

Seeing in Stereo: The Ecology and Evolution of Primate Binocular Vision and Stereopsis

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Primates are the most visually adapted order of mammals. There is a rich history within anthropology of proposed explanations for the adaptive significance of binocular vision, especially pertaining to primate origins and evolution. Depth perception and orbit morphology have been hypothesized to be functionally related to specialized locomotor or feeding behaviors. Many of these arguments continue to this day. An understanding of specific primate visual adaptations, including binocular vision, can shed light on these long-term and heated debates.

Primates exhibit highly derived neurological processing of spatial form and contrast, depth and motion perception, and multiple variants of color vision. One of the most conspicuous primate visual specializations is the large area of overlap between the fields of vision of the two eyes.^{1,2} Indeed, the wide binocular field is functionally related to many other specializations of the primate visual system, including high visual acuity, specializations of visual pathways in the brain, changes in the visuomotor system (Box 1), and elaboration and differentiation of the visual cortex. Visual-field overlap also correlates with orbital convergence, that is the degree to which

the bony orbits face in the same direction (Fig. 1).^{1,3–5} The relationship between these two variables is linear and roughly isometric in mammals, with primates plotting at the high end of both distributions.^{6,7} For a given body size, strepsirhine primates have somewhat less convergent orbits than do anthropoids; nevertheless, strepsirhine orbits are more convergent than are those of many nonprimates.^{3–11} This is also true of the earliest omomyiforms and adapiforms.^{6,8,11,12} High orbital convergence and wide visual-field overlap thus appear to be inherited from primate ancestry.

ADAPTIVE SIGNIFICANCE OF PRIMATE BINOCULAR VISION: ACROBATIC ARBOREAL LOCOMOTION OR NOCTURNAL VISUAL PREDATION?

For much of the twentieth century, features of primates, including specializations of the visual system, were explained as adaptations to the occupation of an arboreal niche.^{13–16} Collins¹⁴ was the first to suggest that binocular vision and stereopsis, the cortical process that mentally reconstructs a three-dimensional world using binocular visual information,

were required for the accurate judgment of distance in arboreal locomotion, including leaping between arboreal substrates. Depth perception is presumably required for successful judgment of distances between substrates, especially during leaping, where a misjudgment can prove fatal. Robert Martin later incorporated elements of these ideas in his fine-branch niche hypothesis of primate origins in which visual specializations for depth judgment would prove effective during acrobatic locomotion that navigates a network of fine arboreal supports.^{17,18} Crompton¹⁹ expanded on this idea, suggesting that stereoscopic depth perception and orbit convergence evolved in early primates so that they could accurately judge distance during nocturnal vertical clinging and leaping, a specialized form of high-speed ricochet arboreal locomotion used by several taxa of extant primates. Importantly, Crompton invoked the demands of maneuvering through branches and other substrates in a low-light, visually complex environment to locate target food (fruit and possibly insects). The common component to Collins', Martin's, and Crompton's proposals is the need for accurate judgment of distance among arboreal substrates to avoid a catastrophic error in distance estimation during arboreal leaping.

The functional link between the visual demands of arboreal locomotion and binocular vision has been criticized, most notably by Cartmill.^{3–5} Although Cartmill directed his arguments against Collins and other proponents of the arboreal hypothesis of primate origins, and predated the

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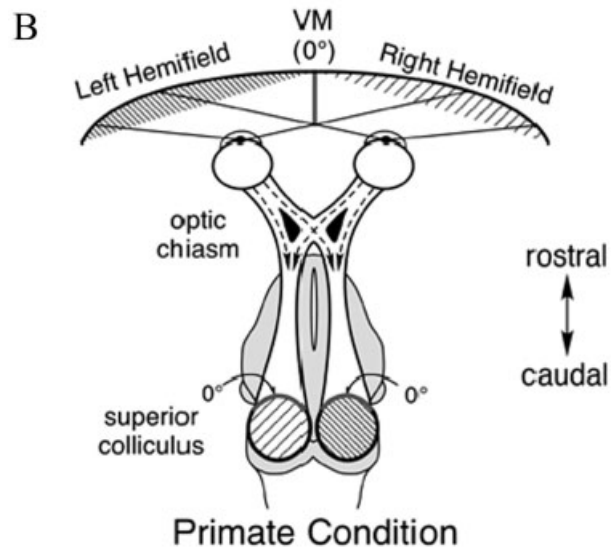
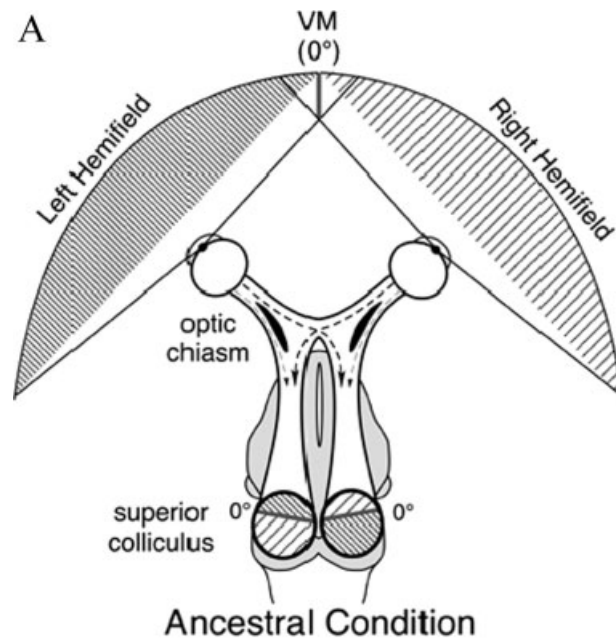
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Box 1. The Primate Retinotectal Pathway and Visual Targeting

There are four main targets of visual information from the retina. The main terminus of retinal information is the pathway to the primary visual cortex via the lateral geniculate nucleus of the thalamus. The supra-chiasmatic nucleus of the hypothalamus and the pretectum, which are subcortical targets, respectively influence or control circadian rhythms and pupillary light responses. The retinotectal pathway, which targets fibers to the superior colliculus in the midbrain portion of the brainstem, is a critical component of the system for planned and coordinated eye movements.

Comparative studies by Pettigrew and coworkers have demonstrated that primates, dermopterans ("flying lemurs"), and some megachiropterans (fruit bats) all have, as compared to most other mammals, a unique morphology and sensorimotor representation in the superior colliculus.⁸⁸

The superior colliculus is a component of a major brainstem structure known as the tectum, which integrates visual, auditory, and somatosensory information (Box 1, Fig. 1A). The superior colliculus of most mammals has a complete map of the visual field seen by the contralateral eye (that is, the left superior colliculus contains information collected by the right eye, Box 1, Fig. 1A). The superior colliculi of primates have segregated information so that each side contains information on the contralateral visual field (Box 1, Fig. 1B). This arrangement integrates information from each eye. While fruit bats and flying lemurs are similar to primates in that visual field representation in the superior colliculus comes from both eyes, they also retain some overlap and redundancy in visual field components that is dissimilar to the situation in all primates. Integrated visual field topography of the superior colliculus is not simply a function of increasing binocular visual field overlap. For example, cats, which have substantial binocular overlap, retain the typically mammalian pattern of contralateral eye representation in the colliculus.^{1,89}



Box 1, Figure 1. This schematic, reproduced from Preuss,¹⁰³ is based on the work of Pettigrew and colleagues.⁸⁸ Reprinted with kind permission of the author and Springer Science and Business Media.

Although this point has been debated, a major function of the superior colliculus in primates is to redirect the eyes, especially the zone of maximal binocular visual field overlap, to an object of interest.⁹⁰ The primate tectum has precisely coordinated visual to visuomotor maps related to ex-

traocular eye muscle function.⁹¹ Allman¹ argues that the lack of redundancy in the visual map of the primate superior colliculus potentially eliminates ambiguity of targeting, which otherwise might make primates' ability to fixate on an object of interest less rapid and accurate.

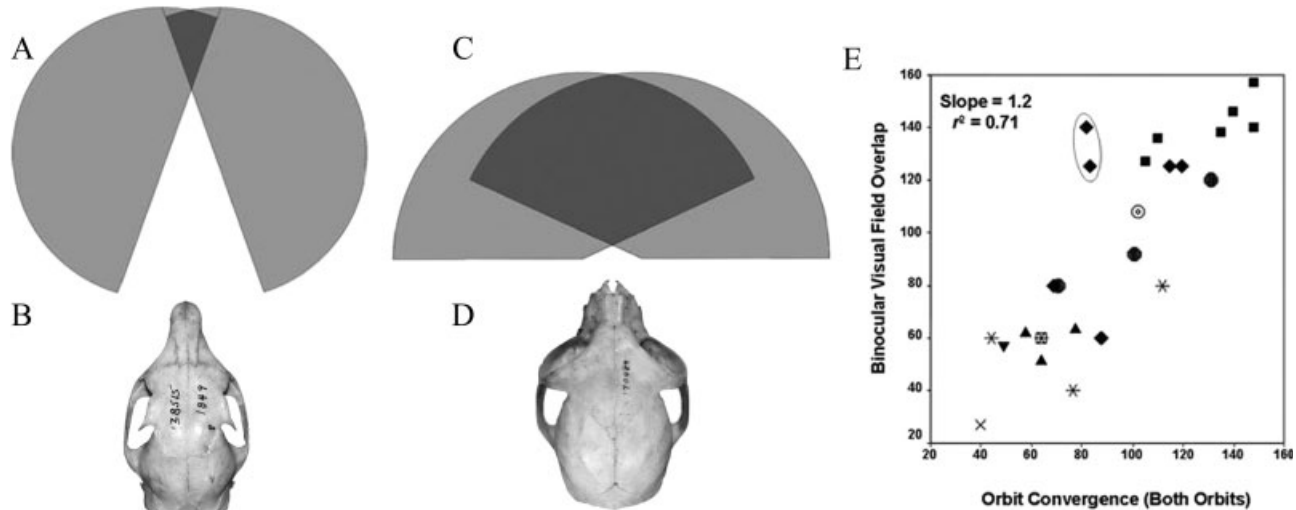


Figure 1. Relationship between orbit orientation and visual field overlap. A. Panoramic visual fields are composed of monocular visual fields (lighter shaded regions) that minimally overlap and are associated with small regions of binocular overlap (darker shaded region). B. Skull of the squirrel *Sciurus 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 strepsirhine primate *Propithecus verreauxi*, which has convergent (similarly facing) orbits and possibly a large binocular visual field (skulls not to scale). E. The correlation between orbit convergence and binocular visual field overlap is significant (Spearman's $\rho = 0.832$, $P < 0.01$, $n = 27$); the confidence intervals of the reduced major axis slope include isometry. Both variables are presented in degrees. The ellipse denotes the positions of the outliers. *Sminthopsis crassicaudata* and *Dasyurus hallucata*. Key: \blacktriangle - Artiodactyla, \bullet - Carnivora, \odot - Chiroptera, \times - Lagomorpha, \blacklozenge - Metatheria, \blacktriangledown - Perissodactyla, \blacksquare - Primates, \ast - Rodentia, \square - Scandentia. (Reprinted from Heesy,⁹ by permission of S. Karger AG, Basel).

work of Crompton and Martin, his objections are equally applicable to all of these hypotheses. The strongest argument against a link between arboreal habits and orbit orientation is that arboreality is not unique to primates, and yet other groups of arboreal mammals, such as rodents, sloths, and some tree-dwelling hyraxes, all have divergent orbits and panoramic visual fields.^{3-5,7,9,20} Locomotion in a complex arboreal environment does not require large binocular and stereoscopic fields. Many arboreal taxa with panoramic vision successfully locomote in this environment.³⁻⁵ For example, arboreal mammals that leap across discontinuous substrates, such as between branches, do not require convergent orbits and expansive binocular visual fields, as demonstrated by the fact that nonprimate arboreal leapers, such as the squirrel *Sciurus*, successfully traverse discontinuous arboreal substrates despite having divergent orbits and limited binocular visual fields.³⁻⁵ Indeed, many gliding rodents, including most anomalurids (scaly-tailed flying squirrels) and petauristines ("normal" flying squirrels), which successfully tra-

verse distances exceeding 100 m between trees, have relatively divergent orbits and, by extension, small binocular visual fields.

Additional criticisms of the connection between arboreality and orbit orientation can be based on studies of the visual information available to most animals during locomotion, irrespective of the size of their binocular field or orbit orientation. Optic flow fields, which are generated by the visual perception of global motion of objects in the environment during locomotion, are based on the movements of projected images across the retina²¹ (Fig. 2a). In other words, movement causes visual information from the environment to flow or radiate across the retina. These optic flow fields provide information on locomotor heading, velocity, and time-to-impact relative to objects or environmental substrates.²¹⁻²³ Optic flow fields are generated by the visual angles subtended by an object and are inversely proportional to the distance from that object to the observer.²² During locomotion, perception of the distance to contact with an object is a function of the ratio of the perceived

distance relative to the rate of change in visual angle of the object. Stated more simply, a locomoting animal perceives objects close to it as larger and moving more quickly than are those that are farther away, which it perceives to be smaller (Fig. 2b). In the simplified case of moving straight forward, points in visual space radiate outward and toward the observer.

The utility of optic flow during locomotion has been most extensively studied in humans and birds.²³⁻²⁵ Although, to the best of my knowledge, optic flow has not been studied in strepsirhine primates, extrapolating from the available data on macaques and humans, as well as avians, supports the hypothesis that arboreal strepsirhines and, for that matter, most animals, probably use optic flow perception to determine heading, velocity, and time-to-impact during locomotion. It is reasonable to question whether the large binocular fields of primates have evolved to use optic flow. Although several studies suggest that binocular cues improve locomotor performance using optic flow in humans,^{26,27} it is notable that the birds that have been demonstrated

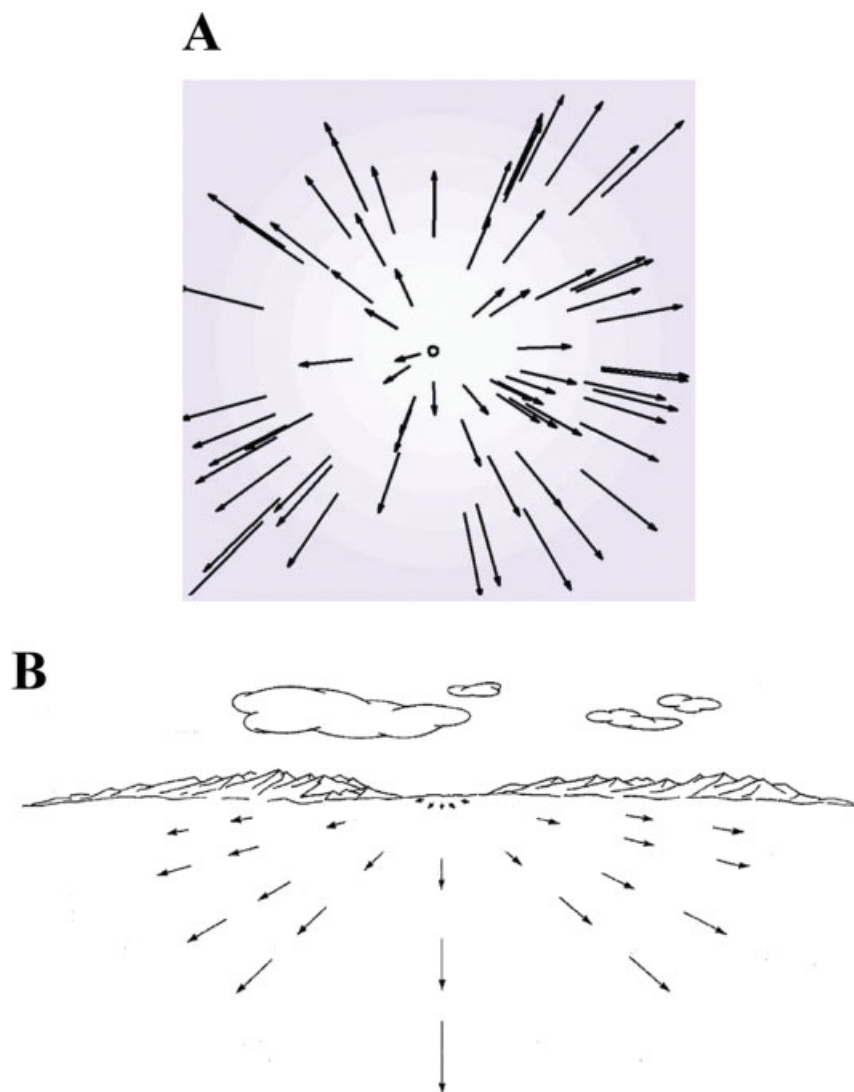


Figure 2. A. In the simplified case of moving straight forward, the points in visual space flow outward from the center. When followed over time, the length and direction of each line provide information on direction and velocity. (Reprinted by permission from Macmillan Publishers Ltd: (Nature) from Cumming,¹⁰² copyright 1998). B. In the pilot's-eye view of traveling forward, there is a gradient of increasing flow of visual cues from the horizon toward the viewer (redrawn and modified from Gibson²¹). (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

to use optic flow fields for heading judgments during flying have small binocular visual fields, yet obviously are very successful at locomoting.²⁸ The avian data certainly suggest that large binocular fields are not necessary to take advantage of optic flow information during locomotion.

An alternative to the locomotion component of the "arboreal theory" has been proposed by Cartmill,³⁻⁵ Allman,¹ and Pettigrew²⁹⁻³¹ to explain the functional and adaptive advantages of orbit convergence and

binocular visual field overlap. Cartmill³⁻⁵ proposed the "visual predation hypothesis" to explain an adaptively cohesive suite of morphological, ecological, and behavioral traits of primates. The influence of activity pattern, specifically nocturnality or light-limited environments, on the optical system was explicated later by Allman and Pettigrew.^{1,29,30} Although Cartmill's hypothesis potentially explains the adaptive significance of multiple traits, here I review only those components related to evolu-

tion of visual system. High orbit convergence and binocular visual field overlap are hypothesized to be adaptations to the nocturnal visual predatory habits of the last common ancestor of all primates. This hypothesis is based on several key points: comparative orbit morphology among mammals, comparative optics, and the functional attributes of stereopsis.

In addition to his observation that many nonprimate arboreal mammals have divergent orbits, Cartmill noted that various mammals possess orbit convergence similar to that of extant strepsirhine primates. In a series of allometric studies that controlled for relative orbit size, Cartmill demonstrated that relatively high orbit convergence values are characteristic of predatory mammals that rely on vision to target, track, and seize prey.^{3,4} He found that orbit convergence values among these predatory mammals were similar to those of small-sized predatory strepsirhine primates such as some loriforms, as well as the haplorhine *Tarsius*. Based on these observations, Cartmill hypothesized that traits of the primate visual system could be best explained as adaptations for a visually directed predatory ancestral habit.³⁻⁵ Further consideration of some of the grasping adaptations and dietary ecology of small predatory strepsirhines led Cartmill to suggest that ancestral visual predation habits were directed toward insects of the forest canopy and undergrowth.⁵ However, Cartmill did not explicitly state a nocturnal activity pattern for primate origins.

Allman¹ and Pettigrew^{29,30} contributed to the visual predation hypothesis by providing a functional explanation that links orbit convergence to the alignment of the orbital, optical, and visual axes, specifically in nocturnal taxa. The optical axis is defined as the axis of symmetry through the cornea and lens, whereas the visual axis is defined as the line that fits through the point of fixation, nodal points, and area centralis (or fovea in taxa that possess one). The orbital axis is the line of symmetry of the orbit. Pettigrew's work was first directed toward avians, but was later expanded to include mammals.^{29,30} Theoretical optical effects of

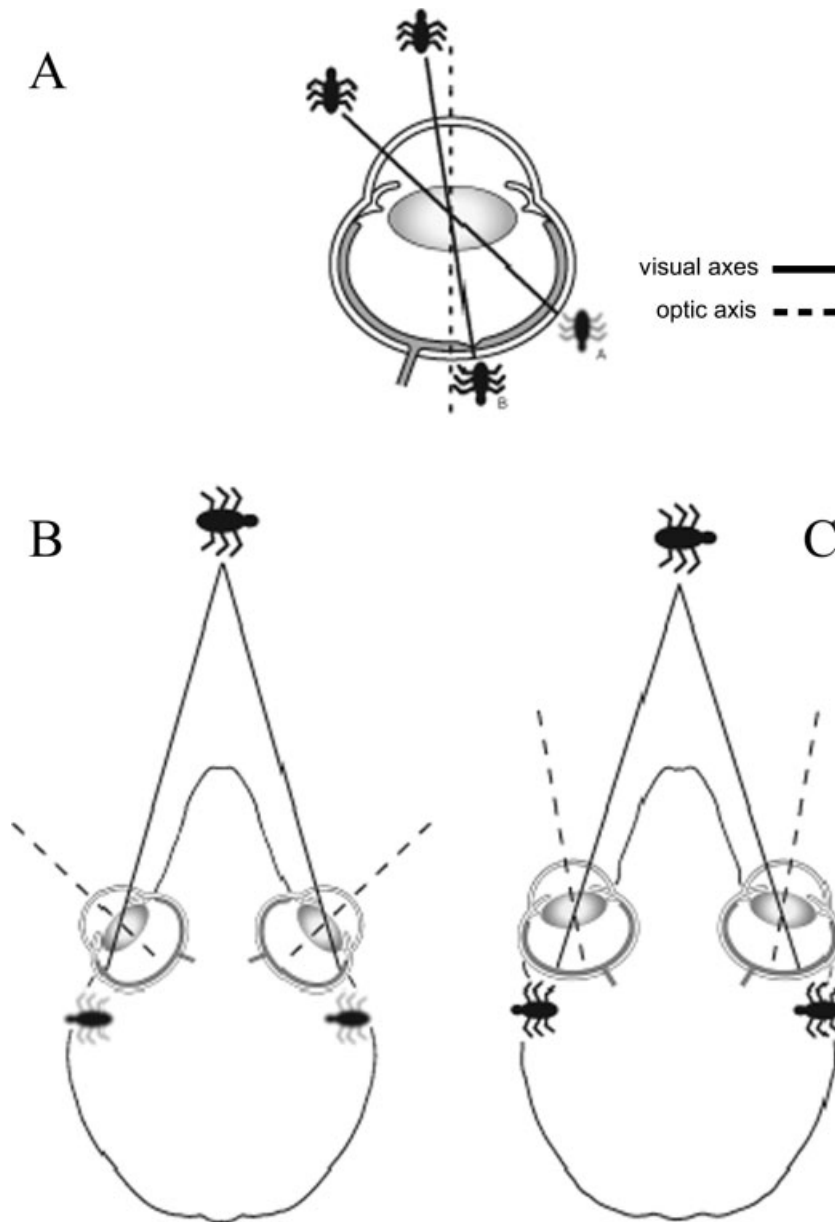


Figure 3. Visual axis reorientation. A. Schematic diagram illustrating the relationship between orientation of the optic axis and visual axis. B. and C. show these relationships in, respectively, an animal with divergent orbits and one with convergent orbits. See text for a detailed discussion of this figure. Please note that refraction and aberration of the path of light are not detailed here. (Figure provided by C. F. Ross).

visual axis alignment in taxa with divergent and convergent orbits are illustrated in Figure 3. In taxa with divergent orbits and optic axes (Fig. 3b), the visual axes converge on an object in front of the animal; light traveling along these axes consequently traverses the most curved portion of the lens of the eye. High curvature of lenses will alter the path of light and

degree of curvature of the lens surface.³² Passage of light through the more curved portions of the lens produces spherical aberration,³² which reduces image quality in optical systems and has a potentially detrimental effect on visual acuity by decreasing image focus on the retina.³²⁻³⁴ The reduction in image quality is lessened in animals having a spherical-shaped lens and, therefore, a uniform angle of

approach. Diurnal animals can avoid the image aberration and poor visual acuity caused by spherical aberration by reducing the diameter of the pupil, thereby allowing light to pass only through the center of the lens. The lens center is optically superior because it is the least curved and allows light to pass through this paraxial zone with less reorientation of the light path than is caused by light passing through the peripheral portion of the lens. Nocturnal animals, however, need to capture as much light as possible from the environment to produce a sufficiently bright image on the retina and therefore cannot reduce pupil size to the same degree as can diurnal taxa.^{1,29,30,35-37} However, by reorienting the eyes and orbits so that the visual and optic axes are more closely aligned, light from the object of interest can pass through the center of the lens (Fig. 3c). This close alignment of the optic and visual axes allows nocturnal animals to view objects or prey within binocular fields without compromising light-gathering capabilities.

The nocturnal visual predation hypothesis is a composite of the comparative work conducted by Cartmill with the optical arguments of Allman and Pettigrew.⁵ The nocturnal visual predation hypothesis is supported by comprehensive analyses of extant comparative data on orbit convergence (Box 2). In addition, phylogenetically based character analyses of activity pattern support another prediction of the nocturnal visual predation hypothesis, that ancestral primates were nocturnal (Box 3). On the other hand, the nocturnal visual predation hypothesis has been criticized based on phylogenetic and ecological arguments. In order to address these criticisms, it is necessary to distinguish those depth cues that are available to all animals from those functional qualities that are exclusive to binocular vision.

OPTICAL MECHANISMS FOR JUDGING DEPTH ARE AVAILABLE TO ALL MAMMALS

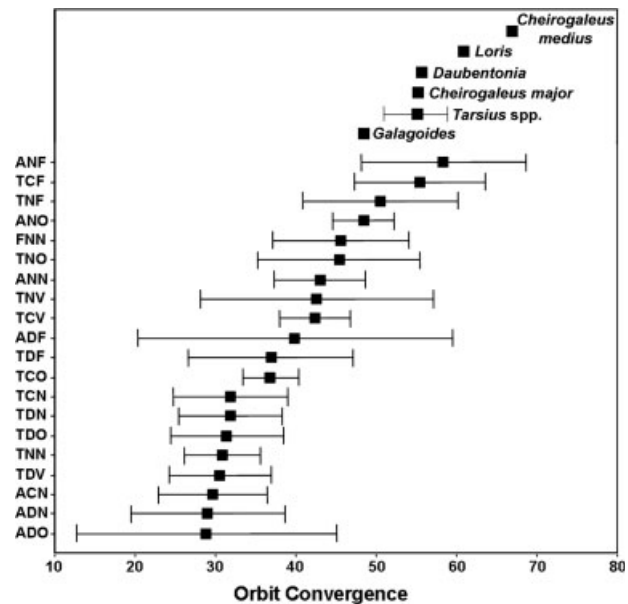
Many researchers have concluded that primate binocular vision evolved to allow improved depth perception.

Box 2. Orbit Convergence and Nocturnal Visual Predation Revisited

One critical prediction of the nocturnal visual predation hypothesis is that convergent orbits occur in mammals that use visual cues to detect, track, and capture prey at night. Correlative data on orbit morphology and feeding ecology in a sample of mammals fueled Cartmill's original exposition of the nocturnal visual predation hypothesis.^{3,4} Two recent studies have revisited this issue using larger and more diverse sampling across mammals.

Ravosa and Savakova¹¹ reexamined the relationship between orbit convergence and dietary ecology in didelphid marsupials; herpestid, procyonid, and felid carnivorans; pteropodids (fruit bats); scandentians (tree shrews); dermopterans ("flying" lemurs); plesiadapiforms; and several extant and fossil primates. The authors found that when allometric factors are taken into account, nocturnal arboreal frugivores such as pteropodids exhibit relatively low levels of orbital convergence, similar to values found in tupaiids, dermopterans, herpestids, and plesiadapiforms. Eocene primates are similar to nocturnal primate and felid analogs in possessing relatively convergent orbits.

I also recently studied the ecological factors associated with high orbit convergence in mammals.⁹ Data on orbit orientation for over 321 extant taxa of marsupial and eutherian mammals were combined with data on activity pattern, degree of faunivory, and substrate preference. Taxa were sorted by considering activity pattern, degree of faunivory, and locomotor substrate together. For example, all mammals that could be categorized as diurnal, terrestrial, and nonpredatory (no animal matter in the diet) were averaged into a single group regard-



Box 2, Figure 1. Ranked ecological composite categories based on orbit convergence (nonprimate eutherian mammals). Groups are ranked by mean orbit convergence. Strepsirhine taxa are added at top for comparison. Top, beginning with ANF, has the highest mean convergence; bottom, ADO has the lowest mean convergence. Filled squares indicate mean bracketed by error bars. Abbreviations for group codes are: ADO, arboreal diurnal omnivore; ANF, arboreal nocturnal faunivore; TCF, terrestrial cathemeral faunivorous; ANO, arboreal nocturnal omnivore; ANN, arboreal nocturnal nonpredator; TNO, terrestrial nocturnal omnivore and arboreal diurnal nonpredator; FNN, aerial or flying nocturnal nonpredator; TNV, terrestrial nocturnal, variably faunivorous; TCV, terrestrial cathemeral, variably faunivorous; ADF, arboreal diurnal faunivore; TDF, terrestrial diurnal faunivore; TCO, terrestrial cathemeral omnivore; TCN, terrestrial cathemeral nonpredator; TDN, terrestrial diurnal nonpredator; TNN, terrestrial nocturnal nonpredator; TDV, terrestrial diurnal, variably faunivorous; ADV, arboreal diurnal, variably faunivorous. Data from Heesy.⁹

less of taxonomic classification. I found that, in general, mammals that are nocturnal and cathemeral (active during night or day) have significantly more convergent orbits than do diurnal taxa, both within and across orders. Faunivorous eutherians, both nocturnal and diurnal, have higher mean orbit convergence than do opportunistically foraging or nonfaunivorous taxa (Box 2, Fig. 1). However, substrate preference, including arboreality, is not associated with higher orbit convergence or, by extension, greater visual field overlap. Strepsir-

hine primates have a range of orbit convergence values similar to that of nocturnal or cathemeral predatory nonprimate mammals (Box 2, Fig. 1).

The Ravosa and Savakova¹¹ and Heesy⁹ studies differ in species sampling and methodology, but the results are entirely consistent. Both studies found that faunivorous eutherian mammals living in light-limited visual environments possess relatively more convergent orbits. These results entirely support the predictions of the nocturnal visual predation hypothesis.

However, multiple cues to perceiving depth are used by animals with either panoramic or binocular visual fields. Any discussion of the rele-

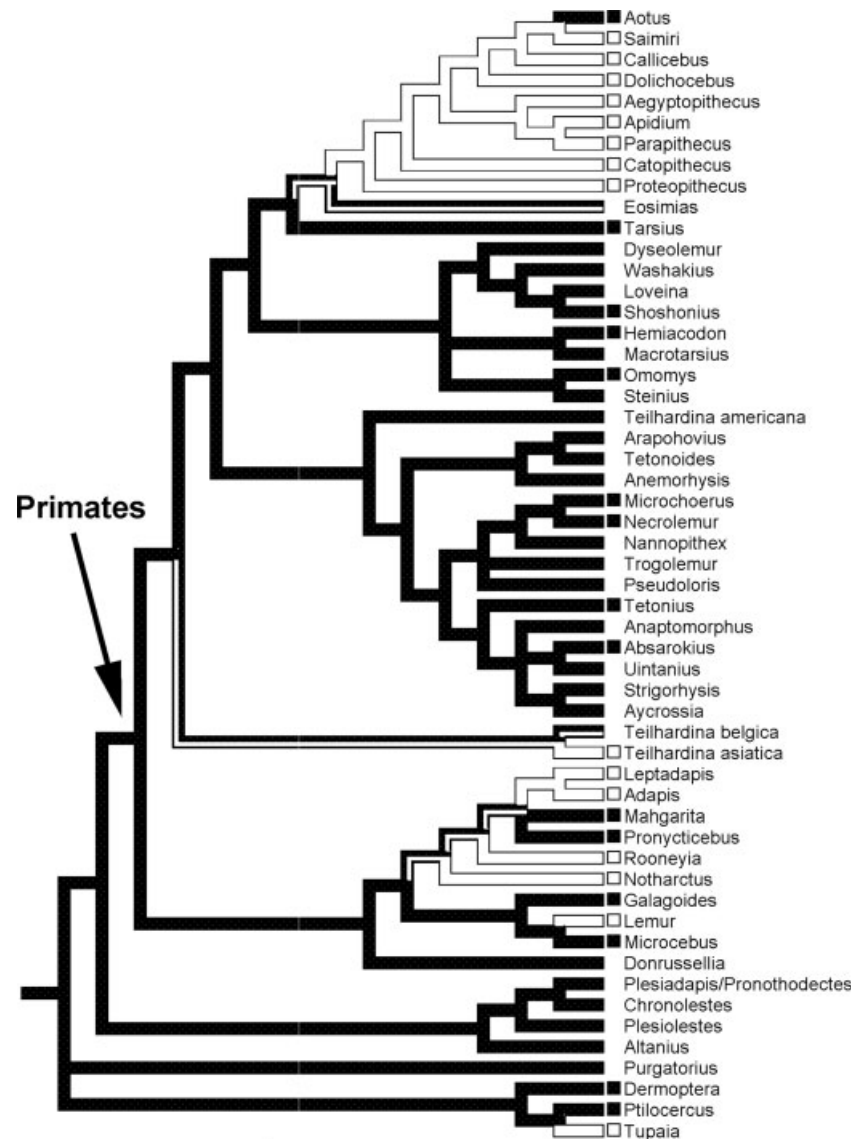
vance of depth perception to primate visual system evolution necessitates distinguishing those depth cues available to animals irrespective of

visual field form from those depth and visual benefits available solely to animals with substantial binocular visual field overlap.

Box 3. The Nocturnal Origin of Primates

Activity pattern, defined as the time of day that an animal is awake and active, is considered to be a critical component of several hypotheses for the origin of primates because of the profound influences of light available to the morphology and function of the visual system.^{36,37} (However, see Ankel-Simons and Rasmussen¹⁰⁴ for an alternative view on the importance of activity pattern to evolution of the primate visual system). Early work by Martin and Charles-Dominique suggested that, based on the distribution of activity pattern in some strepsirhines, the primitive activity pattern of primates was nocturnality.^{17,92} Recently, however, primates have been hypothesized to be primitively diurnal on the basis of two lines of evidence, the distribution of color-sensitive photoreceptor opsin genes in several extant strepsirhines,^{93,94} and reconstruction of the activity pattern of the fossil omomyiform, *Teilhardina asiatica*.¹² The problems with the applicability and interpretation of the genetic data are discussed in detail elsewhere.^{82,95,96}

The possibility of a diurnal ancestry for primates has been raised again recently by Ni and co-workers¹² in their recent description of the basal omomyiform *Teilhardina asiatica* from the earliest Eocene deposits of the Lingcha Formation, China. The skull of *T. asiatica* (IVPP V 12357) is complete enough to allow estimates of orbit diameter and skull length, facilitating the use of orbit-to-skull length scaling to infer activity pattern.⁹⁷ This activity pattern inference, with the addition of the reconstruction of faunivory in *T. asiatica* and a phylogenetically based character analysis of activity pattern, led the authors to suggest that the last common ancestor of primates was a diurnal and visually directed predator. In addition, if the most primitive omomyiform described to date was diurnal, it differs from all later omomyiforms, which were nocturnal,^{95,97}



Box 3, Figure 1. Re-analysis of activity pattern character optimization on the cladogram from Ni and colleagues.¹² Key: Black nodes and branches are nocturnal, white nodes and branches are diurnal, lined nodes and branches are equivocal. Taxa with boxes at left are those for which character states are either known or inferred; they were included in the character optimization.

implying that nocturnality is derived within omomyiforms.

Ross and Martin,⁹⁸ as well as Bloch and Silcox,⁹⁹ have suggested that the extremely small size of *Teilhardina asiatica* precludes the use of extant scaling prediction equations for the purpose of reconstructing activity pattern because *Teilhardina* falls so far below the size range of

extant primates. On the other hand, two critical qualities of the tree topology employed by Ni and co-workers may have influenced the phylogenetically based character analysis of diurnality at the basal primate node. First, in the tree constructed by Ni and coworkers, Malagasy strepsirhines are not monophyletic, with *Galagoides demidoff*, a loriform and

Microcebus murinus, a lemuriform, forming a clade to the exclusion of *Lemur catta*, a lemuriform, a topology that is not supported by molecular analyses of strepsirrhine relationships.¹⁰⁰ Malagasy strepsirrhines are the most variable clade of primates in terms of activity patterns; there are numerous nocturnal, diurnal, and cathemeral species. The position of *Lemur catta* at the base of the strepsirrhine clade forces a diurnal character optimization at the basal node of this clade. Given the influence that this node has on character

optimization at the basal primate node, it is essential to examine topologies and character distributions that accurately reflect known strepsirrhine phylogenetic relationships. Second, the only outgroup to primates included in the analysis is “Scandentia,” which was coded by Ni and coworkers coded as diurnal. However, tree shrews (the Order Scandentia) include a nocturnal species, the pen-tailed tree shrew *Ptilocercus lowii*. Coding scandentians as diurnal implies that diurnality is primitive for the order, an assumption for

which there is no supporting evidence. In addition, at least for the purposes of activity pattern character evolution, it is important to note that dermopterans, which are the sister taxon either to scandentians or primates, are also nocturnal.¹⁰¹ When activity pattern character data are optimized onto Ni and coworkers’ cladogram modified to include *Ptilocercus lowii* and dermopterans, and constrained to enforce strepsirrhine monophyly, nocturnality is reconstructed at the basal primate node (Box 3, Figure 1).

Artists have long understood and used several depth cues, although these are not often cited in relation to the evolution of primate vision. For example, interposition, or object ordering, is a depth cue whereby an object is judged to be farther away than another object that is partly obscuring the first object. Perspective cues are also familiar to every art student. The most common example is of lines that appear to converge in the distance, such as train tracks, but are assumed by the visual system to be parallel, thereby generating the impression of depth.^{38,39} We can additionally generate powerful depth cues with motion parallax by moving the head from side to side. Closer objects appear to move relatively quickly (and opposite to head motion) when projected across the retina, whereas more distant objects appear to move more slowly.^{38,39} Accommodation, the process by which the lens changes shape to focus on near objects, can provide a strong depth cue. Also, near-field depth cues can be generated by vergence eye movements, which reorient the eyes to focus on close objects. All of these cues for judging depth are available to animals regardless of orbit orientation. Interposition, perspective, motion parallax, vergence eye movement cues, accommodation, and optic flow are almost certainly used by arboreal taxa with divergent orbits to determine depth during locomotion.

Advantages of Binocularity

In addition to the depth information available to animals using these

cues, at least three potential visual advantages are unique to animals with large binocular visual fields, such as primates. These advantages are enhanced light sensitivity, contrast discrimination, and expanded stereoscopic depth perception. Binocular visual fields increase the probability of capturing light within the

At least three potential visual advantages are unique to animals with large binocular visual fields: enhanced light sensitivity, contrast discrimination, and expanded stereoscopic depth perception.

region of overlap by a factor of approximately 1.25–2.^{37,40} This can be especially beneficial to nocturnal taxa or ones that are otherwise scotopically (vision in low light) adapted. On a moonless night, light levels can be 100 million times dimmer than daylight; also, there is tremendous variation in light availability from dusk to full night.^{36,37,41} There are examples of mesopelagic fishes (those dwelling 200–900 m under water) that have evolved dorsally oriented tubular eyes and dorsal binocular overlap to increase visual sensitivity to the

region above their heads, from which light is comparatively more abundant.⁴² Binocularity also improves contrast discrimination, defined as the ability to detect luminance differences in adjacent objects or multiple parts of the same object. This improved contrast discrimination is made possible by physiological summation of the doubled visual information extracted from the similar images presented to each eye.^{40,43} Binocular contrast helps distinguish unwanted “noise” from useful information by physiological summation along the visual pathway.^{40,43,44} Simply put, the ability to detect contrast differences, especially subtle differences, is substantially improved within the binocular visual field as compared to monocular performance.

STEREOPSIS: THE CORTICAL COMPUTATION OF THREE-DIMENSIONAL STRUCTURE AND DEPTH FROM THE BINOCULAR FIELD

Basic Mechanisms of Stereopsis

We inhabit a three-dimensional world, but our retinæ can only capture it in two dimensions.⁴⁵ Stereopsis is the cortical process that mentally reconstructs a three-dimensional world that has been simplified into two dimensions by the retinal capture of light from the environment. More formally, stereopsis is the computation of object solidity and depth based on binocular disparity cues.^{45–47} Stereoscopic depth perception is a

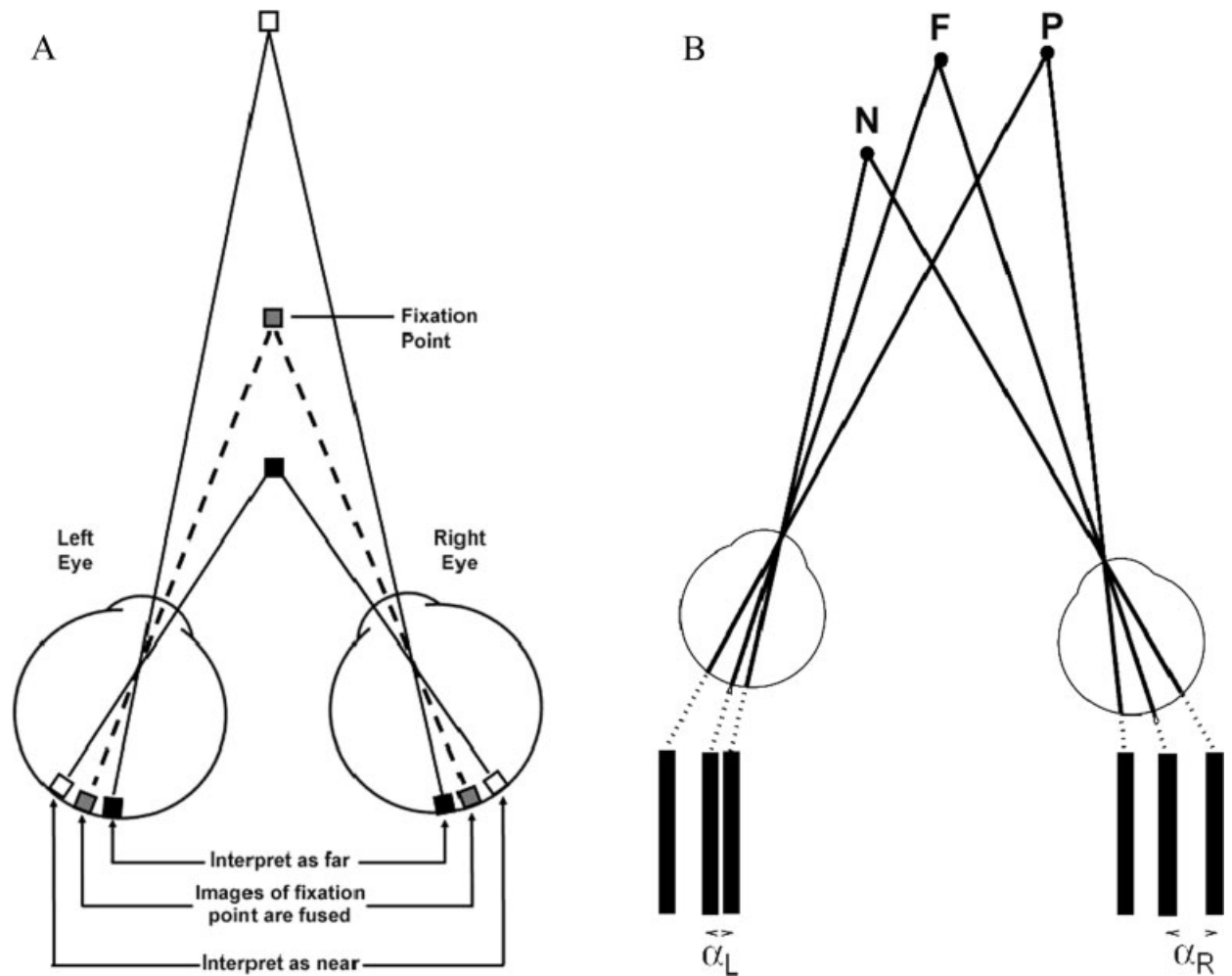


Figure 4. Basic geometry of binocular disparity. A. In an idealized case, the eyes are both directed toward a single fixation point that projects onto corresponding positions on each retina. Closer points project onto more lateral (and noncorresponding) parts of the retina, whereas more distant points project onto more medial noncorresponding retinal positions. These noncorresponding points produce binocular disparity. (Redrawn from Wurtz and Kandel⁵⁹). B. Binocular disparity is a geometric calculation. In this illustration, both eyes are looking toward vertically oriented bars. The appearance of these bars present to each eye are illustrated schematically behind the eyes. Both eyes fixate on a bar, labeled F, and the image of the bar falls onto the fovea (or area centralis for nonhaplorhine mammals, which are afoveate). These images for F fall onto corresponding points on each retina. Images from a bar located within the binocular field closer to the eyes, labeled N, fall onto noncorresponding points. The angular distances between the fixated points for F and from N are illustrated as α_R and α_L on the projected images of bars behind the eyes. The difference between these angles is binocular disparity (disparity = angle R – angle L). Similar angles of disparity are calculated from other points, such as P, within the same binocular field (redrawn from Cumming⁴⁷).

physiological process founded on neurons sensitive to binocular disparities that are responsible for the perception of depth, object solidity, and binocular fusion. Binocular neurons require input from each eye.⁴⁸ Cortical stereoscopic processing integrates or fuses percepts of retinal images from each eye into a singular mental visual image.^{45–48}

Binocular visual field overlap is a prerequisite for stereoscopic depth perception because this is the portion

of the visual field from which binocular parallax cues are collected. Binocular parallax is generated by the slightly different views of objects projected onto each retina (Fig. 4a). Generally speaking, points that project to slightly discrepant or noncorresponding points on each retina provide cues to relative object location within the binocular field when compared to the retinal positions of each eye's visual axis. These slight discrepancies, called binocular disparities, provide

the cues from which stereoscopic depth is computed (Fig. 4a). In the schematic case illustrated in Figure 4b, the angular deviations between the retinal positions for points F (representing the visual axis) and N differ between eyes. Simple subtraction between the angular value for angle R and angle L gives the disparity value for point N. Expansion of the binocular field, as in primates, leads to an increase in the number of points seen by both eyes, facilitating

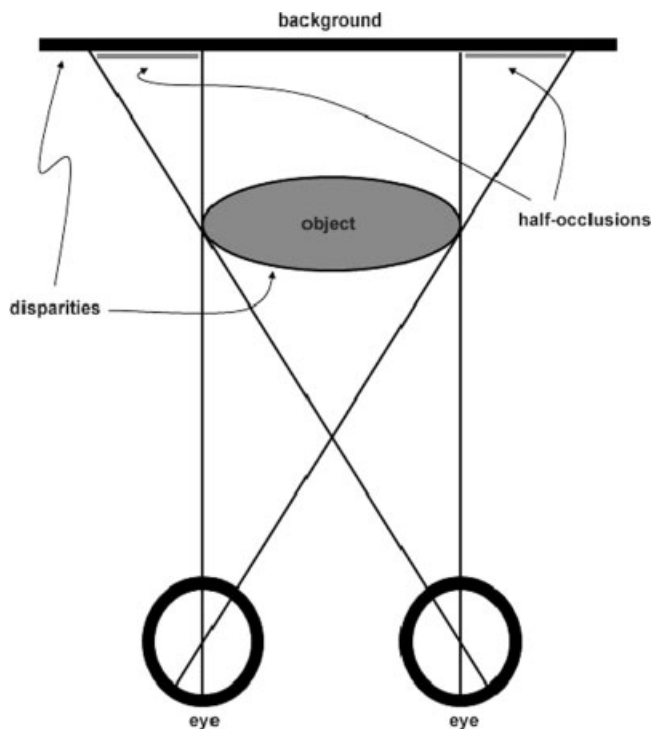


Figure 5. Da Vinci stereopsis. The nearer object occludes the background surface, which creates features visible to only one eye. The partially occluded regions are called here "half-occlusions" or monocular zones. The portions of the object and background visible to both eyes contribute binocular disparity cues for stereoscopic perception, whereas the monocular regions are free of disparity cues. Stereopsis and monocular zones combine to generate the perception of object "pop out," which rapidly draws attention to a target of interest. Basic and da Vinci stereopsis facilitate object detection and object ordering. (Redrawn from Anderson⁵⁴).

richer stereoscopic perception. The amount of parallax available to an animal is partly a function of the distance between the two eyes: the greater the interocular distance, the greater the parallax. Interocular distance therefore limits the functional utility of stereopsis to a short range. Behavioral data show that the maximum range over which stereopsis functions is quite limited in amphibians and birds (<1m), and mammals probably also have a short range over which stereopsis functions.^{49,50} The earliest true primates were likely extraordinarily small⁵¹ and, for this reason, probably had a small distance between the eyes and, therefore, limited optical parallax and a short distance over which stereopsis would be effective. This limitation applies to the scaling of arboreal leaping relative to effective stereoscopic range. Generally speaking, the distance an animal can leap is probably negatively allometric: bigger animals may

leap absolutely greater distances that are otherwise shorter relative to body length or mass. However, interorbital distance and binocular parallax are proportional to head size. At the extraordinarily small body sizes of the earliest primates, effective stereoscopic range was undoubtedly substantially shorter than the maximum possible leaping distance. This discrepancy between the ranges of stereoscopic depth and leaping distance contradicts the hypothesis that primate binocularity evolved to judge distance for arboreal leaping.

Monocular Occlusion Within the Stereoscopic Field: Da Vinci Stereopsis

An additional form of stereoscopic vision that has not previously been introduced into discussion of the evolution of primate binocular vision nonetheless has possibly played a

vital role. Euclid, Galen, and, most notably, Leonardo da Vinci commented on the impression of depth generated by the partial, or monocular, occlusion of an object.⁵² Monocular occlusion or, as it has been called by some authors, da Vinci stereopsis, generates depth information from the differences in views presented to each eye by the partial occlusion of a background object by a foreground object.⁵²⁻⁵⁵ Da Vinci stereopsis differs from interposition, described earlier, because some portion of the occluded object is viewed by one eye. Figure 5 illustrates a simplified case of the da Vinci stereopsis phenomenon. When an object that is relatively close to the viewer is positioned in front of a background object, it blocks or occludes a portion of that background to both eyes. In addition, there are regions of the background that are occluded to only one eye, not the other. These partially occluded zones are named half-occlusions or monocular zones.^{52,54} Each monocular zone is specific to one eye. The right eye views a monocular zone to the right of the foreground (occluding) object that is blocked from the view of the left eye, whereas the left eye views a monocular zone to the left that is blocked from the view of the right eye (Fig. 5).

Da Vinci stereopsis produces an impression of depth because our brains interpret occlusion as strong evidence for the existence of an object.^{56,57} The mammalian visual system is highly attuned to detecting edges and contours.^{56,58,59} Edges or contours effectively distinguish objects from the background because our visual systems assume that an occluded object must lie in the background.^{56,57} Also, if an occluded object lies in the background, then logically an object in the foreground must be occluding the background object, even if that object is not necessarily immediately apparent. The power of object occlusion to generate depth information is exemplified by the famous Kanisza triangle illusion⁶⁰ (Fig. 6). Our visual system interprets the Kanisza illusion as a white-edged triangle that is partially obscuring a black-edged triangle and three black filled circles, which we

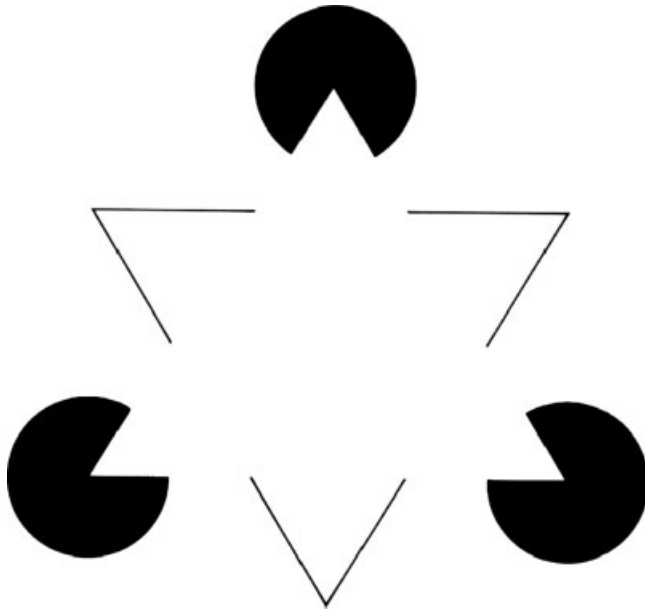


Figure 6. Kanisza triangle demonstrates the phenomenon of illusory contours. Contours are mentally constructed even when these are not present in the figure. In addition, the subjectively constructed triangle acquires the appearance of being whiter than the background.

interpret as lying in the background. Our brains even go so far as to imagine and construct edges to the white foreground triangle.

Da Vinci and standard stereopsis also work simultaneously and congruently to reconstruct depth and object ordering,⁵⁴ which may add to the speed of depth processing, as well as enhanced object recognition. Disparity cues for standard stereopsis are available from the foreground object and common background zones, but not monocular zones (Fig. 6). The combination of processing standard stereopsis information from the binocular portion of the visual field while simultaneously recognizing monocular or stereopsis-neutral zones can cause the perception of an object to “pop out” relative to the background.⁶¹ Nakayama and Joseph⁶¹ have suggested that standard stereopsis and monocular occlusion combine to delineate the geometry of objects relative to the background, especially when those objects are hidden or camouflaged. Disparity is critical to determine whether image fragments are part of a single object or are segregated as parts of separate surfaces.⁶² Standard stereopsis allows object detection

even when the object is similar in color and texture to the background. Da Vinci stereopsis assists in edge detection, while standard stereopsis links components of an object into a percept of a single solid object.⁶¹ Object “pop out” probably rapidly draws or concentrates visual attention to that object, allowing the targeting of an object of interest within a densely populated or otherwise visually confusing scene.⁶³ The combination of standard and da Vinci stereopsis is responsible for immediate object detection and object ordering. An introduction to how various forms of camouflage work is necessary to understand how stereopsis effectively functions to detect obscured objects.

HOW STEREOPSIS NEUTRALIZES CAMOUFLAGE

Animals subjected to intense predation pressure may evolve multiple defenses. Examples include camouflage, morphological and chemical defenses, predator signaling, warning displays, and Müllerian and Batesian mimicry, among others.⁶⁴ Pertinent to the current discussion is camouflage defense, which, as defined by

Endler,⁶⁵ has three types: crypsis, disruptive coloration, and masquerade. Cryptic prey evolve overall body coloration, as well as patterning, that resemble the visual background these animals tend to inhabit.⁶⁵ Animals with disruptive coloration evolve body coloration patterns, some of which can be conspicuous, but nonetheless function to obscure the edges of their body outlines, making detection less probable.^{65,66} Disruptive coloration obscures the edges of an animal to make the edges of the prey animal blend into the background. Masquerade camouflage is used by insects that are shaped and colored to resemble less palatable items, such as sticks or leaves.⁶⁵ The effectiveness of crypsis and disruptive coloration probably differs based on environment; disruptive coloration of animal edges is less dependent on the background, whereas disruptive and cryptic coloration away from the edges, toward the center of the body, tends to require better matching to the background.⁶⁷ Although the functional properties of crypsis and disruptive coloration differ, both have been demonstrated to be effective.^{66,68–70}

Julesz first proposed that stereopsis evolved to counter camouflage.⁷¹ The crypsis-countering effect of stereopsis is a natural product of the retinal disparity of viewing three-dimensional objects in a binocular field.⁷¹ There is disparity between a cryptic prey animal, which is nearer to the viewer, and the background on which it sits, which is relatively further away. Therefore, stereopsis allows the depth ordering of these objects, and the relative and absolute distances between the prey and background can be computed. The functional properties of standard and Da Vinci stereopsis can work in conjunction for prey detection. Stereoscopic fusion of depth cues from a cryptic colored animal will break camouflage by the differential perception of depth from the prey animal and background. Da Vinci stereopsis is especially suited to the detection of edges, even when those edges are obscured through disruptive coloration. Combining stereoscopic depth cues and the edge

Box 4. New Views on the Evolution of Primate Binocular Vision

Changizi and Shimojo¹⁰⁵ recently suggested that the ability granted by a binocular visual field to see around obscuring objects in a visually cluttered environment like a forest has been underappreciated in primate evolutionary studies. Their argument is reminiscent of Da Vinci stereopsis, but the emphasis is on the potential to look around an object in the foreground in order to see visually interesting objects in the background. This can be easily demonstrated. If the reader holds up one thumb about five inches in front of the eyes (it will not work if it is much farther away), a portion of the background is still seen by each eye despite the obscuring finger. This creates the illusion that the thumb is partially transparent because the background can be seen by each monocular field. Changizi and Shimojo¹⁰⁵ call this an X-ray effect because the viewer can “see through” an object. Specifically they hypothesize that “X-ray vision” evolved to cut through the clutter of leaves in a forested environment. Changizi and Shimojo ignore one unresolved allometric element:

Early primates were very small and most environmental objects, like leaves, would be so large relative to their interocular distance (and parallax) as to negate early primates’ ability to see around them. Nevertheless, the “X-ray” effect may indeed potentially be an added benefit to high binocular visual field overlap, especially in the portion of visual space that is very close to the animal.

In a multifaceted synthetic hypothesis for primate brain evolution, Isbell¹⁰⁶ suggested that predation on primates by snakes applied a major selective pressure on specializations of primate brains, including multiple components of the visual pathway, specifically for the rapid visual detection of snakes. Visual input to several brain structures, such as the amygdaloid complex, which is responsive to fearful stimuli, as well as the superior colliculus, which is important for motion tracking, may be expanded or specialized in primates specifically for predator detection. Input to these structures may covary across primate groups based on his-

torical exposure to snake predation. Several parts of Isbell’s hypothesis are difficult to evaluate at present because the functions for one key visual pathway (called koniocellular) are poorly understood due to the paucity of data on the functional properties of this pathway, as well as its distribution across primates.¹⁰⁷ More importantly, Isbell’s hypothesis highlights the importance of sorting salient visual stimuli from the tremendous flood of sensory data that are constantly acquired. A major new emphasis in visual neuroscience is the vital role of visual attention, which can be thought of as selective processing of some visual information at the expense of other sensory information, visual and otherwise, at the neurophysiological and conscious levels.¹⁰⁸ The new paradigm is to determine how only salient features are recognized, captured, and then processed. Isbell’s snake-brain covariation hypothesis illustrates, correctly in my opinion, the fundamental importance of ecologically relevant sensory stimuli on primate sensory system evolution.

detection properties of Da Vinci stereopsis can generate the perception of the camouflaged prey animal “popping out” relative to the background. Expanding the binocular and stereoscopic field also widens the zone over which cryptic or disruptively colored prey can be detected. In addition, enhanced binocularity increases the ability to gauge the distance to cryptic or evasive prey items without unnecessary head movements, which could alert a prey animal to the presence of the predator prior to ambush.⁴

PRIMATE BINOCULAR VISION IN PHYLOGENETIC AND FUNCTIONAL PERSPECTIVE

The predictions of the nocturnal visual predation hypothesis are

strongly supported by comparative data on orbit convergence in mammals (Box 2) and analyses of activity pattern evolution (Box 3). These data conform to the theoretical expectations of nocturnal optics as well as the functional components of stereopsis, both of which would aid in detecting camouflaged prey items in a light-limited environment. However, criticisms of the nocturnal visual predation hypothesis have been leveled on multiple grounds. The most prominent of these criticisms relate to either the phylogenetic origin of primates or dietary ecology. Because these objections have been linked by some, I will review them together. I also summarize new ideas on binocular vision in Box 4.

When Cartmill first proposed the “visual predation hypothesis,” he explicitly sought to provide an adaptive

explanation for a cohesive suite of morphological, ecological, and behavioral traits.³⁻⁵ Specifically, he linked orbit convergence and stereopsis for prey detection, with grasping extremities and claw loss for prey capture.

Recent phylogenetic analyses of newly recovered and described plesiadapiforms has reopened the debate on the morphological origin of primates.⁷²⁻⁷⁴ These analyses have led Bloch and colleagues to suggest that plesiadapiforms are stem primates. Furthermore, these authors have suggested that their phylogenetic reconstruction can be used to test the predictions of the nocturnal visual predation hypothesis, especially the order of trait evolution. Their results suggest that grasping and visual adaptations evolved asynchronously in primates. Specifically, they found that adaptations for man-

ual and pedal grasping thought to characterize primates evolved in plesiadapiforms.^{74,75} Visual features evolved only at the primate (that is, crown clade) node. In addition, Bloch and coworkers argue that insectivorous dental adaptations are found neither in plesiadapiforms nor the early fossil primate groups such as omomyiforms and adapiforms. Instead, they argue that a dietary shift toward increased herbivory is characteristic of the origin of primates.^{74,76}

Although the paleontological evidence for dietary and locomotor adaptations in plesiadapiforms is compelling, additional lines of evidence are worth considering. Silcox and coworkers suggest that the association between visual adaptations and diet is tenuous because adapiforms are often considered frugivorous and omomyiforms are considered omnivorous or frugivorous.⁷⁴ When omomyiforms and adapiforms are considered as whole groups, this appears to be the case. However, dietary reconstruction in the earliest omomyiforms is a notably difficult exercise, with results varying based on the size surrogate used in the analysis.⁷⁷ Depending on the methodology employed, some of the phylogenetically and morphologically most primitive omomyiforms, *Teilhardina americana* and *Steinius vespertinus*,^{78,79} had either insectivorous or frugivorous mixed feeding diets. Other small-bodied omomyiforms, such as *Shoshonius cooperi*, *Loveina zephyri*, *Omomys lloydi*, and *Utahia kayi*, had undisputed insectivorous diets.⁷⁷ Nevertheless, it is difficult to conclude, based on the ambiguity inherent in some results, that omomyiforms were primitively omnivorous or frugivorous. The phylogenetic and comparative analyses conducted by Ni and colleagues,¹² as part of their description of *Teilhardina asiatica*, suggest that not only is it the most primitive omomyiform known, but also that it most likely had an insectivorous diet. It is also worth noting that the cercamoniine adapiform *Donrussellia*, which is often considered to be phylogenetically close to the origin of all adapiforms, has been interpreted as having also been

insectivorous.^{78,80,81} Phylogenetically based character reconstruction of diet also finds faunivory or insectivory at the basal primate node.⁸² The extremely small sizes of the earliest undisputed primates strongly suggests that an insect protein must have been a major dietary compo-

It may be that grasping precedes the evolution of primate visual adaptations, but it is difficult to accept that the mosaic evolution of visual and postcranial specializations invalidates the entire nocturnal visual predation hypothesis.

nent. It is certainly possible, given the preceding evidence, that primates were primitively insectivorous and later diversified into broader and more complex diets incorporating more plant matter.⁸³ At the very least, the question of dietary specializations in the very earliest primates must be considered as yet unanswered.

An additional point to consider is the evidence of a contemporaneous increase in temperature and herbivorous insect diversity (and, presumably, abundance) during the late Paleocene-Eocene, a period that roughly coincides with the diversification of omomyiform and adapiform primates.^{84,85} Much of the evidence of increased herbivorous insect abundance comes from the western interior of North America as well as Patagonia, although it is as yet unclear whether global diversity and abundance levels of insects were similar. Although the continent of origin for primates is currently debated, it appears that the diversifi-

cation of early primates roughly coincides with a dramatic increase in insect diversity. The massive increase in insect availability has also been associated with the rapid diversification of echolocating insectivorous bats during the late Paleocene-Eocene.^{86,87} Evaluating whether the timing and area of origin for primates (and bats) coincides with increased insect resources seems a worthwhile line of inquiry.

Orbit convergence and broad stereopsis are among the most important traits that characterize Primates as a monophyletic group. All of the data on binocular vision and stereopsis reviewed here support the functional and adaptive predictions of the nocturnal visual predation hypothesis, which is certainly applicable to explanations relating to the origin of primates. It may be that grasping precedes the evolution of primate visual adaptations, but it is difficult to accept that the mosaic evolution of visual and postcranial specializations invalidates the entire nocturnal visual predation hypothesis.⁷⁴ At best, this calls into question Cartmill's theories linking manual grasping to visual traits as an adaptively cohesive suite of morphological traits that evolved simultaneously. As new evidence emerges, evolutionary primatologists must, of course, always be willing to adapt theory. However, it is also easy to theorize that the evolution of grasping may have set the stage for selective pressure for improved primate vision, especially for accurate grasping during prey capture. The most important issue is one of understanding the selective factors at work when all adaptive traits are linked together. The nocturnal visual predation hypothesis is a useful tool to aid in interpreting the ecological context surrounding primate origins.

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REFERENCES

- 1 Allman J. 1977. Evolution of the visual system in early primates. In: Sprague JM, Epstein AN, editors. *Progress in psychobiology and physiological psychology*. New York: Academic Press. p 1–53.
- 2 Allman J, McGuinness E. 1988. Visual cortex in primates. In: Steklis HD, Erwin J, editors. *Comparative primate biology*, vol. 4. Neurosciences. New York: Alan R. Liss, p 279–326.
- 3 Cartmill M. 1972. Arboreal adaptations and the origin of the Order Primates. In: Tuttle R, editor. *The functional and evolutionary biology of primates*. Chicago: Aldine de Gruyter p 97–122.
- 4 Cartmill M. 1974. Rethinking primate origins. *Science* 184:436–443.
- 5 Cartmill M. 1992. New views on primate origins. *Evol Anthropol* 1:105–111.
- 6 Ross CF. 2000. Into the light: the origin of Anthropoidea. *Ann Rev Anthropol* 29:147–194.
- 7 Heesy CP. 2004. On the relationship between orbit orientation and binocular visual field overlap in mammals. *Anat Rec* 281A:1104–1110.
- 8 Ross CF. 1995. Allometric and functional influences on primate orbit orientation and the origins of the Anthropoidea. *J Hum Evol* 29:201–227.
- 9 Heesy CP. 2008. Ecomorphology of orbit orientation and the adaptive significance of binocular vision in primates and other mammals. *Brain Behav Evol* 71:54–67.
- 10 Ravosa MJ, Noble VE, Hylander WL, Johnson KR, Kowalski EM. 2000. Masticatory stress, orbital orientation and the evolution of the primate postorbital bar. *J Hum Evol* 38:667–693.
- 11 Ravosa MJ, Savakova DG. 2004. Euprimate origins: the eyes have it. *J Hum Evol* 46:355–362.
- 12 Ni X, Wang Y, Hu Y, Li C. 2004. A euprimate skull from the early Eocene of China. *Nature* 427:65–68.
- 13 Jones F. 1917. *Arboreal man*. New York: Hafner Publishing.
- 14 Collins ET. 1921. Changes in the visual organs correlated with the adoption of arboreal life and with the assumption of the erect posture. *Trans Ophthal Soc UK* 41:10–90.
- 15 Smith GE. 1924. *The evolution of man*. London: Oxford University Press.
- 16 Le Gros Clark WE. 1959. *The antecedents of man*. Edinburgh: Edinburgh University Press.
- 17 Martin RD. 1979. Phylogenetic aspects of prosimian behavior. In: Doyle GA, Martin RD, editors. *The study of prosimian behavior*. New York: Academic Press. p 45–77.
- 18 Martin RD. 1990. *Primate origins and evolution: a phylogenetic reconstruction*. Princeton: Princeton University Press.
- 19 Crompton RH. 1995. "Visual predation," habitat structure, and the ancestral primate niche. In: Alterman L, Doyle GA, Izard MK, editors. *Creatures of the dark: the nocturnal prosimians*. New York: Plenum Press. p 11–30.
- 20 Heesy CP. 2005. The function of the mammalian postorbital bar. *J Morphol* 264:363–380.
- 21 Gibson JJ. 1986. *The ecological approach to visual perception*. Hillsdale New Jersey: Lawrence Erlbaum.
- 22 Lee DN. 1980. The optic flow field: the foundation of vision. *Philos Trans R Soc London B* 290:169–179.
- 23 Lee DN, Reddish PE. 1981. Plummeting gannets: a paradigm of ecological optics. *Nature* 293:293–294.
- 24 Wylie DRW, Bischof WF, Frost BJ. 1998. Common reference frame for neural coding of translational and rotational optic flow. *Nature* 392:278–282.
- 25 Warren WH Jr, Kay BA, Zosh WD, Duchon AP, Sahuc S. 2001. Optic flow is used to control human walking. *Nature Neurosci* 4:213–216.
- 26 van den Berg AV, Brenner E. 1994. Why two eyes are better than one for judgements of heading. *Nature* 371:700–702.
- 27 Gray R, Regan D. 1998. Accuracy of estimating time to collision using binocular and monocular information. *Vision Res* 38:499–512.
- 28 Martin GR, Katzir G. 1999. Visual fields in short-toed eagles, *Circetus gallitus* (Accipitridae), and the function of binocularity in birds. *Brain Behav Evol* 53:55–66.
- 29 Pettigrew JD. 1978. Comparison of the retinotopic organization of the visual wulst in nocturnal and diurnal raptors, with a note on the evolution of frontal vision. In: Cool SJ, Smith EL, editors. *Frontiers of visual science*. New York: Springer Verlag. p 328–335.
- 30 Pettigrew JD. 1986. The evolution of binocular vision. In: Pettigrew JD, Sanderson KJ, Levick WR, editors. *Visual neuroscience*. London: Cambridge University Press. p 208–222.
- 31 Pettigrew JD. 1991. Evolution of binocular vision. In: Cronly-Dillon JR, Gregory RL, editors. *Vision and visual dysfunction*, vol. 2. Evolution of the eye and visual system. Boca Raton: CRC Press. p 271–283.
- 32 Charman WN. 1991. The vertebrate dioptric apparatus. In: Cronly-Dillon JR, Gregory RL, editors. *Vision and visual dysfunction*, vol. 2. Evolution of the eye and visual system. Boca Raton: CRC Press. p 82–117.
- 33 Hughes A. 1977. The topography of vision in mammals of contrasting lifestyle: comparative optics and retinal organisation. In: Crescitelli F, editor. *The visual system in vertebrates*. New York: Springer-Verlag. p 613–756.
- 34 Land MF, Nilsson D-E. 2002. *Animal eyes*. New York: Oxford University Press.
- 35 Land MF. 1981. Optics and vision in invertebrates. In: Autrum H, editor. *Handbook of sensory physiology*, VII/6B. New York: Springer-Verlag. p 471–592.
- 36 Warrant E. 2004. Vision in the dimmest habitats on earth. *J Comp Physiol A* 190:765–789.
- 37 Warrant E. 2008. Nocturnal vision. In: Basbaum AI, Kaneko A, Shepherd GM, Westheimer G, editors. *The senses: a comprehensive reference*, vol. 2, Vision II. San Diego: Academic Press. p 53–86.
- 38 Rock I. 1984. *Perception*. New York: Scientific American Library.
- 39 Kandel ER. 1991. Perception of motion, depth, and form. In: Kandel ER, Schwartz JH, Jessell TM, editors. *Principles of neural science*, 3rd ed. Connecticut: Appleton and Lange. p 440–466.
- 40 Pirenne MH. 1943. Binocular and unocular threshold of vision. *Nature* 152:698–699.
- 41 Martin GR. 1990. *Birds by night*. San Diego: Academic Press.
- 42 Warrant E, Locket N. 2004. Vision in the deep sea. *Biol Rev* 79:671–712.
- 43 Campbell FW, Green DG. 1965. Monocular versus binocular visual acuity. *Nature* 208:191–192.
- 44 Blake R, Sloane M, Fox R. 1981. Further developments in binocular summation. *Percept Psychophys* 30:266–276.
- 45 Poggio GF, Poggio T. 1984. The analysis of stereopsis. *Ann Rev Neurosci* 7:379–412.
- 46 Howard IP, Rogers BJ. 1995. *Binocular vision and stereopsis*. New York: Oxford University Press.
- 47 Cumming BG, DeAngelis GC. 2001. The physiology of stereopsis. *Ann Rev Neurosci* 24:203–238.
- 48 Poggio GF. 1984. Processing of stereoscopic information in primate visual cortex. In: Edelman GM, Gall WE, Cowan WM, editors. *Dynamic aspects of neocortical function*. New York: John Wiley. p 613–635.
- 49 Collett T. 1977. Stereopsis in toads. *Nature* 267:349–351.
- 50 McFadden SA. 1994. Binocular depth perception. In: Davies MNO, Green PR, editors. *Perception and motor control in birds: an ecological approach*. Berlin: Springer-Verlag. p 54–73.
- 51 Gebo DL. 2004. A shrew-sized origin for primates. *Yearbook Phys Anthropol* 47:40–62.
- 52 Howard IP, Duke PA. 2003. Monocular transparency generates quantitative depth. *Vision Res* 43:2615–2621.
- 53 Nakayama K, Shimojo S, Silverman G. 1989. Stereoscopic depth: its relation to image segmentation, grouping, and the recognition of occluded objects. *Perception* 18:55–68.
- 54 Anderson B. 1998. Stereovision: beyond disparity computations. *Trends Cogn Sci* 2:214–222.
- 55 Anderson B, Nakayama K. 1994. Toward a general theory of stereopsis: binocular matching, occluding contours, and fusion. *Psychol Rev* 101:414–445.
- 56 Ramachandran VS. 1990. Perceiving shape from shading. In: Rock I, editor. *The perceptual world*. New York: W.H. Freeman & Co. p 127–138.
- 57 Kandel ER, Wurtz RH. 2000. Constructing the visual image. In: Kandel ER, Schwartz JH, Jessell TM, editors. *Principles of neural science*, 4th ed. New York: McGraw-Hill. p 492–506.
- 58 Hubel DH, Wiesel TN. 1959. Receptive fields of single neurones in the cat's striate cortex. *J Physiol* 148:574–591.
- 59 Wurtz RH, Kandel ER. 2000. Central visual pathways. In: Kandel ER, Schwartz JH, Jessell TM, editors. *Principles of neural science*, 4th Ed. New York: McGraw-Hill. p 523–547.
- 60 Kanizsa G. 1955. Margini quasi-percettivi in campi con stimolazione omogenea. *Rivista di Psicologia* 49:7–30.
- 61 Nakayama K, Joseph J. 1998. Attention, pattern recognition, and pop-out in visual search. In: Parasuraman R, editor. *The attentive brain*. Cambridge: MIT Press. p 279–298.
- 62 Nakayama K. 1996. Binocular visual surface perception. *Proc Nat Acad Sci USA* 93:634–639.
- 63 He Z, Nakayama K. 1995. Visual attention to surfaces in three-dimensional space. *Proc Natl Acad Sci USA* 92:11155–11159.
- 64 Ruxton G, Sherratt T, Speed M. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. Oxford University Press.
- 65 Endler J. 2006. Disruptive and cryptic coloration. *Proc R Soc London B* 273:2425–2426.

- 66 Stevens M, Cuthill IC. 2006. Disruptive coloration, crypsis and edge detection in early visual processing. *Proc R Soc London B* 273:2141–2147.
- 67 Schaefer H, Stobbe N. 2006. Disruptive coloration provides camouflage independent of background matching. *Proc R Soc London B* 273:2427–2432.
- 68 Merilaita S, Lind J. 2005. Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proc R Soc London B* 272:665–670.
- 69 Merilaita S, Lyytinen A, Mappes J. 2001. Selection for cryptic coloration in a visually heterogeneous habitat. *Proc R Soc London B* 268:1925–1929.
- 70 Stuart-Fox D, Moussalli A, Whiting MJ. 2008. Predator-specific camouflage in chameleons. *Biol Lett* 4:326–329.
- 71 Julesz B. 1971. *Foundations of Cyclopean perception*. Chicago: University of Chicago Press.
- 72 Bloch JI, Boyer DM. 2002. Grasping primate origins. *Science* 298:1606–1610.
- 73 Bloch JI, Silcox MT, Boyer DM, Sargis EJ. 2007. New Paleocene skeletons and the relationship of plesiadapiforms to crown-clade primates. *Proc Natl Acad Sci USA* 104:1159–1164.
- 74 Silcox M, Sargis E, Block J, Boyer D. 2007. Primate origins and supraordinal relationships: morphological evidence. In: Henke W, Tattersall I, editors. *Handbook of paleoanthropology*, vol 2: Primate evolution and human origins: Springer Verlag. p 831–859.
- 75 Kirk EC, Lemelin P, Hamrick MW, Boyer DM, Bloch JI. 2008. Intrinsic hand proportions of euarchontans and other mammals: implications for the locomotor behavior of plesiadapiforms. *J Hum Evol* 55:278–299.
- 76 Szalay FS. 1968. The beginnings of primates. *Evol* 22:19–36.
- 77 Strait SG. 2001. Dietary reconstruction of small-bodied omomyoid primates. *J Vert Paleol* 21:322–334.
- 78 Rose KD, Bown TM. 1991. Additional fossil evidence on the differentiation of the earliest euprimates. *Proc Natl Acad Sci USA* 88:98–101.
- 79 Rose KD. 1995. The earliest primates. *Evol Anthropol* 3:159–173.
- 80 Covert HH. 1986. Biology of early Cenozoic primates. In: Swindler DR, Erwin J, editors. *Comparative primate biology*, vol. 1: Systematics, evolution, and anatomy. New York: Alan R. Liss p 335–359.
- 81 Gebo D. 2002. Adapiformes: phylogeny and adaptation. In: Hartwig WC, editor. *The primate fossil record*. New York: Cambridge University Press. p 21–43.
- 82 Heesy CP, Ross CF. 2004. Mosaic evolution of activity pattern, diet, and color vision in haplorhine primates. In: Ross CF, Kay RF, editors. *Anthropoid origins: New visions*. New York: Kluwer Academic/Plenum Publishers. p 665–698.
- 83 Gilbert C. 2005. Dietary ecospace and the diversity of Euprimates during the Early and Middle Eocene. *Am J Phys Anthropol* 126:237–249.
- 84 Wilf P, Labandeira CC. 1999. Response of plant-insect associations to Paleocene-Eocene warming. *Science* 284:2153–2156.
- 85 Curran ED, Wilf P, Wing SL, Labandeira CC, Lovelock EC, Royer DL. 2008. Sharply increased insect herbivory during the Paleocene-Eocene thermal maximum. *Proc Natl Acad Sci USA* 105:1960–1964.
- 86 Eick G, Jacobs D, Matthee C. 2005. A nuclear DNA phylogenetic perspective on the evolution of echolocation and historical biogeography of extant bats (Chiroptera). *Mol Biol Evol* 22:1869–1886.
- 87 Teeling E, Springer M, Madsen O, Bates P, O'Brien S, Murphy W. 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science* 307:580–584.
- 88 Pettigrew JD, Jamieson BGM, Robson SK, Hall LS, McAnally KL, Cooper HM. 1989. Phylogenetic relations between microbats, megabats and primates (Mammalia: Chiroptera and Primates). *Philos Trans R Soc London B* 325:489–559.
- 89 Lane R, Kaas J, Allman J. 1974. Visuotopic organization of the superior colliculus in normal and Siamese cats. *Brain Res* 70:413–430.
- 90 Grantyn AA, Moschovakis AK. 2004. Structure-function relationships in the superior colliculus of higher mammals. In: Hall WC, Moschovakis A, editors. *The superior colliculus: new approaches for studying sensorimotor integration*. New York: CRC Press. p 107–145.
- 91 Schiller P, Stryker M. 1972. Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey. *J Neurophysiol* 35:915–924.
- 92 Charles-Dominique P, Martin RD. 1970. Evolution of lorises and lemurs. *Nature* 227:257–260.
- 93 Tan Y, Li W-H. 1999. Trichromatic vision in prosimians. *Nature* 402:36.
- 94 Tan Y, Yoder AD, Yamashita N, Li W-H. 2005. Evidence from opsin genes rejects nocturnality in ancestral primates. *Proc Natl Acad Sci USA* 102:14712–14716.
- 95 Heesy CP, Ross CF. 2001. Evolution of activity patterns and chromatic vision in primates: morphometrics, genetics and cladistics. *J Hum Evol* 40:111–149.
- 96 Perry GH, Martin RD, Verrelli BC. 2007. Signatures of functional constraint at eye-eye opsin genes: the potential of adaptive color vision in a nocturnal primate. *Mol Biol Evol* 24:1963–1970.
- 97 Kay RF, Cartmill M. 1997. Cranial morphology and adaptations of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea, ? Primates), with a description of a new genus and species. *J Hum Evol* 6:19–35.
- 98 Ross CF, Martin RD. 2007. The role of vision in the origin and evolution of primates. In: Preuss TM, Kaas J, editors. *Evolution of nervous systems*, vol. 4: The evolution of primate nervous systems. Oxford: Elsevier. p 59–78.
- 99 Bloch J, Silcox M. 2006. Cranial anatomy of the Paleocene plesiadapiform *Carpolestes simpsoni* (Mammalia, Primates) using ultra high-resolution X-ray computed tomography, and the relationships of plesiadapiforms to Euprimates. *J Hum Evol* 50:1–35.
- 100 Karanth KP, Delefosse T, Rakotosamimanana B, Parsons TJ, Yoder AD. 2005. Ancient DNA from giant extinct lemurs confirms single origin of Malagasy primates. *Proc Natl Acad Sci USA* 102:5090–5095.
- 101 Janecka JE, Miller W, Pringle TH, Wiens F, Zitzmann A, Helgen KM, Springer MS, Murphy WJ. 2007. Molecular and genomic data identify the closest living relative of primates. *Science* 318:792–794.
- 102 Cumming B. 1998. A sense of direction: going with the flow. *Nat Neurosci* 1:6–8.
- 103 Preuss TM. 2007. Evolutionary specializations of primate brain systems. In: Ravosa M, Dagosto M, editors. *Primate origins: adaptations and evolution*. New York: Springer Science+Business Media. p 625–675.
- 104 Ankel-Simons F, Rasmussen DT. 2008. Diurnality, nocturnality, and the evolution of primate visual systems. *Yearbook Phys Anthropol* 51:100–117.
- 105 Changizi MA, Shimojo S. 2008. “X-ray vision” and the evolution of forward-facing eyes. *J Theor Biol* 254:756–767.
- 106 Isbell LA. 2006. Snakes as agents of evolutionary change in primate brains. *J Hum Evol* 51:1–35.
- 107 Casagrande VA, Khaytin I, Boyd J. 2006. The evolution of parallel visual pathways in the brains of primates. In: Preuss TM, Kaas J, editors. *Evolution of nervous systems*, vol. 4: The evolution of primate nervous systems. Oxford: Elsevier p 87–108.
- 108 McAlonan K, Cavanaugh J, Wurtz RH. 2008. Guarding the gateway to cortex with attention in visual thalamus. *Nature* 456:391–395.

