

Latitudinal variation in light levels drives human visual system size

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Ambient light levels influence visual system size in birds and primates. Here, we argue that the same is true for humans. Light levels, in terms of both the amount of light hitting the Earth's surface and day length, decrease with increasing latitude. We demonstrate a significant positive relationship between absolute latitude and human orbital volume, an index of eyeball size. Owing to tight scaling between visual system components, this will translate into enlarged visual cortices at higher latitudes. We also show that visual acuity measured under full-daylight conditions is constant across latitudes, indicating that selection for larger visual systems has mitigated the effect of reduced ambient light levels. This provides, to our knowledge, the first support that light levels drive intraspecific variation in visual system size in the human population.

Keywords: latitude; light levels; eyeball size; visual cortex size; day length

1. INTRODUCTION

The association between ambient light levels and visual system size is well established in birds [1,2] and primates [3–10]. Lower light conditions during dawn singing in birds [2] or nocturnal activity in primates (e.g. [7]) necessitate larger eyes. These allow larger corneas and pupils and more numerous high-summation (many photoreceptors per retinal ganglion cell) rods, enhancing sensitivity. This is traded against decreased acuity (the distance between points that can be distinguished), which in contrast requires denser cones with low summation, but is nonetheless also positively associated with eye size [11,12].

Enlarged eyes enable parallel increases in sensitivity and acuity, in that they both enhance light-gathering capacity through larger corneas and increase retinal image size, functionally reducing summation because each receptor field corresponds to a smaller proportion of an image [13]. Along these lines, it has been suggested that increasing eyeball size allowed derived nocturnal *Tarsius* and *Aotus* haplorrhines to increase visual sensitivity while simultaneously maintaining relatively high acuity [13], probably for nocturnal predation [7].

Both illuminance (the amount of light incident on the Earth's surface) and minimum day length decrease

with increasing absolute latitude [14], and seasonally shorter day lengths create time pressures that require activity during the mesopic (intermediate light levels between rod saturation and the minimum threshold for cone function) and scotopic (when only rods are active) conditions of dawn and dusk [14]. Lower illuminance means that, even during fully photopic (daylight) conditions, high latitude humans may require larger eyes to attain the *same* level of acuity as those living at lower latitudes. By contrast, under dawn/dusk light levels, higher latitude larger eyed humans may well demonstrate markedly *higher* acuity than lower latitude individuals, owing to greater light capture through an enlarged cornea in combination with larger retinal images.

Visual system component size, from eyeball to both primary visual (V1) and extrastriate cortical areas, are highly correlated in mammals independently of overall cortex size, allometry and phylogeny [3,6], as are eye and brain size in birds [15]. Within humans, there is a point-to-point representation between retina and V1 [16], associated with isometric scaling of the optic tract and lateral geniculate nucleus [17], which, owing to the hierarchical organization of the primate visual system [18,19], translates into tight scaling with upstream visual areas V2 and V3 [20,21].

This close association between retina and V1 [16,22] means that changing retina size directly influences V1 volume. For instance, human disorders such as albinism or those associated with defects in the *PAX6* gene cause malformed or absence of fovea and are associated with reduced grey matter volume in the occipital pole (the V1 region representing the fovea) [23]. A similar effect associated with domestication has been noted in cats: reduction in cone density has resulted in a 30 per cent reduction in visual path volume, and hence overall brain volume [24]. In humans, V1 cortical volume is positively associated with visual acuity, indicating that anatomical differences translate into significant functional effects [25].

Decreasing ambient light levels should select for increasing eye and visual cortex size in order to increase sensitivity and maintain acuity. We thus predict a latitudinal increase in human orbital volume (which is proportional to eyeball size [26,27]). Since enlarged visual systems should be selected to counteract the potential negative impacts on visual processing of decreasing light levels, we also predict that visual acuity measured under ambient photopic conditions should be maintained at a constant level across latitudes regardless of the decrease in light levels.

2. MATERIAL AND METHODS

We measured cranial capacity (CC), orbital volume and foramen magnum (FM) dimensions for 73 healthy adult crania from the Oxford University Museum of Natural History and Duckworth Collection, University of Cambridge (see the electronic supplementary material). We then set a minimum criterion of three skulls per population to minimize outlier-effects in calculating population means, yielding 55 skulls from 12 populations (electronic supplementary material, table S1). Analyses were carried out on full ($n = 73$) and subset ($n = 55$) samples, as well as on population means ($n = 12$). The results were consistent, so we present only the population mean analyses, controlling for possible dependence between individuals within populations. We controlled for phylogeny using phylogenetic general linear model (see the electronic supplementary material).

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To measure orbital volume with 1 mm diameter glass spheres, we lined the orbits with laboratory film. To measure CC, apertures were blocked with white tack, and the cranial cavity filled with wax beads (approx. 5 mm diameter and 2 mm thick). We measured volumes using graduated cylinders. Precautions were taken to maximize reliability (see the electronic supplementary material). We calculated FM cross-sectional area from length and inter-condyle width as a proxy for body mass [28] (see the electronic supplementary material).

All find-site or central country latitudes and longitudes were found using Google latitude [29]. We calculated altitude of the Sun at noon for each latitude/longitude coordinate using [30,31] and log illuminance (lux) following the study of Seidelmann ([32]: 492, table 9.34.1). Minimum illuminances were identified and transformed into raw form for linear regression. We used Google maps [33] to find the nearest town/city to the latitude/longitude coordinates and obtained mean minimum temperatures (converted to °C) from Weatherbase [34]. These data were not available for Uganda and Micronesia, so the lowest mean monthly temperatures were substituted.

We obtained visual acuity data for native adults measured under ambient photopic conditions from Myers [35] and Rivers [36] (electronic supplementary material, table S2).

None of the variables deviated significantly from a normal distribution (Kolmogorov–Smirnov one-sample tests).

3. RESULTS

A significant positive relationship was found between absolute latitude and orbital volume (figure 1a: $t_{10} = 6.686$, $p < 0.001$, $r^2 = 0.817$), controlling for phylogeny (see electronic supplementary material, figure S1; for all equations, see electronic supplementary material).

To account for scaling relationships between eyeball and brain size, we included the interaction between standardized CC and absolute latitude in a two-block multiple linear regression. The model without the interaction term gives a significant partial correlation between absolute latitude and orbital volume ($t_9 = 4.422$, $p = 0.002$, $r_{\text{adj}}^2 = 0.778$) independently of CC, which itself was not significantly correlated with orbital volume once latitude was partialled out ($t_9 = -0.212$, $p = 0.837$). Adding a cranial capacity \times absolute latitude interaction term does not change this result ($t_8 = 5.933$, $p < 0.001$, $r_{\text{adj}}^2 = 0.855$; partial cranial $t_8 = -7.98$, $p = 0.448$), even though the interaction term itself is significant ($t_8 = -2.401$, $p = 0.043$). As the data are in standardized units, the negative interaction term implies that orbit volume increases faster with absolute latitude than does CC (figure 1b). This indicates that the latitudinal increase in human orbital volume is greater than that predicted by positive allometry with total brain size *per se*. In other words, any relationship between eyeball and brain volume is mediated by the positive association between human brain size and latitude [37].

Backwards stepwise regression removed FM area (indexing body size) without significant reduction in r^2 , producing a best model showing a main effect of absolute latitude independent of interaction effects between absolute latitude and/or FM area and CC (electronic supplementary material, table S3). Phylogeny made no difference (electronic supplementary material, table S5).

An alternative explanation for latitudinal increases in orbital volume is that eyes require progressively more insulative fat in colder climates. However, orbital volume remained significantly associated with minimum

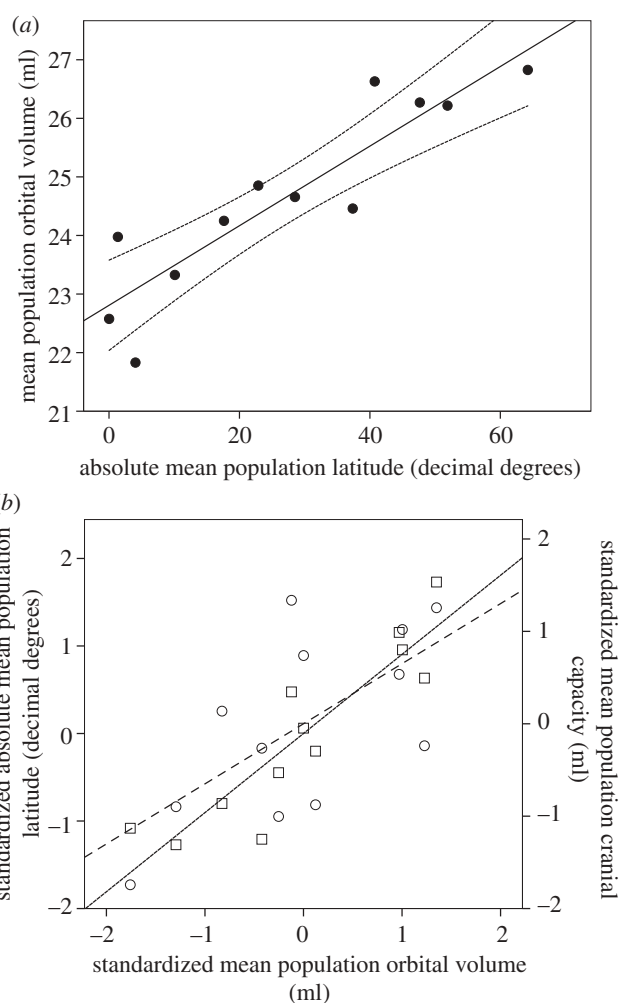


Figure 1. (a) Mean orbital volumes for 12 human populations plotted against absolute mean latitude. Dashed lines show 95% confidence intervals. r^2 linear = 0.817. (b) Standardized absolute mean population latitude (squares and short-dashed line, $r^2 = 0.817$) and cranial capacity (circles and long-dashed line, $r^2 = 0.423$) plotted against standardized orbital volume.

illumination ($t_9 = -3.394$, $p = 0.008$, $r_{\text{adj}}^2 = 0.789$) when mean minimum temperature ($p = 0.734$) was partialled out.

If ambient light levels select for eyeball enlargement to maintain constant photopic visual acuity, then acuity measured under natural daylight conditions should not vary systematically with absolute latitude; instead, enlarged eyes should compensate for associated decreases in illuminance, thus causing the acuity curve to flat line. As predicted, acuity and latitude are not correlated (figure 2), either when controlling for phylogeny (electronic supplementary material) or when the sample is restricted to populations measured using a standard method ($n = 10$).

4. DISCUSSION

We have shown that human orbital volume significantly increases with absolute latitude independently of phylogeny, brain size and body mass, suggesting that there has been selection for larger eyeballs under progressively lower light conditions. This holds true even when controlling for minimum temperature, indicating

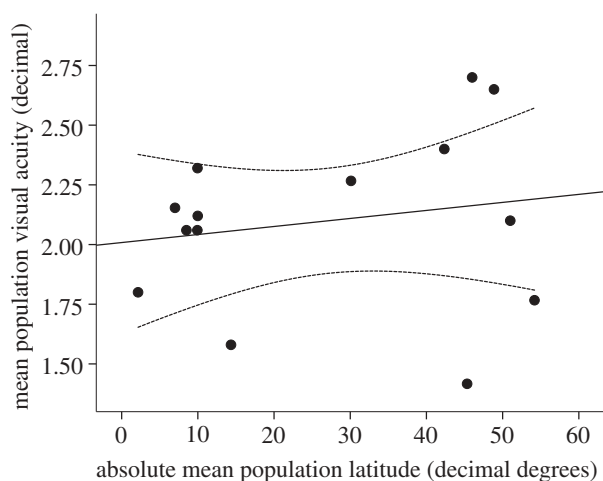


Figure 2. Visual acuity for various human populations [35,36] plotted against absolute latitude. Dashed lines show 95% confidence intervals. r^2 linear = 0.033.

that selection is on eyeball size rather than on insulating packing. In addition, our finding that human visual acuity under latitude-specific photopic conditions remains constant across latitudes implies selection for enlarged eyeballs to allow decreases in light levels to be tracked as humans occupied successively higher latitudes. If this is so, then we predict that measurement under standardized (i.e. optimal) light conditions should yield increasing acuity with absolute latitude, particularly at meso/scotopic light levels. Finally, owing to tight scaling between visual system components, larger eyeballs will necessitate proportionately enlarged visual cortices, and hence, a parallel positive latitudinal trend in these brain regions.

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