Anthropological Review • Vol. 79 (2), 143–149 (2016)

DE GRUYTER
OPEN

Anthropological Review
Available online at: https://doi.org/10.1515/anre-2016-0011

The relationship between latitudinal light variation and orbit and cranial size in humans

Alice Short

Anthropological and Comparative Anatomy Unit, School of Medicine,
The University of Adelaide, Australia

Abstract: Increased orbit size is suggested to be an adaptation for enhanced visual acuity and sensitivity in conditions of reduced light quality. Whilst light ambience has a well established correlation with eye size in birds and primates, evidence in humans is very limited. The aim of this study was to analyse the anatomical compensations of the eye and visual cortex as a result of varying levels of light exposure. It was hypothesized that humans of higher latitudes will have an increased orbit size to improve visual sensitivity and acuity in conditions of decreased light, and thus greater cranium size due to enlarged visual cortices. Craniometric measurements of 1,209 male and 1,021 female individuals from 27 series coming from different latitudes were sourced from William W. Howells Craniometric Data Set. Mean cranial and orbit size was calculated by combining linear craniometric measurements of length, width and height for individual males and females at each latitude. Linear regressions of orbit and cranial size on latitude were created and significance was measured using Pearson's r and P value. Partial correlations were calculated to test whether orbit size correlates with latitude independent of cranial size. Significant positive correlations were found between i) orbit and cranial size and ii) orbit size and latitude and iii) cranial size and latitude in males and females. Additionally, partial correlation values for latitude and orbit size were significant in both males and females. The relationship between visual system size and increasing latitude among humans is currently understudied. Significant relationships between visual system size and increasing latitude suggest that enlarged eyes were an evolutionary mechanism for individuals with compromised light availability. Other factors related to varying geographic location may also play a role.

Key words: eye size, illuminance, visual acuity, visual sensitivity, males, females

Introduction

Light ambience has a well established correlation with eye size in birds and primates.

Studies performed on primates have discovered that nocturnal species have significantly larger orbit size when compared with diurnal species (Garamszegi et al. 2002; Kay and Kirk 2000). The increased orbit size can be seen as an accommodation for enlarged eyes, an adaptation to allow enhanced visual acuity and sensitivity in conditions of lesser light quantity and quality (Kay and Kirk 2000). Studies comparing the avian eye

Original Article Received: January 22, 2016; Accepted for publication: May 27, 2016
DOI: 10.1515/anre-2016-0011

with activity levels and habits discovered that nocturnal birds have significantly greater eye volume when compared to those of diurnal nature. This is possibly a compensation mechanism in response to low light levels, as a larger eye allows for an increased number of photoreceptive cells and hence more light to be received by the retina (Garamszegi et al. 2002).

Light gathering ability, or visual sensitivity, is determined by the size of corneal diameter.

Enlargement of the cornea allows an increased pupil diameter, which increases the amount of light that can enter the eye. Another important quality of eyes is visual acuity, the ability to differentiate two shapes from one another. An increased axial length creates a larger retinal image, which improves the ability to resolve different objects and thus enhances visual acuity (Hall 2007). Heightened light sensitivity also occurs as a result of increase in retinal summation (Pearce and Dunbar 2012). Retinal summation describes the number of photoreceptor cells for the number of bipolar cells in the retina and is an adaptation that occurs to increase light sensitivity. In the case of high summation, a greater ratio of photoreceptor cells synapse to bipolar cells, which allows for response to weak stimuli. Increased retinal summation results have been observed in primates of nocturnal nature when compared to diurnal species. However, increased retinal summation in order to heighten light sensitivity comes at a price of reduced visual acuity. Visual acuity is negatively impacted under high-summation as individual light rays are indistinguishable to the brain (Veilleux and Kirk 2014). It has been suggested that an overall increased eye size would result in an improvement in both an increase in visual sensitivity and acuity. An eye with a greater axial length and corneal diameter is capable of perceiving more light and detail when compared to individuals with smaller eyes. However, due to large variations in environment there is no ideal eye design, rather that humans are expected to optimize eye shape for their specific needs of their environment (Hall and Ross 2007).

This knowledge can be applied to humans living in varying regions of the world. The amount of total light on the Earth's surface (illuminance) decreases as day length decreases. Regions of higher latitude experience greater polarities of both minimum and maximum day length. Whilst average day length of countries remains the same throughout the world, the unequal distribution of daylight at regions of greater latitude results in periods of extended darkness during wintertime (Pearce and Dunbar 2011), and thus activity of retinal photoreceptors varies accordingly (Schubert 2006). According to Pearce and Dunbar (2011), there are three different ranges of vision that are each activated by different levels of illuminance. Scotopic vision relates to vision at low light levels, such as nighttime and overcast days, and involves only rod activation. Photopic vision is active at high levels of light (e.g. daylight), by which vision is mediated by cones. Mesopic vision involves the activation of both rods and cones during periods of early twilight or moonlight. Locations of low latitude experience more day lengths with greater illuminance, and thus habitants are largely active during photopic conditions, increasing the level of light exposure to the eye and maximizing cone activity. Contrastingly, those in locations of increased latitude will have greater levels of activity during mesopic and scotopic conditions. Humans used fire for at least 1.5 million years to provide some light at night, and since the advent of agriculture, various ways of providing relatively steady sources of light at night such as oil-fuelled lamps and candles were introduced. These sources provided low-intensity light compared with daylight, extending periods of mesopic vision. It was only with the introduction of enhanced-air-flow lamps in the last 250 years (whale oil powered and then kerosene and gas powered lamps) that the illuminance in the vicinity of artificial light sources could reach at night levels attributable to photopic vision. It, of course, was reaching photopic levels since the introduction of electric light sources about 150 years ago.

The human orbit does not contain the eyeball alone. However, along with the lacrimal apparatus and surrounding muscles, it is considered to accurately reflect the size of the adult eye (Pearce and Bridge 2013). A study on human orbits has confirmed a positive relationship between orbital and eyeball volume independent of brain size, thus suggesting the measurement of the human orbit a reliable measure of eye size (Pearce and Bridge 2013).

Eye size and the underlying functional meaning behind its variation has received little attention in humans. The aim of this study is to analyse the anatomical compensations that occur to the eye and brain as a result of varying levels of light exposure. It is hypothesized that humans from higher latitudes will have an increased orbit size to improve visual sensitivity and acuity in conditions of periodically decreased light, and thus greater cranium size due to enlarged visual cortices.

Methods

Craniometric measurements from 1,209 male and 1,021 female skulls, originating from a range of 27 latitudinal points, were sourced from William W. Howells Craniometric Data Set (Howells 1973). Calculations of craniometric dimensions were performed to find the cranial and orbital size for each individual using formula for cranial and orbital size.

$$\text{Cranial size} = (\text{GOL} + \text{XCB} + \text{BBH})/3$$

$$\text{Orbital size} = (\text{OBH} + \text{OBB})/2$$

where: GOL – Glabella-Occipital Length
XCB – Maximum Cranial Breadth
BBH – Basion-Bregma Height
OBH – Orbital Height
OBB – Orbital Breadth

The mean cranial and orbit size was then calculated for both males and females of each country. All latitudinal points were recorded using Google Latitude.

Linear regressions were performed for 1) orbit size vs cranial module; 2) cranial module vs latitude; and 3) orbit size vs latitude. To test whether orbit size was changing independently of cranial size, the partial correlation was calculated whilst holding cranial size constant.

Results

Significant correlations were found between orbit size of individuals and latitude in both male and female cohorts ($r=0.285$, $p<0.01$; $r=0.312$, $p<0.01$ respectively). Additionally, significant positive correlations occurred between individual cranial and orbit sizes in both males ($r=0.408$, $p<0.01$) and females ($r= 0.426$, $p<0.01$). Finally, a significant positive relationship occurred between individual cranial size and latitude for males (r=0.276, $p<0.01$) and females (r=0.282, $p<0.01$).

The partial correlation between orbit size and latitude whilst holding cranial size constant displayed a significant coefficient of correlation for females (r=0.221, $p<0.01$) and males (r=0.193, $p<0.01$).

Discussion

Both male and female data displayed significant partial correlations between latitude and orbital size, independently of cranial size (r=0.193, $p<0.01$ and r=0.221, $p<0.01$ respectively).

This suggests that orbit size increases independently from brain size at regions of greater latitude. These data support previous findings by Pearce and Dunbar (2011) where significant interactions between orbital size and latitude were also deemed independent of cranial size.

The correlation between both male and female orbit size and increasing latitude was significant (r=0.285, $p<0.01$; r=0.312, $p<0.01$ respectively). These data provide a strong argument to suggest that an enlarged orbit results from a developmental mechanism to enhance visual image quality of individuals, thus supporting the hypothesis. An increase in orbit size can be attributed to an enlarged cornea, thus increasing pupil diameter (Pearce and Bridge 2013). This consequentially increases the amount of light gathering and thus improving visual sensitivity. Increased axial length and hence an increase in retinal image size will improve visual acuity (Hall and Ross 2007). Enlarged orbit size will increase retinal summation, therefore increasing the number of photoreceptor cells in the eye. These adaptations result in an increased eye size, and improve visual detection of weak stimuli in poor light conditions including artificial light of open fires, candles and oil lamps. These data can be supported in both avian and primate models, which attribute increased orbit size to decreased light quality adaptations result in an increased eye size, and improve visual detection of weak stimuli in poor light conditions (Kay and Kirk 2000; Garamszegi et al. 2002; Hall and Ross 2007). The significant partial correlation figures for males (r=0.193, $p<0.01$) and females (r=0.221, $p<0.01$) provide a strong indication that orbit size increases independently of cranial size, rather than enlarged eyes being simply a morphological consequence of an enlarged brain.

Significant positive relationships between cranial and orbit size were observed in both male (r=0.59, $p=0.0044$) and female cohorts (r=0.72, $p=0.00034$). These results may suggest the development of larger visual cortices to allow for greater neural pathways and connections as a result of the increasing number of photoreceptors in the retina. This can be seen as a coevolutionary mechanism in order to achieve behavioral adaptations of increased visual sensitivity and acuity. This would therefore prove useful in environments of decreased illuminescence including artificial light of open fires, simple lamps and candles.

Given that all anthropometric data used here date back to pre- and early history, prior to the invention of electrical light (Sonnebom 2007), individuals would not have survived in regions of high latitude had they not developed the physiological adaptations to assist in eye sight. Poor eye sight in these conditions of low light levels would have led to decreased ability to work, commute, self protect, farm and prepare food. Among

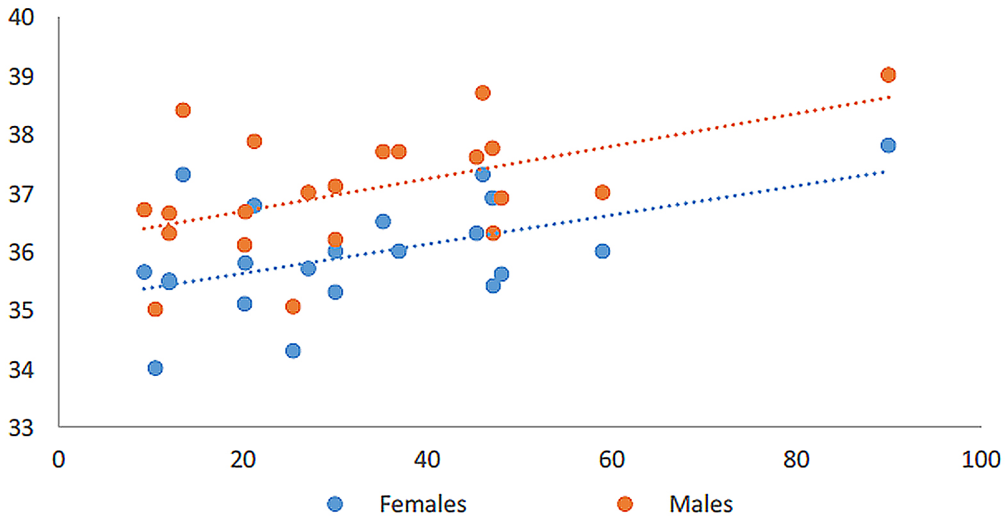

Fig. 1. Correlation of orbit size with increasing latitude in females and males . Absolute latitude in degrees on the x-axis, orbit size on the y-axis.

hunters and gatherers, individuals with heightened visual sensitivity and acuity would have improved chance of survival by greater ability to protect oneself from predators. It can therefore be suggested that this increase in orbital and cranial size was a mechanism to maximise the amount of information gathered from the retinal image, and thus improve visual perception by humans in regions where there is minimal to no light for extended periods of the year.

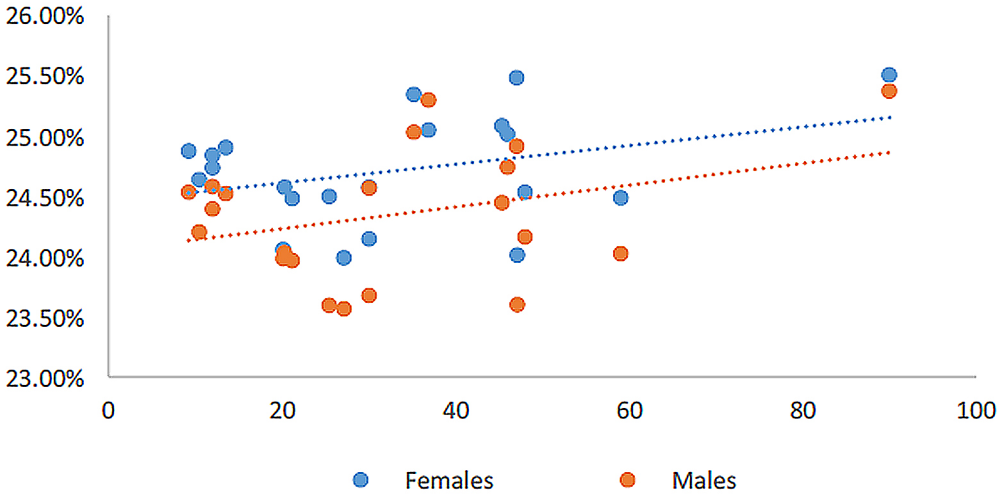

Fig. 2. Increasing orbit volume with latitude when standardized against cranial volume . Absolute latitude in degrees on the x-axis, orbit volume as a pecentage of cranial volume on the y-axis.

A significant positive relationship between cranial size and latitude was found in both males (r=0.276, $p<0.01$) and females (r=0.282, $p<0.01$). These data support the findings of Ash and Gallup (2007) and Pearce and Bridge (2013), both of whom have documented similar correlations of increased cranial size at greater latitudinal points. The independent increase of orbit size with latitude suggests that increased eye size may at part explain the reason for increased cranial volume. One study tested whether the positive scaling of orbital volume is associated with visual cortex volume in humans, in which a significant correlation was found (Pearce and Bridge 2013). This supports the second part of the hypothesis, which predicted that increased cranium size would be observed at higher latitudes due to an increased visual system size.

Whilst the relationship between visual system size and latitude has been deemed significant in a study by Pearce and Dunbar (2012), their results in are limited by a small sample size of 55 skulls across 12 populations. The large sample size in this analysis (2,230 individual skulls across 22 latitudinal points) provides strong reliability, which can support these previous findings.

One limitation of this investigation is the inability to distinguish whether an increase in cranial size is due to enlarged visual cortices, or rather that of already established variables such as the decrease in temperature or vitamin D exposure. Additionally, variation in diet amongst communities at different latitudinal points may have an effect on total brain size.

Therefore, rather than measuring the entire cranium, an alternate method for analysing visual cortex size could be electrophysical monitoring of the visual cortex using electroencephalogeny (EEG). This may eliminate this limitation in future studies, by allowing measurement of activity specific to the visual cortex rather than that of the entire brain.

Suggestions for future research into the relationship between orbit and cranial size and varying latitudes would be to undergo measurements of modern humans after the establishment of artificial light.

Conclusion

Whilst the correlation between orbit and cranial size at varying levels of light has been well documented in other species, the relationship among humans is understudied. An increase in eye size assists in the improvement of visual acuity and visual sensitivity, qualities that are increasingly important in environments where light quality and availability is reduced.

Significant relationships between both orbit and cranial size with increasing latitude were discovered, supporting the hypothesis that visual system size increases with increasing latitude. This is proposed to be an evolutionary mechanism in order to increase chances of survival in regions of compromised light availability.

Acknowledgements

Sincere thanks are due to Maciej Henneberg for consultation and assistance with statistical methods.

Corresponding author

Alice Short, Alice Short 9 Fairford Street,
Unley, SA 5062, Australia

e-mail address:
alice.short@student.adelaide.edu.au

References

Ash J, Gallup GG Jr. 2007. Paleoclimatic Variation and Brain Expansion during Human Evolution. Hum Nat 18:109–24.

Garamszegi LZ, Moller AP, Erritzoe J. 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proc Biol Sci 269:961–7.

Hall MI, Ross CF. 2007. Eye shape and activity pattern in birds. J Zool 271:437–44.

Howells WW. 1973. Cranial variation in man. A study by multivariate analysis of patterns of difference. Among recent human populations. Papers of the Peadbody Museum of Archaeology and Ethnology 67:1–259.

Kay RF, Kirk EC. 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. Am J Phys Anthropol 113:235–62.

Pearce E, Bridge H. 2013. Is orbital volume associated with eyeball and visual cortex volume in humans? Ann Hum Biol 40:531–40.

Pearce E, Dunbar R. 2011. Latitudinal variation in light levels drives human visual system size. Biol Lett 8: 90–3.

Schubert EF. 2006. Human eye sensitivity and phometric quantities. Cambridge, UK:
Cambridge University Press. 275–9.

Sonnebom L. 2007. The Electric Light: Thomas Edison's Illuminating Invention. New York: Infobase Publishing.

Veilleux CC, Kirk EC. 2014. Visual acuity in mammals: effects of eye size and ecology. Brain Behav Evol 83:43–59.