Binocularity and brain evolution in primates

R. A. Barton*

Evolutionary Anthropology Research Group, Department of Anthropology, University of Durham, 43 Old Elvet, Durham DH1 3HN, United Kingdom

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Primates are distinguished by frontally directed, highly convergent orbits, which are associated with stereoscopic vision. Although stereoscopic vision requires specialized neural mechanisms, its implications for brain evolution are unknown. Using phylogenetic comparative analysis, I show that evolutionary increases among primate taxa in the degree of orbital convergence correlate with expansion of visual brain structures and, as a consequence, with the overall size of the brain. This pattern is found across the whole primate order and is also repeated within each of the two major primate subtaxa. The visual expansion associated with increased binocularity is specific to the parvocellular visual pathway, consistent with recent evidence implicating this pathway in fine-grained stereopsis. The results support the hypothesis that brain size evolution in primates was associated with visual specialization.

stereoscopic vision

Extreme orbital convergence (1) is one of a suite of features distinguishing the primate visual system. These features are largely associated with the binocular integration of stimuli in the central visual field and include (*i*) a concentration of ganglion cells in the central retina, together with a greatly expanded representation of the central field in visual cortex; (*ii*) a distinctive pattern of projections between eye and brain in which each side of the visual cortex receives extensive fibers from both retinae; (*iii*) a distinctly laminated lateral geniculate nucleus (LGN), within which information from the same hemifield of each retina is brought into visuotopic register in separate layers before converging on numerous single binocular neurones in the visual cortex; and (*iv*) anatomically and physiologically distinct magnocellular and parvocellular layers of the LGN, with central vision served primarily by parvocellular projections (2, 3). This suite of visual features was a fundamental component of the adaptive shift in the evolution of the first primates (2, 4). There is, however, substantial variation among extant primate species in the degree of orbital convergence (1) and the size of the binocular field (5), and this variation provides an opportunity to examine the implications of binocularity for the evolution of the visual system and brain. A previous study demonstrated that brain size variation in primates is associated with relative expansion of the visual system, including the visual cortex and the parvocellular LGN (6). The present study reports a test of the hypothesis that increased reliance on binocular mechanisms underlies the expansion of visual brain areas and overall brain size.

Methods

Data. Comparative data on orbital convergence in 76 primate species were obtained from ref. 1, in which convergence is defined as the degree to which the orbital margins face in the same direction. Body weights (160 species) were obtained from recent compilations of wild-caught samples (7, 8). Values used were the means of male and female weights. Data on the volume of visual brain structures, the neocortex, and the rest of the brain (43 species) are from ref. 9, with supplementary data on separate LGN layers from ref. 10, and are, together with data on activity timing, available from Barton (6) (www.pubs.royalsoc.ac.uk/proc_bio_electapp_iframe.shtml). The main visual structures analyzed were the LGN and primary visual cortex (area V1). I also tested whether the whole neocortex exhibited correlations similar to those of the LGN and V1. In primates, a large proportion of the neocortex (>50% in macaques) consists of visual areas (including the secondary and tertiary visual cortex, in addition to area V1), and even "association" areas have major visual inputs (3, 11). Previous analyses have shown that neocortex size correlates closely with the size of purely visual structures (6, 12). Hence, it is of interest to determine whether the volumetric evolution of the neocortex as a whole reflects selection on visual mechanisms. Brain weights were taken from ref 13. Sample sizes vary according to how many species values were available for the relevant variables in each analysis.

Analysis. I used the CAIC 2.6 computer package (14), which implements a modified version of Felsenstein's method of independent contrasts (15–17). The program computes standardized contrasts in trait values between pairs of taxa at each node of the phylogeny, allowing analysis of correlated evolutionary change in those traits. For analysis of continuous variables, contrasts were computed at each independent node of the phylogeny. In addition, the association between continuous variables (such as orbital convergence) and activity timing, a categorical variable (nocturnal versus diurnal), was analyzed according to established procedures (14). Part of the variation in orbital convergence is thought to be a side effect of "allometric factors relating to skull construction" (1), without necessarily having any functional corollary. That being the case, tests for associations between orbital convergence and visual brain expansion must control for allometric (size) effects. This was done in two ways: by multiple regression (incorporating body mass as an independent variable) and by computing residuals for brain size based on the bivariate regression between brain size and body size. Least-squares regression was used to generate residuals, as this is the only method that produces residuals uncorrelated with the independent variable, a desirable property of analyses designed to remove the effects of size. An alternative method, the reduced major axis, makes no use of the covariance between x and y, and it is not now recommended for allometric analysis (16). The phylogeny used, including branch lengths, was taken from ref. 18. All regressions were forced through the origin (14, 16). Because the error variances associated with body-weight estimates tend to be relatively high, using the same set of body-weight estimates to correct two different variables can have the undesired effect of adding a correlated source of error variance to each variable, such that spurious positive correlations can result (19, 20). It is therefore advisable to use independent body-weight samples, taken from different populations of each species, to transform variables that are then to be correlated. I did this for the analysis of the correlation between body-size-corrected orbital convergence and body-size-corrected brain weight, by using separate samples, subject to a sample size constraint ($n > 3$ for both adult male and adult female weights), for wild populations given in the summary sources (7, 8). This procedure is conservative (20), and similar results were obtained

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Abbreviation: LGN, lateral geniculate nucleus.

*E-mail: r.a.barton@durham.ac.uk.

when only a single set of body-mass estimates was used to generate residuals. Assumption checking was carried out in accordance with the CAIC 2.6 manual (14). All statistical tests of significance were two-tailed.

Results

Orbital Convergence, Allometry, and Visual Brain Expansion. As predicted (1), independent contrasts in orbital convergence are positively correlated with contrasts in body size ($r^2 = 0.24$, $t = 4.34$, df = 61, $P < 0.001$). This regression suggests, however, that allometry explains only one-quarter of the variance in orbital convergence. Multiple regressions with body size, visual structure size, and size of the rest of the brain as independent variables indicate that orbital convergence correlates with visual structure size and not with the size of the rest of the brain (LGN: $t = 3.1$, df = 3,25, $P = 0.005$; visual cortex: $t = 2.3$, df = 3,25, $P = 0.033$; whole neocortex: $t = 2.9$, df = 3,25, $P = 0.008$; $P > 0.1$ for the rest of the brain in each case). In a slightly different analysis, the effects of variation in the size of the rest of the brain were removed before testing for associations with orbital convergence. This was done by calculating residuals from the regression of visual-structure-size contrasts on contrasts in the size of the rest of the brain, and correlating these residuals with relative orbital convergence (residuals from the regression on body weight). Hence, this analysis tests whether visual structures are expanded relative to the size of the rest of the brain in lineages with high orbital convergence. Relative orbital convergence is, indeed, significantly positively correlated with the relative size of the LGN ($r^2 = 0.32$, df = 25, $t = 3.41$, $P = 0.002$), area V1 ($r^2 = 0.23$, df = 25, $t = 2.69$, $P = 0.012$), and whole neocortex ($r^2 = 0.34$, df = 25, $t = 3.55$, $P = 0.002$).

Orbital Convergence and Brain Size. Brain-size and orbital-convergence contrasts are significantly correlated after the effects of body weight have been removed from each ($r^2 = 0.15$; $t = 2.63$, df = 40, $P = 0.01$; independent body-weight samples used to compute each set of residuals).

Replication of Results Within Independent Primate Subtaxa. Anthropoid primates (monkeys and apes) have significantly greater orbital convergence than do strepsirhines (lemurs and lorises), and this fact has been attributed to structural constraints arising from a reduction in relative orbit size associated with diurnality in anthropoids (1). However, there does not appear to be a general association between orbital convergence and activity period: of four independent contrasts between nocturnal and diurnal taxa, two show greater orbital convergence in nocturnal primates and two greater convergence in diurnal primates, and the mean difference between nocturnal and diurnal lineages is insignificant ($t = 0.16$, df = 3, $P = 0.89$). Hence, the increased degree of convergence in anthropoids may be related to enhancements of stereoscopic vision rather than being a side effect of orbit-size reduction. The results bear this out: even within purely diurnal anthropoids, variation in orbital convergence correlates with brain evolution. As for the whole sample, relative orbital convergence is positively correlated with the relative size of visual brain structures ($n = 11$; LGN: $r^2 = 0.64$, $t = 4.25$, $P = 0.002$; V1: $r^2 = 0.30$, $t = 2.09$, $P = 0.06$; neocortex: $r^2 = 0.48$, $t = 3.0$, $P = 0.01$) and with overall brain size relative to body size ($n = 31$; $r^2 = 0.21$, $t = 2.8$, $P = 0.009$). There were not enough independent contrasts to repeat this analysis within purely nocturnal strepsirhines, but, when both nocturnal and partly diurnal strepsirhines are included, the same overall pattern emerges ($n = 13$; LGN: $r^2 = 0.36$, $t = 2.57$, $P = 0.02$; V1: $r^2 = 0.23$, $t = 1.87$, $P = 0.08$; neocortex: $r^2 = 0.41$, $t = 2.88$, $P = 0.014$; brain size relative to body size: $r^2 = 0.24$, $t = 1.89$, $P = 0.07$).

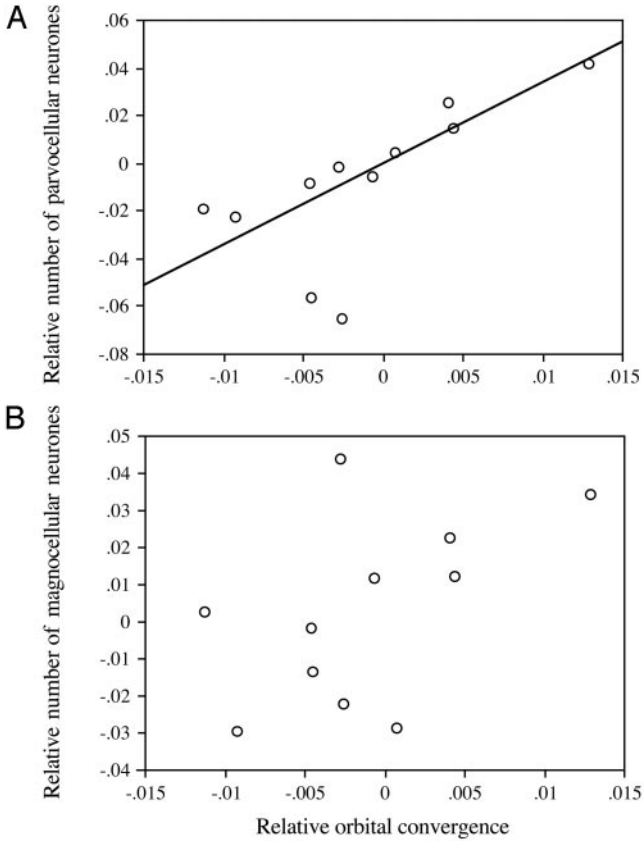

Fig. 1. Correlated evolution of orbital convergence and the LGN of primates. The graphs plot relative phylogenetic contrasts in the number of neurons in parvocellular (*A*) and magnocellular (*B*) layers against relative contrasts in the degree of orbital convergence. There is a significant positive regression for parvocellular layers (*A*: $r^2 = 0.50$, $t = 3.13$, df = 10, $P = 0.01$) but not for magnocellular layers (*B*: $r^2 = 0.21$, $t = 1.67$, df = 10, $P = 0.13$).

Constraints Imposed by Olfactory Mechanisms. It is possible that increases in orbital convergence are not directly associated with visual brain expansion but are merely side effects of decreases in snout size related to olfactory reduction. This hypothesis would predict a negative correlation between olfactory bulb size and orbital convergence after controlling for size. There was, however, no significant negative correlation, either across all primates ($t = -1.7$, df = 3,25, $P = 0.10$) or within either subtaxon (strepsirhines: $t = -1.9$, df = 3,9, $P = 0.09$; haplorhines: $t = 1.6$, df = 3,12, $P = 0.14$). This point is reinforced by the fact that the haplorhine primates with the largest snouts, the baboons (genus *Papio*), nevertheless have a high degree of orbital convergence for that suborder (1).

Parvocellular Versus Magnocellular Visual Pathways. Analysis of the number of neurons in separate layers of the LGN shows a significant correlation between relative orbital convergence and the relative number of neurons in parvocellular layers, but shows no correlation for magnocellular layers (Fig. 1). The same is true when the volume, rather than the neuron number, of each layer is correlated with orbital convergence (parvocellular volume: $r^2 = 0.48$, $t = 3.04$, df = 10, $P = 0.01$; magnocellular volume: $r^2 = 0.25$, $t = 1.82$, df = 10, $P = 0.10$).

Discussion

These results support the hypothesis that the evolution of stereoscopic vision had significant costs in terms of associated brain expansion, and they implicate parvocellular, rather than

magnocellular, visual projections. The latter result is not predicted by one influential model of primate visual processing, which assumes that stereopsis (the recovery of depth information from binocular disparity) is mediated by the magnocellular-dominated "where" visual stream (21). The results accord instead with more recent experimental evidence that implicates parvocellular pathways in fine-grained stereopsis (22, 23) and that indicates neurons sensitive to depth are located in cortical area V4, within the parvocellular-dominated ventral stream (24). Fine-grained stereopsis is likely to be critical for the visually guided, delicate manipulation of plant foods, which has been proposed as a key adaptation of ancestral primates (25). This latter idea may relate to the present findings in the following way. The nasal margins of the orbits in primates with more laterally positioned eyes may place a mechanical constraint on the ability to verge the eyes toward near objects, particularly those in the lower visual field, where manipulation by the hands occurs. Manipulated objects held close to the eyes require considerable vergence for binocular fusion to occur, and binocular disparity signals may have an additional function in the control of such vergence eye movements (26). Hence, the increase in visual brain size in primates with more convergent orbits might reflect enhancements of stereo acuity and vergence-control mechanisms specifically related to the visually guided grasping and close-range manipulation of food items, an ability that would have paved the way for advanced tool-making and tool use. An alternative hypothesis for the evolution of binocular vision in primates relates it to visually guided predation on insects and other small prey (4). Although plausible, this hypothesis places less emphasis on parvocellular-mediated acute visual discrimination and more on the magnocellular-mediated tasks of movement detection and rapid orientation to moving stimuli.

These results may help to resolve a paradox about the evolution of the parvocellular pathway. Most mammals lack a clearly differentiated parvocellular pathway, and its function in primates has been linked to photopic vision associated with a diurnal lifestyle, notably color processing (2, 3, 6, 21, 23). However, the primitive condition for primates is thought to be nocturnality (4, 27); if that is correct, the original emergence of the parvocellular pathway must have been associated with scotopic, probably monochromatic, vision. Although the subsequent evolutionary elaboration of the parvocellular pathway seems to be associated with diurnality and, hence, photopic functions (6, 10, 28), fine-grained stereopsis may provide a more general explanation for its evolutionary origin in primates.

Stereopsis is not the only possible function of binocularity. Binocular summation (the increased sensitivity to faint visual stimuli afforded by a double input to the same neurones) also has been proposed as a possible reason for the evolution of orbital convergence (5, 28). Only stereopsis, however, is likely to have significant computational, and hence neural, costs. Extra neurons would be required to compute disparity, but not to simply sum the signal from two inputs. Furthermore, whereas the binocular summation hypothesis was put forward to explain orbital convergence as an adaptation for scotopic vision in the night-active ancestral primates, the present study found that relative orbital convergence is not, as predicted by that hypothesis, correlated with evolutionary transitions in activity period.

Orbital convergence, an expanded visual cortex, and a large brain relative to body size were fundamental components of the adaptive shift in the evolution of the first primates (2, 4). The results reported here show that the evolutionary relationship among these traits was not confined to a single adaptive shift at the origin of primates, but comprises a general relationship capable of explaining variance in brain size amongst extant species. Because brain tissue is metabolically expensive, there must be distinct information-processing benefits associated with increased brain size. Nevertheless, specific information-processing benefits of increased brain size have been notoriously difficult to identify (29). Stereopsis, together perhaps with other aspects of visual specialization such as color processing (6), appears to provide such benefits.

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