Brief Communication: Assessing Eye Orbits as Predictors of Neandertal Group Size

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KEY WORDS group size; social cognition; Neandertals; orbital aperture diameter; neocortex

ABSTRACT *OBJECTIVES*: The objective is to investigate the hypothesis that Neandertal eye orbits can predict group size and social cognition as presented by Pearce et al. (Proc R Soc B Biol Sci 280 (2013) 20130168).
MATERIALS AND METHODS: We performed a linear regression of known orbital aperture diameter (OAD), neocortex ratio, and group size among 18 extant diurnal primate species. Our data were derived from Kirk (J Hum Evol 51 (2006) 159–170) and Dunbar (J Hum Evol 22 (1992), 469–493; J Hum Evol 28 (1995) 287–296).
RESULTS: There is a positive correlation between OAD and group size; a positive correlation between neocortex and group size; and a positive correlation between OAD and neocortex size. The strength of the collinearity between OAD and neocortex ratio accounts for any significance of OAD in a model. The model that best accounts for variation in group size is one that includes only neocortex ratio; including OAD does not strengthen the model. OAD accounts for 29 percent of the variation in group size.
DISCUSSION: Larger orbits are correlated with larger group sizes in primates, although not significantly when controlling for neocortex ratio. Moreover, the amount of variation in group size that can be explained by OAD is negligible. The larger orbits of Neandertals compared to the average modern human population do not permit any interpretation of cognitive ability related to group size. Am J Phys Anthropol 157:680–683, 2015.

Neandertals living in Europe and Western Asia between ~200,000 and 30,000 years ago are well represented by both skeletal remains and ancient DNA. Neandertals overlapped with contemporary Middle Stone Age Africans in many aspects of behavior, including ornamentation, organization of space, and the production of compound tools such as hafted spears (Vaquero and Pastó, 2001; Zilhão et al., 2010; Finlayson et al., 2012; Zilhão, 2012). Nevertheless, researchers have suggested that the relative size of brain regions is a more reliable source of evidence about behavior and cognitive capabilities than the archaeological record (Aiello and Dunbar, 1993; Dunbar, 2003; Pearce et al., 2013).

Pearce et al. (2013) attempt to demonstrate that the brains of Neandertals were different from those of modern humans in a way that reflects lower cognitive capacity for social interactions. They note that in primates, the size of the eye orbit has a small correlation with the volume of the eyeball, and that the volume of the eyeball has a small correlation with the volume of the visual cortex. Based on a series of statistical correlations between orbit and eye size, and between eye size and visual cortex volume, Pearce et al. (2013) argue that larger orbits predict a larger visual cortex for Neandertals (Fig. 1). With more brain tissue devoted to the visual cortex, Neandertals would have had less neocortical volume available for social cognition, as reflected by group size. Hence, they conclude that the larger orbits of Neandertals resulted in a smaller average group size and less sophisticated social abilities than contemporaneous anatomically modern humans (AMHs).

Smith et al. (1996) have criticized paleoanthropological studies for relying uncritically upon estimates drawn from series of regressions across primates, arguing that it is statistically unsupportable to estimate a dependent value (in this case, group size) from a regression when the independent variable (total endocranial volume minus visual cortex size) has not been observed, but was itself predicted from another regression. Estimation errors propagate across multiple steps, such that error from the first regression is compounded through the use of the second. Pearce et al. (2013) compound not two regressions, but a series of regressions (Fig. 1). Smith et al. (1996) argue that biologists have a better alternative: they can directly observe relevant biological measurements in living species and thereby avoid compounding regression upon regression.

We adopt the null hypothesis that Neandertals were socially handicapped due to their large eye orbits. This hypothesis would be supported by evidence that a) primates with larger orbits tend to have smaller social groups, and/or b) living humans with orbit sizes similar to Neandertals have unusually simple social interactions. We test a) with a critical examination of the argument presented by Pearce et al. (2013) using a biologically appropriate set of comparisons, and address b) in the discussion.

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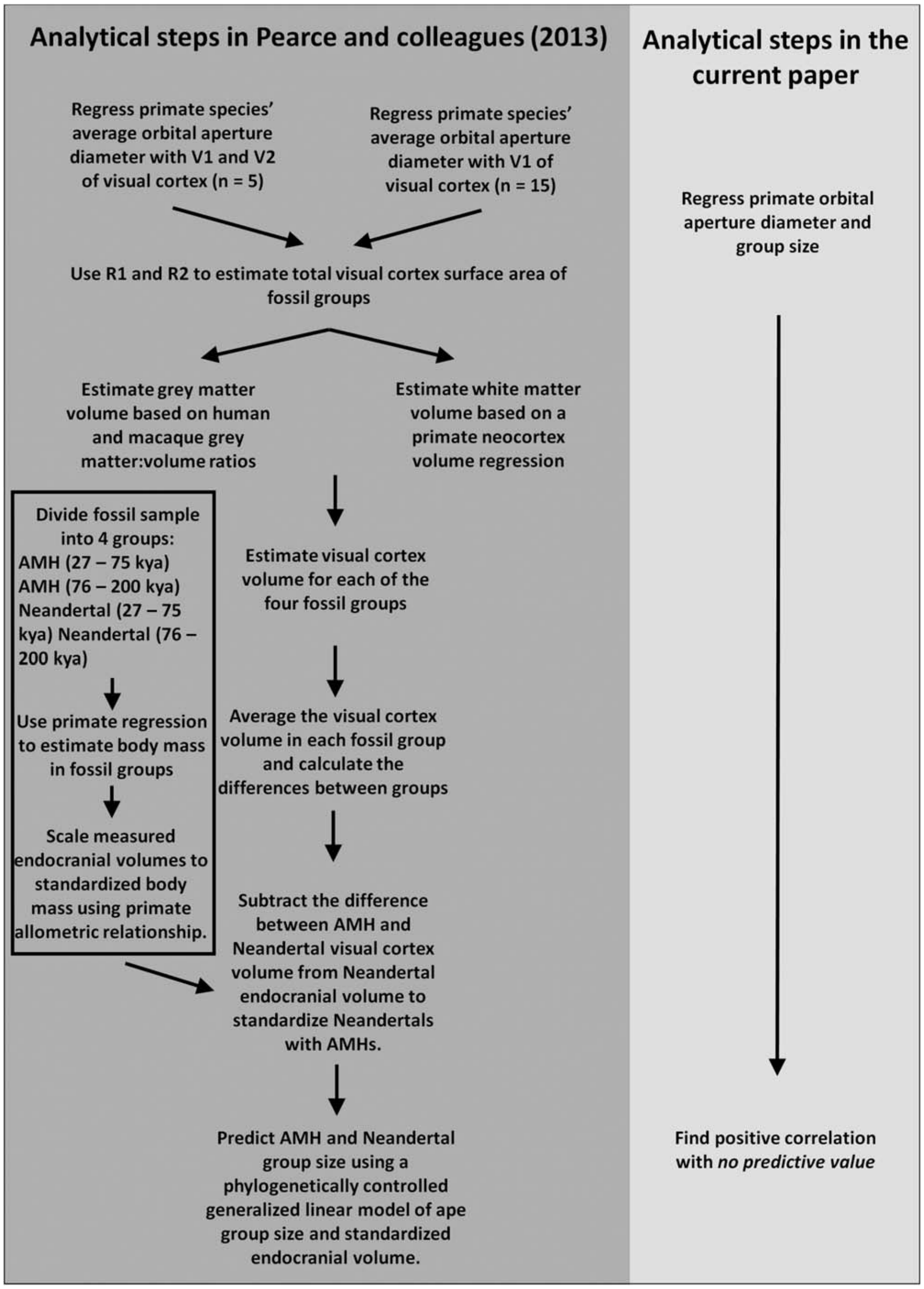

Fig. 1. Analytical steps in the work by Pearce et al. (2013) vs. analytical steps in the current paper.

MATERIALS AND METHODS

To test whether primates with larger orbits have smaller group sizes, we compared three measured values across primates: group size, orbital aperture diameter (OAD), and the ratio of neocortex area to overall brain size (i.e., neocortex ratio). By testing the hypothesis in this way, we examine the argument by Pearce et al. (2013) for small Neandertal group size without compounding regressions of brain areas that we have not directly measured. Rather, we regress three known variables to assess their relationships to each other.

We adopted Dunbar's (1992, 1995) values for mean group size in different primates, which was initially published in the work by Smuts et al. (1987). These averages are from a very heterogeneous set of observational data from different field research studies. Dunbar (1992, 1995) established that neocortex ratio and mean group size have a significant positive correlation within primates. OAD data were taken from Kirk (2006), who examined OAD in a parasagittal plane, equal to the orbit height used by many other authors. The neocortex ratio data were acquired from Dunbar (1992, 1995), and in each species the neocortex ratio is equal to the volume of the

TABLE 1. Primate sample

Taxon	OAD (mm)	Neocortex ratio	Mean group size
Saguinus	10.3	1.6	5.2
Cacajao	22.7	2.3	5.0
Callithrix	9.9	1.5	8.5
Cebus	13.9	2.4	18.1
Saimiri	14.6	2.2	32.5
Procolobus	18.6	2.2	35.0
Papio	26.1	2.8	51.2
Pan	30.8	3.2	53.5
Hylobates	22.6	2.1	3.4
Alouatta	22.8	1.8	8.2
Ateles	22.0	2.4	17.0
Cercopithecus	22.2	2.4	23.9
Lagothrix	22.9	2.2	23.4
Erythrocebus	23.5	3.0	28.1
Macaca nemestrina	24.7	2.4	34.2
Macaca fasicularis	22.4	2.2	28.0
Macaca mulatta	22.7	2.4	40.8
Macaca radiata	23.9	2.3	30.8

OAD = orbital aperture diameter (Kirk, 2006). Neocortex ratio = (neocortex volume)/(total brain volume-neocortex volume) (Dunbar, 1992). Group size = total mean group size for genus (Dunbar, 1992 citing relevant chapters from Smuts et al., 1987).

neocortex divided by the volume of the remainder of the brain, which is the total brain volume minus the neocortex volume. We note that in each sample, the value for a species is an average of a potentially small number of individuals measured opportunistically, and therefore may deviate substantially from the species' true mean.

Nocturnal species of primates are omitted from this comparison because of their extreme ocular adaptations to low light. Additionally, nocturnal activity and feeding ecology may constrain group size in these primates irrespective of the allocation of brain tissue to visual processing (Dunbar, 1992). No one to our knowledge has argued that Neandertals were significantly more nocturnal in their behavior than modern humans. Therefore, we included 18 species of diurnal anthropoids in these comparisons (Table 1). Dunbar (1992) refers to primate taxa in terms of genera, but when the information was available in both Kirk (2006) and Dunbar (1995), we included the species as well.

Despite an apparent curvature in some of the data (Fig. 2), the linear regression model provides a better fit for both OAD and neocortex ratio. We carried out both a linear regression for OAD and neocortex ratio separately, as well as a multiple linear regression analysis of the two variables.

RESULTS

Like neocortex ratio, OAD exhibits a positive correlation with group size (Figs. 2 and 3). However, OAD is not satisfactorily predictive of primate group size. At any given OAD, the range of group sizes is highly variable, for example at OADs between 22.0 and 22.9 mm, group sizes range from 3.4 to 40.8 individuals (Fig. 2).

Pearce et al. (2013) predict that OAD is negatively correlated with neocortex size, thereby concluding that the Neandertal neocortex, and by extension group size, were smaller. Based on the positive correlation between all three variables in living primates (Figs. 2–4), there is no support for their argument. Contrarily, the great degree of collinearity between OAD and neocortex ratio leads to the opposite conclusion.

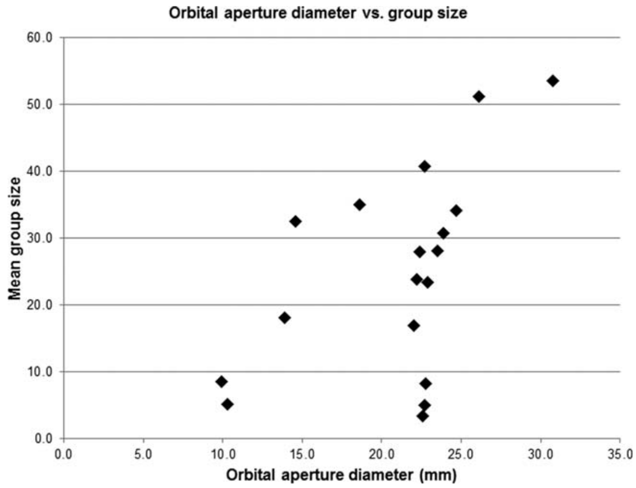

Fig. 2. Primate OAD data from Kirk (2006). Mean group size of primate taxa data from Dunbar (1992, 1995).

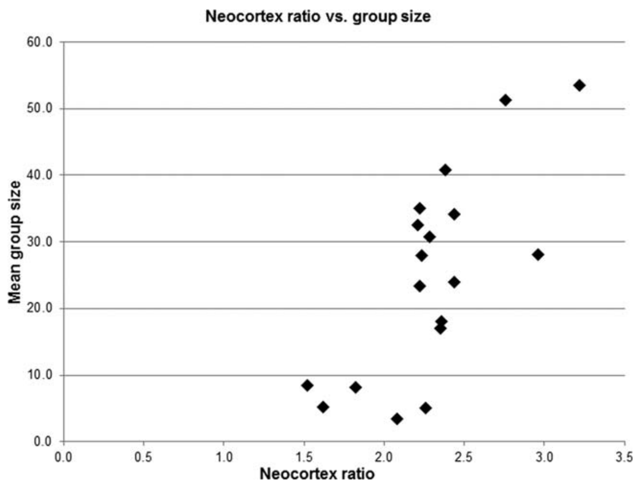

Fig. 3. Primate regression of neocortex ratio and group size. Data from Dunbar (1992, 1995).

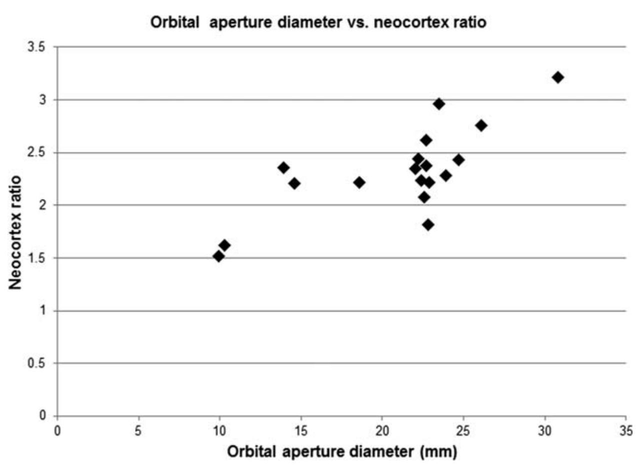

Fig. 4. OAD vs. neocortex ratio. Data from Dunbar (1992, 1995), Kirk (2006).

OAD explains 29 percent of the variance in group size among the 18 primate species considered here. Species with larger orbits have larger groups, on average (Fig. 2). However, that positive correlation of OAD is entirely explained by its correlation with neocortex ratio, which by itself explains 45 percent of the variance in group size (Fig. 3). Using a nested model F test, the multiple regression of OAD and neocortex ratio does not explain more of the variance in group size than neocortex ratio alone. The significance of OAD alone in a regression ($p = 0.02$) can be explained by the collinearity of OAD with neocortex ratio (Fig. 4). If we nevertheless include OAD in a multiple regression with neocortex ratio to predict group size, the regression coefficient of OAD is positive ($p = 0.76$, not statistically significant). Thus, there is no basis for concluding that eye size is inversely correlated with group size. Rather, the comparative data from these other primates suggest the opposite: larger orbits are associated with larger groups.

DISCUSSION

Why did we obtain opposite results from Pearce et al. (2013)? The answer lies in the strengths of our respective methods. We followed Pearce et al. (2013) in examining OAD instead of orbit volume, and drew from the same species samples in our correlations. According to Schultz (1940), eyeball volume accounts for only 83 percent of the orbit volume in primate species. When Chau et al. (2004) studied this relationship in one modern human population, they found that the correlation between orbit volume and eyeball volume was distressingly low ($r = 0.13$). Because no Neandertal eyeballs have been preserved, any regression involving eyeball size must build upon an estimated value for Neandertals, not a measured value. We used the measured value of OAD and eliminated the need to estimate eyeball size, visual cortex gray matter volume, total visual cortex volume, and neocortex ratio, thereby avoiding the compounding of regression error across many steps. In contrast, the conclusions by Pearce et al. (2013) seem to be driven by the compounded regression errors, which in at least one case (visual cortex surface area) depended on data from only five species. By regressing their measured value, OAD, with their predicted value, group size, we have shown that Neandertal OAD should lead Pearce et al. (2013) to predict a Neandertal group size comparable to that of AMHs.

We further observe that human groups vary in orbit height, a comparable craniometric measurement to OAD. The range of orbit height in modern humans (26–41 mm; Howells, 1973) is greater than the difference in averages between modern human (33.66 mm) and Neandertal adults (average of 37.1 mm, with a range of 33.4–38.6 mm[1]). The variation of orbit sizes in living people, although greater than the Neandertal–modern human difference, is simply not useful for testing hypotheses about social behavior among living groups.

We suggest that the same logic be applied to the study of archaic human behavior. Among recent modern human groups living as hunter-gatherers, defining group size is complicated because humans scale their group size according to different environmental and social demands (Binford, 2001). An average derived from group sizes that vary over time, between populations, and among individuals, is of unclear significance for understanding social cognitive abilities. Humans today are highly flexible in their group size in ways that greatly surpass their orbit size variation. Our results challenge the utility of eye orbits for assessing group size and social cognition.

[1]The sample includes the following specimens: Amud 1, Saccopastore 1, Saccopastore 2, Spy 1, Gibraltar 1, La Chapelle, La Quina 5, Shanidar 1, Shanidar 5, Monte Circeo, La Ferrassie 1, Krapina 3 (C), Krapina 6 (E), Tabun C1.

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