for binocular visual fields are enhanced light sensitivity and contrast discrimination, both of which would benefit nocturnal taxa (Lythgoe, 1979; Ross et al., 2005). *Sminthopsis* is cathemeral, active at all light levels, and *Dasyurus* is nocturnal (Arrese et al., 1999). Although speculative, one possible reason for the larger binocular zone in these two animals may relate to their nocturnal and predatory habits. However, both of these taxa exhibit relatively low levels of visual acuity as well as retinal physiological traits similar to other mammals that spend some or their entire activity budget under nocturnal conditions (Arrese et al., 1999), so it is not apparent what benefit the expansion of binocularity would provide these animals. Yet, under certain conditions, functionally converging the visual axes may occasionally be required for some visual tasks, and the ophthalmoscopic measurements may reflect this ability.

Considered as a whole, these results are perhaps not entirely surprising considering the well-documented retinotopic organization of the visual cortex (Allman and Kaas, 1971; Kaas, 1978; Allman and McGuinness, 1988), which probably at least partly constrains the processing of binocular visual data. Mobility of the eyes may permit expansion of the field of binocular overlap, but enlarged fields may not project to primary cortical areas that contain neurons selective to binocular disparity (Cumming and DeAngelis, 2001). This would provide a reasonable explanation for the high correspondence between retinotopic topography, orientation of the globe and nasal and temporal hemifields of the eyes, and the orientation of the bony orbital margins.

Binocular and Stereoscopic Vision in Basal Primates

Anthropoid primates have the highest orbit convergence values among mammals, and strepsirrhine primates inhabit the highest end of the range of eutherian taxa (Cartmill, 1972, 1974; Ross, 1995; Heesy, 2003). This implies that, based on the data presented in this study, primates have among the largest binocular visual fields among eutherian mammals. The phylogenetic history of primate binocular vision is partly preserved in the fossil record. For example, the recently described basal omomyiform *Teilhardina asiatica* from the early Eocene of China has an estimated orbit convergence value of 51° (Ni et al., 2004), similar to extant small-sized strepsirrhine primates (Ross, 1995; Heesy, 2003). High convergence in *Teilhardina* and other early primates when considered together with the distribution of orbit convergence among extant primates suggests that high convergence and binocular vision are primitive for primates (Cartmill, 1972, 1974; Allman, 1977; Ross, 1995; Heesy, 2003; Kirk et al., 2003). This phylogenetic view provides additional support for the hypothesis that has come to be known as the nocturnal visual predation hypothesis of primate origins, which explains orbit convergence and binocular visual field overlap as a unified component of a visual system that was adapted for predatory behavior in a light-limited

environment (Cartmill, 1972, 1974, 1992; Allman, 1977, 1999; Pettigrew, 1978, 1986; Heesy and Ross, 2001; Kirk et al., 2003; but see Ni et al., 2004).

In summary, this article demonstrates that orbit convergence and binocular visual field overlap are isometric and significantly correlated in mammals. These data support previous studies that have used orbit convergence as a proxy for binocularity, particularly for studies of primate evolution (Collins, 1921; Cartmill, 1972, 1974, 1992; Allman, 1977, 1999; Pettigrew, 1978, 1986; Heesy, 2003).

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