The Effects of Latitude on Hominin Social Network Maintenance

Eiluned Pearce

Linacre College

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Abbreviations

AMH	Anatomically Modern Humans
kya	Thousands of years ago
ESA	Earlier Stone Age
MSA	Middle Stone Age
LSA	Later Stone Age
LP	Lower Palaeolithic
MP	Middle Palaeolithic
UP	Upper Palaeolithic
V1	Primary visual area
LGN	Lateral Geniculate Nucleus
PFC	Prefrontal Cortex
PCF	Posterior Cranial Fossa
MRI	Magnetic Resonance Imaging
CT	Computerised Tomography

Eiluned Pearce, Linacre College 'The Effects of Latitude on Hominin Social Network Maintenance', submitted in Trinity Term 2013 for the degree of Doctor of Philosophy.

Abstract

Social networks have been essential throughout hominin evolution, facilitating cooperative childrearing, transmission of cultural knowledge and the sharing of information and resources. As hominins dispersed out of Africa, these networks needed to be maintained at progressively higher latitudes.

The first part of this thesis explores the impact of latitude on brain organisation and the possible implications for social cognition. I hypothesise that the lower temperatures and light levels found at higher latitudes select for larger bodies and visual systems, which in turn necessitate larger somatic and visual brain areas. Using orbit size to index eye and visual cortex size, I demonstrate a robust positive relationship between absolute latitude and orbit volume in recent humans. I show that Neanderthals, who solely inhabited high latitudes, have significantly larger orbits than contemporary anatomically modern humans (AMH), who evolved in lower latitude Africa and had only relatively recently dispersed into higher latitudes. Since Neanderthals and AMH dated 27-75kya have almost identical endocranial volumes, I argue that if a greater proportion of the Neanderthal brain was required for somatic and visual processing, this would reduce the volume of neural tissue available for other functions. Since, according to the Social Brain Hypothesis, neocortex volume is positively associated with social complexity, I propose that Neanderthals might have been limited to smaller social networks than AMH.

The second part of the thesis explores the challenge of maintaining social networks across greater geographic distances at higher latitudes, where high travelling costs seem to prevent whole tribes from bonding during periodic aggregations. Using a gas model I predict that at lower latitudes daily subsistence mobility allows sufficient encounters between subgroups for the tribe to maintain connectivity, whereas in (Sub)Arctic biomes additional mechanisms are required to facilitate tribal cohesion. This may explain the apparent 'explosion' of Upper Palaeolithic art in Europe: symbolic representations allowed social ties to be sustained in the absence of frequent face-to-face contact.

Overall, this thesis demonstrates that latitude may influence both brain organisation and cultural expression and argues that both can have a substantial impact on the maintenance of hominin social networks at high latitudes.

Chapter 1 Latitude & hominin social networks

The maintenance of social networks has been essential throughout hominin evolution: social bonds facilitate cooperative childrearing, transmission of cultural knowledge and the sharing of information and resources. As hominins dispersed out of Africa, these networks needed to be maintained at progressively higher latitudes. Comparative primate research indicates that both cognition and finite time budgets constrain the size and complexity of social networks and groups. I argue that latitude can potentially affect the relative proportions of different functional areas within the brain in terms of body size, visual processing requirements and cognitive flexibility. The resulting organisation of the brain might influence the amount of neural tissue available for processing social complexity and thus the size of social network that can be maintained. In addition, I propose that higher latitude hominins are required to maintain their networks over longer distances than their equatorial counterparts. High latitude hominins may thus have greater social time demands in terms of travelling to meet social partners. Here I outline these arguments before giving an overview of the thesis structure.

During hominin evolution a number of taxa have migrated out of Africa and into the higher latitudes of Eurasia. Survival outside the (sub)tropics requires overcoming a set of novel problems, including reduced resource density and greater seasonality in terms of both resource availability and day length. Different hominin species show varying abilities to disperse across habitat boundaries (Lahr and Foley 1998, Stiner and Kuhn 2006) but in general hominins became better able to colonise, rather than just seasonally or ephemerally disperse into, higher latitude areas over time, leaving stronger archaeological signatures and gradually pushing the maximum extension of their ranges further towards the poles. This was probably aided by technological innovations such as clothing, controlled use of fire and the development of a range of tool types that buffered against seasonally low temperatures and helped reduce the risk of failure when hunting. Like all anthropoid primates, hominins have had to solve ecological problems in a social context and seem to have become increasingly reliant on social means to cope with environmental challenges over time, for example through sharing of information and resources, cooperative childrearing and cultural transmission.

Since, generally speaking, resource seasonality increases[1] and resource density and diversity decrease with latitude (Foley 1993, Grove, Pearce, and Dunbar 2012, Nettle 1999), nearer the poles it might become particularly imperative to be able to (i) ensure safe passage during the seasonal round, (ii) share information about the whereabouts of resources and (iii) conserve cultural knowledge about storage processes and the manufacture of reliable and diverse technology. Since these functions are facilitated through social relations, high latitude hunter-gatherers are expected to maintain large cohesive social networks. However, although social bonds can help assuage ecological difficulties, the maintenance of social networks presents both cognitive and time management challenges. These are likely to be exacerbated at higher latitudes, as social networks become spread over greater geographic distances and groups fission[2] into greater numbers of subunits in order to maintain manageable day journey lengths (Grove, Pearce, and Dunbar 2012, Korstjens, Verhoeckx, and Dunbar 2006, Lehmann, Korstjens, and Dunbar 2007a). In this thesis I seek to investigate (i) possible latitudinal variation in brain organisation and the potential cognitive effect of this on the maintenance of social networks/groups (Pearce and Dunbar 2012, Pearce et al. in press, Pearce, Stringer, and Dunbar 2013) and (ii) whether social networks need to be maintained over larger home range areas at higher latitudes and if so how this affects network connectivity (Pearce et al. in press).

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[1] Growing season length decreases and temperature differentials increase.

[2] Fission-fusion social organisation consists of periodic splitting into sub-groups and re-aggregation. This allows individuals to gain the benefit of belonging to a wider social community whilst minimising the costs.

The function and structure of social networks

There is compelling evidence that in living humans the size of an individual's social network and the quality of their social relationships can increase their chances of surviving life-threatening illness and enhance their mental and physical health (e.g. Adams, Madhavan, and Simon 2002, Domínguez and Arford 2010, Holt-Lunstad, Smith, and Layton 2010, House 2001, Iaupuni et al. 2005, Kotler et al. 2001, Kroenke et al. 2006, Pinquart and Duberstein 2010, Tilvis et al. 2012). In ultimate terms increased health should translate into enhanced reproductive success. Indeed, female baboons with larger social networks experience higher offspring survival than their less sociable counterparts (Silk, Alberts, and Altmann 2003, Silk et al. 2009). Social support can also enhance child health and survival in living humans (e.g. Adams, Madhavan, and Simon 2002, Iaupuni et al. 2005) and the same was probably true for all hominins.

Such health and reproductive benefits are likely to arise from an individual's closest social relationships, which can provide the emotional and practical support to buffer against external stressors. The social network of a living human seems to comprise a series of concentric layers or 'psychological groupings' of decreasing intimacy from ego (Roberts 2010, Roberts et al. 2009). The innermost layers of these are the support clique of ~3-5 individuals and the sympathy group of 12-15 individuals. It is probably these layers in particular that allow cooperative childrearing and reduce stress, because it these people that individuals go to for advice and help (Dunbar and Spoors 1995). The support and sympathy groups are nested within the affinity group (~50 individuals), which is in turn part of an ‘active network’[3] of ~150 individuals that ego feels they share a relationship with and with whom they make a conscious effort to keep in contact (Hill and Dunbar 2003, Roberts 2010). All these personal network layers seem to map onto ethnographically observed groupings, which recur in archaeological and anthropological studies, including those undertaken among modern, western populations: Figure 1.1 and Table 1.1 (Binford 2001, Birdsell 1958, Dunbar 1998b, Dunbar 2012b, Goncalves, Perra, and Vespignani 2011, Grove 2010b, Grove 2011, Hamilton et al. 2007b, Layton, O'Hara, and Bilsborough 2012, Lehman, Lee, and Dunbar in press, Murdock 1949, Williams and Wobst 1974, Wobst 1974, Wobst 1976, Zhou et al. 2005). Although ‘group’ and ‘network’ are often treated as identical in the literature, technically speaking groups are physical aggregations of individuals whereas networks represent actual relationships or bonds (edges) between individuals (nodes), which may not extend to all group members. Here, I use the term ‘network’, but rely on group size data as a proxy. This seems justified because (i) individual relationships are not easily distinguished in the archaeological record, (ii) there is a paucity of network data in ethnographic material, (iii) there is apparent numerical matching between the hierarchical layers of personal networks and human groups (Figure 1.1, Table 1.1) and (iv) across primates a network of connected individuals comprises a constant proportion (~75%) of overall observed group size, so in comparative terms the two are roughly synonymous (Kudo and Dunbar 2001).

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[3] In modern terms the active network is roughly equivalent to the total number of household members at the addresses that an individual sends Christmas cards to (Hill, R., and R. Dunbar. 2003. Social network size in humans. *Human Nature* 14:53-72.) or with whom they actively associate in online social networks including Facebook (Dunbar, R. I. M. 2012b. Social cognition on the Internet: testing constraints on social network size. *Philosophical Transactions of the Royal Society B-Biological Sciences* 367:2192-2201.) and Twitter (Goncalves, B., N. Perra, and A. Vespignani. 2011. Validation of Dunbar's number in Twitter conversations. *PLoS ONE* 6:e22656.).

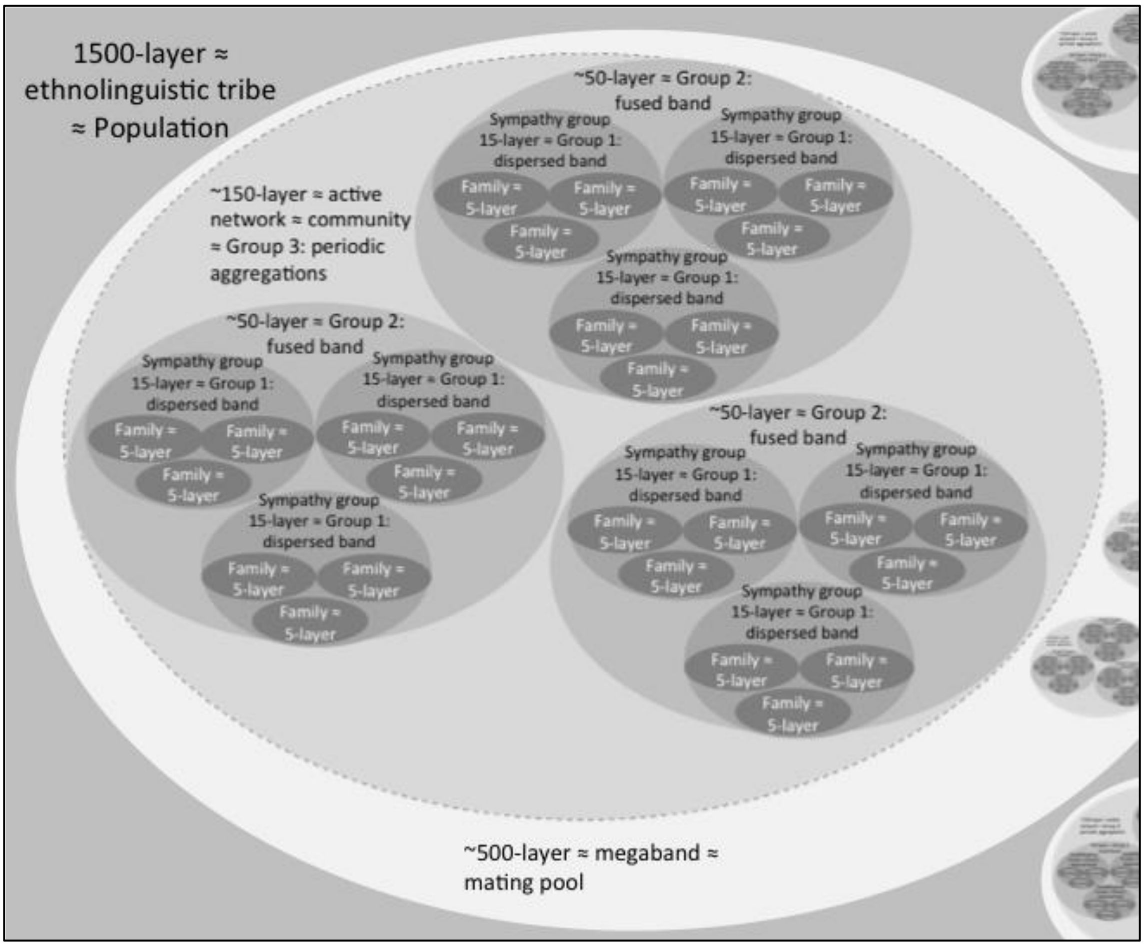

Figure 1.1: The concentric layers typical of living human social organisation, illustrating the scaling ratio of ~3 between layers and giving the assumed equivalencies used in this thesis between (i) personal social network layers (ii) hunter-gatherer grouping levels observed ethnographically and (iii) Binford's (2001) terminology, which is particularly pertinent in Chapters 6 & 7. To ensure visibility the two additional nested groups within the mating community and ethnolinguistic tribe are reduced in size, but in reality the number of members in all component units would be roughly equal. The dashed line around the active network represents the fact that periodic aggregations of hunter-gatherer bands (Binford's Group 3 units) do not numerically distinguish between the active network (median aggregation size is ~150 individuals) and the megaband (maximum aggregation size is ~500 individuals). The constant ratio of ~3 between the cumulative total number of individuals in adjacent layers has been observed not only within human societies, but also across mammals (Hamilton et al. 2007b, Hill, Bentley, and Dunbar 2008, Lehman, Lee, and Dunbar in press, Zhou et al. 2005).

Table 1.1: The assumed equivalencies used in this thesis for the concentric layers of social organisation in living humans.

‘Idealised’ layers based on those identified by Zhou et al (2005)	**Personal network layers**	**Hunter-gatherer grouping layers**	**Binford’s (2001) hunter-gatherer groups**
5	Clique	Nuclear family	Family
15	Sympathy group	Foraging party	Group1 (band during the dispersed phase of the seasonal round)
50	Affiliation group	Residential band	Group 2 (band during the aggregated phase of the seasonal round)
150	Active network		Group 3 (periodic aggregations of bands)
500		Megaband/ endogamous mating pool	
1500		Ethnolinguistic tribe	Population

Much of the tension that is dissipated by clique and sympathy group partners results from the fact that cliques are embedded within a larger group or network in the first place. These inclusive wider groupings or network layers must therefore provide some additional benefit in order for individuals to continue to maintain them. Such advantages might include mating opportunities and access to resources through inter-group competition and cooperative defence. In addition, extensive social networks allow individuals to guard against the risk of failing to obtain sufficient resources. In order to pool ecological risk effectively individuals need to maintain bonds with independent units. At the lowest level, family units in bands pool risk associated with foraging by sharing unpredictable resources such as meat (Hames 1990, Hawkes 1990, Kaplan, Hill, and Hurtado 1990, Winterhalder 1996). If the environment is sufficiently heterogeneous for scarcity in one region to parallel abundance in another, exchange of information and resources may occur between adjacent and more distant residential groups. At the highest level, such exchange may occur across the entire megaband (~500 individuals in an endogamous mating pool) and ethnolinguistic tribe (~1500 individuals). These are the outermost grouping layers beyond an individual's active network (Figure 1.1) and rarely appear to be seen as on-the-ground groups. Rather, social bonds within the megaband and tribe probably exist as indirect ties between the overlapping active networks of individual members. This idea is supported to some extent by that Wiessner's (1982) observation that her !Kung informants sometimes reported feeling a sense of obligation to individuals with whom they were indirectly linked in a chain of hxaro[4] exchange. Incorporating these 'weaker ties' into the total network allows individuals access to a wider variety of resources and information covering a greater geographic area.

Connections across an extended network not only allow the sharing of knowledge and resources, but also facilitate other strategies for coping with resource fluctuations: technology (Torrence 1983, 2001), storage (Testart 1988), diversification of exploitation strategies and the 'seasonal round' of mobility (e.g. Colson 1979, Mauss and Beuchat 1950/1979). For instance, large-scale storage requires the coordinated effort of a relatively large group of people to obtain, transport and process resources. Moreover, a minimum group size may be required to ensure knowledge of the techniques involved continue to be transmitted and to support their cumulative improvement (Henrich 2004, Powell, Shennan, and Thomas 2009). Thus, relatively large social networks are required to enable large-scale storage, as well as other adaptive behavioural strategies that require social learning, such as the manufacture of the technology required to obtain heterogeneous resources. In addition, the capacity to exploit diverse resources usually depends both on having current

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[4] A system through which non-food objects such as arrowheads, beads and clothing are circulated through a !Kung population, with each individual maintaining reciprocal delayed exchange partnerships with a number of close consanguinal kin, as well as their spouse (creating indirect ties with affines).

information about the state of those various resources and the ability to move between them. Movement (whether residential or logistic: Binford 1980, 1982) requires that the group (i) knows the conditions of resources at their destination and (ii) that they will be able to access those resources when they arrive. In order to access resources in lands associated or shared with another group, visitors need to maintain friendly ties with that group, at least in order to gain local intelligence about resource location and coordinate efficient foraging.

In brief, an individual with a larger social network should be better able to cope with local resource failure than someone with a smaller network, due to the more numerous independent sources of help available to them. Furthermore, in general a larger network will provide more mating opportunities and allow shared childrearing, so local populations might be less likely to die out. Similarly, larger networks might be better able to conserve cultural knowledge because the reservoir of 'experts' would be larger. Overall, it might seem that the benefits of large networks should drive continual network expansion. However, total network size is limited by both cognition and finite time budgets.

Constraints on social network maintenance

Cognitive constraints: the 'Social Brain Hypothesis'

In haplorrhine primates (anthropoids: monkeys and apes) there is a strong quantitative relationship between bonded social group (community/active network) size and the relative size of the neocortex, perhaps particularly the 'non-visual' neocortex[5] (Aiello and Dunbar 1993, Barton 2012, Dunbar 1992, Dunbar 1998b, Dunbar 2003a,

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[5] 'Non-visual neocortex' is total neocortex minus the primary visual (V1) area here. Group size is associated with non-V1 neocortex volume independently of V1 volume but not vice verse (Joffe & Dunbar 1997), although the latter might be due to there being visual areas included in 'non-V1-neocortex' in these analyses.

Dunbar 2011b, Dunbar and Shultz 2007a, Dunbar and Shultz 2007b, Joffe and Dunbar 1997, Perez-Barberia, Shultz, and Dunbar 2007, Shultz and Dunbar 2010a). An association between brain size and social complexity is supported by tight linkage in primates between phylogenetic state-changes from (i) asocial to social and (ii) small to large brains, implying that transitions in either brain or group size independently of the other are historically rare (Perez-Barberia, Shultz, and Dunbar 2007). In addition, neuroimaging studies have shown significant positive intraspecific relationships between the volume of particular areas of the frontal and temporal lobes and social network size in both macaques (Sallet et al. 2011) and humans (Kanai et al. 2011, Lewis et al. 2011, Powell et al. 2012). This suggests that in order to maintain a larger network, individuals require more neural tissue to enable them to remember and manipulate information about more numerous, and thus potentially more diverse, social relationships. Social network size and structure is thus at least partially cognitively determined and hence constrained by brain organisation.

More precisely, in living humans the relationship between the size of the orbital (ventromedial) prefrontal cortex (PFC) and the number of individuals someone can maintain within their social network seems to be mediated by their capacity to track other peoples' mental states (Lewis et al. 2011, Powell et al. 2012, Powell et al. 2010). In other words, neural architecture seems to determine social cognitive competence (mentalising), which in turn determines social network size (Powell et al. 2012, although the causal pathway could be reversed in terms of development). Social cognition includes Theory of Mind: the ability to comprehend that other individuals have mental states (beliefs, desires, motivations) that may differ from one's own. A measure of 'mentalising' ability is the 'level of intentionality' that an individual can attain, which denotes the number of nested minds that can be understood, not just in terms of information storage but also in terms of being able to manipulate that information in order to act in a complex social world. For example, *"I suspect (1st order intentionality) that he thinks (2nd order intentionality: Theory of Mind) that she wants (3rd order intentionality) him to ask her out for dinner"*. The greatest number of nested minds an individual can keep track of at any one time (i.e. their level of intentionality) constrains the number of people that they can integrate into their most intimate support clique (Stiller and Dunbar 2007). Given the scaling relationship between the number of individuals incorporated into adjacent network layers (Hamilton et al. 2007b, Hill, Bentley, and Dunbar 2008, Lehman, Lee, and Dunbar in press, Zhou et al. 2005), clique size translates into the size of their sympathy group[6]. This in turn seems to set a limit on the size of an individual's active network size and thus presumably on the size of the overall group that can remain cohesive through indirect ties connecting overlapping active networks (Hamilton et al. 2007b, Hill, Bentley, and Dunbar 2008, Kudo and Dunbar 2001, Zhou et al. 2005).

Group size does not increase isometrically with clique size in primates, but instead larger groups tend to comprise greater numbers of more constantly sized cliques (Kudo & Dunbar 2001). Larger groups therefore have to overcome the difficulty of bonding and coordinating larger numbers of subunits, which is cognitively demanding. However, by incorporating independent constituents into a smaller number of encompassing units and treating these as unitary elements at the next network layer, individuals may be able to keep mental track of more individuals in total. If each subgroup is considered to have a single representative or 'consensus mind', the number of subgroups that can be coordinated may also be linked to mentalising capacities. Johnson (1982) suggests that information processing constraints on decision-making limits the number of interacting

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[6] Although the size of the sympathy group may depend more on memory than mentalising competence *per se* (Stiller, J., and R. I. M. Dunbar. 2007. Perspective-taking and memory capacity predict social network size. *Social Networks* 29:93-104.).

units to six, emphasising a nested hierarchy in the organisation of social networks that has been corroborated ethnographically (Hamilton et al. 2007b, Wilmsen 1973). In addition, Knosse (1990) has suggested that universal thresholds in long-term memory create a bias towards hierarchical organisation of conceptual categories bounded by similar numerical thresholds, such as 'folk' biological taxonomy and the layering of social networks. Overall, the size and organisation of an individual's brain, specifically the size of particular frontal and temporal areas, dictates the degree of complexity that they can assimilate into their mental models of their social world. Factors that influence the size of these brain areas will therefore affect the degree of cognitive complexity that can be handled.

Time constraints on social network maintenance

As well as cognitive constraints on the number of individuals that can be mentally tracked, the size of an individual's network is also limited by the finite time available to create and maintain relationships. If individuals only interact face-to-face very infrequently, the emotional intensity of the relationship tends to decay and social partners will drift towards the outer layers of ego's network (Roberts and Dunbar 2011a, Roberts and Dunbar 2011b). If a minimum time investment is required to keep a relationship 'active' at a particular level of intimacy, the total time budget available will limit the number of relationships that can be incorporated into each layer of ego's network and thus total network size.

For instance, non-human primates predominantly create and maintain social bonds through grooming, which facilitates endorphin release (Keverne, Martensz, and Tuite 1989). However, finite time budgets and other essential activities such as feeding and travelling limit the grooming time available, constraining the number of coalition partners each individual can maintain and therefore clique size. Thus, like mentalising abilities, finite social time indirectly places a limit on overall network and group size, because without adequate coalitionary buffers in terms of a sufficiently large clique, individuals cannot function successfully within the overall group and the group is likely to fission.

Comparative primate analyses suggest that in order to maintain an active network of 150 individuals, modern humans would be required to spend more than four hours grooming per day, yet cross-culturally humans spend an equal amount of time socializing as other primates: up to ~2.4 hours per day or ~20% of day-light hours (Dunbar 1998a, Lehmann, Korstjens, and Dunbar 2007b). In order to achieve this, modern humans appear to have developed mechanisms by which multiple individuals can be ‘groomed’ simultaneously: laughter, singing, synchronous physical activity such as dance, and language (Aiello and Dunbar 1993, Cohen et al. 2009, Curry and Dunbar 2013, Dezecache and Dunbar 2012, Dunbar 2012a, Dunbar et al. 2012a, Dunbar et al. 2012b). However, such mechanisms only function if individuals are aggregated in one place. The more dispersed the members of a network are, the greater the time costs of travelling to meet for face-to-face contact, the less frequent the interpersonal interactions and the greater the difficulty of maintaining cohesion.

The effects of latitude on social network maintenance

Cognitive constraints

In addition to potentially creating greater cognitive demands in terms of coordinating fissioned subgroups and taking absent individuals into account (Grove, Pearce, and Dunbar 2012, Pearce et al. in press), living at high latitudes may also impact on social network maintenance by affecting the underlying neural architecture. If latitude influences brain size and organisation, then this might impact on the size of brain areas involved in the cognitive processing of social complexity and thus on the size of the social network that typically could be cognitively maintained at different latitudes. Higher latitude individuals generally have larger cranial capacities than their equatorial counterparts across all hominins (Ash and Gallup 2007, Potts 1996, Potts 1998)[7], as well as specifically in recent modern humans (Beals et al. 1984) and in *Homo erectus* (Shultz, Nelson, and Dunbar 2012). Furthermore, the endocranial volume of Neanderthals increased over time after their speciation in higher latitude Eurasia (Shultz, Nelson, and Dunbar 2012). There are at least three explanations for a positive relationship between brain size and latitude: (i) a need for enhanced cognition to deal with greater environmental variability, (ii) larger body size and (iii) higher visual processing requirements due to lower light levels nearer the geographic poles.

A larger brain generally implies a larger neocortex, which in turn suggests a larger social network could be cognitively supported. However, if a greater proportion of that neocortex were taken up by visual processing, leaving a smaller non-visual neocortex, the associated social network would also be relatively smaller as well. Likewise, a larger body might require larger somatic brain areas for muscle control, which might reduce the amount of neural tissue available for other brain functions. Thus, differences in the relative strength of selection for the three factors listed above could yield differences in brain organisation and thus differences in the cognitive limits placed on social network size.

Occupying higher latitudes presents cognitive challenges, for instance in relation to the increased seasonality of resources. Such fluctuations may select for a larger brain to allow flexible behavioural strategies and innovation. For instance, Sol et al. (2010) found

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[7] Although it has been argued that this might be an artefact of the increase in latitudinal range after 1.8mya (Henneberg, M., and C. de Miguel. 2004. Hominins are a single lineage: brain and body size variability does not reflect postulated taxonomic diversity of hominins. *HOMO - Journal of Comparative Human Biology* 55:21-37.).

that migratory birds have relatively smaller brains than species that are resident at a location all year around (see also Shultz and Dunbar 2010b). Whereas permanently resident birds need to cope with seasonally fluctuating resources, migrating birds just track preferred habitats. Having a larger brain allows birds to adopt flexible strategies to deal with seasonal variation (Shultz and Dunbar 2010b, Sol et al. 2005, Sol et al. 2010). In addition, birds with larger relative brains are better at establishing themselves in novel environments through more innovative behaviour (Sol et al. 2005). Moreover, relative brain size is associated with the size of stable flocks (as opposed to unstructured aggregations) (Shultz and Dunbar 2010b), which may be advantageous in fluctuating environments by facilitating information exchange about the location of resources. A similar situation is seen in primates: relatively larger-brained species are able to buffer themselves more effectively against seasonal fluctuations, dampening the amplitude of resource variation (van Woerden, van Schaik, and Isler 2010, van Woerden et al. 2011). The raised energetic requirements of having a larger brain may feed back into selection for greater behavioural flexibility in the acquisition of the necessary high-energy resources, thus selecting for an even larger brain.

Since larger brains allow both anthropoid primates and birds to have larger and more complex social groups (Dunbar and Shultz 2007a, Dunbar and Shultz 2007b, Perez-Barberia, Shultz, and Dunbar 2007, Shultz and Dunbar 2010b) and larger-brained species do better in seasonal environments, it may be reasonable to suggest that more social species are better able to ride out resource fluctuations than solitary ones. Similarly, greater seasonality and colder winters may have selected for larger brains in high latitude hominins to allow ecological problems to be solved (i) directly through more flexible behaviour and enhanced innovative capacities and/or (ii) indirectly through having larger networks, the maintenance of which requires sufficient neural architecture. Social responses may be particularly beneficial in the face of unpredictability due to their inherent flexibility in the type and timing of help. Consequently, the cognitive constraint on group size could have been progressively raised as hominins came under selection for strategies to deal with resource fluctuations and declining temperatures as they dispersed into higher latitudes.

However, enhanced cognition and consequent behavioural flexibility may not be the (sole) reason for positive trends between absolute latitude and brain size in hominins. For instance, higher latitude individuals generally have greater body masses than lower latitude individuals and it is widely acknowledged that larger bodies are associated with larger brains (Beals et al. 1984, Dubois 1933, Henneberg 1998, Holloway 1981, Isler et al. 2008, Ruff 2002). Accordingly, as hominins moved into higher latitudes their brains may have enlarged purely allometrically. If so, brain areas associated with social cognition would not be expected to increase with latitude.

Hominins dispersing into higher latitudes would also have encountered declining light levels further away from the equator. To enhance visual sensitivity (the ability to pick out a point from its background) and maintain adequate visual acuity (the distance between points that can be distinguished, or the degree of detail in the visual environment that can be discerned) under these lower light levels, high latitude hominins might have been under selection for larger eyes (Pearce and Dunbar 2012, Pearce, Stringer, and Dunbar 2013). This would probably have necessitated larger visual areas in the brain to deal with the greater visual input and this might have translated into high latitude individuals having larger brains. In living humans cortical areas devoted entirely or primarily to vision account for 23% of the adult human neocortex (Van Essen and Drury 1997), so any selection acting to increase the size of these areas would have a substantial effect on the partitioning of brain tissue. Although humans have smaller visual thalami (lateral geniculate nucleus: LGN) and primary visual areas (V1) than expected from total brain size, this may be due to the fact that humans have a greater number of more specialised visual areas compared to monkeys (de Sousa et al. 2010). Variation in the size of different brain areas reflects differences in neuron numbers and consequently would impact on the neural networks within the brain (Gabi et al. 2010). Furthermore, neuron density is highest in primary sensory areas (Collins et al. 2010), so an increase in the volume of the sensory visual areas would particularly escalate the proportion of neurones in the brain associated with visual processing. As with the impact of body size, if larger brains nearer the poles are associated with larger visual areas, the size of brain areas associated with social cognition would not necessarily be expected to increase with latitude.

In summary, the cognitive challenges of maintaining increasingly larger and more complex social networks are associated with coordinating and keeping track of the whereabouts, reputations and relationships of both present and absent individuals. Factors that lead to variation in the size and organisation of the brain within and between hominin species might yield differences in the brain areas underlying complex social cognition. High latitude hominins have larger brains than their equatorial counterparts, but how these brains are organised might affect their associated capacity for social cognition. The brain cannot expand indefinitely due to energetic constraints on the total amount of this expensive tissue that can be sustained (Aiello and Wheeler 1995). Selection for larger visual systems and bodies may thus limit expansion in brain areas underlying ‘higher’ cognition. On the other hand, behavioural flexibility, innovation and increasingly cultural niche construction might buffer against selection on visual function and body size. Either scenario would have implications for brain organisation and the amount of neural tissue available for understanding a complex social world. In this thesis I focus particularly on the novel hypothesis that lower light levels at high latitudes may have affected hominin brain evolution and hence cognitive limits on the number of individuals they could link into their social networks.

Time constraints

As well as affecting the maintenance of hominin social networks indirectly through brain organisation, latitude could also potentially influence network cohesion by dictating the geographic area over which a network is spread and thus the frequency with which network members encounter each other face-to-face. Where seasonality is high and the diversity and density of resources is relatively low, as at high latitudes, social networks may extend over larger areas, meaning that independent options of aid are available if local resources fail (Collard and Foley 2002, Mace and Pagel 1995, Moore et al. 2002, Nettle 1996, 1998, 1999, Whallon 2006)[8]. However, in order to benefit from these extended networks, high latitude hominins need to be able to maintain network cohesion across those greater distances (Grove, Pearce, and Dunbar 2012, Kelly 1995, Pearce et al. in press). High latitude hominins would need to maintain coordination between at least as many fissioned subgroups as equatorial hominins, but over much larger areas (Grove, Pearce, and Dunbar 2012). Network dispersion would reduce the opportunities to create and maintain social ties through face-to-face contact, as well as increasing the time required to visit and aggregate with other groups.

Mechanisms for simultaneously bonding large numbers of individuals might become more numerous, diverse and frequent nearer the poles in order to take advantage

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[8] In contrast, smaller home ranges in the tropics may be selected by high pathogen stress, because having in-group assortative sociality and out-group avoidance, coupled with limited dispersals, would reduce the likelihood of falling prey to foreign diseases (Fincher, C. L., and R. Thornhill. 2008. Assortative sociality, limited dispersal, infectious disease and the genesis of the global pattern of religion diversity. *Proceedings of the Royal Society B: Biological Sciences* 275:2587-2594.).

of periodic aggregations as a means of facilitating network cohesion. However, travel costs might limit the proportion of the total tribe that could gather together and thus be bonded in this way. If the frequency of face-to-face interactions decrease and the time costs of travelling for social visits rise at higher latitudes, mechanisms to bond networks where social partners are separated in space and over time (i.e. *in absentia*) should become paramount. These might include the exchange of objects to represent social obligations and hominins would need to factor the manufacture of such artefacts into their finite time budgets. The time available for the manufacture of 'social objects' might create further time constraints on the number of individuals that could be incorporated into the network via material representations.

Thesis chapter overview

In this thesis I examine the effect of latitude on the maintenance of hominin social networks. I argue that latitude can influence brain organisation in terms of body size and visual processing requirements and that this may impact on the size of brain areas given over to dealing with social complexity (and other 'higher order' functions). Furthermore, I argue that if social networks were spread over greater geographic areas at higher latitudes, sustaining them would require overcoming time constraints on maintaining cohesion through face-to-face bonding and finding alternative ways of sustaining connectivity, for example through additional cultural scaffolding. Since social networks were probably crucial for hominin reproduction and survival, solving the challenge of maintaining contact over separations in space and time would have been imperative. Understanding the ways in which anatomically modern humans (AMH) in particular managed to solve such problems should provide insight into both human brain evolution and the geographic and temporal variation in material culture expressed during the late Pleistocene.

In Chapter 2 I test whether orbit (eye socket) size can accurately index visual cortex size and thus be applied to examining the internal brain organisation of fossil hominins (Pearce and Bridge 2013). In Chapter 3 I go on to test whether latitudinal variation in light levels can drive visual system size in a hominin species, using recent historical humans as an example (Pearce and Bridge 2013, Pearce and Buck in prep, Pearce and Dunbar 2012). In Chapter 4 I examine possible brain organisation differences associated with differences in body and visual system size between Neanderthals, who evolved in and solely inhabited high latitudes, and contemporary AMH, who evolved in lower latitude Africa and dispersed into higher latitude Eurasia relatively recently (Pearce, Stringer, and Dunbar 2013). I go on in Chapter 5 to discuss possible cognitive implications of brain organisation differences between these two taxa, specifically in relation to active network sizes and mentalising abilities (Pearce et al. in press, Pearce, Stringer, and Dunbar 2013).

In Chapter 6 I turn to the effect of latitude on the area over which social networks are maintained. By comparing the size of recent hunter-gatherer home ranges with Pleistocene lithic transfer distances[9] I seek to establish the maximum extent of Neanderthal and contemporary AMH social networks, in terms of both nested social layers and geographic range. Any differences could have had implications for the material culture and survival ability of these closely related taxa. I examine the time costs involved in face-to-face interaction, social travelling and manufacture of exchange objects in order to explore limitations on the distance over which social contact can be sustained through personal contact. In Chapter 7 I use a gas modelling approach to investigate whether such social time costs could be mitigated by basic subsistence mobility, which might

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[9] Transfer distances refer to the distance between the raw material source and the archaeological site where artefacts are recovered. If these exceed assumed foraging distances, they may indicate social interaction between neighbouring groups.

coincidently allow sufficiently high contact frequencies between groups to maintain tribal cohesion. I use the model to predict the latitude at which additional, culturally-mediated, social bonding mechanisms might become necessary. In Chapter 8 I discuss my findings, particularly within the context of potential mechanisms for social network maintenance and the implications of this for interpretations of the archaeological record.

Chapter 2 Do orbital dimensions index the size of the visual cortex?

In order to estimate the size of the visual cortex independently of overall brain volume it is theoretically possible to use the size of a skull's orbits (eye sockets). However, to do so requires that orbital dimensions accurately represent eye and visual cortex size. Here I show that both within living humans and across diurnal primates, orbital size is significantly positively associated with eye and visual cortex size independently of brain volume or body weight (in the case of humans a proxy for body weight, foramen magnum area). This suggests that it is reasonable to use the size of hominin orbits as a proxy for eye and visual cortex volume in order to investigate internal brain organisation in terms of visual processing.

Introduction

The problem with attempting to investigate potential latitudinal selection on visual cortex size in fossil hominins is accessing the internal structure of their brains. Previous studies of fossil brain morphology have either (i) used endocasts, which are notoriously ambiguous and in any case only provide information on the external shape and overall size of the brain[10] (Holloway 2009), or (ii) relied on extant primate comparisons that estimate the size of specific components of the brain from total brain size (Conroy and Smith 2007), which assumes identical internal organisation for a given brain volume. As a baseline it seems fairly reasonable to assume that if there is a general pattern across primates, this is likely to apply to extinct as well as extant species. However, this is unlikely in terms of visual cortex size because living humans have a primary visual cortex (V1) smaller than expected for their brain size (de Sousa et al. 2010, Holloway 2007). In addition, when comparing closely related hominins with similarly sized brains, such as Neanderthals and

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[10] Although note that endocasts give the negative of the impressions made by the meninges rather than the brain itself.

AMH (Chapter 4), it should not be assumed (i) that they did not deviate from an allometric trend or (ii) that their respective residuals would be identical. As Holloway (2001) argues, it is the residuals from the general trend that are often the most interesting, because these may highlight specific adaptations that draw a particular taxon away from their estimated 'typical-primate' value. The solution proposed here is to use individual skull orbit dimensions as a proxy for eye and therefore visual cortex size. Orbital dimensions have been previously used to model the degree of summation between photoreceptors and the optic nerve in extinct primates (Kay and Kirk 2000) and may also provide information about the size of all the soft tissue constituents of the visual system.

Although brain areas with different functions may vary independently of each other to some extent, within a functional system the components are more likely to covary, so that function is not impaired. Indeed, functional and anatomical scaling between components of the visual system along the neural pathway from the eye to the visual cortex in the occipital lobe is fairly well established in modern humans (Andrews, Halpern, and Purves 1997, Bridge et al. 2009, Bridge et al. 2012, Chen and Zhu 2001, Dougherty et al. 2003, Free et al. 2003, von dem Hagen et al. 2005, Zhong et al. 2009), mammals more generally (Barton 2007, Stevens 2001, Williams, Cavada, and Reinoso-Suarez 1993) and birds (Garamszegi, Møller, and Erritzøe 2002). However, the aim of the first part of this thesis is to gain insight into the internal brain organisation of fossil hominins by using orbit dimensions to estimate visual cortex volume. In order to attempt this, I need to establish that (i) orbit size is an accurate index of eyeball (ocular) size and (ii) eye/orbit size scales with visual cortex size. In this chapter I test these assumptions in diurnal anthropoid primates as well as specifically in living humans.

Although the modern human eyeball takes up one fifth to one third of the orbit, the orbits also contain the extraocular muscles, nerves and fat (Bron, Tripathi, and Tripathi 1997, Schultz 1940, Whitnall 1921). This might suggest that in contrast to intuition, orbital dimensions do not equate directly with eye size. For instance, the orbit comprises seven bones[11], so theoretically the size and morphology of the orbit can be affected by the developmental trajectories of any or all of these components (Bron, Tripathi, and Tripathi 1997, Whitnall 1921). Indeed, human orbital growth is associated with facial development (Denis, Burguière, and Burillon 1998) and follows a general cranial trajectory (Waitzman et al. 1992). Consequently, adult orbit size is related to overall cranial capacity (Bron, Tripathi, and Tripathi 1997, Whitnall 1921) and length (Chau et al. 2004), as well as body size (at least across primates: Kappelman 1996, Schultz 1940). In addition, diachronic reductions in facial and cranial size as well as changes in facial shape (reduced prognathism) are correlated with reduced orbital volume and breadth but increased orbital height in prehistoric East Asian and Western European adults (Brown and Maeda 2004, Masters 2012). This suggests that changes in face shape can influence orbital morphology. On the other hand, other facial and cranial dimensions showed substantially more variation than orbital variables between African, Asian and European populations (Masters 2008), implying that orbits are independent of facial and cranial morphology to some extent.

Despite correlations between orbital and craniofacial morphology, the eyeball, lacrimal apparatus and oblique muscles are considered the main internal factors influencing the form of the orbital cavity (Bron, Tripathi, and Tripathi 1997, Whitnall 1921). During human development eye and orbit dimensions are significantly positively related (Tomasik et al. 2005a, Tomasik et al. 2005b) and if the eyeball is removed before the orbit is fully formed, the growth of the orbit is checked to some extent in both humans

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[11] Maxillary, palatine, frontal, sphenoid, zygomatic, ethmoid and lacrimal.

and rabbits (Cummings et al. 2012, Hintschich et al. 2001, Sarnat 1982). This suggests that orbit size is at least partly determined by eye growth, particularly during rapid eye growth in early development (Washburn and Detwiler 1943). However, a recent study of strepsirrhine primates suggests a generic mammalian pattern of early orbit expansion following eye growth *in utero*, succeeded after birth by slowed eye growth but continued orbital growth (Cummings et al. 2012). This implies that in the neonate eye and orbit size are closely correlated, but due to a higher rate of postnatal orbital growth, this scaling relationship becomes progressively weaker towards adulthood (Washburn and Detwiler 1943).

Even so, within adult primates (both catarrhines and strepsirrhines) orbital volume still explains ~83% of eyeball volumetric variation (Kay and Kirk 2000, Schultz 1940), although Schultz (1940) nonetheless concluded that, *"the size of the orbit is not closely determined by the size of the eyeball [across primates], but is at best dependent upon it in only a very general way."* However, activity period and diet are well known to affect eye and orbit morphology (e.g. Kay and Kirk 2000, Kirk 2006a, Kirk 2006b, Ross and Kirk 2007): for instance, although nocturnal primates tend to have relatively larger orbits than diurnal primates, only visual nocturnal predators have relatively larger eyes (Kirk 2006a). Consequently, with regard to hominins it is probably more critical to ascertain the strength of the relationship between eye and orbit size when only diurnal taxa are considered, assuming that hominins inherited diurnality from the common ape ancestor[12].

The only previous study to investigate whether the size of the eye leads to correlated orbital volume changes specifically in modern humans failed to find a significant relationship between eye and orbit volume, suggesting that eye size does not

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[12] Note that strictly speaking, modern humans might be considered to be cathemeral to some extent given activity during the night as well as during the day, although this is aided through artificial luminance such as fire.

influence orbit size in humans (Chau et al. 2004). However, Chau et al (2004) used a small, predominantly pathological myopic sample from a single Asian population, where myopia prevalence is particularly high (Ip et al. 2007, Saw 2003, Twelker et al. 2009), perhaps due to peculiarities in orbital and/or ocular (eye) morphology. Their sample thus may not have been representative of scaling in the general human population. The primary aim of this chapter is to use a larger global sample to re-test the hypothesis that orbital volume is significantly positively associated with eyeball volume in living humans.

Here I propose that although orbital morphology may be related to facial, neurocranial and basicranial morphology and body size, orbital size is also associated with eye, and thus visual cortex, size. If this hypothesis were supported, this would lend credence to the method of using orbital volume to index visual cortex volume in hominin fossils. In this chapter I test the specific hypotheses: (i) orbital volume is associated with eye volume and (ii) eye/orbit volume is associated with visual cortex volume. First, I use published data to undertake phylogenetically-controlled regression analyses in diurnal primates. If both the above hypotheses were supported then this would justify using orbit size comparisons between hominin species to examine possible visual cortex differences between taxa (Chapter 4). Second, I use original structural Magnetic Resonance Imaging (MRI) data collected from a comparatively large sample of healthy adult humans (Pearce and Bridge 2013). If significant positive relationships were found between orbit volume and both eye and visual cortex volume in this sample, this would support the use of orbit size to survey visual cortex size variation across the latitudinal range of modern humans (Chapter 3).

In addition, I test whether there is sequential scaling between three visual cortical areas (V1, V2 and V5/MT) (Pearce and Bridge 2013). However, I present the results in

Appendix 1 (Figure A4) rather than here because (i) scaling between the primary visual area (V1: Brodmann Area 17/striate cortex) and extrastriate areas, as well as between different extrastriate areas, has already been established in living humans (although not between V2 and V5/MT) (Dougherty et al. 2003, Song et al. 2011, Zhong et al. 2009) and (ii) the aim of this chapter is to assess whether it is possible to use orbit size to predict total visual cortex volume in hominins, not the size of individual visual areas.

Methods

Primates

Controlling for phylogeny

Parametric regression models assume independence between data-points, but this assumption is violated in comparative analyses because species (or populations) are related through shared ancestry. I thus tested whether relationships between variables remained significant independently of shared history between primate taxa by fitting phylogenetically-controlled general linear models (PGLM) using the pgls function in the R capers package (R-Forge Accessed March 2011). A similar method was applied to the human population comparisons in Chapter 3.

The pgls function requires a phylogenetic tree structure, which is converted into a variance-covariance matrix between taxa, where the diagonal elements (variance) represent the total branch-length for each individual taxon from root to tip and the off-diagonal elements (covariance between taxa) represent the total branch-length shared between two taxa (Freckleton, Harvey, and Pagel 2002). As well as regression model parameters and significance statistics, pgls outputs a lambda estimate optimised via a maximum likelihood method. The lambda value is a multiplier of the off-diagonal elements of the variance-covariance matrix, meaning that it expresses the degree to which the data are explained by phylogeny given the data, the tree structure and a Brownian model of evolution (i.e. traits accumulate variance at some constant rate, in line with a ‘molecular clock’ (Pagel 1997)) (Freckleton, Harvey, and Pagel 2002): the greater lambda is, the greater the weighting that is given to the covariance matrix. In terms of ordinary general linear models, if the optimised lambda value is significantly less than one but not significantly different from zero, that suggests that phylogeny does not explain a significant amount of the covariance between x and y (although it could be theoretically explained using a different tree structure or a different model of evolution). In more familiar terms, a PGLM can be interpreted as a multiple linear regression where ‘phylogeny’ is a covariate. In this scheme, whether the lambda value is significantly different from one or zero is roughly analogous to a p-value expressing whether the phylogeny explains a significant part of the variance in the y-variable that is not explained by the other x variables.

Data & analyses

I obtained orbital and eyeball volume and body weight data for a sample of 18 diurnal primates from Schultz (1940). I used diurnal species only, due to the well-documented differences between diurnal and nocturnal primate visual systems (Kay and Kirk 2000, Kirk 2006a, Ross and Kirk 2007, Stephan, Frahm, and Baron 1984). I excluded *Lasiopyga callitrich*, *Pygathrix rubicundus* and *P. sabanus* from the analyses because the taxonomical classification of these specimens was unclear and therefore prevented their accurate positioning in a current phylogenetic tree. I used eye and orbit diameter data from Kirk and colleagues (Kay and Kirk 2000, Kirk 2006a) for diurnal anthropoids, and endocranial volume[13] and body weight data from Martin (1990). I obtained total visual cortex surface areas (V1 + V2) from Kaskan et al (2005) for 5 diurnal anthropoid primate genera: *Homo sapiens*, *Macaca*, *Saguinus*, *Saimiri* and *Callithrix jacchus*. I took V1 volume data from Stephan et al (1981) for 15 diurnal anthropoids. To test whether orbit diameter is significantly associated with V1 volume independently of endocranial volume and body weight the combined dataset from Kay & Kirk (2000), Stephan et al (1981) and Martin (1990) contained 12 taxa: I removed the outlier *Alouatta*, which only matches for genus and not species, and data were missing for *Miopithecus* and *Saguinus*.

The phylogenetic consensus trees for the PGLM analyses were downloaded from the 10k tree project (Arnold, Matthews, and Nunn 2010): Figure 2.1. All data were $\log_{10}$ transformed in order to fit linear models. Residuals did not differ from normality and did not show excessive heteroscedasticity.

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[13] Endocranial volume is taken as an index of brain size given the isometric scaling between then two (Isler, K., E. C. Kirk, J. M. A. Miller, G. A. Albrecht, B. R. Gelvin, and R. D. Martin. 2008. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. *Journal of Human Evolution* 55:967-978.; Martin, R. 1990. *Primate origins and evolution. A phylogenetic reconstruction.* London: Chapman & Hall.).

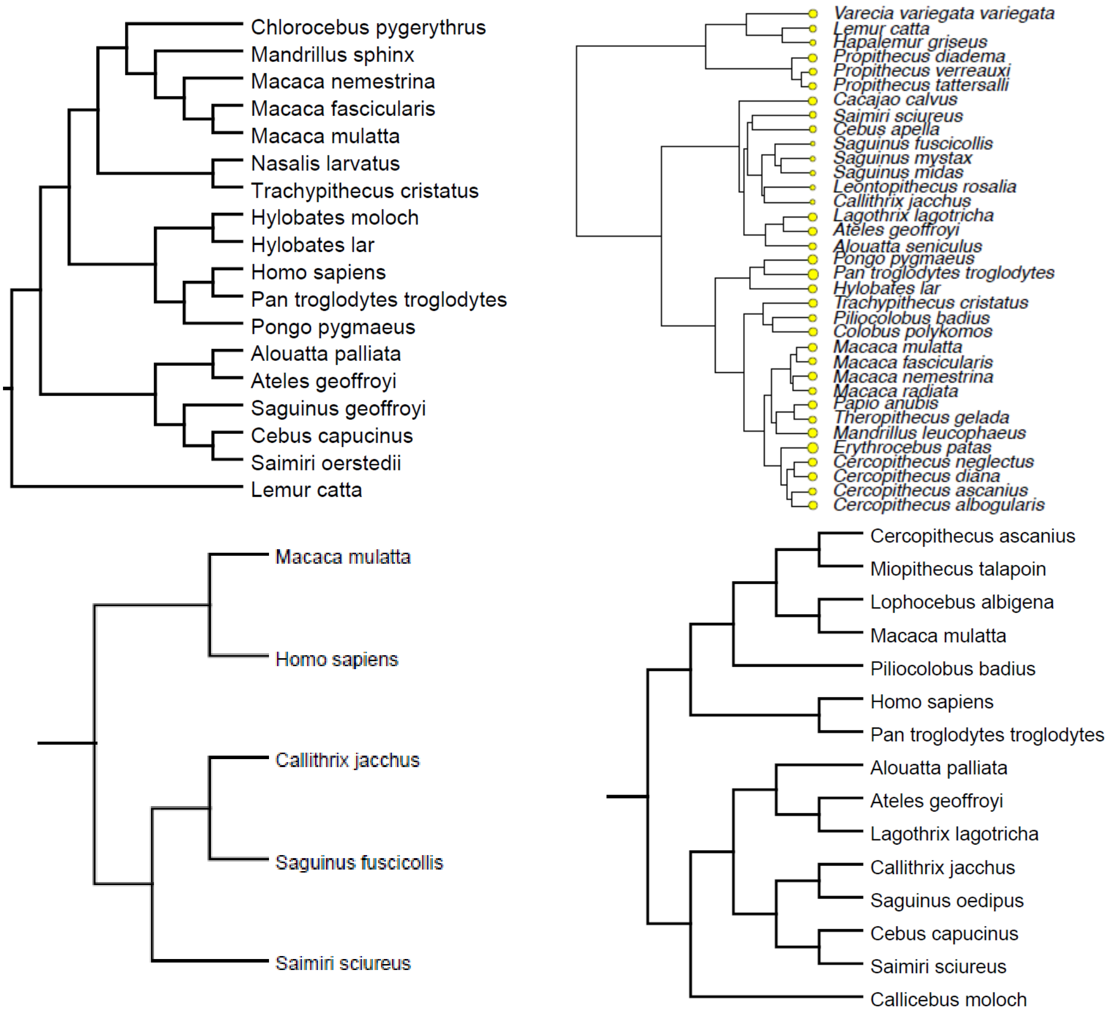

Figure 2.1: TOP LEFT: Phylogenetic tree used in PGLM analysis fitted to $\log_{10}$ eyeball volume plotted against $\log_{10}$ orbital volume for 18 diurnal primates (Schultz 1940). TOP RIGHT: Phylogenetic tree used in PGLM analysis fitted to eyeball traverse diameter plotted against orbital traverse diameter for 35 diurnal primates (Kay and Kirk 2000, Kirk 2006a), showing eye size via the radii of the circles. Cranial capacity data were not available for all taxa (Martin 1990), leaving a sample of 16 diurnal primates. Of the taxa with eye diameter data, the following did <u>not</u> have endocranial volume data and were excluded from the relevant models: Saguinus fuscicollis, Leontopithecus rosalia, Saguinus mystax, Saguinus midas, Lemur catta, Propithecus tattersalli, Macaca fascicularis, Macaca radiata, Cercopithecus albogularis, Colobus polykomos, Trachypithecus cristatus, Cacajao calvus, Cercopithecus diana, Propithecus diadema, Cercopithecus neglectus, Macaca nemestrina, Mandrillus leucophaeus and Erythrocebus patas. BOTTOM LEFT: Phylogenetic tree used in applying a PGLM to $\log_{10}$ total visual cortex surface area (Kaskan et al. 2005) plotted against $\log_{10}$ orbital diameter (Kay and Kirk 2000) for 5 anthropoid primate species (for Macaca the mean orbital diameter of two species was taken) (Arnold, Matthews, and Nunn 2010). BOTTOM RIGHT: Phylogenetic tree used in applying a PGLM to $\log_{10}$ V1 volume (Kaskan et al. 2005) plotted against $\log_{10}$ orbital diameter (Kay and Kirk 2000) for 15 anthropoid primate species (Arnold, Matthews, and Nunn 2010). For analyses including body weight and endocranial volume data were unavailable for Saguinus and Miopithecus (Martin 1990) and these species were excluded.

Living humans

Magnetic Resonance Imaging (MRI) scan sample

MRI scans of 100 normal, healthy subjects were downloaded from the 1000 Functional Connectomes Project (NITRC Accessed 2011), which provides an online collection of scans from a number of research groups across the world, mainly from USA and Europe. Ten imaging centres were selected to cover a range of latitudes (see Chapter 3): Atlanta (USA), Baltimore (USA), Berlin (Germany), Newark (USA), Orangeburg (New York), Oulu (Finland), Oxford (England), Palo Alto (USA), Queensland (Australia), Taipei (Taiwan). The latitudes of the 10 imaging centres were obtained using (Gorissen Accessed July 2008, July 2010). Ten subjects were randomly selected from each of these samples using the Excel RAND( ) function. Where possible 5 females and 5 males were selected, but for the Palo Alto sample the only 2 male subjects were selected alongside 8 randomly selected females. Demographic information was unavailable for the Taipei sample so 10 subjects of unknown sex were selected. Demographic information was also unavailable for 3 of the Orangeburg sample.

One subject was removed from the final analyses because this individual appeared as a very low outlier on all brain-associated plots, leaving 99 subjects: 43 females (age *M*=26.70, *SD*=6.71), 43 males (age *M*=29.21, *SD*=7.58) and 13 subjects of unknown sex (unknown age). In the analyses sex was coded as two dummy variables (male and female) so that all available data could be included in the models.

As well as differing in imaging resolution, scan acquisition protocol and scanner type, the quality of the scans varied considerably between the source imaging centres. Scans were therefore graded for quality with regard to the eye/orbit region: (1) perfect, clear image, (2) complete eye boundary but some blur or slight distortion, (3) incomplete eye boundary, image blurred or distorted, (4) substantial distortion or reconstruction needed in order to delineate the eye in each slice and (5) unmeasurable (for one subject the anterior section of the eye/orbit was cut off in the image). Images graded 1 or 2 provided a sample of 40 subjects: 19 females (age *M*=25.21, *SD*=2.658), 15 males (age *M*=27.13, *SD*=6.885) and 6 subjects of unknown sex (unknown age). The eye and orbit analyses using the better quality sample (scans graded 1 or 2) yielded similar results to the whole sample, but with improved fit. The regression parameters fitted to the higher quality sub-sample lie within the 95% confidence intervals of the whole sample models for the 'eye/orbit-visual-cortex' models. The opposite is true for the 'eye-orbit' models and I give the accompanying statistics for the higher quality sample in Appendix 1. I report only the findings of analyses using the full sample here (Pearce and Bridge 2013). Since scans were graded on the basis of the quality of image regarding the eye and secondarily the orbit, other areas of the scan such as the foramen magnum (FM) remained of unequal quality and sometimes could not be measured. Consequently the sample size for some analyses was reduced.

MRI scan methods

Freesurfer

Freely-available freesurfer software (Rosset Accessed 2011) allows the automatic reconstruction and segmentation of the subcortical and cortical regions of the brain from T_1-weighted images. This process involves using identification of white/grey matter and grey/cerebrospinal fluid boundaries and sulcal/gyral patterns in conjunction with generalised 'masks' or 'model' brains (Desikan et al. 2006, Hinds et al. 2008, Pearce and Bridge 2013). The output provides surface area, grey matter thickness and volume measurements for specific areas of the cortex, as well as hemisphere-specific grey and white matter volumes for the cortex and subcortex.

I first ran the recon-all function, which outputs hemisphere-specific surface area, thickness, volume and curvature measurements for all brain regions that freesurfer identifies (http://www.freesurfer.net/fswiki/recon-all). I converted these into an SPSS database for analysis. Once the full reconstructions were completed I was able to use the ba-labels function[14] to automatically segment 12 Brodmann areas including the V1, V2 and V5/MT visual areas (Fischl et al. 2008, Hinds et al. 2009, Hinds et al. 2008), as well as the motor (Duncan and Jones 2000) and somatosensory areas. Of all the visual areas, V1, V2 and V5/MT are the best documented and most accurately identified across primates and within humans (Lyon and Connolly 2011, Rosa and Tweedale 2005). Furthermore, identification of the V1/V2 boundary has been shown to closely match when identified anatomically using the stria of Gennari and functionally using visual stimuli (Bridge et al. 2005), and locating V1 using gyral and sulcal patterns is in close correspondence to using the stria of Gennari (Hinds et al. 2008). The Brodman Area labelling function again outputs hemisphere-specific text files containing surface area and grey matter thickness and volume measurements, which were converted into SPSS format. Since grey matter volume is a function of surface area and grey-matter thickness, I use volume alone in the following analyses. I summed the volumes of V1, V2 and V5/MT to give ‘total’ visual cortex grey matter volume.

As controls of overall brain size I calculated total ‘non-visual’ or ‘rest-of-cortex’ grey matter volume by subtracting total visual (V1+V2+MT) grey matter volume from the total cortical grey matter volume. I did the same for total brain volume. I also summed cerebellum and brain stem volumes as an index of ‘hindbrain’ size. For all measures hemisphere volumes were combined.

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[14] http://surfer.nmr.mgh.harvard.edu/fswiki/BrodmannAreaMaps

OsiriX

The Orangeburg sample scans were unsuitable for measurement because their skulls had been stripped. In addition, the image for another subject prevented the measurement of eye/orbit volume. I measured the remaining 89 scans using the freely available Osirix software (Ives and Helmus 2011, Rosset Accessed 2011). I first converted the downloaded .nii image files into .hdr and .img files using FSL software (Jenkinson et al. 2012, Smith et al. 2004, Woolrich et al. 2009). I then imported these files into Osirix, creating a new database for each subject. I extracted the image resolution (pixel dimensions for X, Y and Z - slice thickness - dimensions) from the .hdr file using FSL.

Within the OsiriX 2D Viewer I set the image resolution and magnified the image by x1000 (for the Taipei sample the magnification factor was x700 because this enabled the image to remain within a single screen view). Some images required rotating before measurement, so that the nasal region was at the top of the screen. Regions of interest (ROIs) were manually delineated, and lengths, areas and volumes were automatically generated (Figures 2.2-2.7, Table 2.1). Maximum axial eye length was measured in the axial view (Figure 2.2) to identify possible myopes, since axial length and degree of myopia are strongly linked (Gilmartin 2004). Following the advice of optometrists from Aston University, I took 27mm as the cut-off for myopes. However, the three individuals in the full dataset with axial lengths longer than this did not appear as outliers on any data plots and are thus included in all analyses. For each subject linear and areal measurements were taken three times, and volume measurements twice. Means were taken and standard errors (*SE*) and deviations (*SD*) were calculated as measures of intra-observer error. I measured the right eye/orbit only. As well as eye/orbit volumes, I measured eye/orbit areas and height/width (Figure 2.5) to test whether different measures of eye/orbit size correlate with each other. I present these analyses in Appendix 1.

For the multiple linear and area measurements for each variable the maximum *SE*s were <0.1mm/mm^2 (*SD*s <1mm/mm^2). For eye volume (sample mean volume M=6.489cm^3, SD=0.794cm^3, N=88) the maximum *SE* for the two measurements was 0.64cm^3 (SD=0.91cm^3) and for orbital volume (sample mean volume M=26.669cm^3, SD=2.659cm^3, N=88) the SE=3.85cm^3 (SD=5.45cm^3). The maximum *SE* for the orbital volume measures was reduced to 1.01cm^3 (SD=1.43cm^3) when only the higher quality images (N=40) were considered. Paired-sample t-tests indicated significant correlations between the different measurement runs of orbit and eye volume (r=0.866 and 0.856, respectively, N=88) but whilst no significant difference was found between the means of the two measurement runs for orbital volume, a significant difference was found for eye volume (t_{87}=-2.800, p=0.006), although the mean difference was only -0.132cm^3 (SD=0.442cm^3).

As outlined above, orbital size is partially influenced by face and body size. I did not have body weight or stature data for these subjects, so I followed Pearce & Dunbar (2012) in using foramen magnum (FM) size as a proxy for body mass, as suggested by Radinsky (1967). I measured maximum facial width (sample mean volume M=11.558cm, SD=0.802cm, N=78) and maximum nasal height (sample mean volume M=5.340cm, SD=0.720cm, N=75) in coronal view since these were the easiest face-dimension measures to standardise. I also measured foramen magnum area (sample mean volume M=6.272cm^2, SD=1.397cm^2, N=88) in axial view (in the first slice in which the cerebellum was no longer visible). I included these body and face size controls as covariates in multiple Ordinary Least Squares (OLS) regressions testing for a relationship between eye and orbit volumes.

Table 2.1: Measurements taken using OsiriX. The first four variables were used in analyses presented in this chapter, whereas the other variables are dealt with in Appendix 1 or mentioned in the Discussion section of this chapter.

Measurements	**Scan View**	**Tool**	**Slice Choice**	**Position in Slice**
Eye Axial Length (Figure 2.2)	Axial	Length	Where maximum axial length is visible	Maximum length between centre of the cornea and the retina, bifurcating the eye
Orbital/Eye Volume (Figure 2.3)	Axial	Closed Polygon in each slice	Each slice for which the feature is present	Orbit: Bounded by the interior darker nasal wall and zygomatic/frontal bone (depending on vertical position) Eye: Interior boundary of the fluid-filled chambers
Foramen Magnum Area (Figure 2.4)	Axial	Closed Polygon	First slice in which cerebellum is absent	Boundary
Face Height/Width (Figure 2.5)	Coronal	Length	First slice in which zygomatic bone is complete	'Nose' height, Maximum width
Orbital/Eye Area (Figure 2.5)	Coronal	Closed Polygon	First slice in which zygomatic bone is complete	Orbit: Exterior boundary of the white orbital fat. Eye: Interior boundary of the vitreous humour chamber.
Orbital/Eye Height/Width (Figure 2.5)	Coronal	Length	First slice in which zygomatic bone is complete	Orbit: Maximum vertical/horizontal length across white orbital fat. Eye: Maximum vertical/horizontal length across the vitreous humour chamber.
Optic Nerve Width (Figure 2.6)	Axial	Length	Where maximum diameter is visible	Maximum diameter perpendicular to nerve path

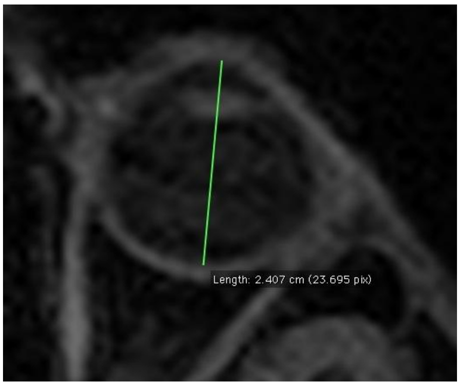

Figure 2.2: Axial eyeball length taken. Due to confidentiality issues with the 1000 Functional Connectomes scans, the example shown in these figures is an MRI scan kindly provided by Holly Bridge.

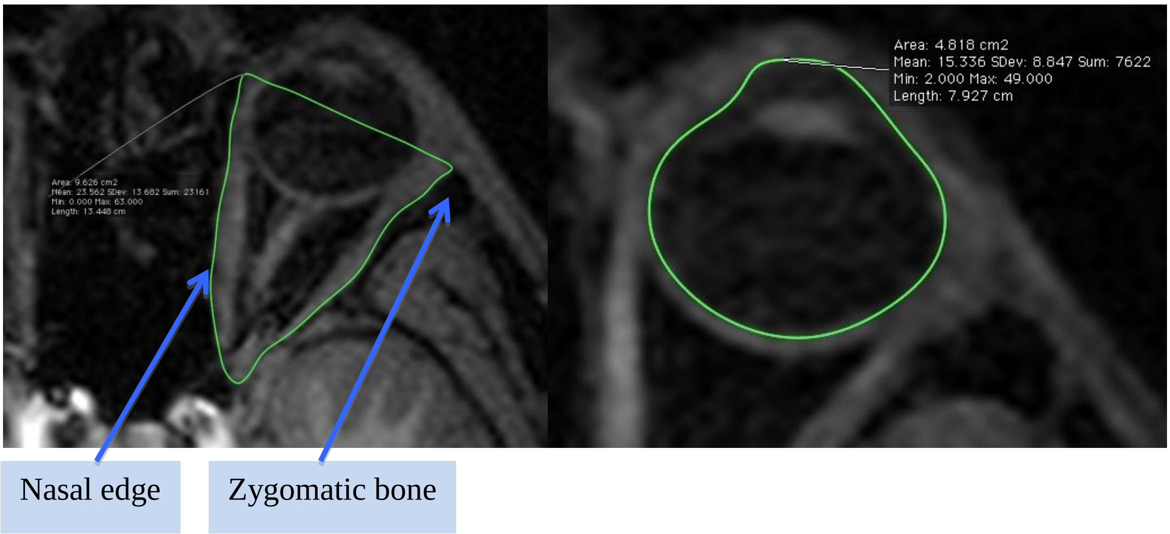

Figure 2.3: LEFT – The orbit delineated in a single slice, marked by the nasal cavity on the left and the zygomatic bone on the right. RIGHT – The eyeball delineated in a single slice, with the boundary identified as the edge of the anterior and posterior chambers. The lens is visible in this slice.

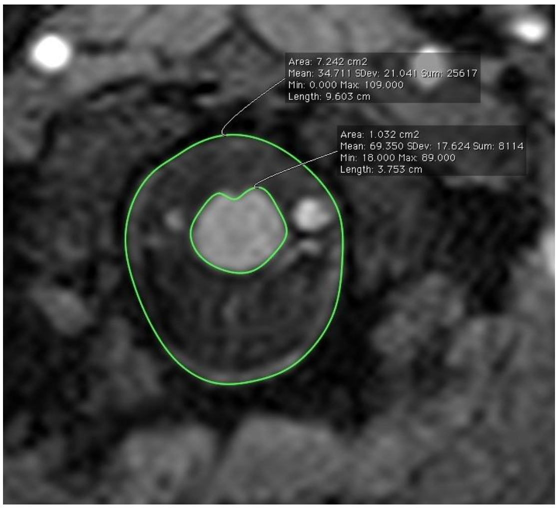

Figure 2.4: Foramen magnum and spinal cord area.

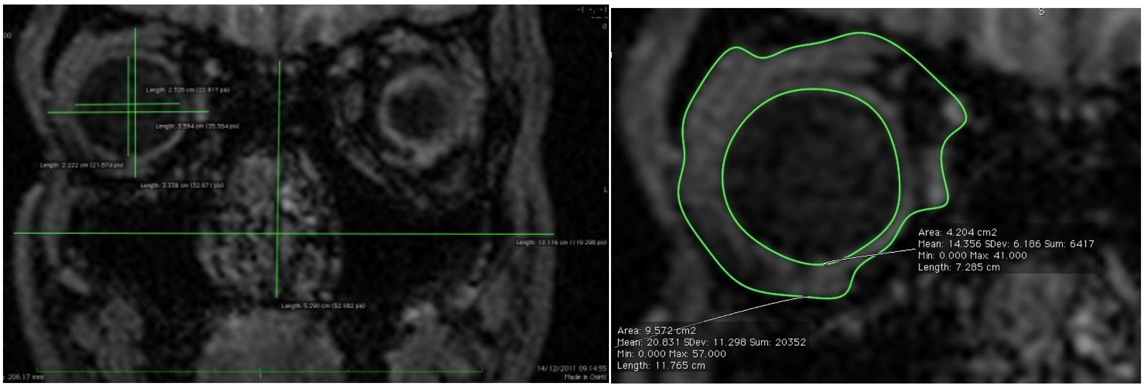

Figure 2.5: LEFT - Eye, orbital and facial height and width. RIGHT – Eye and orbital area. Both taken in coronal view for the first slice in which the zygomatic bone is complete, moving from anterior to posterior slices.

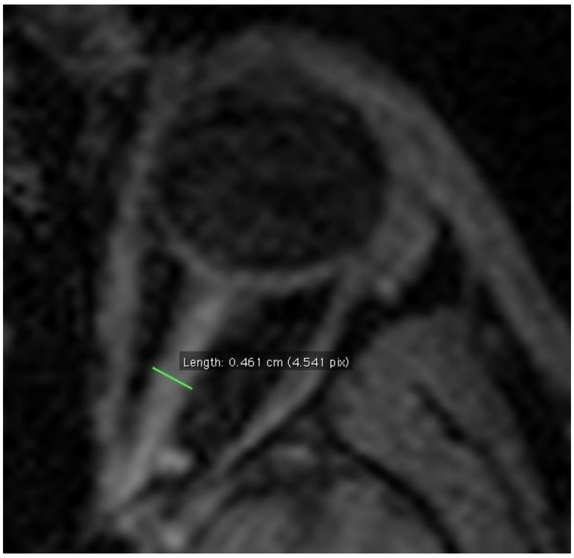

Figure 2.6: Maximum optic nerve diameter.

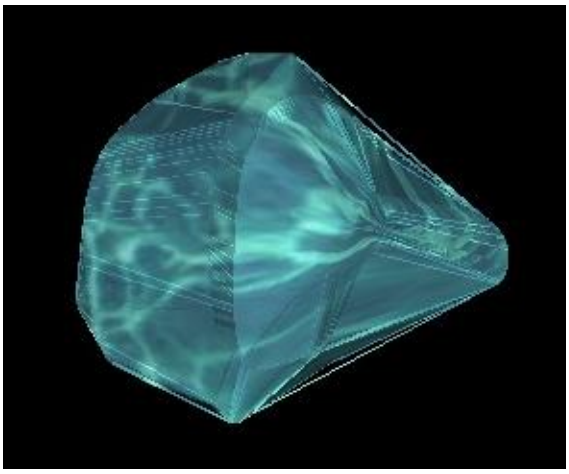

Figure 2.7: The reconstructed volume of the right orbit, comprised of regions of interest delineated in each slice and created using the ‘compute volume’ function.

Analyses

Unless otherwise stated, regression residuals were not significantly different from normal and did not show heteroscedasticity. Furthermore, tolerance and VIF statistics did not show excessive collinearity between independent variables in multiple regressions and the R^2 for simple regressions between covariates was not high enough to cause concern (<0.2).

Note that due to the symmetrical nature of the relationships and the fact that measurement error is expected on both axes, Reduced Major Axis (RMA) regression would have been optimal in these analyses for accurate parameter estimation (Smith 2009). However, OLS regression models provide a conservative test of significance, which is the crucial point here, because such OLS models tend to underestimate the true slope. Nonetheless, the data plots in some cases suggest that the fit of an RMA regression model would have been much stronger, providing elevated R^2 values.

Measuring the accuracy of T_1 scans against optimized T_2 scans

As detailed in the Discussion, the T_1-weighted images used here are not optimised for eye/orbit measurement. I thus attempted to test the accuracy of T_1-measurements against those obtained from more optimal T_2-scans using a sample of T_1- and T_2-weighted scans kindly provided by Holly Bridge (FMRIB, University of Oxford) for 6 subjects. I used the same method as described above to measure eyeball volume twice for the left and right eyeballs in each scan. I took the mean of the two measurements of each eyeball. Unfortunately, because the T_2-weighted scans were taken to examine the optic nerves rather than the eyeballs themselves, in some of the T_2-weighted scans the superior part of the eyeball was cut off and the inferior eyeball became increasingly unclear due to the attenuation of image quality. In some of the T_1-weighted images the previously encountered problem of unclear anterior eye boundaries was also apparent. The measurements taken were thus not ideal.

However, across the full sample and a subset of better quality scans (N=3 individuals) and when split into left or right eyes, the mean absolute difference between T_1 and T_2-weighted image measurements was ~0.5cm^3, with a SD of ~0.5 cm^3, ranging from 0.7-1.28cm^3. For the whole sample R^2=0.787 and for the subset R^2=0.993 for regressions between mean T_1 and mean T_2 eyeball volume measurements. However, these effect sizes should be treated with caution since the residuals showed potential heteroscedasticty and lack of normality, although OLS is fairly robust to assumption violations. Using multilevel models to account for relatedness between right and left eyeballs within subjects made no difference to these results.

Results

Primates

Hypothesis 1: Orbit size is associated with eye size across diurnal primates

Volumes

PGLM analysis revealed that across a sample of 18 diurnal primates $\log_{10}$ eyeball volume was significantly associated with $\log_{10}$ orbital volume independently of phylogeny (Figure 2.8): t_{16}=11.646, p=3.169e^{-9}, overall R^2=0.894, overall *adjusted* R^2=0.888. The optimised lambda value (6.611e^{-5}) was not significantly different from zero (χ^2=-0.0006, p=1) but was significantly different from 1 (χ^2=8.052, p=0.0045), suggesting that phylogeny does not explain variation in eye volume independently of orbit volume.

A significant partial relationship between $\log_{10}$ eyeball volume and $\log_{10}$ orbital volume remained when the effects of $\log_{10}$ body weight, which itself did not show a significant partial relationship (p=0.321), were partialled out: t_{15}=4.314, p=0.0006, overall R^2=0.901, overall *adjusted* R^2=0.888. The optimised lambda remained significantly different from 1 (χ^2=9.253, p=0.002) but not significantly different from zero (χ^2=-0.0007, p=1). The results were unchanged when the outlier Orangutan, whose relatively small visual structures have been previously noted by Stephan et al (1984) (see Figure 2.8), was removed, except that the effect size increased: overall R^2=0.941, overall *adjusted* R^2=0.937.

Since orbit volume is related to body size (Kappelman 1996, Schultz 1940), there is some degree of multicollinearity between orbital volume and body weight. I thus re-ran the analyses using raw relative eyeball and orbital volumes (calculated as ratios to body weight): Figure 2.9. A PGLM analysis showed that relative orbital volume is significantly positively associated with relative eyeball volume independently of phylogeny: t_{16}=9.475, p=5.779e^{-8}, overall R^2=0.849, overall *adjusted* R^2=0.839. The optimised lambda value (0.9999) was not significantly different from one (χ^2=-0.0017, p=1) but was significantly different from zero (χ^2=7.808, p=0.005), suggesting that the phylogenetic tree structure has a substantial effect in the model. Nonetheless, the relationship between relative orbital and eyeball volumes remains despite a strong phylogenetic effect. If the outliers *Lemur catta* (which might be cathemeral: Donati et al. 2013) and *Saguinus geoffroyi* were removed the relationship would have been even stronger.

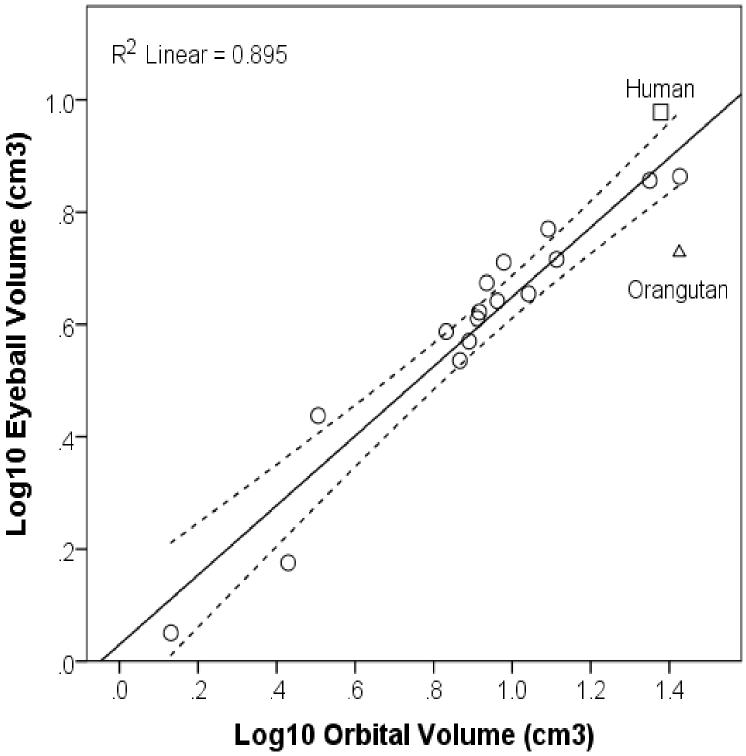

Figure 2.8: Log$_{10}$ eye volume plotted against log$_{10}$ orbital volume for 18 diurnal anthropoid primates (Schultz 1940). The orangutan outlier is represented by a triangle. The dashed lines indicate 95% CIs for the regression line.

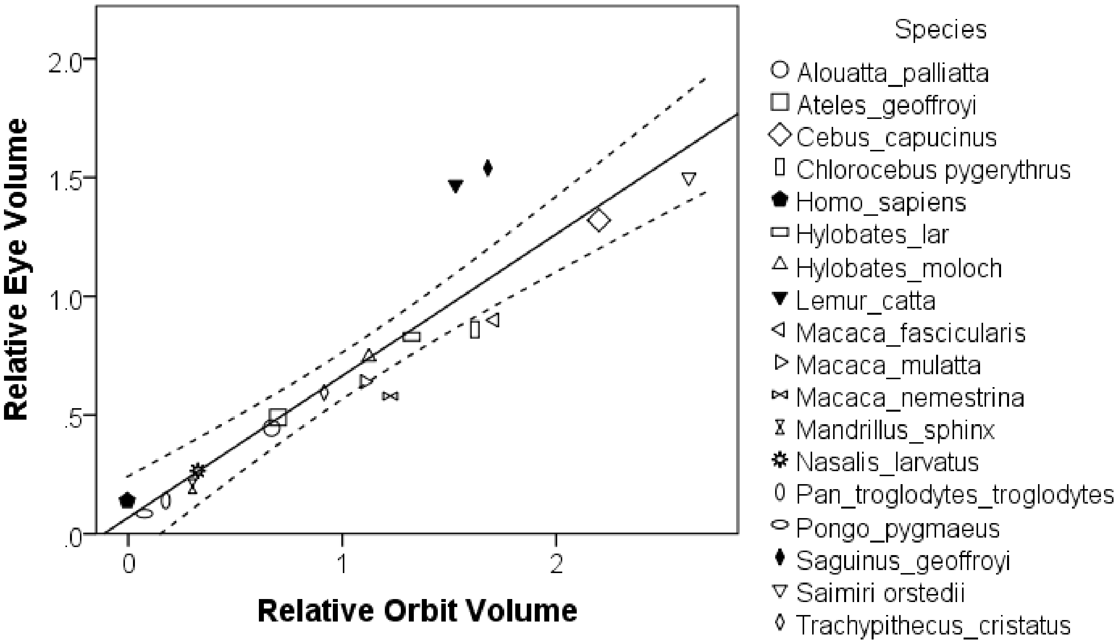

Figure 2.9: Relative eyeball volume plotted against relative orbital volume for 18 diurnal primates. The dashed lines indicate 95% CIs for the regression line.

Linear dimensions

In addition, PGLM analysis revealed that $\log_{10}$ transverse eye diameter remains significantly associated with $\log_{10}$ orbital diameter independently of cranial capacity (partial relationship for orbit diameter: t_{14}=4.721, p=0.0003, R^2=0.900, overall model *adjusted* R^2=0.889, Figure 2.10) or $\log_{10}$ body weight (partial relationship for orbit diameter: t_{14}=3.502, p=0.004, overall model *adjusted* R^2=0.886), which themselves did not show a significant partial relationship with $\log_{10}$ eye diameter (p=0.572 and 0.397 respectively). For both models the optimised maximum-likelihood lambda value was not significantly different from zero (p=1) but was significantly different from one (p=0.003).

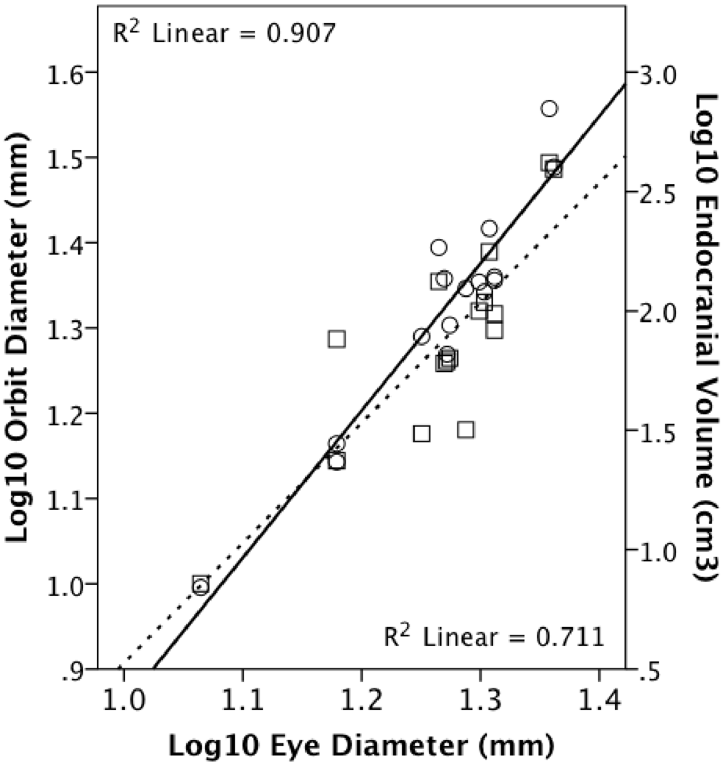

Figure 2.10: $\log_{10}$ orbital diameter (circles, solid line) and $\log_{10}$ endocranial volume (squares, dashed line) plotted against $\log_{10}$ eye diameter for 16 diurnal primates.

To overcome problems of multicollinearity I also regressed relative eye diameter against relative orbital diameter (relative to endocranial volume or body weight). When relativized against endocranial volume, eye and orbit diameters were still positively related independently of phylogeny: t_{15}=29.291, p=1.199e^{-14}, overall R^2=0.983, overall model *adjusted* R^2=0.982, optimised lambda=0.268 (not significantly different from zero, p=0.581, or one, p=0.126). Similarly, when relativized against body weight, eye and orbit diameters were still positively related independently of phylogeny: t_{15}=53.801, p=2.2e^{-16}, overall R^2=0.995, overall *adjusted* R^2=0.995, optimised lambda was zero, but was not considered significantly different from zero, p=1, or one, p=0.078 according to chi-squared tests. Orbit and eye size thus remained significantly associated with each other independently of endocranial volume or body weight across diurnal primates.

Hypothesis 2: Orbit size is associated with visual cortex size in diurnal primates

The PGLM analysis revealed a significant positive linear relationship between $\log_{10}$ orbital diameter and $\log_{10}$ total visual cortex surface area independently of phylogeny (Figure 2.11): t_3=10.374, p=0.002, overall R^2=0.973, overall *adjusted* R^2=0.964. The same was true for the PGLM fitted to $\log_{10}$ V1 volume regressed on $\log_{10}$ orbital diameter (Figure 2.11): t_{13}=8.412, p=1.286e^{-6}, overall R^2=0.845, overall *adjusted* R^2=0.864. For both models lambda was not significantly different from zero or one.

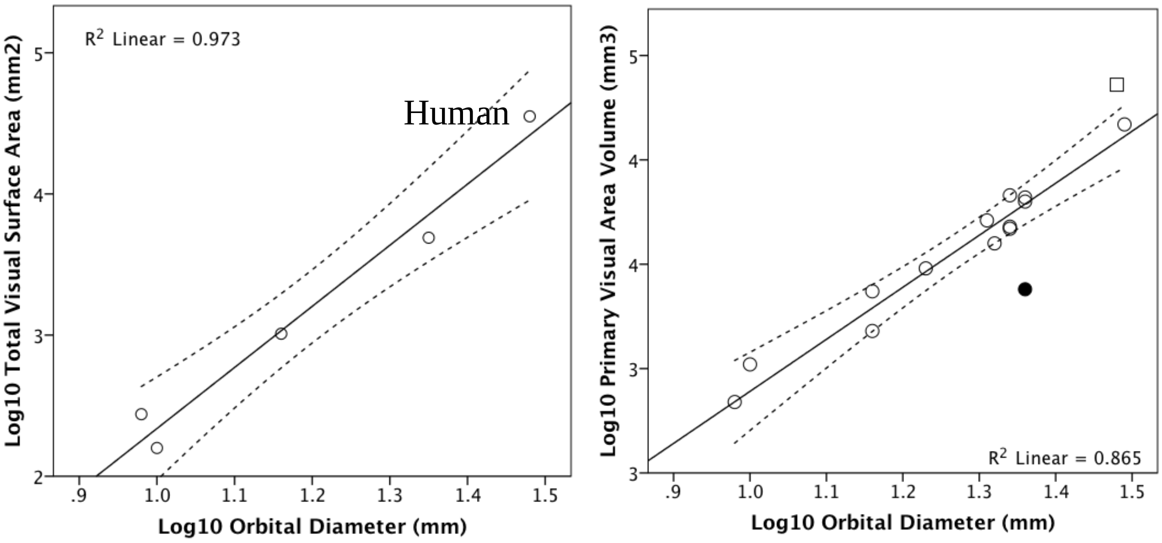

Figure 2.11: $\log_{10}$ total visual cortex surface area (LEFT) and $\log_{10}$ V1 volume (RIGHT) plotted against $\log_{10}$ orbit diameter for diurnal primates. The dotted lines give 95% confidence limits for the regression line. The shaded circle in the right-hand figure denotes the outlier Alouatta and the square represents Homo sapiens.

Controlling for overall brain and body size

Of all the visual brain areas, V1 should be most strongly related to eye size because sensory input is directly into this brain region. Given this and the fact that V1 volume data were available for a larger sample of diurnal primates, here I present only the multiple linear regression analyses between orbit size and V1 volume controlling for brain and body size. Visual cortex (V1+V2) surface area did not remain significantly associated with orbital size once overall neocortex was taken into account (Appendix 1), but this is probably due to an insufficient sample size and the lower degrees of freedom once further covariates were included in the model.

Controlling for overall neocortex size

When the outlier *Alouatta* (Figure 2.11) was removed[15], PGLM analysis revealed significant partial relationships with V1 volume for both $\log_{10}$ orbital diameter (t_{11}=3.141, p=0.009) and $\log_{10}$ rest-of-neocortex (i.e. total neocortex minus V1) volume (t_{11}=4.444, p=0.0001): overall R^2=0.980, overall *adjusted* R^2=0.976. To overcome the potential multicollinearity between orbital and non-visual neocortex volumes, I re-ran the PGLM analyses on relative measures of orbit diameter and V1 volume, as ratios against rest-of-neocortex volume. Relative orbital volume remained significantly positively associated with relative V1 volume, independently of phylogeny, even when the outlier was included: t_{13}=9.728, p=2.476e^{-7}, R^2=0.879, *adjusted* R^2=0.870.

Controlling for overall brain size and body weight

The PGLM analyses indicated that orbital diameter is significantly associated with V1 volume independently of endocranial volume (t_5=3.320, p=0.021, overall R^2=0.986, overall *adjusted* R^2=0.980) or body weight (t_5=5.130, p=0.004, overall R^2=0.985, overall

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[15] When the outlier is included, the PGLM run with $\log_{10}$ orbital diameter and $\log_{10}$ rest-of-neocortex volume predicting $\log_{10}$ V1, only $\log_{10}$ rest-of-neocortex volume showed a significant partial relationship with V1 volume (t_{12}=5.062, p=0.003), with $\log_{10}$ orbital diameter not being significantly associated with V1 volume independently of rest-of-neocortex volume (t_{12}=1.064, p=0.309).

adjusted R^2=0.979). Moreover, orbital diameter is significantly associated with V1 volume independently of cranial capacity and body weight when both variables are included together as covariates (t_5=3.194, *p*=0.033, overall R^2=0.987, overall *adjusted* R^2=0.978). In all models, neither endocranial volume nor body weight showed significant partial relationships with V1 volume.

Living humans

Data structure

The data collected are hierarchical, because they were sampled from 10 different imaging centres and therefore subjects sampled from the same centre may not yield independent data-points. The accuracy of results obtained from OLS regression analyses was therefore checked against the output of mixed/multilevel model analyses, but since these hierarchical linear models did not yield different results and because I am interested in whether relationships are significant, rather than optimising parameters, I report only the OLS analyses here.

Sex differences

Independent t-tests found that males had significantly larger orbital volumes and larger visual and rest-of-cortex grey matter volumes, than females: Table 2.2. In contrast, no significant sex difference in eye volume (*p*=0.339, females: *M*=6.45, *SD*=0.67, *N*=41, males: *M*=6.62, *SD*=0.87, *N*=37) or FM area (*p*=0.241, females: *M*=6.24, *SD*= 1.29, *N*=40, males: *M*=6.53, *SD*=1.58, *N*=36) was found.

Table 2.2: Sex differences in eye, orbit, visual cortex grey matter and rest-of cortex grey matter volumes and FM areas for a sample of living humans.

	Males			**Females**			**t**	**p**	**R^2**
	N	**Mean**	**SD**	**N**	**Mean**	**SD**			
Orbit volume (cm^3)	37	28.19	2.35	41	25.45	2.25	5.277	$1.2e^{-6}$	0.27
Visual cortex volume (cm^3)	43	42.51	5.98	43	38.83	5.22	3.046	0.003	0.10
Rest-of-cortex volume (cm^3)	43	440.34	51.74	43	398.15	43.53	4.092	$9.8e^{-5}$	0.17
Eye volume (cm^3)	40	6.62	0.87	41	6.45	0.67	n/a		
FM area (cm^2)	36	6.53	1.58	40	6.14	1.29	n/a		

Hypothesis 1: Orbital volume is associated with eye volume in living humans

OLS regression revealed that mean orbital volume was significantly positively associated with mean eyeball volume: $t_{86}=4.119$, $p=8.711e^{-5}$, $R^2=0.165$. This relationship remained significant when an outlier (Figure 2.12) was excluded from the analysis.

Orbital volume remained significantly associated with eyeball volume ($t_{85}=4.426$, $p= 2.829e^{-5}$) independently of brain-minus-visual-cortex-grey-matter volume, which itself failed to show a significant partial relationship with eye volume ($p=0.125$): overall *adjusted* $R^2=0.169$. Controlling for rest-of-grey-matter (i.e. non-visual) cortical volume, cerebellum plus brainstem or subcortical grey matter volume yielded similar patterns. For subjects for whom the data were available, controlling for FM area and face height and width[16] (proxies for body and face size respectively) made no difference to the results. Similarly, including sex in the model made no difference.

To check these findings, I calculated relative eyeball and orbital volumes as ratios against rest-of-cortex grey matter volume. An OLS regression analysis revealed that

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[16] Neither eye nor orbit volume is significantly related to FM area or face height and only orbital volume, but not eye volume, shows significant relationships with face width ($t_{86}=2.938$, $p=0.004$, $R^2=0.103$) and brain volume ($t_{86}=4.040$, $p=1.159e^{-4}$, $R^2=0.159$; when two outliers are excluded $R^2=0.205$).

relative eyeball volume is significantly positively associated with relative orbital volume (Figure 2.13): t_{86}=8.508, p=4.938e^{-13}, R^2=0.457. This relationship remained unchanged when the sex was added to the model.

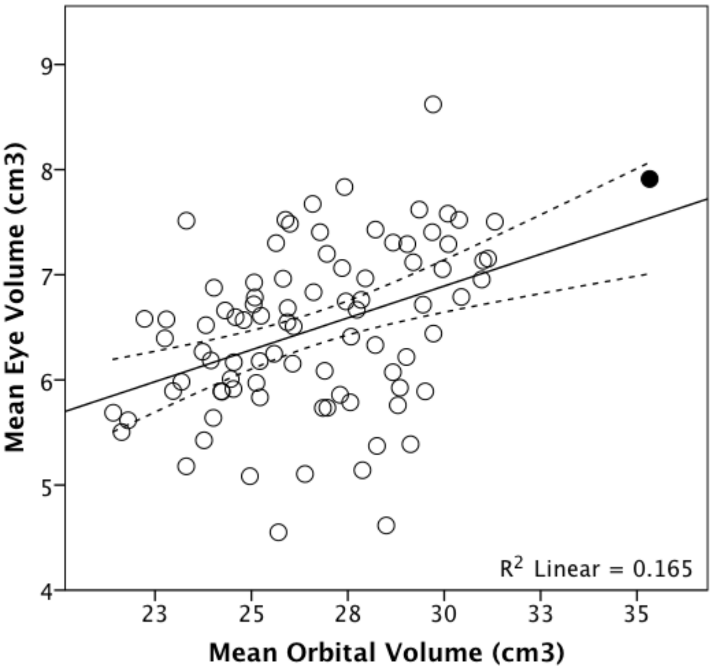


Figure 2.12: Mean eyeball volume plotted against mean orbital volume for 88 living humans. The dotted lines represent 95% confidence intervals for the regression line. Removing the shaded outlier makes no difference to the outcome of the analyses.

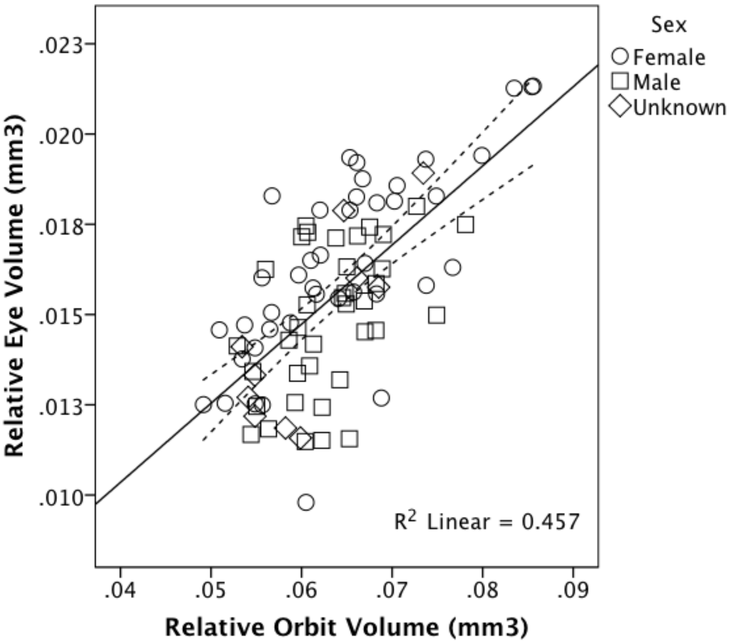


Figure 2.13: Relative eyeball volume plotted against relative orbital volume for 88 living humans, labelled by sex, with the dashed lines indicating the 95% confidence intervals of the regression line.

Hypothesis 2: (i) Eyeball and (ii) orbit volume is associated with visual cortex grey matter volume in living humans

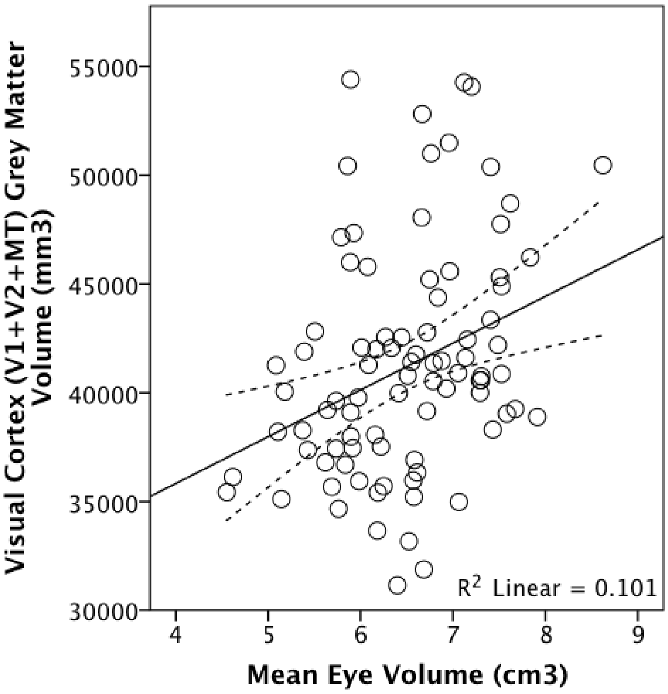
OLS regression analyses revealed a significant positive relationship between eyeball volume and total visual cortex (V1+V2+V5/MT) grey matter volume: t_{86}=3.100, p=0.003, R^2=0.101, Figure 2.14. This relationship remains independently of all measures of overall brain size, including motor or somatosensory cortex volumes (Table 2.3). Adding sex into the models makes no difference. Similar patterns are observed when only V1 is considered (Appendix 1).

Table 2.3: OLS regression statistics for partial relationships between eyeball and 'total' visual cortex grey matter volume, controlling for various measures of overall brain size.

Eyeball volume predicting visual cortex grey matter volume, controlling for:	**OLS Regression Statistics**					
	t	**df**	**p**	**Partial R^2**	**Over all R^2**	**Overall adjusted R^2**
Total brain volume	3.353	85	0.001	0.117	0.305	0.288
Brain minus visual	3.360	85	0.001	0.117	0.286	0.269
Subcortical grey matter	3.394	85	0.001	0.119	0.243	0.225
Cerebellum + Brainstem	3.338	85	0.001	0.116	0.202	0.183
Non-visual grey matter	2.969	85	0.004	0.094	0.385	0.370
Motor cortex	2.127	85	0.036	0.051	0.310	0.294
Somatosensory cortex	2.073	85	0.041	0.048	0.374	0.359

Orbital and total visual cortex volumes are significantly associated independently of subcortical grey matter (t_{85}=2.531, p=0.013, overall R^2=0.201, overall *adjusted* R^2=0.182), motor cortex (t_{85}=2.551, p=0.027, overall R^2=0.314, overall *adjusted* R^2=0.298) and cerebellum + brain stem volume (t_{85}=2.713, p=0.008, overall R^2=0.169, overall *adjusted* R^2=0.150) whether or not the outlier is excluded (Figure 2.14). The relationship between orbital volume and total visual grey matter volume does not remain independently of non-visual cortical grey matter volume and is significant independently of non-visual (t_{84}=2.299, p=0.024, overall R^2=0.243, overall *adjusted* R^2=0.225) or total brain volume

(t_{84}=2.190, p=0.031, overall R^2=0.259, overall *adjusted* R^2=0.242) only when the outlier has been removed.



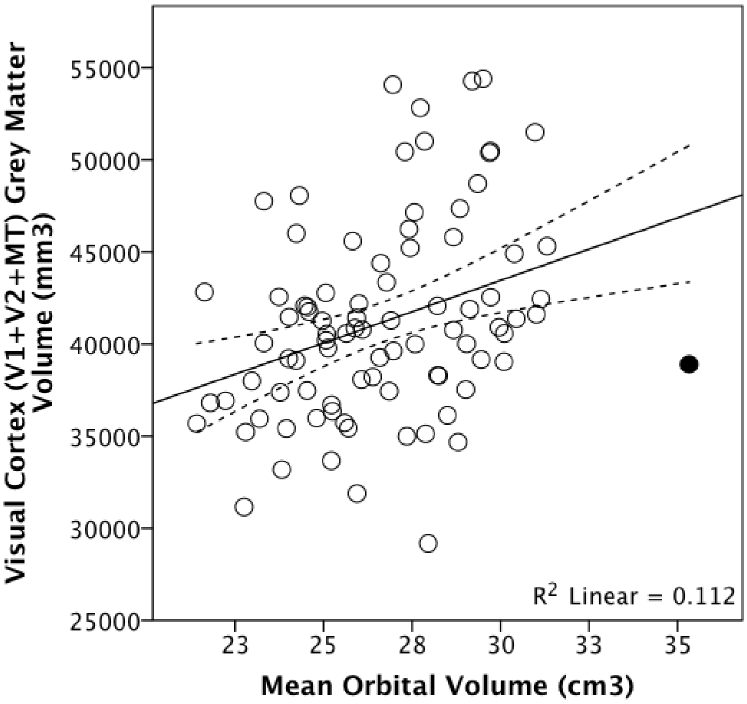


Figure 2.14: Total visual cortex grey matter volume plotted against eyeball (TOP) and orbital (BOTTOM) volume for 88 living humans, with the outlier shaded. The dotted lines represent 95% confidence intervals for the ordinary least squares regression line. It should be noted that for visual cortex volume plotted against either eye or orbit volume, a reduced major axis regression with a steeper slope would have produced a stronger fit to the data than the more conservative OLS model applied here.

Discussion

The results presented here show that contrary to previous reports (Chau et al. 2004), orbital and eyeball volumes are significantly positively associated in living humans, independently of overall brain, face and body (indexed by FM area) size. I also showed that across diurnal primates orbital volume is strongly positively associated with eyeball volume independently of brain size, body weight and phylogeny. Together these findings indicate that it is valid to use fossil hominin orbit size to index eyeball size: on average a larger orbit will mean a larger eye.

According to my model human orbital volume explains ~17% of the variance observed in eyeball volume across the full sample, but this rises to ~40% when only the better quality scans are considered. The strength of the relationship between eyeball and orbital dimensions presented here is likely to be an underestimate, for a number of reasons. Firstly, the type of MRI scan available to me was not optimised for orbital and ocular measurements. Since the 1000 Functional Connectomes scans were taken in order to study the brain, they were T_1-weighted, enabling the clear differentiation of white-and grey-matter, whereas T_2-weighted images are optimal for delineating the eye (Chau et al. 2004, Singh, Logan, and Gilmartin 2006). Moreover, T_1-weighted images show fluid and bones as the same shade (dark/black) meaning that the true extent of the orbit was difficult to ascertain and I had to depend on the external boundary of orbital fat (white), which may not always necessarily follow the orbital walls perfectly.

Secondly, the clarity and focus of the images in the ocular area was not ensured. This resulted in 49 of the available 89 scans requiring ‘reconstruction’ of the eyeball boundary in some slices. In combination, these factors likely gave rise to measurement error, thus artificially inflating the unexplained variance in the relationship between orbital and eye volumes. Despite this, the relationship remained significant.

To test the closeness of the relationship between human orbital and eyeball size further, it would be necessary to take one of two directions. The first option would be to run optimised T_2-weighted image scans of the eyeball as well as taking computerised tomography (CT) scans of the same subjects for measurement of the boney orbit. Alternatively, the components of the visual system from orbit to V1 could be measured physically postmortem. The first option seems preferable in terms of the ease of collecting the measurements, access to larger samples sizes, ethics approval and the opportunity to collect live body weight data. On the other hand, the latter option could enable the measurement of retina size and rod and cone numbers, in order to investigate the extent to which macro size-scaling reflects neural scaling, as observed across primates (Stevens 2001).

In addition to demonstrating significant positive scaling between orbit and eyeball volume in living humans, I have shown that orbital and eyeball volumes are significantly positively related to visual cortex grey matter volume independently of sex, various measures of overall brain size and motor/somatosensory cortex volume. This supports the idea of mosaic brain change. For instance, thalmic and cortical components of the visual system show a 2-3 fold variation in size between modern human individuals (Andrews, Halpern, and Purves 1997, Ejima et al. 2003), but the inter-individual variation in total brain mass is much lower (~30%), suggesting that the former can vary independently of overall brain size (Andrews, Halpern, and Purves 1997). Independent change in different brain systems is further supported by a twins study showing that genetic clustering distinguishes the occipital lobe from other brain regions, suggesting that occipital development and adult morphology, to the extent that it depends of gene expression, can vary independently to that of other brain units (Chen et al. 2012). Consequently, an enlarged eye should translate into a larger visual cortex, but this would not necessarily correspond to an increase in size of non-visual brain areas.

The diurnal primate analyses also suggested that orbital size is significantly positively associated with V1 volume independently of overall neocortex/brain and body size. Given that V1 is known to scale with downstream visual areas (Barton 2007, Dougherty et al. 2003, Song et al. 2011, Zhong et al. 2009), this relationship likely holds for extrastriate visual areas as well, given sufficient sample size. The significant partial relationship between orbit and visual cortex volumes strongly indicates that scaling between visual system components from orbit to the visual cortex is not solely due to overall scaling of the orbit to cranial or body size.

Factors influencing orbital size in addition to eye size include the degree of orbital convergence and cornea size (Kirk 2006a). However, the degree of orbital convergence is significantly positively associated with lateral geniculate nucleus (LGN) and V1 volumes in primates (Heesy, Kamilar, and Willms 2011), so this probably implies a mediating scaling relationship between orbital volume and the size of the LGN and V1. Overall, the findings presented here suggest that orbital dimensions can be used to look at possible differences in the size of visual brain areas between primate taxa independently of total brain volume and other aspects of cranial morphology.

In theory scaling between orbit/eyeball and V1 might seem somewhat surprising given that across progressively larger primate retinal areas, both foveal diameter (the retinal area of highest cone density and acuity: Franco et al. 2000) and cone number (Finlay et al. 2008) remain fairly constant, whereas the number of rods increases. Given the high degree of rod summation on retinal ganglion cells, one might expect that eye enlargement would not increase the cross-sectional area of the optic nerve very much, if at all. Furthermore, since the fovea is 'overrepresented' in terms of neural tissue volume in the V1 compared to more peripheral areas of the retina (the magnification factor), one might predict that only an increase in the size of the fovea would substantially increase the size of the V1. However, many more rods, even with high summation, would increase the size of the optic nerve. Since V1 scales with positive allometry compared to the LGN (Bush and Allman 2004), V1 might follow a similar scaling pattern regarding the optic nerve as well. A small increase in optic nerve diameter would therefore translate into a proportionally larger increase in visual cortex size even if eye enlargement yields only greater numbers of rods and not cones. Although measured (Figure 2.6), the optic nerve was generally too unclear in the images used here to provide accurate data to infer the degree of summation between photoreceptors and retinal ganglion cells across eye sizes and latitude (see Chapter 3). Consequently, in this chapter I simply sought to test whether 'total' visual cortex volume scales with total eye size. However, future work should aim to assess such scaling effects in finer detail in terms the contributions of rods (periphery) and cones (fovea), especially in relation to the light level hypothesis put forward in Chapter 3.

The findings presented here have several implications for application to fossil hominins. Firstly, it should be noted that when eyeball volume is plotted against orbital volume for diurnal primates, the value for humans lies outside the 95% confidence intervals of the regression line (Figure 2.8), meaning that estimates of eyeball volume from orbital volume probably underestimate actual eye size for humans and perhaps other hominins, especially given the double logged plot. The same is true when visual cortex is plotted against orbital diameter (Figure 2.11): the value for humans lies above the upper 95% confidence limit for the regression line. On the other hand, neither human value falls outside the 95% prediction intervals of the data. Nonetheless, in terms of using an equation to predict visual cortex size from orbit size in fossil hominins, this just means that estimates are likely to be conservative. Furthermore, since it is the relative size of the visual cortex in Neanderthals compared to AMH that is tackled in Chapter 4, the absolute values of estimated surface areas are not paramount. Secondly, although I have corroborated previous findings of significant sex differences in orbit size but not eye size (Chau et al. 2004), the sex of fossil hominins is largely unknown. Given that the primary interest here is in using orbits to infer visual cortex size and that the sex differences observed here are in these two variables, a larger orbit will equate with larger visual brain areas irrespective of whether the reason is linked to the individual's sex or not.

In this chapter I have demonstrated that within living humans and across diurnal primates orbital volume explains variance in both eyeball and visual cortex grey matter volumes independently of overall brain (and body) size. The scaling of orbit to eye to visual cortex size, both within living humans and across diurnal anthropoid primates, means that I am justified in using orbit size to estimate visual system size in fossil hominins and historical humans. The fact that this scaling between visual system components occurs independently of total brain size means that it is possible to use orbit dimensions to explore differences in organisation between two brains of the same absolute size. In the next chapter I use the orbital volumes of two samples of recent historical *Homo sapiens* to test whether latitudinal variation in light levels can drive differences in visual system size within a hominin taxon.

Chapter 3 Do latitudinal trends in light levels drive visual system size in recent historical humans?

Ambient light levels influence visual system size in both birds and primates. Here I argue that the same is true specifically for hominins. Since light levels decrease with increasing latitude, I hypothesise that higher latitude hominins develop larger eyes in order to maintain adequate visual function. To test this I use a sample of recent historical humans (living in the last ~200 years) as an exemplar hominin species, using orbit volume as an index of eye and visual cortex volume. In two independent datasets I demonstrate a significant positive relationship between absolute latitude and recent human orbital volume, the slope of which is identical in the two samples. Due to the scaling between visual system components demonstrated in Chapter 2, this orbital trend is expected to translate into enlarged visual cortices at higher latitudes. I test this using MRI data and verify a significant positive relationship between visual cortex volume and absolute latitude in living humans independently of overall brain size. I also establish that visual acuity measured under full-daylight conditions is constant across latitudes in recent humans, implying that selection for larger visual systems mitigates the reduced ambient light levels found nearer the poles. This provides the first support that light levels drive normal intraspecific variation in visual system size in the modern human population. If this is the case in one hominin species, it could be the case in others. Furthermore, latitudinal light levels might drive differences in brain organisation between hominin species that evolved in and/or inhabited different latitudes.

Introduction

The association between ambient light levels and visual system size is well established across both birds (Thomas et al. 2002, Thomas et al. 2006) and primates (Barton 1996, Barton 1998, Barton 2007, Barton, Purvis, and Harvey 1995, Kirk 2004, Kirk 2006a, Kirk 2006b, Ross and Kirk 2007). In general, lower light conditions during dawn singing in birds (Thomas et al. 2002) or nocturnal activity, particularly hunting mobile prey, in both primates (e.g. Kirk 2006a) and birds (Garamszegi, Møller, and Erritzøe 2002) necessitate larger eyes. Larger eyes allow greater maximum pupil dilation as well as more numerous high-summation[17] rods, enhancing sensitivity. However, higher sensitivity is usually traded against decreased acuity, which in contrast requires denser cones with low summation, but is nonetheless also positively associated with eye size (Kiltie 2000, Walls 1942). Although acuity and sensitivity are generally inversely related, selection for an increase in either could lead to ocular expansion.

Isometric enlargement of the eye improves potential visual acuity by increasing the number of photoreceptors over which the image is spread without changing the image brightness, so that acuity can be increased without loss of sensitivity (Ross and Kirk 2007). Enlarged eyes could enable parallel increases in both sensitivity and acuity, in that they simultaneously (i) enhance light gathering capacity through larger maximum pupil diameters and (ii) increase retinal image size, functionally reducing summation because each receptor field corresponds to a smaller proportion of an image, so more details can be differentiated (Kay and Kirk 2000). Along these lines, it has been suggested that increasing eyeball size allowed the secondarily nocturnal hapolorrhine primates *Tarsius* and *Aotus* to increase visual sensitivity whilst at the same time maintaining relatively high acuity (Kay and Kirk 2000), probably for nocturnal hunting (Kirk 2006a). Selection for enhanced sensitivity and/or acuity under low light levels is thus expected to result in larger eyes.

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[17] That is, many photoreceptors synapsing with each retinal bipolar and in turn ganglion cell.

In general, light availability is lower at high latitudes. Both illuminance[18] and minimum day length decrease with increasing absolute latitude (Powers 1966). Seasonally shorter day lengths create time pressures that likely require activity during the mesopic[19] and scotopic conditions of twilight at dawn and dusk nearer the poles (Stockman and Sharpe 2006, USA Astronomical Applications Department Accessed 2011). Furthermore, compared to the tropics, at higher latitudes twilight lasts longer (Figure 3.1). This means that higher latitude humans are exposed to these lower ambient light levels for a greater proportion of the day, as well as for longer periods of time cumulatively over a year. Although the rate of dark adaptation keeps pace with decreasing daylight at dusk, it does so marginally, meaning that canopy or cloud cover could require additional responses to maintain visual function (Lythgoe 1979). 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. In contrast, under dawn/dusk light levels, larger-eyed humans living at high latitudes may well demonstrate markedly higher acuity than lower latitude individuals.

Given the above, I predict a latitudinal increase in orbital volume and, by implication eyeball size, in modern humans. I test this hypothesis using two independent orbit volume datasets of recent human skulls measured using different methods: (i) the traditional bead method (Pearce and Dunbar 2012) and (ii) imaging software on computerised tomography (CT) scans (Pearce and Buck in prep). Larger eyes should translate into larger visual cortices at higher latitudes and I test this using the MRI data from Chapter 2 (Pearce and Bridge 2013). Since enlarged visual systems should be

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[18] The amount of light incident on the Earth’s surface, which is a function not only of the curvature of the Earth but also of the increased cloudiness, particularly regarding low-level cloud, above ~45˚ latitude, especially in the Northern hemisphere (Wetherald, R. T., and S. Manabe. 1986. An investigation of cloud cover change in response to thermal forcing. *Climatic Change* 8:5-23.).

[19] Mesopic: intermediate light levels between rod saturation and the minimum threshold for cone function, scotopic: when only rods are active.

selected to counteract decreasing light levels in order to ensure adequate visual function, I 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. If latitude is associated with eye size in modern humans, latitudinal light levels may have influenced visual cortex size, and thus perhaps overall brain size and organisation, throughout hominin evolution.

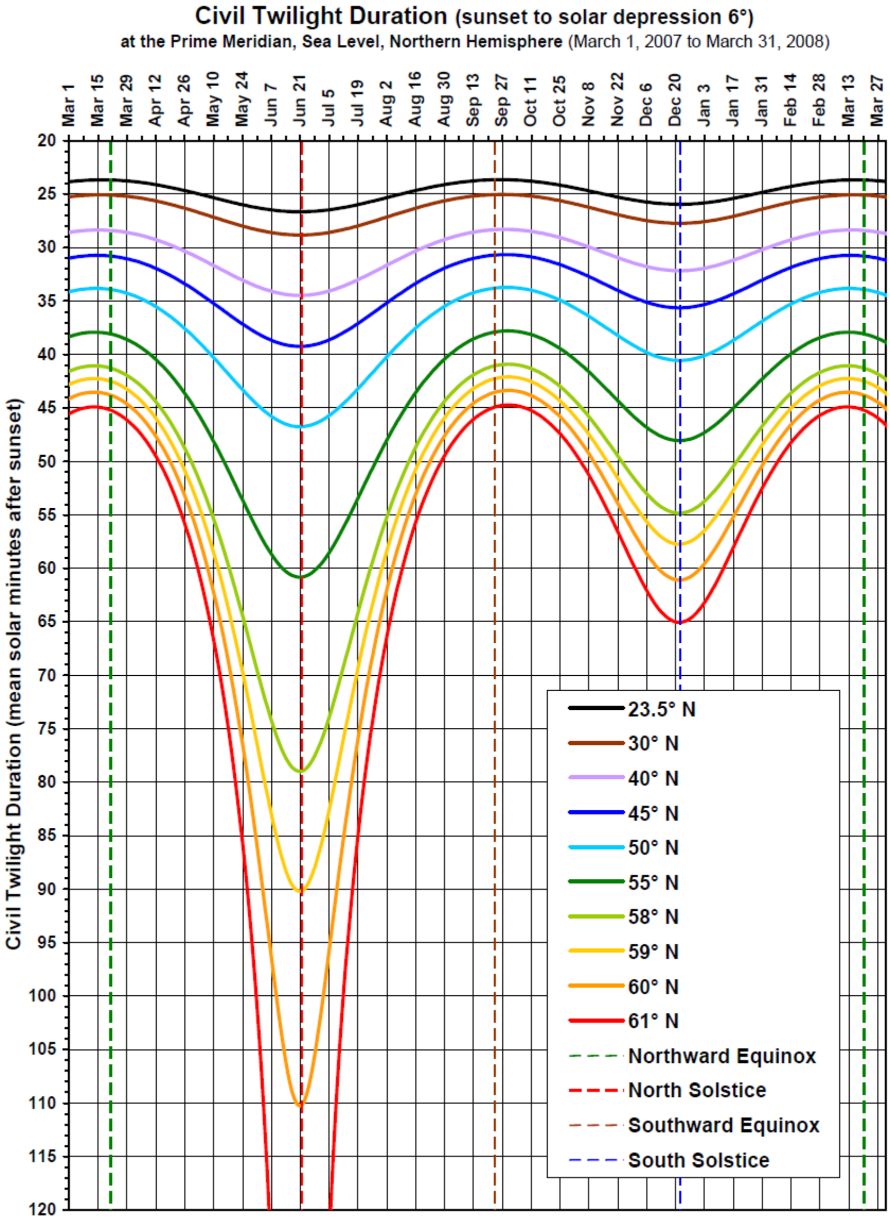

Figure 3.1: Latitudinal and seasonal variation in Civil Twilight duration measured in mean solar minutes after sunset (Bromberg Accessed 2011, permission for use granted).

Method

Morphometric and geographic data for the primary (bead) orbital dataset

I measured endocranial volume, orbital volume and foramen magnum (FM)[20] dimensions for 73 healthy adult crania from the Oxford University Museum of Natural History and the Duckworth Collection, University of Cambridge. I then set a minimum criterion of 3 skulls per population to minimise outlier-effects in calculating population means, yielding 55 skulls from 12 populations (Appendix 2: Table A5) (Pearce and Dunbar 2012: supplementary online material). Since the results were consistent, only the population mean analyses are presented here, because these controlled for possible dependence between individuals sampled from the same population (Pearce and Dunbar 2012). The results presented here were replicated by subsequent, independent analyses using multilevel linear models on the individual-level dataset taking possible differences in intercept and slope across populations into account (Zuur, Pearce, and Ieno 2012).

To measure orbital volume with 1mm diameter glass spheres, I lined the orbits with laboratory film. To measure endocranial volume, apertures were blocked with white tack, and the cranial cavity filled with wax beads (~5mm diameter, ~2mm thick). I measured volumes using graduated cylinders. Precautions were taken to maximise reliability: if the estimates for the two orbital volumes were >2 ml apart (following normal variation (Deveci et al. 2000)), both measurements were repeated and a mean taken. Where only one orbit was intact, the mean of three replications was taken. Where possible I used the mean of both orbits. To check intra-observer reliability, the endocranial volume of four skulls was re-measured, giving an error of ±10ml.

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[20] NB One Australian and one Italian exhibited damaged foramen magna, which could not be measured.

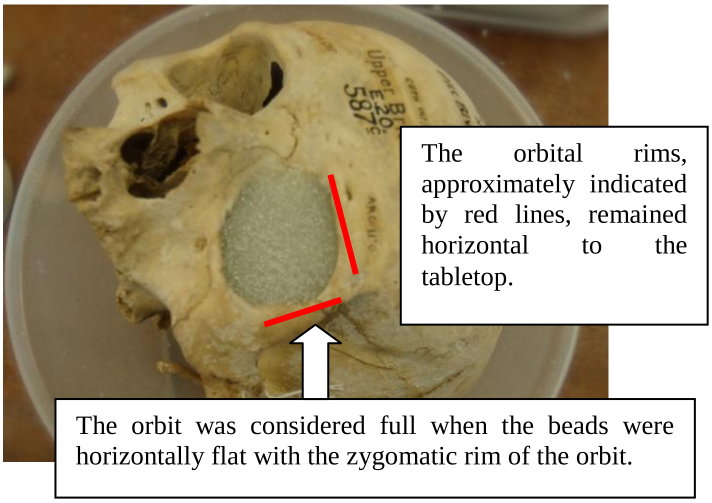
Both orbital volume and brain size are positively related to body mass across primates (Martin 1990, Schultz 1940) and brain size increase with absolute latitude in humans has been linked to body mass effects previously (Beals et al. 1984). Any relationship between orbital volume and absolute latitude could thus be a side-effect of latitudinal body mass increase associated with temperature gradients (Katzmarzyk and Leonard 1998), although note that in Chapter 2 I demonstrated that the relationship between eye and orbit size remains independently of body weight (or a proxy) in diurnal primates and living humans, so orbit increase with latitude could still indicate eyeball increase. To take account of body mass I used FM area to index the volume of neural tissue required for somatic maintenance (Radinsky 1967). Although the use of FM size has limitations because it is correlated with both brain and body size (Martin 1980, Wanner 1971), it is one of the most diagnostic skull measurements for body mass estimates, particularly in hominoids (Spocter and Manger 2007). Since only skulls were available for the present study, FM area remains the best available proxy. I calculated FM cross-sectional area from length and inter-condyle width using the ellipse equation, following Radinsky (1967).

All find-sites or central country latitudes and longitudes were found using http://www.gorissen.info/Pierre/maps/googleMapLocation.php (Gorissen Accessed July 2008, July 2010). I calculated sun altitude at noon for each latitude/longitude coordinate using http://www.ou.edu/research/electron/internet/solarjav.html (Lammi Last modified January 1999, accessed July 2008, Naval Oceanography Portal Accessed July 2008) and calculated $\log_{10}$ illuminance (lux) following Seidelman (1992: 492, Table 9.34.1). Minimum illuminances were identified and transformed into raw form for linear regression. I used http://maps.google.co.uk (Europa Technologies Google) to find the nearest town/city to the latitude/longitude coordinates and obtained minimum mean temperatures (˚C) from www.weatherbase.com (Canty & Associates LLC). Although mean minimum temperature is likely to be more closely related to insulation needs (versus the minimum value of mean monthly temperatures during the year), these data were available for fewer populations than monthly means. However, minimum mean temperature was not available for Somalia, so rather than inflating the variance in the data by combining different temperature measures, I excluded this population from the analyses. Although future work should use historical temperature data, the exact dates and locations of the skulls measured here were unknown, meaning that in these analyses using historical climate data was not possible.

Methods for digital orbit measurement

As well as the glass bead method to measure total orbital volume, partial orbital volumes were measured using Computer Tomography (CT) scans of 27 modern human crania from six populations (Germany, Lithuania, Greenland, Liberia, Australia and India). Laura Buck (currently Roehampton University) conducted measurement using AVIZO 5.0 software (Mercury Computer Systems, Chelmsford, MA, USA) and kindly provided the method on which this description is based, as well as the accompanying figure. I undertook all analyses.

Contrary to the beads method, measurement of the whole volume of the orbit was not possible, because although CT scans and the associated AVIZO software enable the manipulation of 3D reconstructions of the skull, this method does not allow alteration of the original slice orientation: these are fixed images of a cross-section of the original object taken at a particular angle. Measurement of a physical skull allows the lined orbit to be filled up to a imaginary surface horizontal to the orbital rim, whilst the skull is held in position with the occipital resting on a table-top in such a way that the superior and zygomatic rims of the orbit are parallel to the table-top (Figure 3.2). In contrast, manipulation of the CT slices fails to allow this, presumably because the former bead method necessitates a slight downward slant of the nasal area whereas CT slices are likely to be taken vertically in the coronal plane.



The orbital rims, approximately indicated by red lines, remained horizontal to the tabletop.

The orbit was considered full when the beads were horizontally flat with the zygomatic rim of the orbit.

Figure 3.2: Photograph showing the bead method for orbit volume measurement.

In order to allow repeatable measurements, the criterion of measuring orbital volume in coronal view as if it were filled to a flat surface horizontal to the zygomatic rim was followed. This does not completely fill the orbit (Figure 3.3) but does allow consistent measurements to be taken (individual mean errors were <0.55mm^3 for multiple measurements of the same skull) and thus comparisons between specimens to be performed. Once the slice where the zygomatic rim first disappears from view was identified, the orbital rim was delineated in each slice starting from the first slice in which the zygomatic rim was visible and in subsequent slices working posteriorly towards the optic foramen. These accumulated regions of interest (cross-sectional areas delineated in each slice) were segmented out of the overall image and used to calculate volume using the AVIZO toolkit, taking slice thickness into account. The partial volumes of the left orbits (or right orbits when the left one was damaged) were calculated three times and a mean taken.

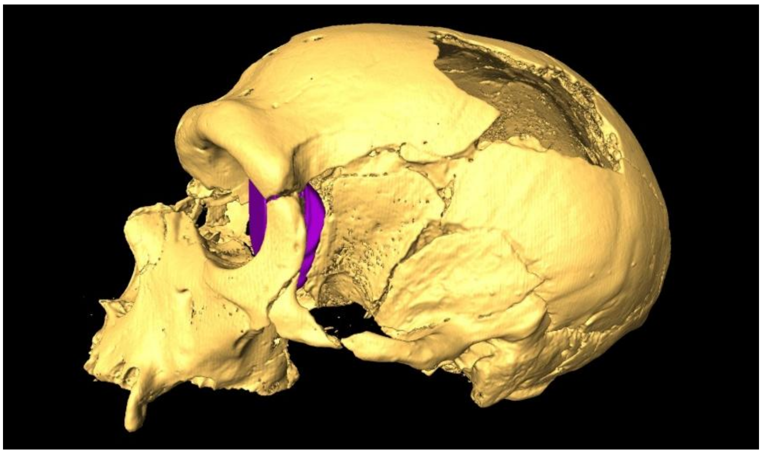


Figure 3.3: The selected orbital volume within the cranium of La Chapelle-aux-Saints. NB although this is a fossil Neanderthal, the measurement method used was identical in the recent human sample.

Phylogenetic controls

To ensure that shared ancestry between populations was not creating spurious relationships or masking others, I conducted PGLM analyses using the caper (formerly caic) package in R (R-Forge Accessed March 2011), see Chapter 2 for background information. For the main orbit$_{bead}$ database and the visual acuity analyses I built trees using genetic distance data (Cavalli-Sforza, Menozzi, and Piazza 1994), whereas for the partial orbit$_{CT}$ database I used a geographic distance matrix and a more recently published tree structure (Li et al. 2008): see Appendix 2 and Pearce & Dunbar (2012: supplementary online material) for more details and tree structures.

Visual acuity dataset

I obtained visual acuity data for native adults measured under ambient photopic conditions from Myers (1902) and Rivers (1898) (Appendix 2: Table A6) (Pearce and Dunbar 2012: supplementary online material), which in some cases involved converting fractions to decimals following Rivers (1898). These measures give the ratio between the distance at which a subject can make out the test stimulus and the standard distance at which the print size subtends an angle of 5 degrees. The populations for which visual acuity data were given in Rivers from other sources and those which were explicitly measured using the same E-stimulus method (where the subject is required to indicate the orientation of the letter, which is systematically altered) are indicated in Appendix 2: Table A6. Limiting the analysis to this subset did not alter the results.

Visual cortex

To test whether visual cortex volume shows a latitudinal trend I used the V1+V2+V5/MT grey matter volumes obtained from MRI scans and the absolute latitude of the research centre where the image was recorded (see Chapter 2 for details of method) (Pearce and Bridge 2013).

Statistical assumptions

Unless otherwise stated, Levene's test for homogeneity of variance found no significant difference between groups. Variables to which t-tests were applied and raw residuals from regression models did not differ significantly from normal distributions (Kolmogorov-Smirnov one-sample test with Lilliefors correction) and complied with heteroscedasticity assumptions.

Results

Testing for latitudinal patterns in orbital volume (bead method)

A significant positive relationship was found between absolute latitude and mean orbital volume (Figure 3.4: t_{10}=6.686, p<0.0001, R^2=0.817). This relationship remained significant when the effects of shared ancestry were partialled out (adjusted R^2=0.799). Maximum-likelihood optimised $\lambda = 6.61e^{-5}$ was significantly different from 1 (χ^2=45.64, p=1.42e^{-11}) but not significantly different from 0 (χ^2=3.4e^{-4}, p=1): phylogeny has little effect on the relationship between absolute latitude and orbital volume even though population clades on the tree tended to be geographically clustered. All subsequent analyses also remained unchanged when shared ancestry was taken into account, so I present only the results of the standard OLS analyses.

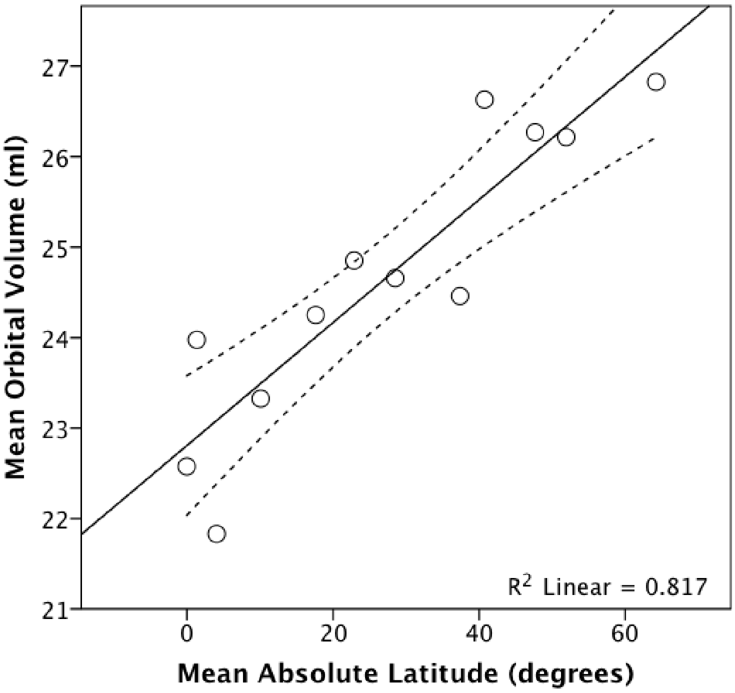


Figure 3.4: Mean orbital volumes for 12 human populations plotted against absolute mean latitude. Dashed lines show 95% confidence intervals.

To account for scaling relationships between eyeball and brain size, I included the interaction between standardised z-scores of endocranial volume and absolute latitude. The OLS model[21] without the interaction term revealed a significant partial correlation between absolute latitude and orbital volume (main effect of absolute latitude: t_9=4.422, p=0.002, overall *adjusted* R^2=0.778) independently of endocranial volume, which itself was not significantly correlated with orbital volume once latitude was partialled out (main effect of endocranial volume: t_9=-0.212, p=0.837). Adding the endocranial volume*absolute latitude interaction term did not change this result[22], even though the interaction term itself was significant (interaction: t_8=-2.401, p=0.043). Since the data

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[21] All variables were standardised z scores.

[22] Main effect of absolute latitude: t_8=5.932, p=0.0003, overall *adjusted* R^2=0.855; main effect of endocranial volume: t_8=-0.798, p=0.448.

were in standardised units, the negative interaction term implies that orbit volume increases faster with absolute latitude than it does with endocranial volume (Figure 3.5). This indicates that the latitudinal increase in human orbital volume is greater than that predicted by scaling with total brain size *per se*. Furthermore, the significant interaction effect but insignificant partial endocranial volume main effect suggests that any relationship between eyeball and brain volume is mediated by the positive association between human brain size and latitude (Beals et al. 1984, Pearce and Dunbar 2012).

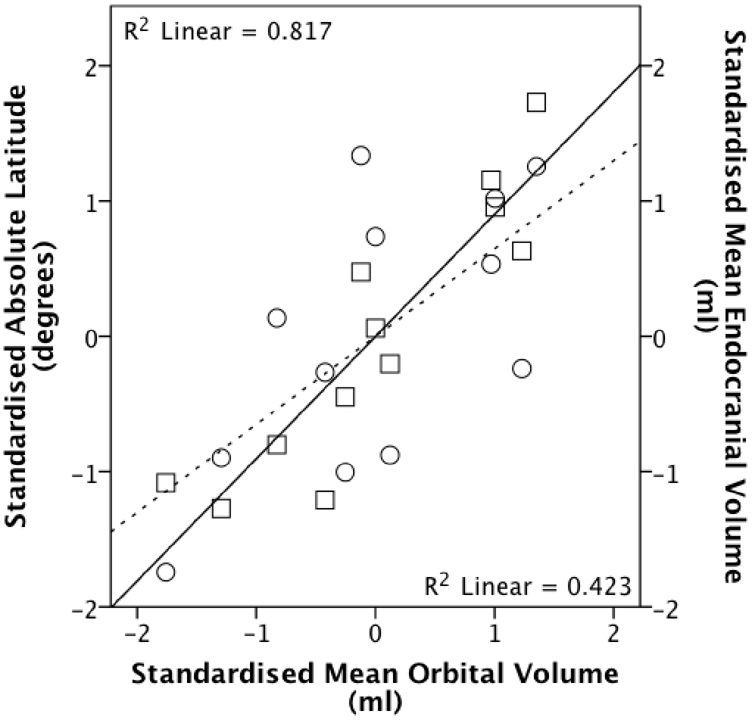

Figure 3.5: Standardised absolute latitude (squares and solid line) and endocranial volume (circles and dashed line) plotted against standardised orbital volume.

Orbital volume remained significantly associated with endocranial volume (t_9=2.712, *p*=0.024, overall *adjusted* R^2=0.365) once the effects of FM area (*p*=0.343), indexing body mass, were partialled out. Furthermore, backwards-stepwise linear regression[23] analysis was conducted from a model predicting standardised orbital volume

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[23] This type of statistical analysis systematically removes variables to produce a best-fit model without significant reduction in R^2. This statistic compares the variance explained by the model to the variance explained in the raw data and is thus not the best measure for comparing fit between alternative models. However, since this material is published I retain the backward regression approach here, but elsewhere I used maximum likelihood for model comparison.

from standardised absolute latitude, endocranial volume and FM area and the two- and three-way interactions between these three independent variables. The best-fit model (Table 3.1) showed a main effect of absolute latitude independent of interaction effects between absolute latitude and/or FM area and endocranial volume. Regardless of the sample used, only absolute latitude consistently showed a significant partial correlation with orbital volume. Overall, this suggests that the latitudinal trend in orbital volume is not merely a manifestation of body enlargement nearer the poles.

Table 3.1: Best-fit model from backward stepwise regression predicting orbital volume for 12 human populations (df=7, overall* adjusted *R^2=0.924).

Model (standardised variables)	**Unstandardised Coefficients**		**Standardised Coefficients**	**t**	**p**	**Collinearity Statistics**	
	B	**SE**	**Beta**			**Tolerance**	**VIF**
(Intercept)	.364	.117		3.098	.017		
Absolute Latitude	1.209	.131	1.209	9.248	.00004	.404	2.475
Endocranial Volume * Absolute Latitude	-.279	.121	-.209	-2.307	.054	.843	1.186
Endocranial Volume * Absolute Latitude * FM Area	-.751	.275	-.451	-2.732	.029	.253	3.951
Absolute Latitude * FM Area	-.644	.216	-.394	-2.987	.020	.398	2.515

Orbital fat and low temperatures

An alternative explanation for latitudinal increases in orbital volume is that eyes require progressively more insulative fat in colder climates. However, although as predicted orbital volume increases as both minimum temperature and minimum illuminance decrease (Figure 3.6), orbital volume remained significantly associated with minimum illuminance (t_8=-2.946, p=0.019, overall adjusted R^2=0.766) when mean minimum temperature was partialled out. In contrast, minimum temperature showed no significant partial relationship with orbital volume independently from illuminance (p=0.934)[24].

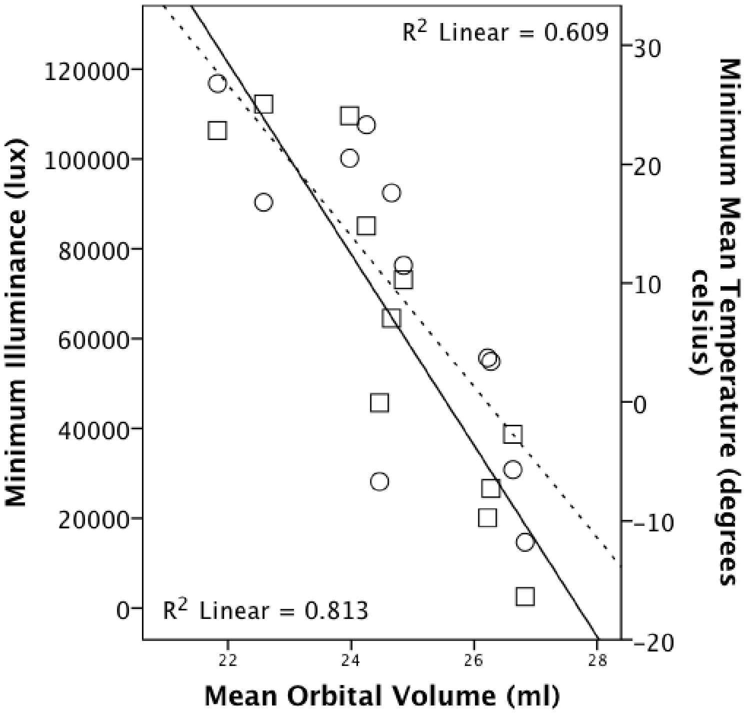

Figure 3.6: Population mean orbital volume plotted against minimum illuminance (lux) (squares, solid line) and minimum temperature (°C) (circles, dashed line).

An issue with this analysis is that both illuminance and temperature are related to insolation (the amount of solar energy received per unit of area and time), which is mediated by latitude and season[25]. I therefore standardised both minimum illuminance and minimum mean temperature by calculating their z-scores and used these to calculate the interaction between them to represent covariance with insolation. Backwards step-wise regression with initial input of standardised minimum illuminance, standardised minimum temperature and the interaction between them predicting standardised orbital volume yielded a best-fit model with minimum illuminance predicting orbital volume (t_7=-6.245,

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[24] These statistics are calculated on revised data and therefore differ slightly from those reported in Pearce & Dunbar (2012).

[25] Although VIF>0.2 (0.315) and Tolerance<10 (3.172), suggesting that multicollinearity between illuminance and temperature was not a severe problem (Field, A. 2009. *Discovering Statistics Using SPSS. 3rd Edition.* London: SAGE Publciations Ltd.).

p=1.505e^{-4}, R^2=0.827): minimum temperature and the interaction term were both dropped with no significant reduction in the variance explained by the model.

Corroborating the latitudinal effect on human orbital volume in an independent dataset

I sought to corroborate this latitudinal trend in orbit size by analysing an independent sample of recent human orbital volumes. After testing for a relationship between these partial[26] orbital volumes (orbit$_{CT,}$ N=27) and absolute latitude, I compared these orbit$_{CT}$ models to the orbit$_{bead}$ total volumes models.

A significant OLS relationship was found between absolute latitude and partial orbit$_{CT}$ volume at the individual level: t_{25}=2.403, p=0.024, R^2=0.188. Excluding outliers made no difference. This confirms the latitudinal trend found in the original orbit$_{bead}$ sample.

As Figure 3.7 suggests, although the slope of the orbit$_{CT}$ line falls within the 95% confidence interval (CI) of the orbit$_{bead}$ regression slope, the orbit$_{CT}$ intercept lies outside the corresponding confidence interval due to the partial versus full volumes used. Removing the outliers (Figure 3.7) increases the slope of the individual-level orbit$_{CT}$ model so that it no longer falls within the 95% confidence intervals associated with the orbit$_{bead}$ models (Table 3.2). However, an ANCOVA (in SPSS: univariate general linear model) revealed that regardless of whether outliers are removed, the orbit$_{CT}$ and orbit$_{bead}$ slopes are not significantly different from each other. The ANCOVA model used 'method' (a dummy variable coding the beads and CT samples as two groups), 'absolute latitude'and the 'method*absolute_latitude' interaction, to predict 'orbital volume'. Both absolute latitude ($F_{1,96}$=16.476, p=0.0001) and method ($F_{1,96}$=95.490, p=4.596e^{-16}) showed

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[26] See Method for an explanation of why we could not measure total orbital volume from the CT scans.

significant main effects, whereas the interaction term ($F_{1,96}$=0.004, p=0.947) did not show a significant relationship with orbital volume (overall *adjusted* R^2=0.785). The significant main effect of method corroborates a significant difference in intercept between the two different method groups. The main effect of absolute latitude indicates that orbital volume measured by either method increases with absolute latitude. However, the lack of a significant partial relationship between the interaction term (method*absolute_latitude) and orbital volume suggests that the way in which orbital volume is related to absolute latitude does not differ significantly between the two groups once scaling associated with the intercept is removed: the slopes of the two lines do not differ significantly from each other and thus the lines are not significantly different from parallel. As stated previously, removing outliers does not alter these results.

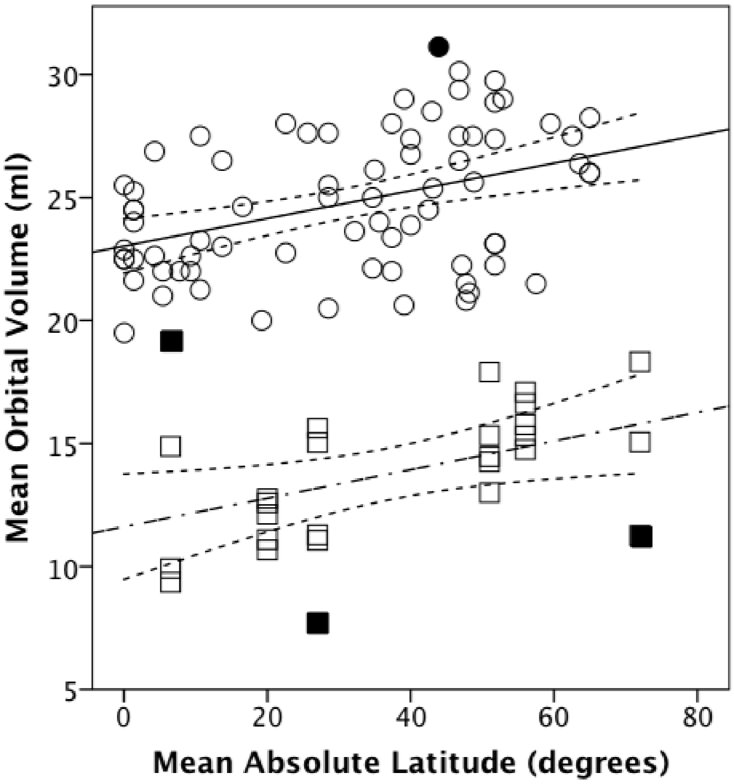

Figure 3.7: Comparison between partial (interrupted line, N=27) and total (solid line, N=73) orbital volumes plotted against absolute latitude, identifying outliers (shaded). 95% confidence intervals are shown for the regression lines.

Table 3.2: Intercepts, slopes and 95% CIs for orbital volume regressed against absolute latitude for the two different methods and for different sub-samples.

Sample Level	**Sample size**		**Bead Method**			**CT Method**		
	Bead	**CT**	**Parameter**	**SE**	**95% CIs**	**Parameter**	**SE**	**95% CIs**
			SLOPES					
All Individuals	73	27	0.056	0.015	0.026 - 0.086	0.058	0.024	0.008 - 0.108
Individuals excluding outliers	72	24	0.054	0.015	0.025 - 0.083	0.091	0.017	0.055 - 0.126
Individuals (populations with ≥3 individuals)	55		0.066	0.014	0.038 - 0.093			
Populations [excluding outliers]	12	6	0.068	0.010	0.046 - 0.091	0.051 [0.087]	0.021 [0.007]	-0.008 - 0.111 [0.068-0.106]
			INTERCEPTS					
Individuals	73	27	23.028	0.554	21.922 - 24.133	11.618	1.04	9.475 - 13.760
Individuals excluding outliers	72	25	23.024	0.539	21.948 - 24.100	10.510	0.738	8.981 - 12.040
Individuals (populations with ≥3 individuals)	55		22.927	0.504	21.916 - 23.937			
Populations [excluding outliers]	12	6	22.807	0.346	22.036 - 23.578	11.863 [10.65]	0.964 [0.31]	9.185 - 14.540 [9.78-11.51]

To overcome the problem of lack of independence between individuals sampled from the same population, I calculated mean orbital volume for each of the orbit$_{CT}$ populations (Table 3.3). Plotting these against absolute latitude yielded two clusters (Figure 3.8) corresponding to ‘high’ (>40˚) and ‘low’ (<40˚) latitude groups. An independent sample t-test revealed that higher latitude populations (*M*=15.260, *SD*=0.566,

N=3) had significantly larger orbits than lower latitude populations (M=12.44, SD=0.784, N=3): t_4=5.051, p=0.007, R^2=0.864. Removing outliers made no difference. These findings were replicated when controlling for shared ancestry via a PGLM, with high and low latitude groups coded as a dichotomous dummy variable.

Table 3.3: The populations used in the CT method sample, giving mean population orbital volumes and their standard deviations.

Population	N	Absolute Latitude	Latitude Group 1=Low 2=High	Mean Orbit Volume (ml)	SD (ml)	Mean Orbit Volume, Outliers Excluded (ml)	SD (ml)
Australia	5	27	1	12.14	3.24	13.25	2.41
Germany	5	51	2	14.99	1.83		
Indian	5	20	1	11.85	.92		
Greenland	3	72	2	14.88	3.54	16.69	2.31
Liberian	4	6	1	13.33	4.61	11.39	3.04
Lithuanian	5	56	2	15.91	.95		

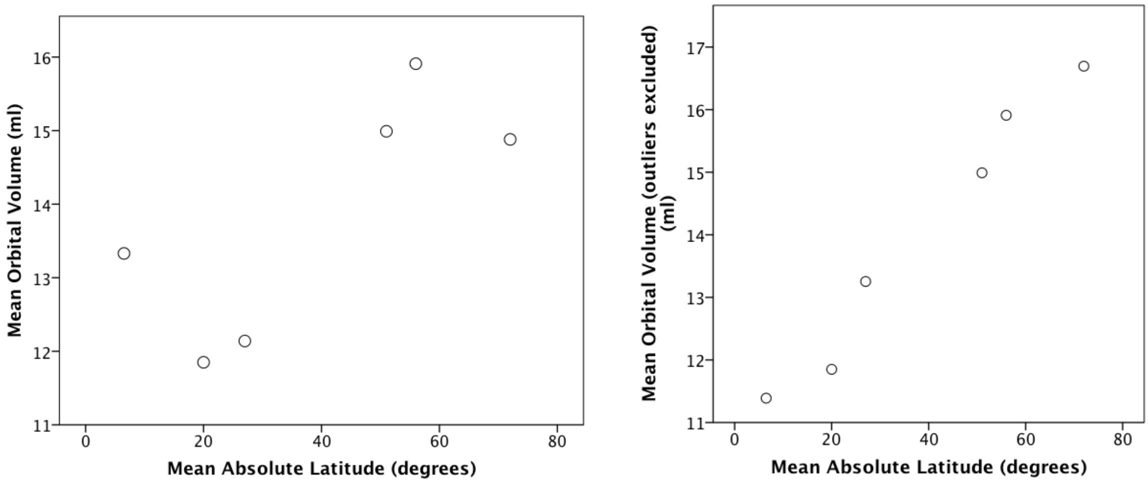

Figure 3.8: Population mean orbital volumes from the CT method plotted against absolute latitude, including (LEFT) and excluding (RIGHT) outliers. OLS regression revealed a significant positive relationship when outliers were excluded (t_4=12.520, p=2.341e^{-4}, R^2=0.975) but not when they were included (t_4=2.388, p=0.075). The slopes of both these models lie within the 95% confidence intervals of the population-level orbit$_{bead}$ model slope and vice verse (Table 3.2).

Testing for latitudinal patterns in visual acuity

If ambient light levels select for eyeball enlargement to maintain constant photopic visual acuity, acuity measured under natural daylight conditions should not vary systematically with absolute latitude; instead, I hypothesise that enlarged eyes should compensate for decreases in illuminance, thus causing the acuity curve to flat-line. As predicted, acuity and latitude are not significantly correlated (Figure 3.9), even when the sample is restricted to samples measured using a standard method (*N*=10). This result supports the hypothesis that larger visual systems allow humans to mitigate the lower light levels of higher latitudes.

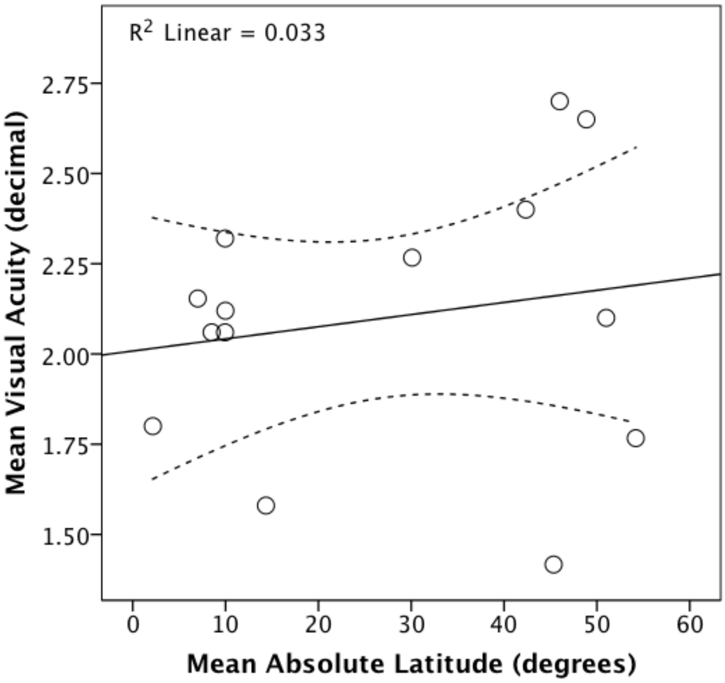

Figure 3.9: Visual acuity for 14 human populations (Myers 1902, Rivers 1898) plotted against absolute latitude. Dashed lines show 95% confidence intervals for the regression line.

Absolute latitude and visual cortex volume

OLS regression revealed that total visual cortical grey matter volume was significantly positively associated with absolute latitude (t_{96}=3.275, *p*=0.001, Figure 3.10) independently of rest-of-cortex grey matter volume (t_{96}=7.701, p<10^{-36}): overall *adjusted*

R^2=0.428. This result was replicated when controlling for the alternative measures of overall brain volume (see Chapter 2) and when sex was also included in the models. In the full sample absolute latitude also shows a positive relationship with eyeball volume (t_{86}=2.045, p=0.044, R^2=0.046), which remains independently of non-visual brain volume, brain stem + cerebellum volume and subcortical grey matter volume. In the higher quality scan sample both orbital and eye volume are positively related to absolute latitude, but not significantly (orbit: t_{38}=0.845, p=0.403; eye: t_{38}=0.797, p=0.430).

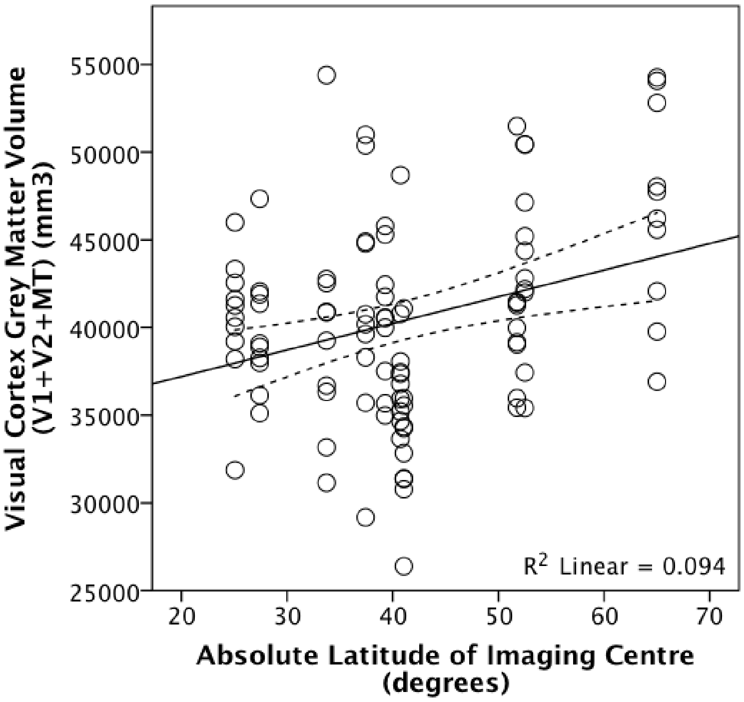

Figure 3.10: Visual cortex (V1 + V2 + V5/MT) grey matter volume plotted against the absolute latitude of the imaging centres where the MRI scans were taken for 99 living humans (see Chapter 2). The dotted lines represent 95% confidence intervals for the regression line.

Discussion

Using two independent datasets collected using different methods, I have shown that in recent historical humans orbital volume significantly increases with absolute latitude independently of shared ancestry, brain size and an index of body mass. Furthermore, despite the constraints imposed by the CT method, both total (bead) and partial (CT) orbit measurements demonstrated the same volume increase per unit latitude: standardised beta was 0.433 and 0.408 respectively for the full sample individual-level models. In addition, the fact that the relationship between minimum illuminance and total orbital volume holds true even when controlling for minimum temperature implies that selection has acted on eyeball size rather than insulating packing. Overall, these analyses provide strong support for a robust positive relationship between absolute latitude and modern human orbital volume, implying enlarged eyes and visual cortices in humans nearer the poles.

Furthermore, the MRI data analysed here directly support the hypothesis that higher latitude living humans have larger visual brain areas compared to those living nearer the equator, even though (i) the subjects likely used more powerful and pervasive artificial lighting, so any latitudinal effect on visual system size was expected to be less pronounced than in historical populations, and (ii) the subjects may not have been local to the area where they were scanned, meaning that they might have expressed the visual system sizes of their ancestral or natal latitude rather than that of the research centre. Consequently, a more controlled sample would probably demonstrate a much stronger effect. One implication of increasing visual cortical volume with latitude is that this might help explain the enlargement of the human brain in individuals living further from the equator (Beals et al. 1984). That is, larger visual areas may translate into brain increase overall. Preliminary examination of the data presented here and in Pearce and Dunbar (2012) would seem to support this: there is a ~20% increase in both orbital volume (thus eyeball size) and endocranial volume (thus brain size) between equatorial Micronesians and high latitude Scandinavians.

The finding that human visual acuity under ambient photopic conditions remains constant across latitudes implies selection for enlarged eyeballs as modern humans occupied successively higher latitudes, so that visual function could be maintained despite decreasing light levels. If this is so, then measurement under standardised light conditions should yield increasing acuity with absolute latitude, particularly at meso/scotopic levels. Along parallel lines, Reimchen (1987) argued that higher prevalence of colour-blindness in higher latitudes manifests an adaptation to high acuity under twilight conditions. In support of this association, adult Norwegians born above the Arctic circle have been found to be less sensitive to colour (measured under constant light levels), especially if born in the autumn when light levels are lowest (Laeng et al. 2007). However, in laboratory tests no differences in scotopic sensitivity or perception have been found between red-green colour-blind or monochromat subjects compared with colour-normal control subjects (Simunovic, Regan, and Mollon 2001). Nonetheless, further work into the effect of latitude on vision could benefit from merging the hypothesis presented here with that of Reimchen.

A pertinent question is whether these apparent visual system size differences are genetically encoded adaptations that have arisen over the last ~45 thousand years (ky) of modern human colonisation of higher latitudes (Benazzi et al. 2011, Higham et al. 2011, Hoffecker 2009, Pavlov, Svendsen, and Indrelid 2001), particularly during the last 13ky or so since the retreat of the Last Glacial Maximum (LGM) (Barton et al. 2003). The relatively high heritability (25-50%) of occipital lobe morphology (Bakken et al. 2012) might support a genetic component to this latitudinal trend. Such a genetic basis would imply that individuals that migrate away from their ancestral latitude should show ‘residual’ or ‘lagging’ visual system sizes. Alternatively, eyeball increase and the accompanying enlargements in other visual system components could be purely developmental: created each generation in response to childhood lighting conditions. This is supported to some extent by evidence for a link between light levels and the eyeball elongation associated with myopia (e.g. Deng and Gwiazda 2011, Fulk, Cyert, and Parker 2002, Mandel et al. 2008, McMahon et al. 2009, Mutti and Marks 2011, Rose et al. 2008a, Rose et al. 2008b, Vannas et al. 2003). Light levels might also determine normal ocular growth.

Taken together, the findings presented in this chapter suggest that latitudinal decrease in light levels leads to increasing visual system size in recent modern humans. Since latitudinal variation in light levels appear to drive intraspecific variation in humans, the same might be true within other hominin species. Furthermore, such an effect could translate into taxonomic differences between hominin species that evolved at different latitudes. By comparing the orbital dimensions of these different taxa, it should be possible to uncover potential differences in visual cortex volumes between them. Such differences might indicate variation in internal brain organisation hitherto hidden inside endocasts of surface morphology. In the next chapter I take Neanderthals and contemporary AMH as a case study in order to explore whether these closely related taxa differed in the proportion of their brains dedicated to visual processing.

Chapter 4 Using cranial morphometrics to investigate brain organisation in Neanderthals and Anatomically Modern Humans

Neanderthals evolved in and solely inhabited high latitudes, whereas contemporary AMH evolved in lower latitude Africa and had dispersed into higher latitude Eurasia more recently. Given the positive relationship between absolute latitude and orbital size in recent modern humans, I hypothesise that Neanderthals have larger orbits than contemporary AMH. Using three independent datasets I show that although the size of Neanderthal orbits are not positively related to latitude (probably because their latitudinal range is restricted compared to that of recent modern humans), Neanderthals do have significantly larger orbits than contemporary AMH. I also demonstrate that there is no significant difference in absolute endocranial volume between Neanderthals and AMH dated 27-75kya. In addition to the larger visual cortices implied by their larger orbits, Neanderthals probably had larger somatic brain regions associated with their greater body mass. I show that taking the proposed differences in body and visual system size into account yields significantly smaller 'standardised' endocranial volumes for Neanderthals compared to contemporary AMH. I conclude that in conjunction, larger visual and somatic regions within a similar sized brain suggest that (i) Neanderthals and AMH had differently organised brains and (ii) Neanderthals would have had less neural tissue available for other brain regions compared to AMH. I discuss avenues for future research in terms of the influence of phylogeny and facial morphology on orbit size.

Introduction

Neanderthals and AMH provide an interesting case study to investigate the stresses placed on hominin social network maintenance at different latitudes. Whereas Neanderthals seem to have evolved from *Homo heidelbergensis* in Eurasia ~130 thousand years ago (kya), AMH evolved from African *Homo heidelbergensis* populations ~200kya, with a most recent common ancestor ~400-600kya (Klein 2009, Langergraber et al. 2012, Scally and Durbin 2012, Stringer 2012)[27]. Although the increasing evidence that Neanderthals inter-bred with AMH (Condemi et al. 2013, Endicott, Ho, and Stringer 2010, Green et al. 2010, Neves and Serva 2012, Sánchez-Quinto et al. 2012, Sankararaman et al. 2012, Yang et al. 2012) (but see Eriksson and Manica 2012) has been used to question their classification as a separate species, most would agree that these two hominin populations are anatomically and genetically distinct. In any case, examples of interspecific breeding have been reported for other primates (Jolly et al. 1997). Regardless of low levels of interbreeding, Neanderthals and AMH differ at numerous loci and were geographically isolated for long enough for substantial morphological, behavioural and cognitive differences to have arisen through both drift and selection arising from their different latitudinal environments.

Similar overall brain size, asymmetry[28] and sulcal patterns have been taken as evidence that Neanderthals and AMH had the potential for similar cognitive capacities, assuming corresponding neural similarities (Gabi et al. 2010, Herculano-Houzel et al. 2007, Herculano-Houzel and Kaas 2011, Holloway 1981, Holloway 1985, Lent et al. 2012). However, the widespread focus on overall brain size as one of the only features unambiguously available from the fossil record may mask other important aspects of comparisons between AMH and Neanderthal brain anatomy and cognition (Holloway 1983, Holloway 2001, Holloway 2007, Holloway and Post 1982). For instance, there is no guarantee that the brains of Neanderthals and AMH were organised internally in the same way in terms of the relative sizes of different anatomical and functional regions. Whilst there is some overlap in cranial trait variation, when means and combinations of traits are

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[27] Note that others have argued for a common ancestor, *H. helmei*, 300-250kya (Lahr, M. M., and R. A. Foley. 1998. Towards a Theory of Modern Human Origins: Geography, Demography, and Diversity in Recent Human Evolution. *Yearbook of Physical Anthropology* 41:137-176.)

[28] Most show typical left-occipital and right-frontal petalia.

considered there is clear separation (Weaver, Roseman, and Stringer 2007). Endocranial shape differences appear early in ontogeny, followed by more rapid[29] and possibly differently shaped developmental trajectories in Neanderthals compared to AMH (Bastir, O'Higgins, and Rosas 2007, Gunz et al. 2012, Gunz et al. 2010, Ponce de Leon and Zollikofer 2001). For instance, AMH undergo a ‘globularisation’ phase soon after birth, which is absent in both Neanderthals and chimpanzees (Gunz et al. 2012). Differences in ontogeny and external adult morphology might reflect differences in internal brain organisation between Neanderthals and AMH.

Neanderthals evolved under lower light levels and in generally colder, more seasonal, less resource-dense habitats than AMH. These environmental differences may have selected for differently organised brains in these two taxa. However, to what extent specific brain areas can change under selection independently of other brain regions remains a matter of debate (Barton 1996, Barton 1998, Barton 2001, Barton 2007, Barton and Harvey 2000, Barton, Purvis, and Harvey 1995, Finlay and Darlington 1995, Finlay, Darlington, and Nicastro 2001, Finlay et al. 2008). At one extreme is the view that across mammals the size of all brain areas depends on total brain volume. At the opposite end of the spectrum, each brain area is considered to be under independent selection, creating a mosaic of areas whose relative sizes differ between taxa, reflecting their specific niche requirements. In reality it is probable that phylogenetic, developmental and functional constraints set a general framework for brain structure, with selection on specific subsystems producing variation between brains. Even the chief proponents of unitary brain evolution acknowledge that the ‘unexplained error’ in their model leaves room for taxa straying from the allometric line (Finlay and Darlington 1995, Finlay, Darlington, and

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[29] Contrasting with stature, where the rate of growth is slower in Neanderthals, probably due to nutritional stress (Martín-González, J. A., A. Mateos, I. Goikoetxea, W. R. Leonard, and J. Rodríguez. 2012. Differences between Neandertal and modern human infant and child growth models. *Journal of Human Evolution* 63:140-149.).

Nicastro 2001). In other words, taxon-specific brain organisation remains possible, with the reduction of some brain areas and expansion of others relative to total brain size. Indeed, there is evidence that areas comprising particular subsystems in the brain have undergone correlated size changes independently of other subsystems (Barton and Harvey 2000, Barton, Purvis, and Harvey 1995, de Winter and Oxnard 2001). In this regard, particular attention has been paid to the scaling of the visual system independently of other neural systems, both across mammals (Barton 2007), within primates (Barton 1996, Barton 1998) and now in living humans (Chapter 2, Appendix 1). Specific selection on the size of visual brain areas is thus possible.

As detailed in Chapter 3, in recent modern humans larger eyeballs seem to be necessary in order to attain adequate visual acuity and/or sensitivity under the lower light levels of higher latitudes (Pearce and Dunbar 2012). Similarly, since Neanderthals exclusively inhabited higher latitudes above 30 degrees North, they might be expected to have larger eyeballs than contemporary AMH, who had dispersed into such areas relatively recently (Pearce, Stringer, and Dunbar 2013). Due to scaling between visual system components from eyeball to V1 and through successive visual areas (Chapter 2, Appendix 1 and Pearce and Bridge 2013, Pearce and Dunbar 2012), larger Neanderthal eyeballs may have translated into volumetric enlargement throughout their visual cortex (Pearce, Stringer, and Dunbar 2013). This is supported by the fact that compared to AMH Neanderthals have relatively larger occipital lobes (Balzeau, Holloway, and Grimaud-Hervé 2012). Furthermore, differences between these taxa have been identified in Brodmann’s Area 19 in the extrastriate (peristriate) cortex and Brodmann’s Area 37, which overlaps the fusiform gyrus region associated with face, body and word recognition (Holloway 1985).

Visual areas in the occipital lobe project to association areas in the parietal lobes, and to some extent these lobes can be considered as a developmentally and functionally integrated unit (Bruner 2010). For instance, the positioning and relative size of the Neanderthal occipital bun[30] has been postulated to be a side-effect of the development of their flattened parietals (Gunz and Harvati 2007). This parietal flattening is the culmination of a general allometric trend in hominins, but Neanderthals additionally show non-allometric superior lateral extension, creating their 'en bombe' posterior cranial profile (Bruner 2010). In contrast, AMH show a non-allometric overall increase in parietal surface area, as well as apparently more complex vascular impressions over the parietal surface (Bruner 2010). Unlike the occipital lobe the parietals also contain non-visual areas, so although the parietals as a whole are smaller in Neanderthals compared to AMH (Balzeau, Holloway, and Grimaud-Hervé 2012), the shape differences could still point to internal differences, including larger visual association areas in Neanderthals. If so, this would necessitate that Neanderthals had smaller areas underlying other parietal functions compared to AMH. I discuss possible differences in temporal and frontal lobe morphology between these taxa in relation to social cognition in Chapter 5, but it should be noted that these lobes also house visual areas. The impact of different visual processing requirements between Neanderthals and contemporary AMH might thus be manifested in specific areas throughout the brain.

In addition to possible visual system differences, Neanderthals show different body proportions, with broader trunks and shorter limbs than AMH (Weaver 2009, Weaver and Steudel-Numbers 2005), as well as a greater overall body mass (Ruff, Trinkaus, and

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[30] Although both classic Neanderthals and early European AMH manifest large occipital buns, perhaps due to prolonged growth of larger brains (Trinkaus, E., and M. LeMay. 1982. Occipital bunning among later Pleistocene hominids. . *American Journal of Physical Anthropology* 57:27-35.), Neanderthals differ in the relative size and positioning of their buns compared to AMH (Gunz, P., and K. Harvati. 2007. The Neanderthal "chignon": Variation, integration and homology. *Journal of Human Evolution* 52:262-74.), suggesting possible organisation differences in the posterior brain between these taxa.

Holliday 1997). These are adaptations to the habitual activity loads (mobility and dietary regimes) and lower temperatures associated with high latitudes (Holliday 1997, Ruff 1994, Sorensen and Leonard 2001, Weaver 2003, Weaver and Steudel-Numbers 2005). Since larger bodies are likely to require more neural tissue for somatic maintenance and control, Neanderthals brains are expected to have had larger somatic areas compared to those of AMH (Dubois 1933, Holloway 1981, Pearce, Stringer, and Dunbar 2013, Ruff, Trinkaus, and Holliday 1997). Thus, their higher latitude range may have been reflected in Neanderthal brain organisation in relation to both vision and somatic control. For a meaningful comparison, fossil AMH and Neanderthal brain volumes need to be adjusted for at least these two effects.

However, since orbital dimensions are influenced by both facial and body size (Chapter 2), any differences in orbit size between Neanderthals and AMH might merely reflect the more robust morphology of Neanderthals. Across primates and between the sexes larger body size is linked to relatively smaller eyes within orbits (Schultz 1940), so the larger bodied Neanderthals might have had larger orbits but the same sized eyes as AMH. Nevertheless, in Chapter 2 I demonstrated that the relationship between eye and orbit size remained significant independently of body weight across diurnal primates, as did the relationship between orbit and visual cortex (V1) size. Regardless of body size differences, therefore, if Neanderthals have larger orbits, it is likely that they also had larger eyes and larger visual cortices. However, different facial morphologies might still play a role. The faces of newborn Neanderthals are already larger and more projecting than those of AMH neonates with similar endocranial volumes and the neonatal orbital shape is clearly distinguishable between these taxa (Gunz et al. 2012). Although the larger Neanderthal supraorbital bar (brow ridge) probably would not affect orbit size (there is no relationship between the two across primates: Ravosa 1991), greater Neanderthal prognathism might. For instance, the tucking of the face under the neurocranium could increase competition for space between the frontal lobe and the contents of the orbits, leading to smaller orbits in AMH compared to Neanderthals (Masters 2008, Masters 2012). A full evaluation of the influence of facial morphology on the relationship between orbit and eye size requires a geometric morphometric approach, which is beyond the scope of this current work. However, here I examine the impact of taking linear measures of face height and breadth into account in the orbit size comparisons between Neanderthals and AMH.

If a greater proportion of the Neanderthal brain was invested in visual and somatic regions, this may have led to (i) Neanderthals having larger brains than AMH overall or (ii) Neanderthals having less brain tissue to facilitate other cognitive processes and thus differently organised brains compared to AMH. Alternatively, previous work suggests that AMH had larger cerebella than Neanderthals (Weaver 2005) and this might ‘counterbalance’ greater Neanderthal investment in somatic and visual brain areas, so that neither Neanderthals nor AMH had a relative reduction in other brain areas compared to the other taxon. However, this would still indicate differential organisation within the same-sized brain. If Neanderthal brains were organised differently, this could have implications for their cognitive capacities, including their ability to keep track of large social networks.

In this chapter I test the following hypotheses: (i) orbit size increases with absolute latitude in Neanderthals, (ii) Neanderthals have significantly larger orbits than contemporary AMH, (iii) Neanderthals have the same sized endocranial volumes as contemporary AMH, (iv) once the size of their bodies and visual cortices (estimated from orbit size) are taken into account, Neanderthals differ in the size of their ‘corrected’ endocranial volumes compared to contemporary AMH and (v) taking account of Neanderthals' smaller cerebella does not remove the difference between the 'corrected' endocranial volumes of Neanderthals and contemporary AMH. In order to test the latter two hypotheses I recalibrate Neanderthal and fossil AMH endocranial volumes for differences in body mass, visual cortex volume and cerebellum volume, by standardising the endocranial volumes to the proportions expected for an average *H. sapiens* individual. This enables comparisons to be made as if Neanderthal and AMH brains were organised in the same way. By doing so, I test whether the predicted differences in the size of visual, somatic and cerebella brain areas might have created substantial differences in brain organisation between these closely related hominin taxa.

Method

Unless otherwise stated, variables and regression residuals did not differ significantly from a normal distribution (Kolmogorov-Smirnov one sample test with Lilliesfors correction) and Levene's test found no significant difference in variance between groups. Effect sizes are reported as R^2. All reported findings are replicated when the AMH sample is limited to specimens found within the approximate Neanderthal range in Eurasia (versus also including AMH from East Asia and Africa).

Endocast volumes

I used endocast volumes for 25 Neanderthals and 39 AMH dated 27-200ky (Holloway 2004), see Table A7 in Appendix 3 (Pearce, Stringer, and Dunbar 2013 supplementary online material). I excluded AMH younger than 27ky so that the AMH specimens were as close in time to the Neanderthal specimens as possible (Neanderthals were extinct by 28kya (Finlayson et al. 2006), although probably earlier (Wood et al. 2013)). I also excluded from the analyses specimens dated older than 200kya as being taxonomically arguable, but include them for reference in Figure 4.6. From the original endocast sample I also excluded children and infants (Engis 2, La Quina 18, Skhul 1, Qafzeh 11, Atapuerca 6, Sungir 3 (De Miguel and Henneberg 2001, Osaka City University Accessed 2011)). I included the Kostenki and adult Sungir specimens, now dated to ~35kya (Marom et al. 2012). I also re-classified the Skhul and Qafzeh specimens as AMH rather than Neanderthals following current consensus. Using alternative endocranial volume databases (Bailey and Geary 2009, De Miguel and Henneberg 2001) produces essentially the same results, indicating that my findings are robust to discrepancies in volume determinations. However, I present only the analyses using the endocast dataset here (Pearce, Stringer, and Dunbar 2013).

In Appendix 3 (Table A8, Figure A10) I present the results of an alternate method, which predicted fossil hominin brain volumes from endocranial volumes before standardising for body and visual system size. In this chapter corrections are made on the endocranial volumes directly in order to reduce the number of estimation steps and the associated compounded error accrued around the mean estimates (Pearce, Stringer, and Dunbar 2013).

Body mass

In order to calculate body mass correction factors, I calculated the ratio between living human and fossil hominin body masses. Multiplying the absolute fossil endocranial volumes by this factor standardised them by the same ratio. This gave the equivalent endocranial volume expected for a living human. Since the relationship between brain and body size is not isometric, I used body mass raised to the 0.646 power in this calculation, which Isler et al. (2008) report as the common slope for ln-transformed endocranial volume regressed on body mass across primates once grades are taken into account. In addition to removing the body mass differences between Neanderthals and AMH, this overcame artefacts of recent secular decrease in *H. sapiens* brain/body size (e.g. Henneberg 1998). Corrections taking sex and latitude into account made no difference to the findings.

I first split my fossil endocranial volume sample into date-groups based on those used in Ruff et al (1997): Table 4.1. This meant that the specimens were allocated body masses depending on date rather than taxonomic allocation *per se*, so in theory the body mass correction procedure is not biased by taxonomic classification of specimens. In reality, all but one date-group corresponds to either AMH or Neanderthals (Table 4.1).

Table 4.1: The system by which the date-groups used here relate to the date-groups outlined in Ruff et al (1997).

Ruff et al (1997) date groups (kya) (used to calculate body mass correction factors in the present study)	Specimens	Date range for the relevant specimens in the present study (kya)	Aggregated date groups used in the present study (kya)
0 (living)	AMH	n/a	n/a
21 – 35	AMH	27 - 35	27 - 75
36 - 75	Neanderthals	40 - 60	27 - 75
	AMH	37 - 70	27 - 75
90	Skhul/Qafzeh AMH	100 - 110	76 - 200
100 - 150	Neanderthals	120 - 170	76 – 200

Although for the calculation of body mass correction factors I maintained the Ruff et al (1997) date-groups, for subsequent analysis I aggregated these into two all-encompassing date-groups: 27-75ky and 76-200ky. Categorisation in this particular way rather than equal division of the whole date-span is due to the discrepancy in body mass between Neanderthals in these two date categories (Ruff, Trinkaus, and Holliday 1997), which I discuss below. In addition, this strategy maximised sample size in both date categories.

Orbital size

Orbital areas were from Kappelman (1996), orbital height (OBH) and breadth (OBB) measurements were supplied by Chris Stringer (who also provided nasion-prosthion height and bimaxillary breadth data) and I measured orbital volumes using the Duckworth Collection at the University of Cambridge and collections at the Natural History Museums of Oxford and London, following the method described in Chapter 3. The specimens used are indicated in see Table A7 in Appendix 3. Volumes did not include brow-ridges, since the orbits were filled with beads up to a line continuous with the lateral and medial rims, following Schultz (1940).

Since eyeballs are not perfectly spherical, it is likely that orbital volume would give the most accurate indication of overall eyeball size (Appendix 1) and therefore retinal and visual cortex size. However, since the bones within the orbit are fairly fragile, very few fossils have survived with fully intact orbits. In contrast, the orbital rims are more robust and therefore more likely to survive post-depositional processes (Kappelman 1996) and therefore measurements of the orbital rims allow larger samples to be compiled. Furthermore, orbital and eyeball diameters rather than volumes have been used to study visual system scaling across primates (Kay and Kirk 2000, Kirk 2006a). In this study, orbital aperture area and orthogonal linear measurements provide an index of eyeball maximum coronal cross-sectional area and diameter respectively.

Due to the logistical issues surrounding access to original fossils, I relied mainly on casts to measure orbital volumes, although I was able to measure the original Gibraltar 1

(Forbes Quarry) fossil[31]. However, the parallel use of areal and linear measurements of actual fossils acts as a test of validity for the orbital volume analysis. I included La Ferrassie and Skhul 5 regardless of their fragmentary orbits because both have some internal orbital bones intact and accurate rim reconstruction is possible (Kappelman 1996). I also included Amud even though the interior orbital bones are missing because the rims of this specimen are fully intact, thus allowing fairly accurate reconstruction of the orbits. Where only one orbit of a cast was unfilled (Brno 3 and Guattari/Monte Circeo 1), it was measured 3 times and a mean calculated. I calculated 'mean orbital volume' by averaging either (i) left and right orbital volumes or (ii) repeat measurements of one orbit when only one orbit was available.

Methods for estimating visual cortex volume differences

I calculated visual cortex corrections using a number of computational steps, which I summarise before giving details below. Insufficient volumetric data are available for primate visual areas beyond V1 to produce an equation relating orbital size directly to total visual cortex volume. Instead, I (i) estimated fossil visual cortical surface areas from orbit height (OBH, the measurement for which I had most fossil data[32]) using a primate-derived equation, and (ii) converted these into volumes by multiplying by cortex depth. I (iii) assumed a 2mm thickness for grey matter to estimate volumes and (iv) used a primate equation to estimate white matter volume from grey matter volume. I then (v) totalled grey and white matter volumes to give 'total' visual cortex volume.

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[31] It should be noted that, in addition, I attempted to use the imaging software OsiriX to measure orbital volume in CT scans of the actual fossils, but similarly to the issues outlined in Chapter 3, the angle of the scanned slices prevented standardised measurements from being taken because (i) the whole orbital rim was not visible in coronal view in the more anterior slices and (ii) it proved impossible to delineate a constant anterior level through the slice sequence in either the sagittal or axial views.

[32] Although the primate data are transverse diameters (widths), non-hominin primate orbits are circular (Kirk, E. C. 2006a. Effects of activity pattern on eye size and orbital aperture size in primates. *Journal of Human Evolution* 51:159-170.) so these are comparable to hominin OBHs.

In order to estimate total visual surface area from orbit diameter in the fossils, I used the PGLM primate equation given in Chapter 2, which predicts $\log_{10}$ visual cortex surface area from $\log_{10}$ orbital diameter (Figure 4.1)[33]: $log_{10}totalvisualSA=-1.99(95\%\ CIs\ -3.60\ -\ -0.38)+4.33(95\%\ CI\ 3.00\text{-}5.66)*log_{10}orbitdiameter$ (*adjusted* R^2=0.964). I used OBH to estimate 'total' visual cortex (V1+V2) surface area for each individual fossil in the endocast volume dataset for which Stringer provided data, and converted these surfaces into total combined grey and white matter volumes. First, I calculated total grey matter volume by multiplying the surface area estimates by 2mm, which is a reasonable estimate of cortical grey matter thickness in both humans (Lukatela and Swadlow 2004, Pakkenberg and Gundersen 1997, Rockel, Hiorns, and Powell 1980) and macaques (Rockel, Hiorns, and Powell 1980). I then estimated white matter volume from grey matter volume using a RMA regression equation, using data from Bush & Allman (2003): $t_{19}=56.28$, $p<0.001$, $R^2=0.994$, $log_{10}white=-0.81(95\%\ CI\ -0.72\ -\ -0.93)+1.32(95\%\ CI\ 1.24 - 1.43)*log_{10}grey$. The parameters of a PGLM do not fall outside these 95% confidence intervals (PGLM: $log_{10}white=-0.79+1.29*log_{10}grey$). However, I chose to use the RMA model because (i) this is more appropriate when there is measurement error on both axes and the relationship between variables is symmetrical (Smith 2009) and (ii) because there was a visual difference in the fitted regressions lines (Figure 4.2) and models based on OLS tend to underestimate the slope. For the OBH-visual cortex model the RMA and PGLM lines are almost identical and I used the phylogenetically-controlled model (Figure 4.1). Finally, I summed the estimated white matter volumes with the grey matter volume estimates to get 'total' (V1+V2) visual cortex volume. Once I had calculated total visual cortex volume estimates for each fossil, I calculated the residual to the AMH mean for each date group

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[33] This equation differs slightly from that used in Pearce et al (2013) because here I use the mean for two macaque species from a single database used for all the primate orbit diameter data (Kay & Kirk 2000), whereas for the publication we used data for a single macaque species from a different database (Kirk 2006a). The fossil estimates thus differ very slightly from those reported in Pearce et al (2013).

for each Neanderthal fossil. I also calculated the difference between the species' means in each date group (27-75ky: 124cm^3, 76-200ky: 64cm^3).

After correcting for body mass differences as outlined above, I standardised the Neanderthal endocranial volumes by subtracting the difference in visual cortex volume between AMH and Neanderthals (individual residuals or differences between date-specific means where OBH was unavailable) from the respective Neanderthal body-mass-standardised endocranial volumes. In other words, all Neanderthal endocranial volumes were recalibrated as if they were organised in the same way as the average AMH brain (i.e. without enlarged visual cortices), whilst also taking individual differences within the Neanderthal species into account as far as possible.

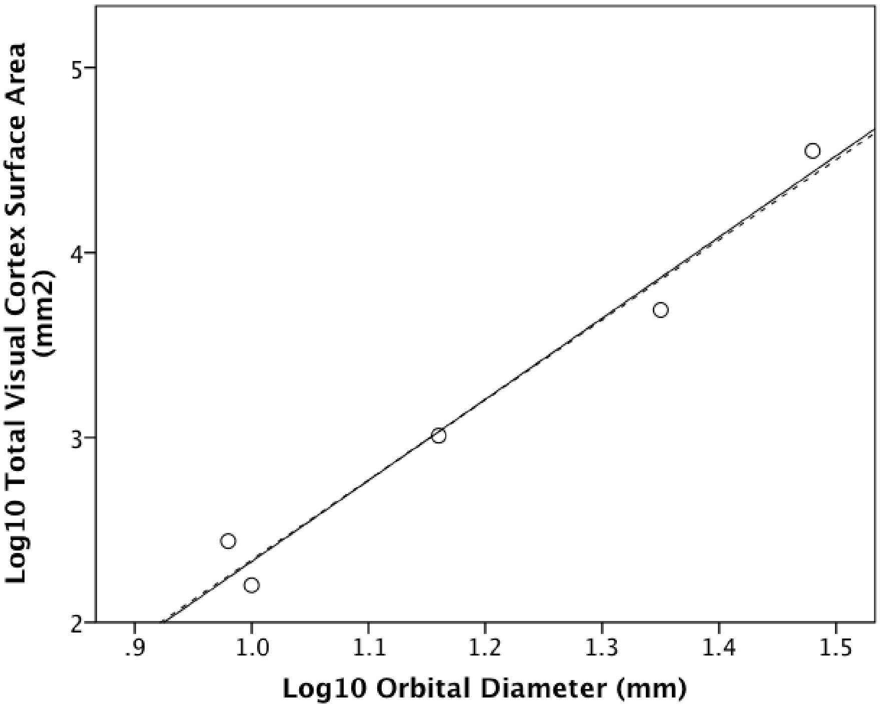

Figure 4.1: Log$_{10}$ total visual cortex volume plotted against log$_{10}$ orbital diameter for 5 primate species. The solid line represents the RMA regression and the dashed line the PGLM equation.

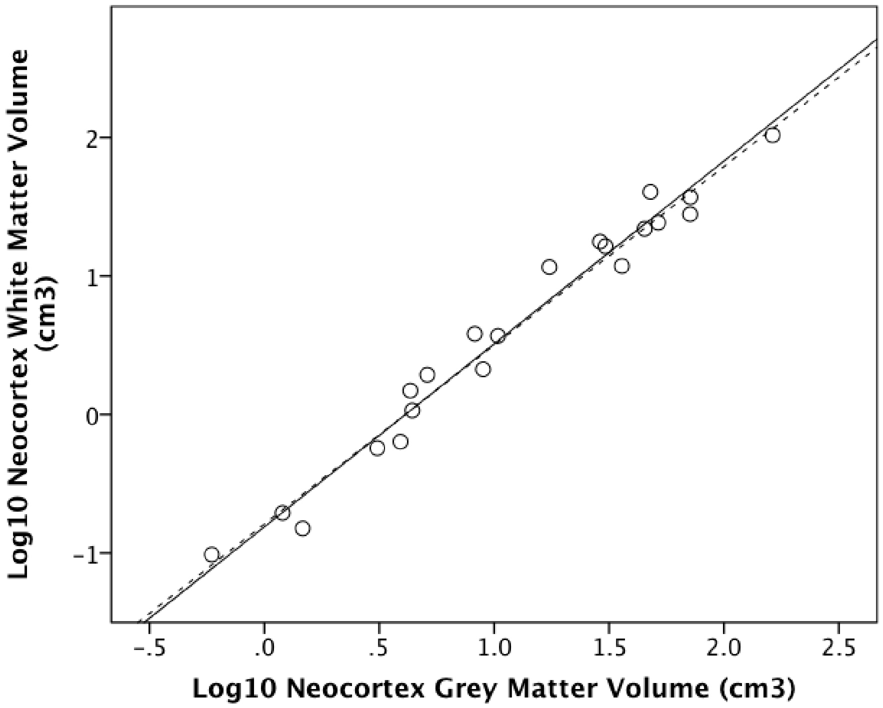

Figure 4.2: Log$_{10}$ neocortex white matter plotted against log$_{10}$ neocortex grey matter volume for 21 primate species (data from Bush 2003). The solid line represents the RMA regression and the dashed line the PGLM equation.

Accuracy of visual cortex volume estimates

To assess how realistic the estimates of visual cortex volume were, I compared the fossil estimates to the MRI measurements of visual cortex grey matter (Table 4.2) for living humans (Chapter 2, Appendix 1). I converted the MRI-derived grey matter volumes into white matter volumes in order to calculate total (grey + white) volumes using the mean modern human neocortex white:grey matter ratio (0.761: Bush and Allman 2004). This gave a mean V1+V2[34] white matter volume of 26.13cm^3. This translates into a total (grey+white) volume of 60.469 cm^3 (range: 37.01 – 84.25 cm^3) for living humans. These values lie within the range of visual cortex estimates for the fossil AMH but not the Neanderthal sample (Table 4.3).

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[34] V1+V2 is more comparable with the primate data used to estimate fossil visual cortex size than also including V5/MT.

Table 4.2: Descriptive statistics for MRI measurements of cortical grey matter volumes for 99 living humans (see Chapter 2 for more details).

	Grey Matter Volume (cm^3)					
	V1	**V2**	**MT**	**V1+V2**	**Non-visual Cortex (Total minus Visual)**	**Brain (mask)**
N	99	99	99	99	99	99
Mean	9.234	25.104	6.095	34.338	419.338	1461.649
Std. Deviation	1.866	3.770	.795	5.325	49.755	179.707
Minimum	5.151	15.863	4.644	21.014	326.609	1118.639
Maximum	14.144	36.450	8.892	47.843	530.429	2033.975

Table 4.3: Descriptive statistics for fossil visual cortex volume estimates. 'Minimum/maximum' values correspond to estimates for individual specimen in the sample. 'Lower/upper' values correspond to cumulative error around the means of these estimates.

Taxon		Estimates for Fossil Visual Cortex Volume (cm^3)		
		Lower	**Mean**	**Upper**
Neanderthals	N	12	12	12
	Mean [SD]	170.66 [24.152]	202.48 [29.004]	242.24 [35.127]
	Minimum for the sample	122	144	171
	Maximum for the sample	208	248	297
AMH	N	15	15	15
	Mean [SD]	78.44 [31.712]	92.24 [37.744]	109.33 [45.302]
	Minimum for the sample	41	47	55
	Maximum for the sample	140	166	197

However, the living human estimates fall outside the 95% confidence limits of both the mean Neanderthal (181.826 – 221.134 cm^3) and mean AMH (71.413 – 113.067 cm^3) visual cortex estimates. Nonetheless, Figure 4.3 shows that the AMH fossil estimates are much more closely aligned with the visual cortex volumes expected for living humans than are the estimates for Neanderthals. Overall, the fossil estimates seem fairly accurate, given the closer correspondence between fossil and living AMH compared to Neanderthals and the fact that the living human values were also partially estimated.

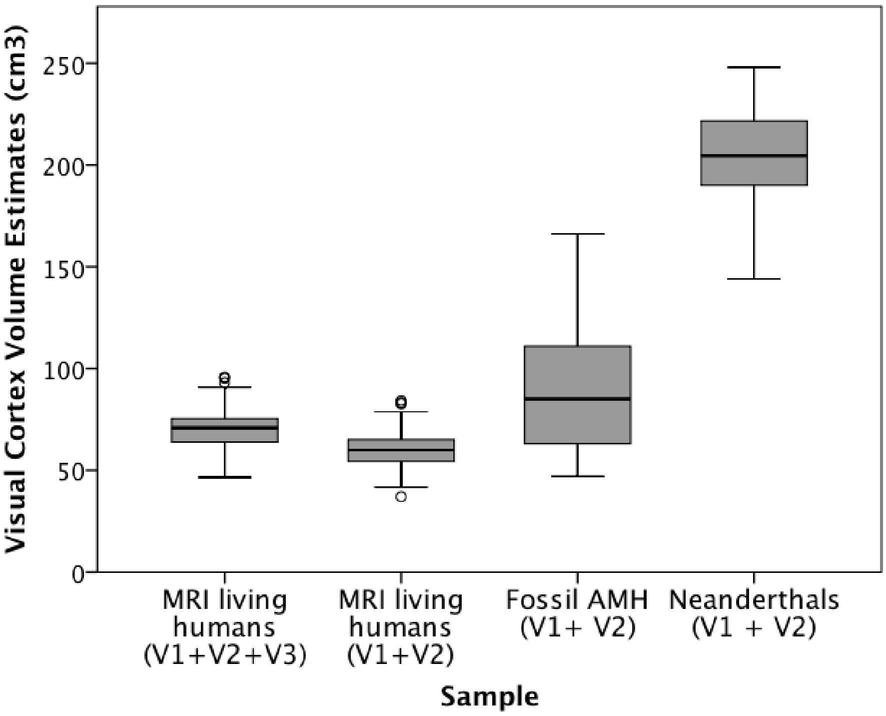

Figure 4.3: Estimated visual cortex volume for living humans (MRI measurements, see Chapter 2) and fossil AMH and Neanderthals. The horizontal lines represent the medians and the grey boxes represent the interquartile range.

Cerebellum volume differences

I calculated the difference between the recently living human (51 populations comprising 1416 individuals) and Neanderthal (La Ferrassie and La Chapelle-aux-Saints) mean cerebella volumes (converted from posterior cranial fossa (PCF) by Weaver (2005)) (139.76 minus 106.35=33.41cm^3), transformed this into mm^3 and added it to the mean body mass and vision corrected Neanderthal endocranial volumes, making them the overall volume that they would be if they belonged to an average (living) human.

These analyses likely overestimated the difference in cerebellum volume between fossil AMH and Neanderthals, since the cerebella difference between the Neanderthals and the almost contemporary Cro-Magnon AMH individual was only 12.57 cm^3. The cerebella correction I used thus provides a conservative test of whether such cerebella differences could mitigate any difference in standardised endocranial volume associated with somatic and visual cortical differences between these two hominin species.

Incorporating estimate error

Computing standardised endocranial volumes requires a series of steps, which each introduce error into the subsequent estimates. In this chapter I am interested in comparisons between taxon means: rather than being interested in the error accrued for the standardised endocranial volume estimate for each individual specimen, what is crucial is the compounded error attached to the calculated mean per taxon group. In other words, the central issue is the parameter (taxon mean) error rather than the population error. I therefore built a model in R to calculate the cumulative standard error of the mean standardised endocranial volume for each taxon/date group by, at each computational step, taking not only the mean estimate but also the mean estimate plus or minus the standard error (*SE*: for means) or standard error of the estimate (*SEE*: for regressions, following (Ruff, Scott, and Liu 1991)). I then took these three values ((i) mean estimate, (ii) mean estimate plus *SE*/*SEE*, (iii) mean estimate minus *SE*/*SEE*) into the next step of the estimation process. Once I had calculated the standardised endocranial volumes, I then calculated the sample mean for the (i) mean, (ii) upper (cumulative 'mean plus SE/SEE' estimates) and (iii) lower (cumulative 'mean minus *SE*/*SEE*' estimates) estimates for each of the taxon and date-group subgroups of specimens. The means of the upper and lower estimates for each sample were taken as representing the cumulative *SE* around the mean. I plot these cumulative standard error bars in Figure 4.6.

Results

Absolute latitude and orbit size

OLS found that none of the measures of Neanderthal orbit size were significantly associated with the absolute latitude of fossil find sites (Figure 4.4).

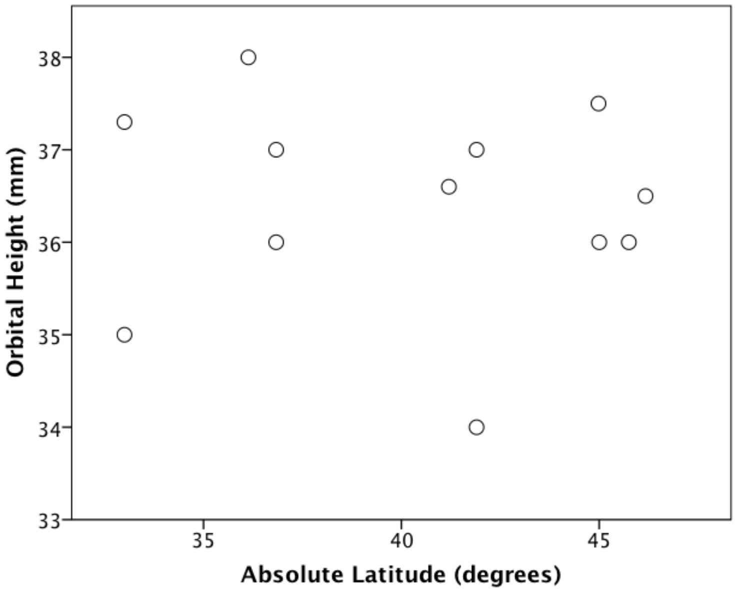

Figure 4.4: Orbital height (OBH) plotted against absolute latitude for 12 Neanderthals, as an example of the lack of a latitudinal trend in Neanderthal orbit dimensions.

The lack of a latitudinal trend may be due to a combination of small sample size and the restricted latitudinal range covered by Neanderthals compared to recent modern humans. This probably also explains the lack of a latitudinal trend in orbit size for the fossil AMH sample, which predominantly also comes from Europe. Taking the date of the fossils into account made no difference to the models.

Orbit size comparisons between Neanderthals and AMH

Independent-sample t-tests confirmed that Neanderthals had significantly larger orbits than contemporary AMH (Table 4.4). These results were repeated when the sample was limited to the 27-75kya date group.

Table 4.4: Orbital dimensions compared between AMH and Neanderthals from all date-groups using independent (two-tailed) t-tests. *Corrected for unequal variances.

Orbit:	**Neanderthals**		**AMH**		**Independent t-test**		
	Mean (SD)	**N**	**Mean (SD)**	**N**	**t**	**p**	**R^2**
Area (mm^2)	1404.98 (94.24)	6	1223.39 (130.00)	10	2.952	0.011	0.38
Height (mm)	36.41 (1.11)	12	30.63 (2.59)	15	7.777*	<0.001	0.71
Breadth (mm)	44.07 (2.19)	11	41.80 (2.78)	15	2.245	0.034	0.17
Volume (cm^3)	34.15 (3.40)	5	29.51 (2.07)	4	2.387	0.048	0.45

Face size

Although facial height and breadth do not differ significantly between Neanderthals and AMH within the 76-200ky date-group sample, within the younger 27-75kya specimens Neanderthals have significantly larger faces both horizontally and vertically (Table 4.5). Figure 4.5 shows orbital height and breadth as ratios against orthogonal (controlling for potential whole-part problems) and parallel facial dimensions (bimaxillary breadth and nasion-prosthion height). Independent t-tests revealed that the OBH/NPH and OBB/ZMB ratios show no difference between Neanderthals and AMH in either date group. In fact, in the 76-200kya date group there are no significant differences for any of the relative orbit measures. However, in the 27-75kya date group both orthogonal ratios show significant differences, but in opposite directions. Neanderthals (N=8) have significantly larger orbit heights relative to facial breadths compared to AMH (N=6): t_{12}=3.264, p=0.007, R^2=0.470. In contrast, AMH (N=9) have significantly larger orbital breadths relative to nasion-prosthion heights compared to Neanderthals (N=8): t_{15}=6.515, p=9.767e^{-6}, R^2=0.739.

Table 4.5: Descriptive and independent t-test statistics comparing nasion-prosthion height and bixmaxillary breadth between Neanderthals and AMH, split by date-group.

Date Group	**Facial Dimension**	**Taxon**	**N**	**Mean**	**SD**	**Independent t-test**			
						t	**df**	**p**	**R^2**
27-75ky	Nasion-Prosthion Height	AMH	9	64.90	5.76	-7.398	15	$2.226e^{-6}$	0.78
		Neanderthals	8	85.78	5.86				
	Bimaxillary Breadth	AMH	6	98.00	3.58	-4.384	13	0.001	0.60
		Neanderthals	9	111.44	6.86				
76-200ky	Nasion-Prosthion Height	AMH	4	73.00	4.02	-2.323	4	.081	n/a
		Neanderthals	2	83.50	7.78				
	Bimaxillary Breadth	AMH	3	107.33	2.08	-.094	1.059*	.940	n/a
		Neanderthals	2	108.00	9.90				
*Corrected for unequal variances.									

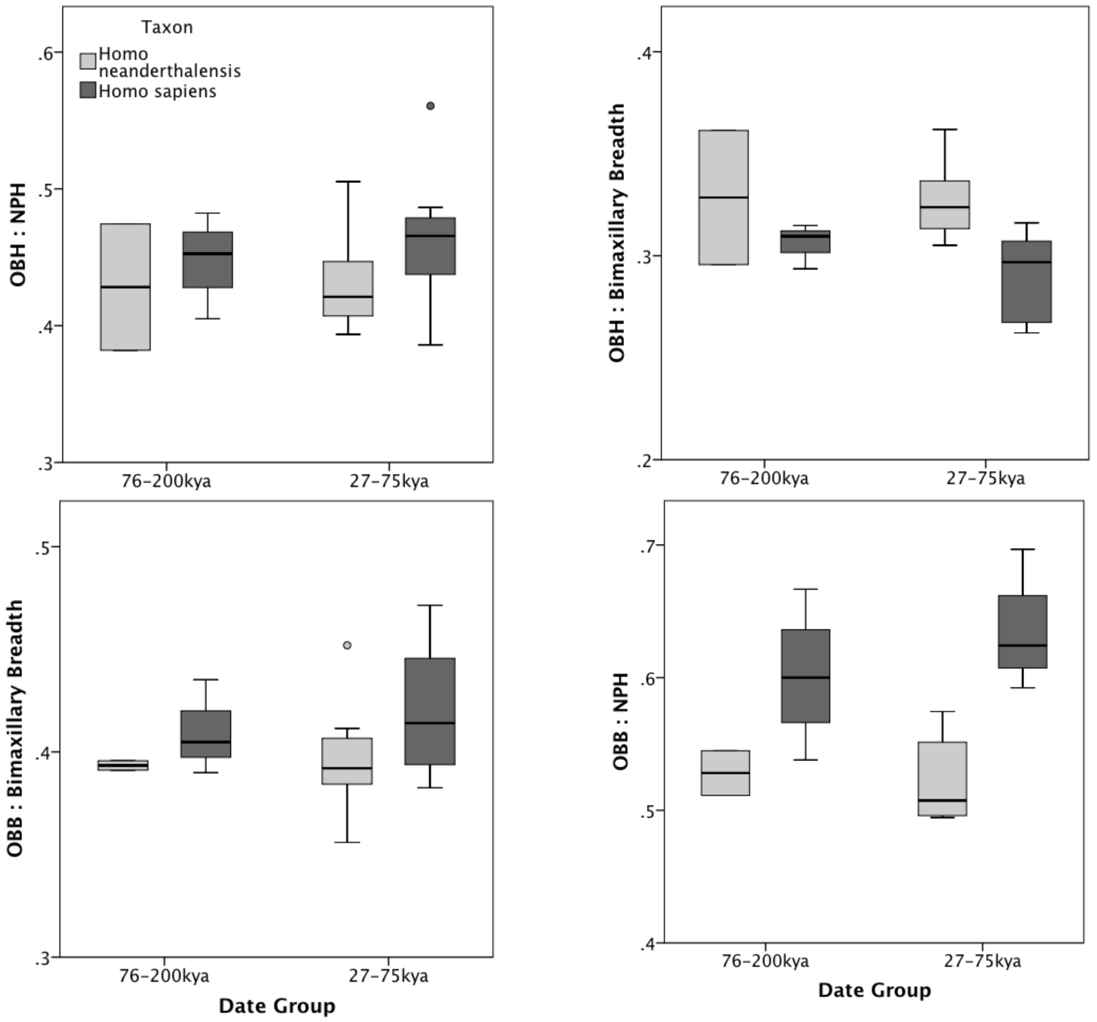

Figure 4.5: Boxplots comparing the ratios between orbital height and nasion-prosthion height (TOP LEFT) or bimaxillary breadth (TOP RIGHT) and between orbital breadth and bimaxillary breadth (BOTTOM LEFT) or nasion-prosthion height (BOTTOM RIGHT) between AMH and Neanderthals in the 27-75ky and 76-200ky date-groups.

Accounting for body mass and visual system size differences

Independent-sample t-tests found no significant difference in raw/absolute endocranial volume between AMH and Neanderthals dated 27-75kya (Figure 4.6, Table 4.6). However, older AMH dated 76-200kya had significantly larger endocranial volumes than Neanderthals of a similar date (Figure 4.6, Table 4.6). Neanderthals dated to 27-75kya had significantly larger endocranial volumes than those dated 76-200kya (t_{19}=3.513, p=0.003, R^2=0.411). AMH date groups showed no significant difference (p=0.061).

Comparison of 'corrected' or 'standardised' endocranial volumes shows that adjusting for differences in body and visual system size results in the disparity between the two Neanderthal date groups disappearing (Figure 4.6). In effect, the younger Neanderthals (27-75kya) show no increase in non-somatic/non-visual brain size compared to the older Neanderthals (76-200kya) and archaic humans. These younger Neanderthal 'standardised' endocranial volumes are significantly smaller than those of contemporary AMH within the 27-75kya date group (Table 4.6). This suggests that later Neanderthal brains comprised a significantly larger proportion of neural tissue associated with somatic and visual function compared to the brains of contemporary AMH.

In the 27-75kya date group, the mean standardised Neanderthal endocranial volume (M=1130 cm^3, *95% CIs*=1033-1227 cm^3, N=13) lies outside the 95% confidence intervals of the mean absolute endocranial volume of recently living humans (M=1373 cm^3, *95% CIs*=1335-1410 cm^3, N=55 living in the last ~200 years, data from Pearce et al (2012) and Chapter 3). In contrast, the living human mean lies within the 95% confidence interval of the fossil AMH mean (M=1332 cm^3, *95% CIs*=1287-1377 cm^3, N=32).

Table 4.6: Independent-sample t-test statistics for comparisons between AMH and Neanderthals for 'raw/absolute' and 'corrected/standardised' endocranial volume, split by date group.

Date Group (kya)	Endocranial Volume Variables		Taxon		Independent t-test (two-tailed)		
			AMH	Neanderthals	t	p	R^2
27-75	Absolute Endocranial Volume (cm^3)	N	32	13	0.008	0.994	n/a
		Mean	1473.84	1473.46			
		SD	135.96	180.92			
	Corrected Endocranial Volume (cm^3)	N	32	13	4.520	<0.001	0.32
		Mean	1332.41	1129.79			
		SD	126.45	158.92			
76-200	Absolute Endocranial Volume (cm^3)	N	6	8	7.169	<0.001	0.81
		Mean	1535.50	1271.00			
		SD	48.87	78.14			
	Corrected Endocranial Volume (cm^3)	N	6	8	8.516	<0.001	0.86
		Mean	1405.11	1092.20			
		SD	48.39	79.136			

Endocranial volumes standardised for differences in visual system size alone also yielded a significant difference between Neanderthals (M=1342, SD=185, N=13) and AMH (M=1474, SD=136, N=32) in the 27-75ky date-group: t_{43}=2.640, p=0.011, R^2=0.139. There is no significant difference when only body mass is taken into account in the 27-75ky date group (p=0.082), although AMH still have larger body-mass-standardised brains than Neanderthals (AMH: M=1332, SD=126, N=32; Neanderthals: M=1254, SD=154, N=13). Both visual-only (t_{12}=8.324, p=2.497e^{-6}, R^2=0.852) and body mass-only (t_{12}=7.297, p=9.517 e^{-6}, R^2=0.816) corrections are associated with significant differences between Neanderthals and AMH in the 76-200kya data group (AMH: visual-corrected M=1536, SD=49, N=6, body-mass-corrected M=1405, SD=48, N=6; Neanderthals: visual-corrected M=1207, SD=86, N=8, body-mass-corrected M=1156, SD=72, N=8).

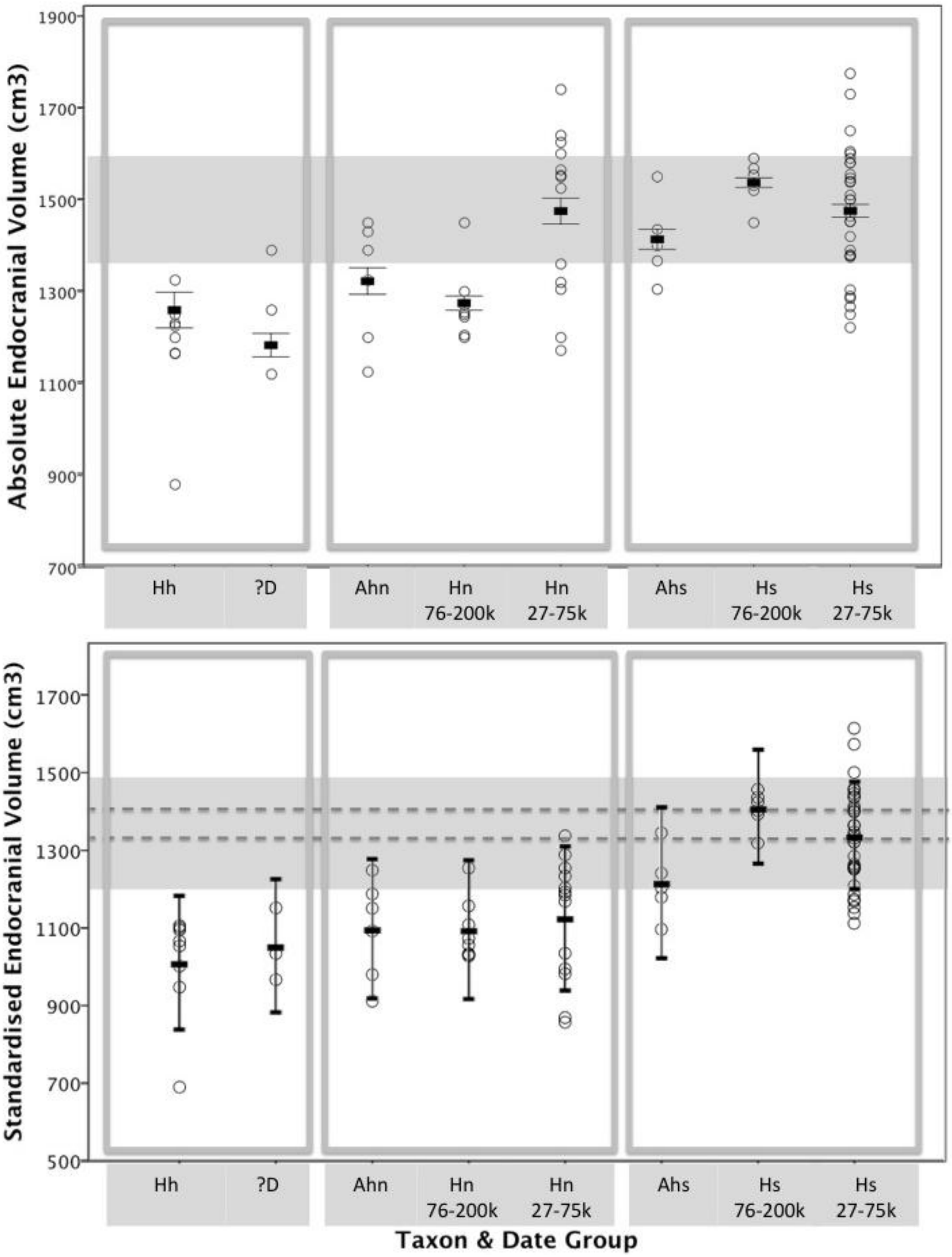

Figure 4.6: Absolute (TOP) and standardised (BOTTOM) endocranial volumes for different hominin taxa, split into date groups (given in thousands of years ago: ky). The three boxes represent, left to right, (i) Homo heidelbergensis (Hh) and possible Denisovans (?D), (ii) the Neanderthal lineage, from archaics (AHn) to Neanderthals (Hn) dated 76-200kya and 27-75kya and (iii) the Homo sapiens lineage, from archaics (AHs) to AMH (Hs) dated 76-200kya and 27-75kya. Circles indicate the mean value for each individual fossil specimen. The horizontal bars show group means ± the (cumulative for BOTTOM) standard error of the mean. The light grey shading illustrates that Neanderthals dated 27-75kya have the same sized brains as AMH in terms of absolute endocranial volumes, but that once body and visual system sizes are taken into account, the Neanderthal means lie outside the cumulative standard errors of the AMH means. The dashed lines in B illustrate the AMH means for both date groups, to ease comparison with the Neanderthal means.

Taking cerebellum differences into account

Independent t-tests revealed that even when Neanderthal endocranial volumes are artificially enlarged in line with a recent-human-like cerebellum volume, there is still a significant difference in standardised brain volume between the Neanderthals and AMH in both 27-75kya (t_{36}=3.420, p=0.002, R^2=0.245) and 76-200kya (t_{14}=4.812, p=2.760e^{-4}, R^2=0.623) date groups. The smaller Neanderthal absolute cerebellum size therefore does not negate the postulated effect of greater neural investment in vision and somatic maintenance in reducing the amount of neural tissue available for other brain areas.

Discussion

The results presented here indicate that Neanderthals had significantly larger absolute orbits than contemporary AMH. Although interactions with overall face and body size may be involved, orbits provide an accurate index of eyeball volume in diurnal primates independently of body mass and overall brain size, a proxy for general head size (Chapter 2). Furthermore, for optical function it is the absolute size of the eye that is imperative, not the size of the eye relative to the face: as long as the skull is large enough to support an eye of a particular size, variation in face size should not significantly impact on eye size. Due to scaling between visual system components independently of brain and body size, larger absolute orbits probably signify that Neanderthals had both larger eyes and larger visual cortices than contemporary AMH. This is corroborated by recent endocast work, which found that Neanderthal occipital lobes are relatively larger than those of AMH (Balzeau, Holloway, and Grimaud-Hervé 2012). In addition, Asian *Homo erectus* also have relatively larger occipitals than their African counterparts (Balzeau, Holloway, and Grimaud-Hervé 2012), a pattern which seems to be paralleled by orbital size (Figure 4.7) and endocranial volume (Shultz, Nelson, and Dunbar 2012), suggesting a latitudinal trend in visual system size in *H. erectus* as well as recent humans.

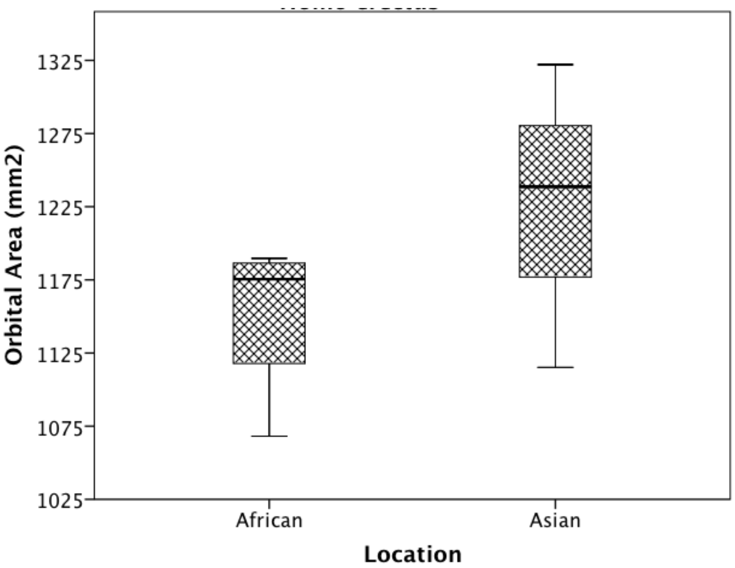

Figure 4.7: Comparison of orbital area between African (N=4) and Asian (N=3) H. erectus (data from Kappelman 1996). The horizontal lines represent the medians, the boxes the interquartile range and the whiskers the minimum and maximum orbital area in each sample.

Variation in visual cortex size might underlie the intraspecific differences in visual function observed in living humans (Halpern, Andrews, and Purves 1999). For instance, larger V1 areas have been associated with both higher visual acuity (Duncan and Boynton 2003), implying that having larger V1 areas may have enabled Neanderthals to attain higher visual acuity than AMH, perhaps particularly under the lower ambient light levels of Pleistocene Europe.

In recent humans (dated to the last ~200 years), larger visual systems seem to translate into larger brains (Chapter 3, this thesis; Pearce and Dunbar 2012). One might therefore expect that larger Neanderthal visual cortices (and somatic areas associated with their bigger bodies[35]) would similarly drive overall brain enlargement in this taxon compared to AMH. However, I have shown that this is not the case for specimens dated 27-75kya: on average, Neanderthals in this date group do not show significantly larger brains than contemporary AMH. This suggests that (i) Neanderthal and AMH brains were organised differently and (ii) by implication, because a greater proportion of overall brain tissue was invested in visual and somatic systems, proportionally less neural tissue was left over for other functional brain areas in Neanderthals compared to AMH (Pearce, Stringer, and Dunbar 2013). Note that my analysis considered only the principal visual areas in the occipital lobe: given that the visual system projects through the parietal and temporal to the frontal lobes, my case might be strengthened if comparative data on these projection areas were available and could be included in the analysis.

Intriguingly, one gene, *CAN15*, for which Neanderthals express the ancestral form but living humans express two fixed amino acid substitutions is associated with the development of the visual system (Green et al. 2010). It may be that such genetic differences underlie the anatomical ones suggested here. It would be productive to test whether similar differences can be found in other genes implicated in the visual phenotype, such as variants of the *GPCPD1* gene, which are associated with the absolute size of the occipital lobe in living humans (Bakken et al. 2012). Expression of the *GPCPD1* gene is also linked to an inverse relationship with the size of the left superior and lateral temporal sulcus: individuals homologous at a particular locus have a relatively larger occipital cortex and a relatively smaller left temporal cortex compared to total cortical surface area,

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[35] With regard to this hypothesis, it is worth noting that I purposefully did not attempt to estimate the volumes of specific ‘somatic’ areas, but rather used a generalised method of standardising the volume of the whole endocranium/brain for differences in body mass, because as yet it is unclear exactly which areas such body size differences would influence. However, since some higher level cognitive abilities are associated with the somatosensory cortex, it may be that the possible AMH-Neanderthal brain organisational differences associated with body size relate predominantly to subcortical brain regions.

and vice verse. This suggests that trade-offs between visual and non-visual brain areas occurs within living humans and is genetically mediated.

Further evidence for a trade-off between visual and other brain areas in living humans comes from the inverse relationship found between the volumes of V1 and the anterior prefrontal cortex (PFC) independently of total cortex volume, although this seems to be driven by opposite scaling relationships with total cortex: negative for V1 and positive for anterior PFC (Song et al. 2011). These data are from living humans and therefore might suggest that the larger visual cortices posited for high latitude historical humans might yield reductions in other brain areas. However, the larger total brain size observed in large-orbited recent human populations seems to argue against this: larger visual cortices in recent humans appear to translate into larger total brain sizes at higher latitudes (Chapter 3). However, such brain area trade-offs might support the idea that larger Neanderthal visual cortical areas were associated with parallel reductions in other brain areas, meaning that their brains were the same size as those of contemporary AMH despite their larger visual areas. In this regard the inverse relationship between occipital and left temporal cortex size is especially interesting, given the association of the latter with auditory and language areas and the fact that differences between Neanderthals and AMH endocasts have been identified in Brodmann areas 22, 40 and 39, which overlap Wernicke's area in the association auditory cortex (Bakken et al. 2012, Holloway 1985). Furthermore, the PFC and some temporal regions are implicated in social cognition (see Chapter 5).

Overall, my findings tie in with the suggestion that the Neanderthal and AMH lineages underwent separate evolutionary trajectories (Bruner, Manzi, and Arsuaga 2003): starting from the brain size of their common ancestor, I suggest that the visual and somatic regions of Neanderthals were enlarged, whereas AMH evolved similarly large brains through increase in other brain regions. Furthermore, it seems that the Neanderthal route followed a more strictly allometric trajectory (Bruner, Manzi, and Arsuaga 2003). Modern human V1s are smaller than expected for a primate of our brain size (de Sousa et al. 2010); larger Neanderthal V1s may thus be more in line with the expectations for a generic large-brained primate, adding support to this argument. This would tie in with Neanderthals carrying the ancestral *CAN15* allele.

However, whereas the enlarged Neanderthal visual and somatic brain areas would have required reduction in other areas compared to AMH, the reverse is not true of AMH and their larger cerebella volumes compared to Neanderthals. Thus, even when compensation is made for the smaller cerebella of Neanderthals, they still exhibit significantly smaller ‘effective’ (standardised) brain sizes than their AMH counterparts. Since the contrast in cerebellum volume between contemporary AMH and Neanderthals was smaller compared to that between these fossil hominins and living humans, this aspect of brain organisation is unlikely to have had a substantial differential effect in Late Pleistocene fossil hominins. However, this does point to potential brain changes within the AMH lineage over the last ~30ky since the time of Cro-Magnon. Larger fossil samples are required to investigate this possibility further.

Although the palaeoanthropological literature often applies regressions derived from extant species to approximate hominin traits (Aiello and Wood 1994, Kappelman 1996, Rightmire 2004, Ruff 2000, Ruff, Trinkaus, and Holliday 1997, Smith 2002, Spocter and Manger 2007), criticisms of such analyses abound. These often relate to (i) the particular combination of baseline species yielding varying curves (Findley 1969, Holloway and Post 1982, Martin 1990, Martin 1982, Radinsky 1982, Wanner 1971), (ii) primate brain databases often representing species using a single individual, ignoring intraspecific variation and (iii) data from different sources being combined, introducing further bias (Healy and Rowe 2007). In reference to (i), regardless of the taxa used or the regression model applied, the comparisons between Neanderthals and AMH remain qualitatively unchanged. Moreover, with regard to (ii) and (iii), I have modelled the cumulative error accrued in the fossil estimates, which should take account of the error associated with small baseline samples and mixed datasets to some degree. If better quality data become available, for example measurements of both orbital and total visual cortex volumes from the same individuals for a large number of diurnal primate species, this error would be substantially reduced. However, the general results should remain fairly consistent because even with sub-optimal data the findings are still significant.

Nonetheless, there are several questions raised by the findings presented here that require further study in order to strengthen or negate the proposed light level hypothesis. For instance, although fossil AMH fall within the recent modern human range of variation at each specific latitude, Neanderthals and *Homo heidelbergensis* have larger orbit volumes than AMH regardless of latitude: Figure 4.8. This pattern is replicated in the orbital area data, with *H. erectus* having orbital areas more in line with AMH than the larger orbits of *H. heidelbergensis* and the Neanderthals (Figure 4.8). Some Neanderthals fall within the modern human range and some modern human outliers overlap with Neanderthals. However, in general, at any given latitude Neanderthals have larger orbits than modern humans from any sample.

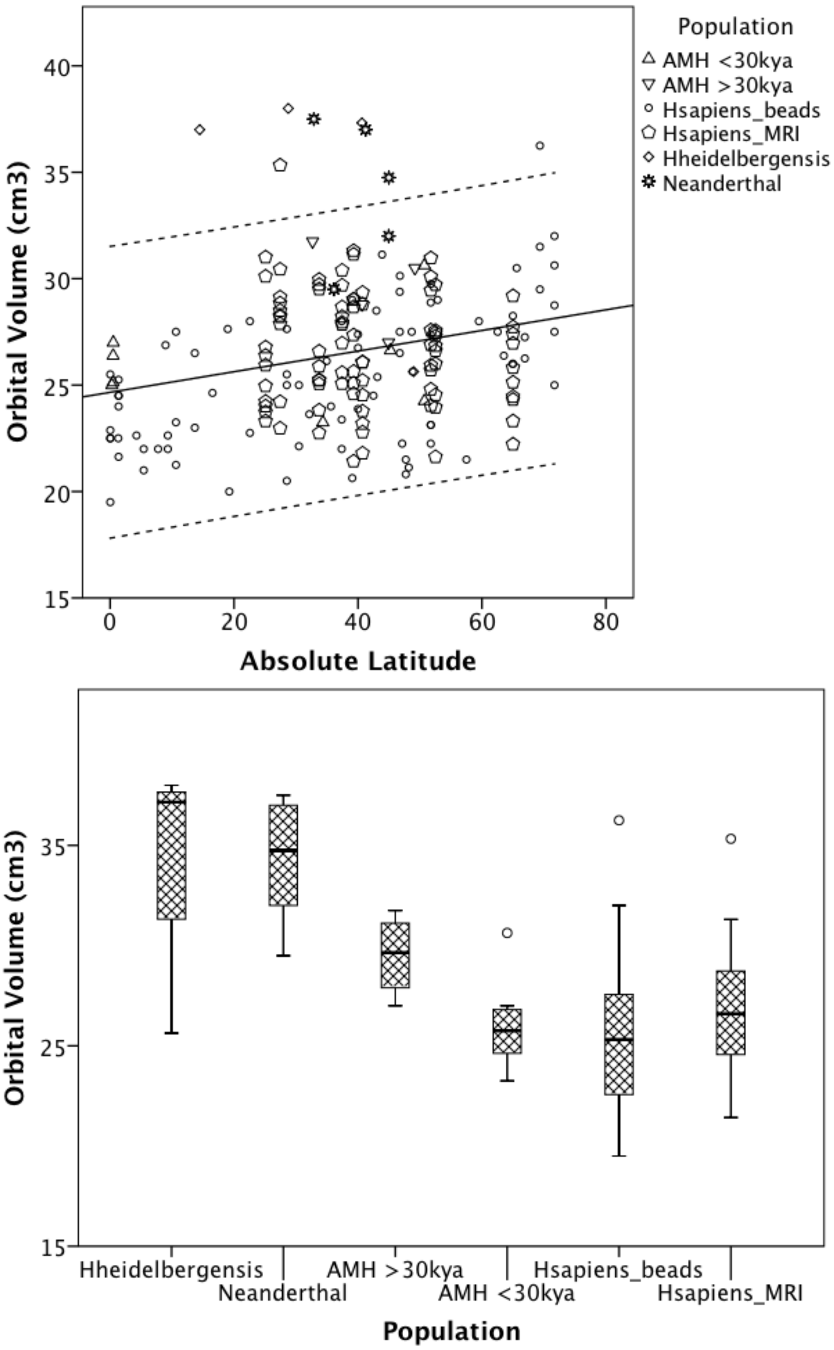

Figure 4.8: TOP Orbital volume plotted against absolute latitude for fossil, recent (bead-measured) and living (MRI) AMH, Neanderthals and H. heidelbergensis. The solid line is the regression for the AMH specimens only; the dashed lines represent 95% confidence limits for the AMH data. BOTTOM The median and inter-quartile range of orbital volume for different hominin taxa and samples. The AMH fossils dated <30kya were not included in the analyses presented here (specimens were casts from the Duckworth collection: Chancelade, Elementeita A & B, Fish Hoek, Makalia burial, Nakuru, Oberkassel 1& 2).

Since Neanderthals had lived in Northern latitudes for at least 100ky whereas AMH have only lived in a similar range for a maximum of 45ky, and only for ~15ky before the Neanderthals went extinct, this difference in orbit size might be due to the time taken to evolve larger visual systems. However, given the essential nature of vision for hominin survival, one would expect any selection of visual function to be strong and the associated changes relatively rapid. Furthermore, if AMH evolved in Southern rather than Eastern Africa (Henn et al. 2011), they might already have been ‘pre-adapted’ to lower light levels outside the subtropics, at least up to ~34 degrees latitude. Although part of the difference in orbit size between Neanderthals and contemporary AMH might be associated with their respective latitudes of speciation, there seem to be other factors involved in addition.

The large *H. heidelbergensis* orbits might indicate that Neanderthal orbits are big due to phylogenetic inertia associated with plesiomorphic robusticity. A potential test of this was examining whether the orbital differences remained after controlling for face size, but the analyses presented above yielded ambiguous results depending on the relative ratios used. This is probably due to differences in orbital shape as well as size and further geometric morphometric study is required to resolve this question. However, given the relationship between orbit and eye size independently of body weight (size) across primates and independently of facial dimensions in living humans (Chapter 2), larger Neanderthal and *H. heidelbergensis* orbits probably still imply larger-than-AMH eyes irrespective of their greater robusticity. If AMH orbital volume is the baseline associated with declining light levels away from the equator, the ‘extra’ volume of Neanderthal/*H. heidelbergensis* orbits might be linked to additional visual function requirements.

For instance, larger Neanderthal orbits compared to living and fossil AMH inhabiting similar latitudinal ranges could be because, in order to fulfil all their subsistence activities, Neanderthals needed to utilise the twilight hours around dawn and dusk to a greater extent than did AMH. That is, perhaps Neanderthals needed to extend their time budgets further beyond daylight hours, particularly in winter, compared to contemporary AMH. Perhaps Neanderthals needed to spend longer periods foraging in order to maintain their larger body sizes or because they did not exploit trapping and bow-and-arrow technology. Alternatively, perhaps AMH adopted the same subsistence strategies but had managed to invent more powerful artificial lighting sources such as animal-fat lamps, buffering against further selection on their visual systems. The extreme of this time budgeting and scheduling line of reasoning is that Neanderthals and *H. heidelbergensis* were nocturnal, evolving from diurnal ancestors in a similar way to secondarily nocturnal *Tarsius* and *Aotus*. One way to test this would be to compare the size of their orbits to the size of their optic foramina in order to assess the relative degree of summation, as has been done to assess the activity periods of other extinct primates (Kay and Kirk 2000). Alternatively, the basicranium might give an indication of the size of the optic nerve and chiasm relative to the orbit/eye.

Otherwise, the larger Neanderthal orbits could be due to Neanderthals living under different diurnal light regimes compared to AMH. For instance, it has been suggested that Neanderthals preferred mosaic habitats including pockets of woodland (Finlayson 2004). Perhaps hunting under forest canopies exacerbated the selective pressure to enlarge their visual systems. On the other hand, variation in light levels associated with planetary eccentricity (shape), obliquity (tilt of the spin axis) and precession (influencing the season of the year when the Earth is nearest the sun) (Dunkerley et al. 1998) cannot be the cause of these visual system size differences, given that Neanderthal orbits are significantly larger than roughly contemporary, as well as living, AMH.

A further, extremely tentative, suggestion is that the domestication of dogs by AMH buffered the selection pressure on their own visual systems, because it lessened the need for humans to have high visual acuity themselves. Neanderthals might not have had this luxury. Although mtDNA analysis of modern breeds has suggested a common origin of domesticated dogs after 16.3kya (Pang et al. 2009), subsequent work argues that extant lineages give inadequate information about the earliest domestication (Larson et al. 2012). Moreover, recent anatomical and genetic evidence from the archaeological record has identified ancient dogs from at least 30kya from the Altai mountains and the AMH Gravettian site of Předmostí (Druzhkova et al. 2013, Germonpré, Lázničková-Galetová, and Sablin 2012, Ovodov et al. 2011). Dogs are hugely beneficial in hunting and would have allowed AMH to exploit resources such as rabbits more easily (Fa et al. 2013, Koster and Tankersley 2012). As yet there is no evidence that Neanderthals also used dogs and this may have been an important difference regarding selection on their visual function.

Work in recent AMH suggests that increased fat for insulation against lower temperatures is not a viable explanation for larger orbits (Chapter 3, this thesis; Pearce and Dunbar 2012). Furthermore, this explanation does not seem to apply to Neanderthals either: contrary to popular understanding, they seem to have preferred warmer habitats than incoming AMH (Aiello and Wheeler 2003, Stewart 2004). However, Neanderthals may have had a subsidiary need to have more protective fat in their orbits to protect their eyes during close-quarter hunting and perhaps interpersonal conflict. This might have led to larger orbits beyond those required purely to house eyeballs of sufficient size to deal with lower light levels (the AMH baseline). However, to what extent additional orbital fat would have made any protective difference under such circumstances is open to debate.

Overall, their differently sized bodies and orbits (which probably imply differently sized eyes irrespective of face/body size) suggest that although Neanderthals had the same absolute brain size as contemporary AMH, their brains were organised differently (Pearce, Stringer, and Dunbar 2013). Macroscopic measures such as regional volumes index neural network characteristics such as the number of neurons and synapses (Andrews, Halpern, and Purves 1997, Gabi et al. 2010). Consequently, differences in the partitioning up of brain tissue might have had substantial implications for cognitive processing in Neanderthals compared to contemporary AMH. For instance, differences in brain organisation might explain the discrepancy between (i) the original group size estimates for Neanderthals derived from total endocranial volumes (Aiello and Dunbar 1993), which suggest similarly sized communities to AMH, and (ii) the smaller and less geographically extensive social networks suggested by the archaeology (e.g. Gamble 1999). Larger visual and somatic areas might have left less neural tissue to underpin the cognitive processing of social complexity in Neanderthals. I explore these potential cognitive differences in Chapter 5.

Chapter 5 Neanderthals and AMH: cognitively different kinds of human?

Investigating the cognitive capacities of fossil hominins is notoriously problematic because they can only ever be looked at indirectly. The links between brain structure, cognition and behaviour in primates can be studied using comparative psychological, behavioural and anatomical data. Once these interactions are understood to some extent, it is feasible to infer possible cognitive capacities for hominins from (i) brain anatomy deduced from hominin braincases and (ii) the behaviours interpreted from the fragmentary archaeological record. In this chapter I examine the way in which these data can be used to compare Neanderthal and AMH cognitive capacities. I argue that even if there was not a great deal of difference between these taxa in terms of technological skill, there may still have been a difference in the taxon-specific degree of social complexity that each was cognitively able to support. Using the standardised endocranial volumes estimated in Chapter 4, I predict cognitive group (active network/community) sizes for Neanderthals and AMH via a comparative primate approach. I also more cautiously predict levels of intentionality (mentalising abilities) for each taxon, since these have been shown to mediate the relationship between orbitofrontal brain volume and network size in living humans. I argue that Neanderthals may not have been able to keep track of as many individuals as could AMH. The associated differences in social network size between taxa may have played a role in why AMH managed to survive whereas the Neanderthals went extinct.

Introduction

In deciphering the cognitive capacities of fossil hominins one must rely on inference, either from behaviour or from neuroanatomy. The problem is that behavioural expression can arise from multiple different and interacting cognitive processes. Furthermore, although one can reasonably infer that if a species performs a particular behaviour, they must posses the necessary cognitive capacity in order to do so, the absence of evidence of a particular behaviour does not equate with a lack of cognitive capacity to execute it. In addition, hominin behaviour has to be inferred from its by-products in the archaeological record, which requires interpretation from incomplete data. In terms of neuroanatomy, the main issue is that brain plasticity and the dispersed network of interconnections between different regions make the mapping of cognitive processes onto the physical brain an incredibly complex task. However, certain functions such as vision are robustly located in the brain and accumulating evidence pinpoints social cognition to prefrontal and temporo-parietal regions (see below). As a result, there is the potential to shed light on hominin cognition through combining comparative primate, archaeological and neuroanatomical data, albeit cautiously and within limits.

The comparative primate literature can be used to examine the relationship between brain morphology and performance on cognitive tasks. One can then apply these relationships to fossil hominins using inferred brain morphology to predict possible cognitive correlates. For example, across primates absolute brain volume is generally a good indicator of executive function (Deaner et al. 2007, Shultz and Dunbar 2010c). Since the endocranial volume of hominin species has enlarged over time, this has been taken to indicate increasing cognitive capacities in parallel with these anatomical changes. However, because the model fit across primates is not perfect (absolute brain size does not exactly match cognitive ability across species: there is some error around the regression line), this implies that different taxa with the same absolute brain size can still show some variation in cognitive ability. This is probably because different facets of ‘intelligence’ are most strongly associated with the size and structure of particular brain areas rather than total brain volume, at least in living humans (Gunz et al. 2012, Luders et al. 2009). This implication has not yet been thoroughly investigated for hominins.

Contrary to popular claims, on average the brains of later Neanderthals (dated 36-60 kya) were not significantly larger than those of roughly contemporary AMH (dated 27-70kya): Chapter 4. On the surface this might suggest that these two hominins had identical cognitive capacities. However, as argued in Chapter 4, even though Neanderthals and AMH had similarly sized brains in absolute terms, it does not necessarily follow that those brains were therefore organised internally in an identical manner. In terms of tissue allocation to different functional systems, any differences in brain structure that evolved since their common ancestor were unlikely to have been massive: *Homo heidelbergensis* already had a brain size that overlaps the lower range of AMH and Neanderthal volumes (Chapter 4: Figure 4.6). Nonetheless, any neuroanatomical differences between Neanderthals and AMH may have translated into cognitive ones.

For instance, compared to Neanderthals, AMH seem to have expanded parietal lobes (Balzeau, Holloway, and Grimaud-Hervé 2012, Bruner 2010). Since working memory is known to activate parietal, as well as frontal, areas in living humans (Cohen et al. 1997, Mottaghy 2006, Salmon et al. 1996), this morphological difference could reflect a need for enhanced working memory in AMH compared to Neanderthals (e.g. Beaman 2007, Coolidge and Wynn 2001, Wynn and Coolidge 2004)[36]. A better working memory might be required, for example, in creating material culture through more complex *châine opératoires* involving a greater number of nested stages (Haidle 2010). For instance, so far no evidence for habitual use of bow and arrow technology has been found associated with Neanderthals (Lombard and Haidle 2012, Shea and Sisk 2010) whereas AMH seem

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[36] In a series of papers Wynn & Coolidge have claimed that in addition to the ‘expert’ long term working memory displayed by Neanderthals, AMH had developed enhanced capacities in working memory associated with a more effective phonological loop (verbal rehearsal) component, which allowed them to exhibit more advanced language skills, cultural innovation and use of symbols. However, Beaman (2007) argues that although working memory might be different between the two taxa in some way, there is no empirical evidence to support Wynn & Coolidge’s claim that the phonological loop is a bottleneck in language processing and that increasing its capacity would lead to more complex AMH language and culture.

to have been using complex projectile technology from at least 71kya (Brown et al. 2012). This is the case even though stone-point hafting has now been dated back to ~500kya, suggesting that it may have been practised by the Neanderthal-AMH common ancestor (Wilkins et al. 2012). Moreover, there is also evidence of adhesive being applied to Neanderthal lithics, implying hafting (see D'Errico 2003 for a review). Lombard & Haidle (2012) argue that although viewed separately the manufacture of a bow or an arrow does not require any extra cognitive capacity beyond that routinely displayed in Middle Palaeolithic (Neanderthal) assemblages, combining both the projectile and its means of delivery requires an extra level of cognitive complexity only displayed by AMH (Lombard and Haidle 2012)[37].

On the other hand, other factors apart from limits on working memory may explain the apparent lack of complex projectile technologies in the Neanderthal record. For instance, Shea & Sisk (2010) argue for energetic and time constraints: since Neanderthals had a larger body mass than contemporary AMH they needed to spend more time obtaining the necessary calories and therefore did not have the spare capacity to invent more efficient or complex technologies. Moreover, Neanderthals inhabited high latitudes, where resources are generally more dispersed, meaning that daily foraging distances would be correspondingly longer and thus time allocation to foraging would probably be higher, even without accounting for their large bodies (Grove, Pearce, and Dunbar 2012). In contrast AMH evolved in lower latitude Africa where, in general, resources would be at higher densities. This may have provided AMH with extra time in which technological innovation was possible: AMH had already developed bow and arrow technology before they too were faced with the time pressures exerted on foraging at higher latitudes. However, the Neanderthals did seem to have had time to develop (whether through

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[37] The same might true for spears and spear throwers.

innovation or emulation) ‘transitional’ industries such as the Châtelperronian (d'Errico et al. 1998a, d'Errico et al. 1998b, Gravina, Mellars, and Ramsey 2005, Hublin et al. 1996, Hublin et al. 2012, Mercier et al. 1991, Zilhao and Errico 1999, Zilhão et al. 2006). If they had time to make these artefacts, which include time-costly bone items, it seems unlikely that insufficient time would explain the lack of bow and arrow technology.

An alternative explanation could be that Neanderthal populations never reached high enough population densities to facilitate the maintenance of cumulative cultural variants, even if the bow and arrow was repeatedly invented in local Neanderthal groups (Henrich 2004, Mellars and French 2011, Powell, Shennan, and Thomas 2009). However, the effects of population density in relation to horizontal cultural transmission are ultimately tied to the number and frequency of contacts between individuals in the population: the higher the density, the more often individuals have the opportunity to exchange information or copy each others’ behaviour. Even if individuals are distributed in space, if lines of contact are maintained over extended distances, then cultural variants can be spread and maintained within the population or group. It is therefore not the population density *per se* that is necessarily important, but the degree of social contact in relation to the density and structure of social ties within the network (Davies 2012). If Neanderthal individuals did not maintain many contacts with individuals outside their residential and neighbouring bands, then their cultural transmission may have been limited. The argument then becomes that Neanderthals may have had the time to invent new technologies, but in general these were ephemeral due to small social networks. Transitional industries may have arisen where network density increased for some reason, for instance if the population was forced into refugia.

Differently sized social networks could have had a number of cognitive correlates in Neanderthals and AMH. For instance, Burke (2012) has suggested that the need to maintain large social networks over large areas may have selected for a different kind of spatial cognition in AMH compared to that expressed by Neanderthals, who in contrast seem to have inhabited relatively small home ranges (Adler et al. 2006, Conard et al. 2011). It is known from studies conducted with London taxi drivers that prolonged and extensive use of complicated cognitive maps leads to enlargement of the posterior hippocampus (Maguire, Frackowiak, and Frith 1997, Maguire et al. 2000, Maguire et al. 2003, Maguire, Woollett, and Spiers 2006). Based on this evidence, Burke (2012) argues that different demands on spatial cognition in AMH versus Neanderthals may have led to progressively larger differences in spatial cognition underpinned by structural brain changes. She proposes that whereas Neanderthals would have had detailed local knowledge of their relatively small home ranges based on landscape navigation, AMH may have developed the ability to translate this egocentric perspective into a cognitive representation resembling a bird's eye view map (Burke 2012). More abstract spatial representations may have aided AMH in exploratory navigation, as opposed to habitual movement through a known area, allowing AMH to colonise new areas such as the open and homogenous environment of the mid-latitude steppe more easily than Neanderthals (Burke 2012).

As well as the hippocampus, the parietal lobe is also known to be involved in spatial cognition (Sack 2009). Furthermore, spatial cognition is linked to working memory (Baddeley 2003, Courtney et al. 1998, Courtney et al. 1996, Curtis 2006, Diwadkar, Carpenter, and Just 2000, Gron et al. 2000, Jonides et al. 1993, Smith, Jonides, and Koeppe 1996), which is also associated with the parietal cortex (see above). For example, working memory is likely to be involved in keeping a set of visually represented directions in mind whilst navigating through a new environment, at the same time as remembering the turns already made during the journey. Thus the parietal differences between AMH and Neanderthals might underlie differences in working memory and/or spatial cognition between these taxa. The larger visual areas attributed to Neanderthals might therefore predominantly relate to sensory areas in the occipital lobe, rather than all the visual association areas in other brain regions.

Burke also suggests that the AMH ability to maintain social networks spread over larger areas was facilitated through more efficient communication of information about the landscape, for instance in the form of schematic maps (Burke 2012). This could equally be achieved through verbal narratives, such as the Australian Aborigine songlines (Chatwin 1987 (1998)). The degree of recursion that can be dealt with in terms of locational cues (in navigation) and manufacturing steps (for instance, in making a bow and arrow set) might all depend on similar underlying cognitive processes. The apparent lack of complex clothing technologies made by Neanderthals might also be linked to the smaller number of steps that they could nest in a causal chain, meaning that Neanderthals were restricted to warmer sites than contemporary AMH (Aiello and Wheeler 2003, Grunstra 2009 unpublished MSc dissertation, Wales 2012). Given possible cognitive limitations on recursion, Neanderthals might also show lower levels of intentionality (the number of minds which an individual can keep track of) than AMH and I explore this possibility below.

Although Burke concentrates on potential cognitive implications of geographically extensive AMH social networks in terms of spatial cognition, it is likely that there would have been consequences for brain structures more directly linked with processing social complexity (Aiello and Dunbar 1993, Dunbar 1992, Dunbar 1998b, Dunbar 2003b, Dunbar

2008, Dunbar 2009, Dunbar 2011a, Dunbar and Shultz 2007a, Dunbar and Shultz 2007b, Joffe and Dunbar 1997, Perez-Barberia, Shultz, and Dunbar 2007). Having larger groups dispersed over wider areas is expected to equate with increased cognitive burden in terms of coordination and taking account of absent individuals. If so, AMH probably required larger brain areas dedicated to processing social complexity compared to Neanderthals. Previous applications of the Social Brain Hypothesis to fossil hominins have estimated similar community sizes for Neanderthals and AMH, due to their similarly sized absolute brain volumes (Aiello and Dunbar 1993, Gamble 2011). In contrast, shorter transfer distances and more limited symbolism in the Neanderthal record compared to that of AMH has been taken to suggest that Neanderthals had smaller social networks (e.g. Gamble 1999, Mellars 1996). This apparent discrepancy between ‘cognitive’ and ‘archaeological’ estimates of network size may arise due to differences in brain organisation between the two taxa. For instance, relatively larger visual and somatic areas in the Neanderthal brain may have limited the neural tissue available for areas associated with social cognition. Taking account of larger Neanderthal visual system and body sizes might yield cognitive limits more in line with archaeological indicators of Neanderthal active network size.

Across primates, mentalising abilitites (levels of intentionality) and the number of individuals that can be successfully integrated into the inner layers of an individual’s social network seem to be most closely associated with non-V1 neocortex, especially the frontal lobe (Dunbar 2003a, Dunbar 2009, Joffe and Dunbar 1997). Specifically, social cognitive competences are linked to particular areas within the frontal and temporal lobes (Dunbar 2011b, Kanai et al. 2011, Lewis et al. 2011, Powell et al. 2012, Powell et al. 2010, Sallet et al. 2011). In living humans performance on mentalising tasks are principally associated with activity in, and the volume of, the (left) temporo-parietal junction and the orbital/medial PFC (Lewis et al. 2011, Powell et al. 2012, Powell et al. 2010, Van

Overwalle 2009). Human social network size is specifically connected to orbital/ventromedial PFC volume via these mentalising capacities (Lewis et al. 2011, Powell et al. 2012, Powell et al. 2010). Analogous associations in macaques suggest that this pattern is shared across primates: in macaques the number of cage-mates is positively associated with the grey matter volume of the mid-superior temporal sulcus and the rostral prefrontal cortex (Sallet et al. 2011). Furthermore, in monkeys living in larger groups there is increased coupling activity (connectivity) between the frontal and temporal lobes (Sallet et al. 2011). Since the macaques did not choose the size of their groups, this seems to suggest a causal relationship: living in larger groups leads to the development of more neural tissue in specific areas of the frontal and temporal lobes. If Neanderthals and AMH differed in their sociocognitive capacities, we might expect differences in specific areas of their frontal and temporal lobes.

Since AMH appear to have relatively enlarged and differently shaped parietal and temporal lobes compared to Neanderthals (Balzeau, Holloway, and Grimaud-Hervé 2012, Bastir et al. 2011, Bastir et al. 2008, Bruner 2010, Bruner, Manzi, and Arsuaga 2003), this implies that AMH may have had a larger temporo-parietal junction area. If so, this may have allowed them to have more complex mentalising capacities, and thus larger social networks, than Neanderthals. Moreover, ‘social memory’ of both people and more abstract social concepts seems to be linked to the anterior temporal cortex (Olson et al. 2013) and AMH seem to have more projecting temporal poles compared to other hominins including Neanderthals (Bastir et al. 2011). Such differences in temporal morphology might suggest differences in social cognitive competences between these closely related taxa.

In terms of frontal lobe comparisons, the findings are more ambiguous. Although Bruner and Holloway (2010) found no difference in the non-allometric widening of the frontal lobe and Bookstein et al (1999) found no difference in internal frontal sagittal profile between Neanderthals and AMH, Balzeau et al (2012) report that Neanderthals had relatively larger frontal surface areas than AMH[38]. This latter result implies that, contrary to predictions, Neanderthals may have had higher social cognitive abilities than AMH. However, it is the internal organisation of macro regions that is crucial to understanding possible differences in cognition. Since Neanderthals had larger bodies, they might have had larger primary motor areas than AMH in order to control their larger muscles, and hence larger frontal lobes overall. However, this does not negate the possibility that AMH had relatively larger PFC areas associated with social cognition within their frontal lobes. Indeed, Bastir et al (2011) found that although both taxa have frontal widening compared to less encephalised hominin taxa, the pattern of widening is different. These external shape differences might underlie internal organisational differences. For instance, AMH have relatively wider orbitofrontal regions (Bastir et al. 2011) and this is particularly pertinent regarding differences in social cognition, given the specific associations between the volume of the orbital PFC and mentalising competences in living humans (Lewis et al. 2011, Powell et al. 2012, Powell et al. 2010).

In addition, frontal lobe function may have been influenced by differences between Neanderthals and AMH in other brain regions. For instance, the role of the cerebellum is increasingly thought to be involved in behavioural control through its connections to the frontal lobe, rather than being purely associated with fine-tuned movement sequences as previously supposed (Barton 2012, Koziol, Budding, and Chidekel 2012). The fact that Neanderthals had smaller cerebella than living and, to a lesser extent fossil, AMH (Weaver

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[38] Note that this does not necessarily mean a volumetric difference, since we do not know the morphology of the internal division between lobes.

2005) might suggest that differences in frontal-based cognitive processes were mediated through differences in cerebella anatomy and function.

Increasing the resolution of analysis to the scale of the orbital prefrontal cortex or temporo-parietal junction in fossil hominins seems a remote, perhaps implausible, possibility, bar the unlikely discovery of a frozen or fossilised Neanderthal brain. In the absence of optimal resolution, possible differences in the internal organisation between taxa need to be accounted for as far as possible. One way to do this is to use a combination of hominin skull dimensions and comparative primate equations to estimate the size of particular brain areas independently of overall brain volume. For instance, estimating the size of the visual cortex from orbit size (Chapter 4; Pearce et al. in press, Pearce, Stringer, and Dunbar 2013) or using the posterior cranial fossa to estimate cerebellum size (Weaver 2005). Since visual areas take a up a relatively large proportion of the neocortex in living humans (Van Essen and Drury 1997), differences in the sizes of these areas might have a substantial effect on the size of other brain areas and thus on the cognitive function of the hominin brain. In Chapter 4 I showed that once the proposed differences in visual system and body size are taken into account, Neanderthals have significantly smaller standardised endocranial (brain) volumes than contemporary AMH. This indicates potential cognitive differences between these taxa. In order to provide a quantitative handle on these possible differences in terms of social cognition, here I use the standardised endocranial volumes from Chapter 4 to estimate cognitive groups sizes and mentalising (level of intentionality) abilities for Neanderthals and fossil AMH via comparative primate equations.

Methods

I developed new primate equations to estimate group size and levels of intentionality from endocranial volume. This is an alternative to previous methods using estimates of fossil brain and neocortex/frontal lobe size derived from endocranial volumes (Aiello and Dunbar 1993, Dunbar 2003a, Dunbar 2009). Using endocranial volume directly reduces the number of computational steps involved, thus minimising the compounded error variance accrued by the estimates. I give alternative methods and results where brain volume is first calculated from endocranial volume and then standardised for body mass and visual system size in Appendix 3 (see also Pearce et al. in press). Both methods yield significant discrepancies between Neanderthals and contemporary AMH. However, the brain-derived estimates are likely to be more accurate because using endocranial volume, which is a step further removed from the specific ‘social cognition’ brain areas, adds variance to the primate relationships with group size and levels of intentionality.

New primate equation predicting community size from endocranial volume

I fitted PGLM and Reduced Major Axis (RMA) regressions to a sample of 25 anthropoid primates (Joffe and Dunbar 1997) as well as to the apes in the database alone (Table 5.1, Figure 5.1). I fitted the PGLMs using a tree downloaded from the 10k tree project: Figure 5.1.

Although there is a phylogenetic RMA model (Ives, Midford, and Garland 2007) that can be fitted using the phytools package in R (Revell 2011 (accessed 2011)), it is not commonly used and its accuracy is thus not well validated. I therefore chose to fit nonphylogenetic RMA regressions, following a comparable method to the original analyses by Aiello & Dunbar (1993).

Table 5.1: Regression equations fitted to log$_{10}$ group size plotted against log$_{10}$ endocranial volume for 25 anthropoid primates or for four apes only.

Model	**t**	**df**	**p**	**R^2**	**slope**	**95% CI for slope**	**intercept**	**95% CI for intercept**
RMA ape	5.46	2	0.032	0.94	1.619	0.807 – 12.089	-2.894	-0.781 - -30.143
PGLM ape	0.91	1	0.530	n/a	1.514	-5.636 – 8.663	-2.661	-22.783 – 17.460
RMA all anthropoids	9.86	23	<0.001	0.81	0.746	0.605 – 1.235	-0.116	0.134 - -0.977
PGLM all anthropoids	3.16	19	0.005	0.31 (adj)	0.452	0.309 – 0.594	0.408	-0.147 – 0.964

Here I present only the fossil group size estimates using the RMA regression fitted to the full anthropoid primate dataset, rather than either of the PGLM estimates or the ape RMA estimates. The RMA regression models are preferable because the relationship between variables is symmetrical and there is likely to be variance on both axes. Furthermore, the PGLM fitted to the full anthropoid sample suggests that the relationship between log$_{10}$ group size and log$_{10}$ endocranial volume remains independently of phylogeny. The small ape sample size and the variance added to the relationship through using absolute endocranial volume rather than brain areas more specifically associated with social cognition means that the ape PGLM is not significant. Given this, I privilege the full anthropoid model over that solely fitted to apes (contra Pearce, Stringer, and Dunbar 2013).

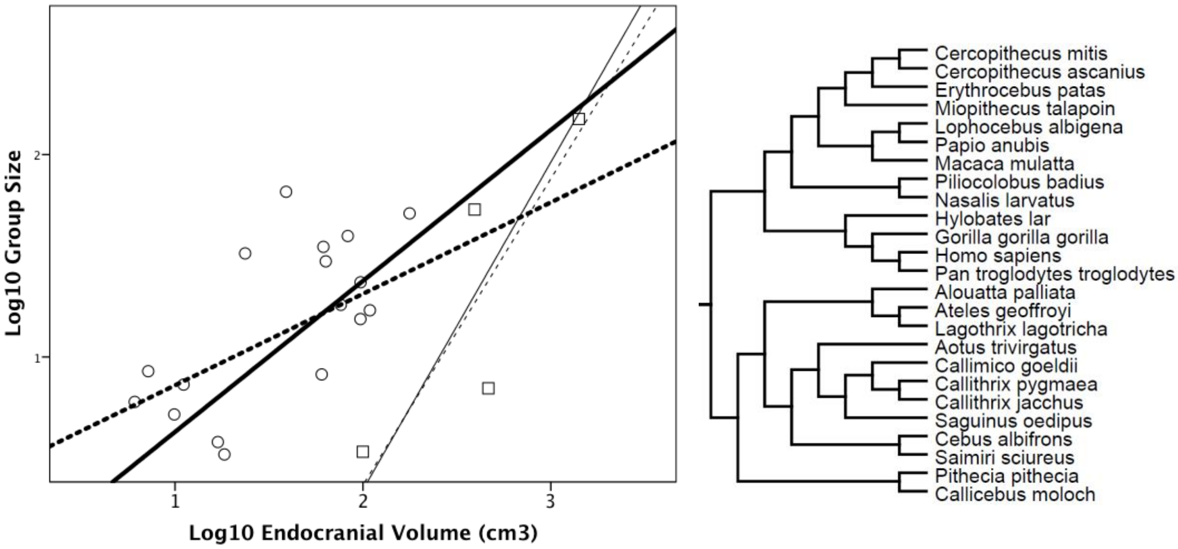

Figure 5.1: LEFT Log$_{10}$ group size plotted against log$_{10}$ endocranial volume for 25 anthropoid primates. The dashed lines indicate PGLM equations whereas the solid lines indicate RMA regression models. The thicker lines are fitted to all taxa and the thinner lines are fitted to the apes only, indicated by squares. RIGHT Phylogenetic tree used in applying a PGLM to log$_{10}$ group plotted against log$_{10}$ endocranial volume for 25 anthropoid primates, downloaded from the 10k tree project (Arnold, Matthews, and Nunn 2010).

Statistics for Reduced Major Axis regression

Unlike OLS regression, which minimises the vertical distance between data-points and the regression line along the y-axis only, in RMA regression it is the triangle between each data-point and the regression line that is minimised. That is, RMA regression minimises the distance between observed data-point (x_i, y_i) and expected data-point (${}_i$, ${}_i$) along both the y- and x-axes simultaneously. Since significance testing is not part of the standard R function for fitting RMA regression models, I wrote a function using the following method. Assuming residuals perpendicular to the regression line and standard co-ordinate geometry (inspired by, but using an different method to MacLeod 2006, accessed 2011, and advised by Tim Holden), I (i) calculated the expected value (${}_i$, ${}_i$) for each data-point (x_i, y_i) in Cartesian space and (ii) calculated the total sum squares (SS_T), regression sum squares (SS_R) and error sum squares (SS_E), (iii) calculated R^2 in order to compare the variance explained by the regression model with the variance in the data, where *n*=sample size, *df*=degrees of freedom, *k*=number of parameters and and are the means of the x and y variables, respectively:

$$\hat{x}_i=((y_i+(x_i/\text{slope})) - \text{intercept})/((1/\text{slope})+\text{slope})$$
$$\hat{y}_i=\text{slope}*\hat{x}_i+\text{intercept}$$
$$SS_T=\Sigma((x_i - \bar{x})^2+(y_i - \bar{y})^2)$$
$$SS_R= \Sigma((\hat{x}_i - \bar{x})^2+(\hat{y}_i - \bar{y})^2)$$
$$SS_E= SS_T - SS_R$$
$$R^2= SS_R / SS_T$$
$$F= SS_R / (SS_E / (n-2)),\ df= (2-k, n-k)$$
$$t=\sqrt{F},\ df=n-2$$

I then calculated the confidence intervals for the slope and intercept. The recommended method for doing this is to calculate the standard errors of the slope and intercept using bootstrapping, in which a set of samples the same size as the original sample are taken with replacement from the original sample and to which the statistic of interest is then applied. The standard deviation of the statistic over these bootstrapped samples is equivalent to the standard error of the original statistic estimated from the original sample (Plotnick 1989).

To do this I used the boot package in R (boot: Bootstrap Functions [online] available at: http://cran.r-project.org/web/packages/boot/index.html (accessed 2011)) to bootstrap slopes for 1000 iterations (Efron and Tibshirani 1986, Plotnick 1989). Since RMA confidence intervals are asymmetrical I then calculated 95% confidence limits for the slope using the Bias Corrected and Accelerated (BCa) method (Carpenter and Bithell 2000, Efron and Tibshirani 1986), which is recommended for skewed distributions (Plotnick 1989). I then followed Trujillo-Ortiz (accessed 2011) to calculate the confidence limits for the intercept, by substituting the lower and upper slope limits into the line equation to find the lower and upper limits of the intercept, respectively.

New primate equation predicting level of intentionality from endocranial volume

Following Dunbar (2003a, 2009) I took the maximum level of intentionality to be 1 for monkeys, 2 for non-human apes and 5 for humans. In humans the maximum level of intentionality that an individual can operate at is measured using vignettes and questions requiring the tracking of different numbers of nested minds (degrees of 'embeddedness'). The maximum level of intentionality is measured as the level where participants first answer incorrectly, taking into account random answering and making mistakes on lower levels while correctly dealing with higher levels. At fifth order intentionality the frequency of participants answering correctly drops substantially and this is taken as the general maximum for living humans (Stiller and Dunbar 2007).

For non-human primates measurement of mentalising abilities is less straightforward, particularly since it is debateable whether subjects demonstrate true mindreading rather than behavioural conditioning. Nonetheless, a number of studies have used perspective-taking in relation to visual stimuli as a proxy for theory of mind (second order: I *know* what you *see*). Chimpanzees are able to understand what a particular conspecific sees and act accordingly in competitive foraging paradigms (Hare et al. 2000, Hare, Call, and Tomasello 2001, Tomasello, Call, and Hare 2003), whereas the evidence for monkeys is more equivocal (Flombaum and Santos 2005, Hare et al. 2003). Furthermore, chimpanzees alter their vocalisations to exaggerate the degree of aggression being shown towards them if a member of their audience matches or surpasses the aggressor in rank (Slocombe and Zuberbühler 2007). In addition, orang-utans modify their gestures to take account of their audience's degree of comprehension and chimpanzees pass second order intentionality false belief tests in experimental settings (Cartmill and Byrne 2007, O'Connell and Dunbar 2003). On the other hand, unlike humans chimpanzees do not perform third party punishment for transgressions (Riedl et al. 2012), suggesting that chimpanzees may not reach third level intentionality.

In contrast, both apes and monkeys have been found to be able to take the intention of human experimenters into account, for example distinguishing between accidental and intentional movement by factoring in constraints on normal action (touching a container with an elbow when the hand was occupied versus unoccupied) (Wood et al. 2007). This could suggest that all non-human primates may be capable of incorporating the mind of another into their worldview (2^{nd} order intentionality). However, given the contradictory evidence and thus the need for more data in this area, I follow Dunbar (2003a, 2009) in setting monkeys at 1^{st} order and apes at 2^{nd} order intentionality. This allows comparison with the original fossil hominin intentionality estimates, where both Neanderthals and AMH are considered to have reached fifth order intentionality (Dunbar 2009).

Mentalising competences show significant linear relationships (i) with frontal lobe volume across primates (Dunbar 2009) and (ii) with both orbital PFC and left temporo-parietal junction volume in living humans (Lewis et al. 2011, Powell et al. 2012, Powell et al. 2010). Since orbital PFC volume is not associated with memory performance and mentalising ability is not associated with dorsal PFC, the size of the orbitofrontal region in particular seems to be specifically associated with social cognition in humans (Powell et al. 2010). Furthermore, path analysis suggests that mentalising competences mediate between orbital PFC volume and network size in humans (Powell et al. 2012), indicating that levels of intentionality are related to the widely accepted relationship between brain and group/network size. Thus, although the relationship between mentalising and brain size is less well established than that between group and brain size, accumulating evidence suggests that mentalising is a key component to social cognition and has a measurable neural basis. Nonetheless, the fossil hominin estimates of intentionality are more tentative than the group size estimates because assigning non-human primates to the different levels remains problematic, whereas group sizes are more easily observable and quantitatively measurable.

Following the method of Dunbar (2003a, 2009), I fitted an PGLM regression predicting level of intentionality from endocranial volume (Dunbar 2009, Martin 1990): $LoI=0.696(SE=0.179)+0.003(SE=0.0002)*ECV(cm^3)$, $t_1=15.727$, $p=0.040$, $R^2=0.996$, adjusted $R^2=0.992$, Figure 5.2. Optimised lambda was not significantly different from zero ($p=1$) or one ($p=0.175$). A fitted RMA regression did not alter the parameters so I used the phylogenetically-controlled model.

Although level of intentionality is a discrete variable and therefore its relationship with brain size is not necessarily one of continuous change, the general idea is that smaller brains place lower limits on the level of intentionality that can be reached. As a species ‘slides’ down the continuous brain volume scale, they will fall within successively lower mentalising ‘bins’ under lower mentalising thresholds, even though it is as yet unknown where the levels of intentionality switches occur in terms of exact brain volume values.

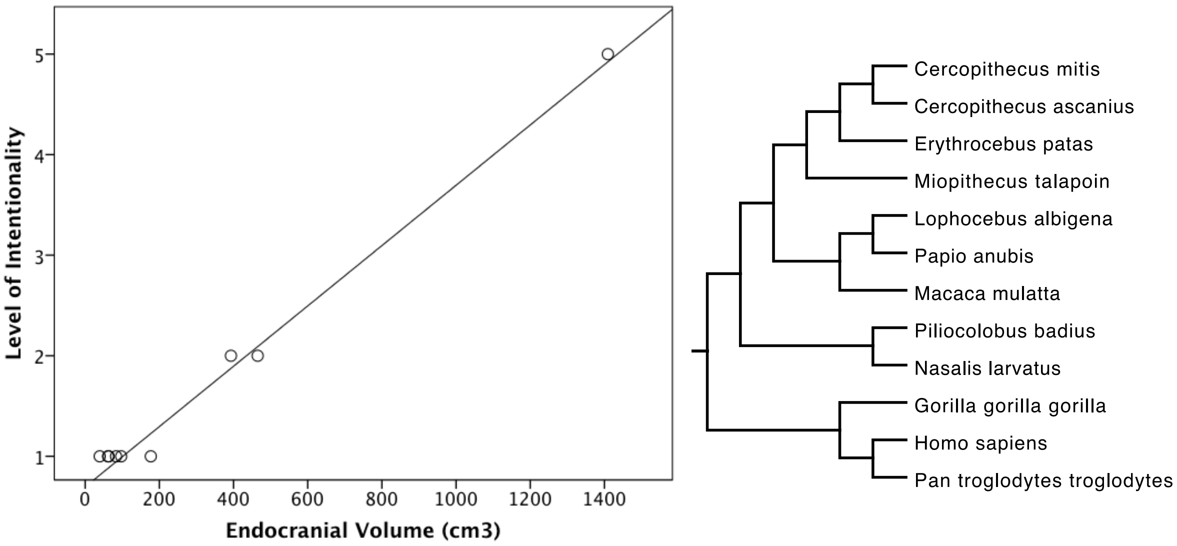

Figure 5.2: LEFT Level of intentionality plotted against endocranial volume for twelve primate species. RIGHT The phylogenetic tree (Arnold, Matthews, and Nunn 2010).

Results

The mean absolute endocranial volumes predict mean active network sizes of 177 for both AMH and Neanderthals in the 27-75ky date group. In the 76-200ky date group the absolute endocranial volumes predict mean group sizes of 182 for AMH and 158 for Neanderthals. The larger absolute endocranial volumes for the older AMH (Holloway 2004) seems to be due to sampling bias associated with the small sample size, because this is not corroborated in the non-endocast datasets (Bailey and Geary 2009, De Miguel and Henneberg 2001). All the other patterns are found irrespective of the dataset or method.

Once endocranial volumes are standardised for body and visual system size, the primate-derived estimates of social cognitive capacities reported here suggest that Neanderthals had significantly smaller groups and lower levels of intentionality compared to AMH. However, the active network sizes estimated from standardised endocranial volumes using the RMA regression fitted to all 25 anthropoid primates are higher than the community size of 150 previously estimated for living humans (Dunbar 1998b) (Figure 5.3). The mean recent human endocranial capacity of 1373 (see Chapter 3; Pearce and

Dunbar 2012) yields a active network size of 168 individuals (95% CI 164-171 individuals). I include a reference line reflecting the recent human values in Figure 5.3 for comparison. It can be seen that the mean fossil AMH active network sizes for both date groups cluster closely around those estimated for recent humans, whereas the estimated active network size of Neanderthals fall below. This is unsurprising given that these group sizes are transformations of the standardised endocranial volume comparisons and will thus show identical patterns. For the 27-75kya AMHs the mean group size estimate is 164 (range=144-190, *N*=32) whereas for Neanderthals the mean estimate is 144 (range 118-165, *N*=13). In the 76-200kya date group the mean for AMH is 171 (range 163-176, *N*=6) and for Neanderthals only 142 (range 135-157, *N*=8). However, note the large cumulative standard errors around these mean estimates, largely linked to the transformation from $\log_{10}$ values (Figure 5.3).

With respect to rounded levels of intentionality, the standardised endocranial volume estimates suggest that whereas Neanderthals seem to have reached 4th order but no further (27-75kya: *M*=4.12, *N*=13, 76-200kya: *M*=4.03, *N*=8), AMH are able to work up to fifth order intentionality (27-75kya: *M*=4.76, *N*=32, 76-200kya: *M*=4.98, *N*=6, recent historical: *M*=4.82, *N*=55)[39]. Figure 5.3 indicates that whereas the mean values for the Neanderthal lineage fall below 4.5, the means for the human lineage exceed 4.5 levels of intentionality. Thus Neanderthals seem to be able to work at 4th but not up to 5th order, whereas in general humans have the potential to reach fifth order intentionality. Furthermore, in contrast with the Neanderthal sample, none of the mean estimates for any of the individual AMH fossil specimens fall below fourth order and some individual specimens exceed the fifth order boundary.

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[39] Note that in a sample of living humans, females scored a mean of 4.72 (*N*=23) and males a mean of 4.63 (*N*=17) (Powell, J. L., P. A. Lewis, R. I. M. Dunbar, M. García-Fiñana, and N. Roberts. 2010. Orbital prefrontal cortex volume correlates with social cognitive competence. *Neuropsychologia* 48:3554-3562.).

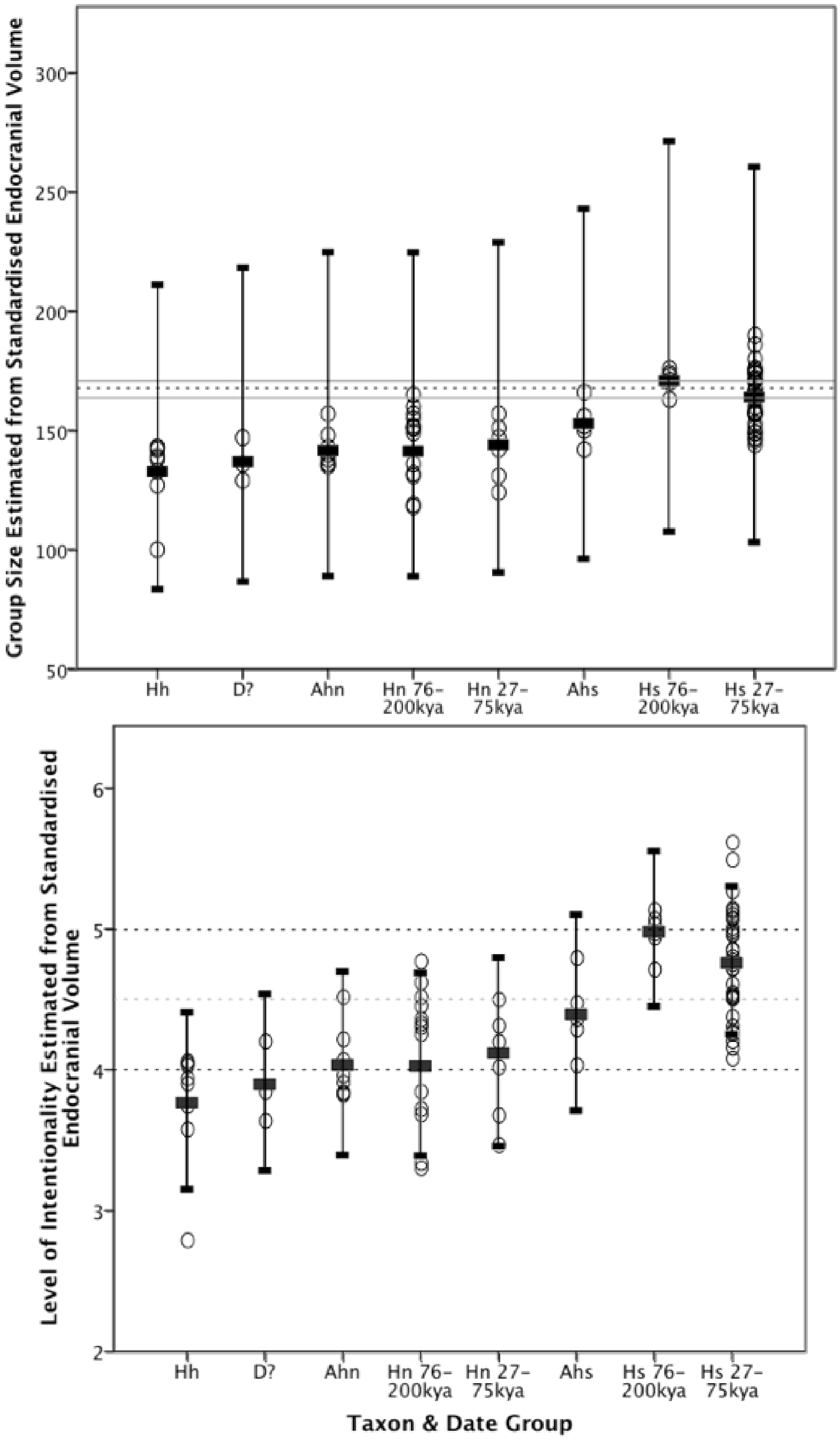

Figure 5.3: Group size (TOP: horizontal lines represent the mean group size estimated for recent humans, with 95% CI) and level of intentionality (BOTTOM: the black dashed lines indicate 4 and 5 orders of intentionality) estimated from standardised endocranial volumes. See Figure 4.6 for the taxon key. The horizontal black bars represent the mean for each taxon/date group and the associated cumulative standard error. Circles indicate the mean estimate for individual specimens.

Discussion

Echoing a large body of previous literature, I have shown that across anthropoid primates endocranial volume is significantly positively related to both bonded community/active network size and level of intentionality (mentalising ability). Thus the smaller endocranial capacities demonstrated for Neanderthals once their proposed larger visual systems and bodies are taken into account (Chapter 4) may have had far-reaching repercussions for their cognition and thus their social and cultural life (Pearce under review, Pearce, Stringer, and Dunbar 2013).

For instance, the analyses presented above suggest that Neanderthals were only capable of working at a maximum of 4 levels of intentionality (that is, oneself and three other minds). This may have limited the Neanderthals' ability to keep track of other individuals' mental states and prevented them from effectively bonding as as large or as many cliques as AMH working at upto five orders of intentionality. Lower mentalising competences might have ultimately constrained the size of Neanderthals' active networks and social groups relative to those of AMH. Thus, whereas fossil AMH have predicted active network sizes inline with those predicted for recent humans using the same primate equation, predicted Neanderthal active network sizes are smaller. Although these network sizes are transformations of the standardised endocranial volume comparisons given in Chapter 4, attaching a numerical value to the average Neanderthal active network size will allow me to estimate the areas associated with Neanderthal grouping layers (Chapter 6).

However, it should be noted that although the overall pattern remains unchanged, the precise estimates differ depending on the method and baseline equation used (for example, contrast the results here with those in Appendix 3: Table A10). The real differences between average active network size between AMH and Neanderthals may have been much larger than suggested here or in Pearce et al (2013). This is because using endocranial volume rather than neocortex or even brain volume adds variance to (and thus lowers the slope of) the primate regression model predicting community size, due to differences in brain organisation between primate species and the variance in the relationship between endocranial and brain volumes. For instance, gorillas (and orangutans) have unusually large cerebella and relatively small neocortices, meaning that their group sizes are smaller than predicted from their total brain size (Dunbar 2011a). When standardised brain (versus endocranial) volume is used to predict community size, Neanderthals have an estimated active network size of 107 (range 70-142) compared to 152 (range=118-196) for AMH dated 27-75kya (see Appendix 3, Pearce et al. in press). The lithic transfer distances recorded for Neanderthals provide stronger support for these brain-derived numbers (Chapter 6), as do widespread findings of 150-strong active networks in living modern humans. Nonetheless, the key message here is that differences in brain organisation could have lead to substantially divergent capacities to deal with social complexity in Neanderthals compared to AMH.

This proposed difference in active network size seems to be supported by the archaeological record. The size of residential groups (inner social layers) can be approximated using floor areas and the number of sleeping (warming) hearths, which suggest a mode of 12-14 individuals and a maximum of ~30 individuals for Neanderthals[40]. The butchery evidence at Mauran suggests a minimum of 30 individuals and perhaps an aggregation of up to several hundred (Farizy 1994, Hayden 2012). These estimates suffer from the palimpsest nature of the archaeological record: even single archaeological strata do not necessarily signify a single occupation period, meaning that

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[40] For Neanderthals three out of six sites predict groups of 12-14 individuals, Molodova-I predicts 14-16 individuals, Tor Faraj predicts 15-18 (or up to 30-36 individuals pending extension of the excavation area) and Abric Romani predicts 23-28 individuals (Hayden, B. 2012. Neanderthal social structure? *Oxford Journal of Archaeology* 31:1-26.).

the division of space as interpreted from the archaeological record may not express the presence of a physical group. Despite this, these data seem to match recent modern human hunter-gather group sizes fairly well: the median size of a recent hunter-gatherer residential group/band size is 14 (*N*=139) during the most dispersed phase of the seasonal round and 37 (*N*=148) during the most aggregated phase of the seasonal round, whereas the median size of periodic aggregations is 150 (*N*=127) (Chapter 6, this thesis; data from Binford 2001). However, the archaeological group estimates suggest a most likely maximum Neanderthal band size of ~30 individuals (which matches the size predicted by the maximum transfer distance associated with Neanderthals: Chapter 6), compared to the recent hunter-gatherer median (versus maximum) of 37. Thus, in support of Hayden (2012) I argue for a quantitative difference in the band sizes of Neanderthals and AMH. Even an incremental difference at the level of the band might have had substantial implications in terms of survival: a small difference in the size of inner social layers exponentially translates into a much larger difference at higher social layers due to the scaling ratio of three between the total membership of adjacent layers (Hamilton et al. 2007b, Hill, Bentley, and Dunbar 2008, Lehman, Lee, and Dunbar in press, Zhou et al. 2005).

Interpretations of smaller total network sizes for Neanderthals are supported by their shorter and less frequent maximum lithic transfer distances compared to AMH, as well as the Neanderthals' apparently lower need for material cultural supports for network maintenance in the form of symbolic artefacts (e.g. Gamble 1999, Layton, O'Hara, and Bilsborough 2012, Mellars 1996, Moutsiou 2011). In their traditional lifestyle exploiting mosaic environments Neanderthals would not have needed as strong or as many ties with individuals in independent distant bands in order to guard against local resource fluctuations, since groups could, within limits, more easily switch between alternative resources within a localised area (Finlayson 2004). The reliance of Neanderthals on cooperative large game hunting may also have led to the concentration of social interaction within bands, even if contact was also maintained with neighbouring bands. I explore the identity of the outermost social layer maintained by Neanderthals in more detail in Chapter 6, using lithic transfer data. However, overall, the archaeological record supports the conclusion that Neanderthals did not experience the same level of social complexity, indexed by group size, as contemporary AMH.

Such social differences may have had profound implications for Neanderthals. First, assuming similar densities, the area covered by the Neanderthals' extended networks would have been smaller than those of AMH (Chapter 6). Consequently, the Neanderthals' ability to trade for exotic resources and artefacts would have been reduced (Horan, Bulte, and Shogren 2005), as would their capacity to gain access to foraging areas sufficiently distant to be unaffected by local scarcity (Whallon 2006). Furthermore, their ability to acquire and conserve innovations may have been limited (Powell, Shennan, and Thomas 2009) and they may have been more vulnerable to demographic fluctuations, causing local population extinctions (Dalén et al. 2012, Hublin and Roebroeks 2009). Consequently, having smaller networks may have played a role in why Neanderthals went extinct whereas modern humans managed to survive. Future work should explore the exact implications of a difference in social network size between Neanderthals and AMH. For instance, through agent-based modelling one could examine how large the difference in total network size would need to be to create differential survival under given parameters of resource fluctuation.

Whether Neanderthal group/network size was ultimately constrained by cognition remains a matter for debate. In living humans the direction of causality between brain structure and social cognition has not yet been robustly demonstrated: individuals with larger orbitofrontal grey matter regions may have larger active networks because learning to deal with that number of people requires the development of extra neural support, or individuals with naturally larger orbitofrontal prefrontal areas may have the ability to maintain relationships with more individuals. The macaque data outlined above suggest that part of the relationship may be developmental (Sallet et al. 2011). This implies that individuals who interact with fewer conspecifics for an extrinsic reason such as low population density might have a smaller orbitofrontal region. Thus any sociocognitive differences between Neanderthals and AMH could potentially be purely developmental.

However, since endocranial differences between these taxa are present from early postnatal development (Gunz et al. 2010, Ponce de Leon and Zollikofer 2001), such cognitive differences may have been at least partly inherited. This is supported by the fact that the cognitive limit on active network size seems to be fairly stable in living humans regardless of the social and ecological environment and thus appears to be species-specific, albeit with individual variation around the mean (Dunbar 1998b, Dunbar 2012b, Goncalves, Perra, and Vespignani 2011, Grove 2010b, Grove 2011, Hamilton et al. 2007b, Zhou et al. 2005). The shorter juvenile period experienced by Neanderthals (Ponce de Leon and Zollikofer 2001, Smith et al. 2010) may also have been genetically constrained and probably would have impacted upon their brain development. The size of non-V1 neocortex positively correlates with both community size and the length of the juvenile period in primates, so a shorter juvenile period might have meant a lower cognitive limit on active network size for Neanderthals (Joffe and Dunbar 1997). Furthermore, fine-tuning of the neural and cognitive processes for handling complex social information seems to continue until adulthood (Blakemore 2008, Deeley et al. 2008, Dumontheil, Apperly, and Blakemore 2010), so if Neanderthals had a shorter adolescence this might have limited such refinements. Moreover, if Neanderthal development occurred in a less complex social context in terms of interaction with fewer individuals, the environmental stimulus for such neural and cognitive refinements may have been absent in Neanderthals, leading to ‘under-developed’ social brain neural networks relative to those of AMH.

Several genes identified as having undergone selective sweeps in AMH but not Neanderthals include those linked to various psychological disorders (schizophrenia and autism, which is especially interesting given the proposed social cognitive differences), cognitive abnormalities (associated with Down Syndrome) and cranial/dental development (Green et al. 2010). Furthermore, the Mezzena Rockshelter Neanderthal carries the ancestral allele of the *Microcephalin* gene, which is associated with brain development, rather than the D haplotype that seems to have undergone recent positive selection in modern humans (Evans et al. 2005, Lari et al. 2010, Mekel-Bobrov et al. 2007). Although normal *Microcephalin* variants in living humans are not associated with total brain size or general mental ability, including ‘prosociality’ as a questionable[41] measure of social intelligence (Rushton, Vernon, and Bons 2007, Woods et al. 2006), differences in allelic expression between Neanderthals and AMH could have had other more subtle effects in internal brain organisation and thus cognition.

Nonetheless, whichever direction the causality is manifested and regardless of the extent to which brain structural changes are inherited, the association between specific brain areas and social network size implies that if Neanderthals did have smaller groups than AMH, there would be associated differences in brain structure between the two taxa irrespective of why the groups were smaller in the first place. Even if smaller groups were initially linked to ecology rather than limited by existing brain architecture, those smaller

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[41] Social intelligence is the ability to mentally manipulate information about a complex social world, not attitudes regarding whether or not to behave altruistically towards others.

groups would likely still be associated with smaller prefrontal and temporo-parietal regions in Neanderthals due to the social environment in which they developed, especially since these neural changes continue into adulthood (Blakemore 2008, Deeley et al. 2008). However, more work is required across primates to elucidate the direction of causality and the involvement of feedback mechanisms, as well as to test the consistency of associations between particular prefrontal and temporo-parietal areas and complex social cognition across a larger number of primate species.

Since Neanderthals and Middle Stone Age AMH seem to have been able to exploit a similar range of resources and utilise similar subsistence strategies (e.g. Adler et al. 2006, Burke 2012, D'Errico 2003, Eren, Greenspan, and Sampson 2008, Fiorenza et al. 2011, Hardy and Moncel 2011, Hardy et al. 2012, Henry, Brooks, and Piperno , Patou-Mathis 2000, Richards et al. 2000, Richards et al. 2008, Roebroeks and Villa 2011, Sorensen and Leonard 2001, Stringer et al. 2008), in terms of technological cognition there may be little to distinguish these taxa. Over time Neanderthals show increased ‘behavioural complexity and diversity’ in terms of the number of burials and instances of raw material modification recorded (Langley, Clarkson, and Ulm 2008). Even lack of evidence that Neanderthals exploited smaller, more mobile prey may be linked to lower Neanderthal population densities and smaller social networks, rather than limited technical cognition (Fa et al. 2013, Kuhn and Stiner 2006, Stiner and Kuhn 2006). Ignoring the suggestion of differences in working memory, it is theoretically plausible that even if Neanderthals and AMH showed no difference in ‘technical’ intelligence, they could still differ in their respective capacities to process complex social information[42]. Although there are overlaps between the two, for example in social learning of tool manufacture and

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[42] It should be noted that both are ultimately linked to solving ecological problems either through (i) direct interaction with the environment or (ii) via cooperation and having to interact with the environment in a social setting, that is, taking other actors into account.

use, social and technical intelligence seem to relate to different yet interacting cognitive domains or systems.

In this sense my argument echoes the suggestion of Mithen (1996a, 1996b) for separate domains of social, technical and natural history intelligence based on the evidence for an intuitive grasp of associated concepts shown by young children as well as apparent cross-cultural universality (see references in Sperber and Hirschfeld 2004). However, my interpretation of the difference between Neanderthal and AMH cognition is somewhat different: whereas Mithen sees Neanderthals as possessing equal ability to AMH within each separate domain and proposes that the difference lies in the cognitive fluidity and domain-sharing/permeability seen only in AMH, I argue for a difference in social but not necessarily technical (or natural history) intelligence. Any differences in the technical behaviour expressed may result from differences in social context, as Mithen points out, but not from differences in technical cognition *per se*.

Comparative primate data seems to support the existence of different social and technical domains. For instance, chimpanzees do as well on object manipulation or mechanistic tasks as 2.5-year-old human children, and both do better than orangutans (Herrmann et al. 2007). However, in relation to social tasks, chimpanzees fail to do as well as the children (Herrmann et al. 2007). This indicates that ape species can differ in social versus technical abilities. Furthermore, across four domains (inhibition, memory, transposition and support) Bayesian modelling has uncovered a species-specific factor and a domain-specific factor (but a minimal role for inter-individual variation), which both independently account for 17% of performance variance across chimpanzees, bonobos, orangutans, gorillas, spider monkeys, brown capuchin monkeys and long-tailed macaques (Amici et al. 2012). This suggests that primate cognition is to some degree modular, so that different domains can undergo separate changes under specific selection pressures. It should be noted that Neanderthals are not being equated with chimpanzees here: any differences in social cognitive abilities between Neanderthals and AMH are likely to have been far less substantial.

A second piece of evidence for a distinction between social and technical cognition relates to the autistic spectrum disorders in living humans. Individuals who score highly on the autism scale are often good at understanding abstract concepts and mechanisms but (i) either consistently fail, or show a marked developmental delay in passing, Theory of Mind false belief tasks, which require understanding that other individuals have mental states that can differ from one's own, and (ii) do poorly at the 'reading the eyes' task involving naming the emotional expression on human faces (Baron-Cohen 2009, Baron-Cohen et al. 1999, Baron-Cohen et al. 2001, Norenzayan, Gervais, and Trzesniewski 2012). This discrepancy has lead to the theory of orthogonal continua of 'systematising' (technical) versus 'empathising' (social) cognition (Baron-Cohen 2009). Most normally functioning adult humans score about equally on both these scales, although females tend to score better in empathising and males better at systematising. Autistics express an extreme male pattern, scoring very highly on the systematising scale but very low on the empathising one. It is conceivable that there might be species differences in the mean scores and relative difference between scores on such scales. I suggest that even if Neanderthals and AMH would have scored similarly on the systematising scale, most AMH individuals would have outdone Neanderthals with their empathising score, at least if the measure was altered to include higher order intentionality tasks and items testing the ability to track and coordinate large numbers of social partners and affiliated/enemy groups. By this model Neanderthals would have exhibited strong emotional attachment to their closest kin and friends and they would have kept in contact and exchanged members with adjacent bands. However, their social world would have played out over a smaller spatial scale and may not have extended to the overall groups sizes expected for AMH ethnolinguistic tribes (see Chapter 6). Although both Neanderthals and AMH were both intelligent, resourceful humans, they were nonetheless different versions of the same theme.

Both Neanderthals and AMH adapted to their environments physically and socially. However, Neanderthals primarily seem to have dealt with the challenges faced in their high latitude environment through physical adaptation (e.g. large body size) and technical know-how (e.g. cooperative big game hunting). In contrast, AMH seem to have followed a different trajectory, which involved greater reliance on the flow of information and cooperation through extensive social networks. The Happisburgh evidence for exploitation of the southern edge of the boreal zone 780kya (Parfitt et al. 2010) suggests that the common ancestor of Neanderthals and AMH may have already possessed a high degree of cognitive flexibility to deal with the demands of high latitudes, for example associated with the controlled use of fire (Roebroeks and Villa 2011). Possible cognitive differences between the descendent taxa may thus have been predominantly associated with visual processing, body size and social complexity. AMH may have been able to expand further North due to the cumulative development of cultural innovations facilitated through their larger social networks, whereas Neanderthals were limited to roughly the same latitudinal range as their ancestors. The flexibility allowed by social solutions to ecological problems ensured the survival of AMH, whereas the technical and physiological adaptations of the Neanderthals seem to have fallen short. However, unlike Neanderthals, high latitude AMH probably would have had to overcome additional difficulties in order to bond the outer layers of their larger networks over larger areas. In Chapter 6 I examine the effect of latitude on the areas over which social networks need to be maintained, as well as the implications of time budget constraints on that maintenance.

Chapter 6 Social network distances and time constraints

Decreasing resource densities and increased reliance on hunting nearer the poles suggests that the area over which a social network needs to be maintained will increase with absolute latitude. I show this to be the case in a sample of recent hunter-gatherers, even accounting for the lack of independence between societies nested within biomes. I take (i) the radii of range areas associated with different recent hunter-gatherer grouping levels and (ii) archaeological transfer distances as indicative of the distance over which social networks are maintained. Using these data I suggest that both Neanderthals and Palaeolithic AMH maintained social layers up to the outermost ethnolinguistic tribe at all latitudes. However, only the infrequent AMH transfers of up to 800km in Europe suggest some interaction between ethnolinguistic units. I argue that the time taken to travel to visit or aggregate with other bands may have been a limiting factor on the distance over which cohesive social links could be sustained. In order to quantify the time costs involved, I model home range areas as circles and estimate the time taken to traverse the radii. I show that for peripheral groups to walk to the centre of the tribal (ethnolinguistic population) range would have taken several days of solid walking in the highest latitude biomes. High travelling times may prevent ethnolinguistic populations from bonding during physical gatherings of all their members. Other mechanisms of cohesion or for reducing travelling times are thus expected at the highest latitudes.

Introduction

Rather than being aggregated in a single location, the members of a hunter-gatherer's social network are distributed over an ecologically determined home range area in a number of residential groups, which disperse and re-aggregate over time. The overarching question tackled in the second part of this thesis is how hunter-gatherers are able to maintain these dispersed connections, particularly at higher latitudes. Decreasing resource density and increased reliance on hunting means that the home range area of hunter-gatherer populations is expected to increase with absolute latitude (Grove, Pearce, and Dunbar 2012, Kelly 1995, Pearce et al. in press). Indeed, at higher latitudes and where seasonality is more pronounced, cultural and language groups span larger geographic areas (Collard and Foley 2002, Mace and Pagel 1995, Nettle 1996, Nettle 1998, Nettle 1999). At the same time, at higher latitudes network size might also increase in order to aid information flow and so that individuals are assured of a number of alternative sources of help if their local resources fail. However, since hunter-gatherer population density decreases with absolute latitude (Grove, Pearce, and Dunbar 2012), if overall network or fused group sizes do increase with latitude, they must do so at a slower rate (have a lower slope) than does area. The offset between network and area size increase will affect the degree of difficulty higher latitude humans face in maintaining their networks, by determining the inter-group spacing (i.e. group density) and thus the distances that need to be circumvented in order to maintain face-to-face contact between groups. Moreover, personal networks might be spread over a greater number of physical groupings at higher latitudes (i) because reduced resource density would increase foraging time and lead to greater and more frequent fissioning (Grove, Pearce, and Dunbar 2012) and conversely (ii) due to energy constraints on the number of individuals that can gather in a single place and be adequately supported by the local resources. Greater dispersion of the network would increase the difficulty of maintaining its connectivity by decreasing the frequency of interpersonal contact between bands.

In this chapter I (i) explore latitudinal and taxonomic variation in range area and total network size in recent and archaeological hunter-gatherers, and (ii) quantify the potential time costs associated with network maintenance at different latitudes. Without actual group geographic distribution and social network data, I use recent hunter-gatherer group size to index network size and assume that the geographic area required for a group of a particular size is the area over which the associated social network is maintained.

Latitudinal constraints on social network maintenance

There are cognitive, energetic and time constraints on the size of a dispersed network in terms of membership numbers and geographical spread (Chapter 1). Regarding cognition, individuals require the memory capacity to coordinate with and take into consideration non-present individuals and sub-groups. Energetic constraints on social network maintenance include access to sufficient resources to support periodic aggregations, as well as building up sufficient energy reserves to allow social activities to be performed. Ultimately this relates to balancing finite time budgets: individuals need to spend sufficient time resting, foraging and travelling as well as socialising. The time spent servicing relationships shows exponential decline across the intimacy layers from ego outwards to the 500-layer (Miritello et al. 2013, Roberts 2010, Roberts et al. 2009, Sutcliffe et al. 2011), so it is likely that the time spent in face-to-face interaction would be greatest for individuals within the band, whose members tend to re-aggregate fairly frequently. Consequently, the time spent in face-to-face interaction with members of ego's inner social layers might not differ significantly across different latitudes[43].

On the other hand, assuming that hunter-gatherer bands are spread across their total home range, rather than habitually clustering throughout the year, a major time cost might be accrued by travelling to visit other groups. If these travel times become prohibitive as home range area increases and frequent face-to-face interaction becomes impractical, additional mechanisms such as increased reliance on material expressions of social relationships might become more important at higher latitudes (Pearce et al. in press,

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[43] Unless band and clique sizes significantly increase with latitude: I test this below.

Shuttleworth 2013). In that case, higher latitude hominins may have to spend a greater proportion of their time in manufacturing exchange objects. The amount of time available for such manufacture might place a limit on the number of, and distance over which, ties could be maintained *in absentia*.

Social interaction in the archaeological record

Raw material transfer distances that exceed the assumed foraging radius of a particular site may represent interaction between social groups. The most basic transfer distance measurements use the distance from the archaeological find-site to the nearest source of a particular type of lithic, assuming that the raw material was not collected from secondary deposits and ignoring accessibility. Raw material transfer distances do not necessarily reflect direct exchanges between two social partners, but may rather represent the summed distance of transfer through a chain of individuals. Nonetheless, maximum transfer distances may provide information on the total area covered by overlapping individual active networks.

Three concentric ‘procurement zones’ are often identified from frequency distributions of transfer distances: (i) the ‘local’ 5km-radius zone accounting for 60-98% of material and representing all stages of the *chaîne opératoire*, (ii) the ‘intermediate’ zone denoting a radius of 5-20km from the site (5-20% of the material consists of prepared cores and finished tools) and (iii) the ‘distant’ zone incorporating the area beyond and consisting of <5% (usually 1-2%) of the material, in which the end stages of reduction are overrepresented (Féblot-Augustins 1993). The local and intermediate zones seem to correspond to the foraging radii of recent human hunter-gatherer bands: 15-25km from base camp (Layton and O'Hara 2010, Layton, O'Hara, and Bilsborough 2012).

Gamble (1998, 1999) incorporates all three transfer zones into his 'local hominid network' or 'landscape of habit', which has an upper limit of 100km and which corresponds to the activities of his 'intimate' (5 individuals i.e. the support clique) and 'effective' (20 individuals i.e. the sympathy layer) groups. Beyond ~100km lies the 'social landscape' incorporating the 'extended'[44] and 'global'[45] social layers (Gamble 1998, Gamble 1999). As he points out, Gamble's landscape of habit overlaps mean Aka visiting distances, 96% of which are <100km and 50% <50km (Hewlett, Koppel, and Cavalli-Sforza 1982). The Aka 'exploration range[46]' is on average ~60km for both sexes combined, which is similar to the mean 'mating range[47]' of ~53km (Cavalli-Sforza and Hewlett 1982, Hewlett, Koppel, and Cavalli-Sforza 1982). Furthermore, the theoretical work of Wobst (Williams and Wobst 1974, Wobst 1974, Wobst 1976) suggests that in closed mating networks of 175-475 individuals living at the lowest density of 0.005 individuals/km, the maximum distance between the central and most distant group (range radius) is 151km and between nearest neighbours <80km. In addition, Steele (1996) used body weight and community sizes estimated from female body weight and total brain volume to estimate home range diameters for early AMH of 10km using a primate equation and ~97km using a carnivore model, yielding radii of 5km and 48.5km respectively. All these observational and simulated data suggest that a habitual range of <100km is fairly realistic.

More recently, Moutsiou (2011) has refined Gamble's approach to propose a 5-layer nested scheme for obsidian transfer distances: local (0-10km), mesolocal (10-50km), regional (50-100km), extended (>100km) and exotic (>200km). From these she inferred

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[44] Comprising 100-400 individuals, which merges the active and mating layers in Dunbar's scheme (Table 1.1) but seems to better equate with periodic hunter-gatherer aggregations: Group 3, see below.

[45] Comprising 2500 individuals, which is greater than Dunbar's 1500-strong ethnolinguistic tribe, but could correspond to the highest confidence limit rather than the average.

[46] The median distance to places visited at least once for each individual.

[47] The distance between the birth places of spouses.

the extent of social interaction throughout hominin evolution and across their latitudinal range. Marwick (2003)[48] raises the bar and suggests a transfer distance of >300km to indicate the existence of exchange networks, which he argues first emerge in Africa ~130kya.

Although Gamble, Moutsiou and Marwick do examine ethnographic mobility data, they do not use these data directly to infer which social grouping layer different transfer distances might represent. Thus, no one appears to have directly compared the areas or radial distances associated with each hunter-gatherer grouping (i.e. areas associated with the foraging party, band, periodic aggregations, endogamous community, ethnic population) with archaeological transfer distances. Doing so might indicate the level of social interactions most likely represented by observed transfer distances. For instance, if maximum transfer distances most closely resemble the range radii associated with recent hunter-gatherer bands, one might infer interaction within, but not between, bands (~50-layer). Since I aim to investigate the upper constraints limiting social network maintenance I concentrate on maximum distances here.

I also compare the obsidian transfer distances associated with AMH and Neanderthals, as well as contrasting them with recent hunter-gatherer radii, in order to ascertain (i) whether AMH maintained their social networks over larger areas than Neanderthals and (ii) whether interaction at a similar maximum social layer is represented for both taxa. Compared to the grooming cliques and communities of other fission-fusion apes (chimpanzees and bonobos), modern human social organisation contains additional layers, yet it is unknown when these additions occurred. Although the size of the

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[48] Marwick suggests that from ~1.9mya hominins show a maximum transfer distance of 13km, which he argues shows greater planning depth compared to chimpanzees, who have similar home range sizes, but move objects over shorter distances. From 1mya he argues that transfer distances increase to 100km and suggest the emergence of protolanguages, which facilitated the pooling of information.

chimpanzee community is numerically equivalent to the human hunter-gatherer band, in terms of cognition and brain size the community layer seems synonymous with the active network, the next layer out (Dunbar 1993, Dunbar 1998b, Lehman, Lee, and Dunbar in press). If so, humans have added the band/50-layer below this (perhaps as reliance on meat forced increased fissioning for foraging as well as the need to share risky resources: Layton, O'Hara, and Bilsborough 2012, Pearce et al. in press). Similarly, Foley & Gamble (2009) argue that further sub-division into family units is a uniquely modern human trait. This is supported by the suggestion that the grooming cliques of other primates equate with living human sympathy groups (~15-layer) rather than support cliques (~5-layer, equivalent to the hunter-gatherer nuclear family) (Kudo and Dunbar 2001)[49]. In addition, although chimpanzee females disperse between communities, there is extreme antagonism between communities, suggesting that the encompassing mating pool of neighbouring communities is not a ‘real’ social unit for chimpanzees in the same way as the ~500-strong endogamous megaband is for modern human hunter-gatherers. Modern humans have also added a layer beyond the megaband comprising the ethnolinguistic tribe. Comparing archaeological transfer distances with the areas expected for their different social network layers might indicate whether Neanderthals, as well as Pleistocene AMH, had added the additional megaband and ethnolinguistic social layers. This will help date the addition of these layers during the evolution of hominin social organisation.

Layton et al. (2012) argue that ethnographically inferred home ranges for a Neanderthal active network (taken as 145 individuals based on absolute brain volume) were well beyond modern hunter-gatherer daily foraging ranges. They argue that 80-96% of raw material in the Neanderthal archaeological record was transported over distances

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[49] How chimpanzee foraging parties map onto this scheme is a matter for empirical study, but the difference may concern ecologically constrained physical groups sizes (foraging parties) and cognitive limits on the number of intense social relationships that can be tracked and manipulated (bonded cliques).

within the estimated home range area for modern hunter-gatherer communities (active networks), implying that Neanderthals were moving throughout the area associated with their communities but perhaps not within the entire area occupied by an associated endogamous megaband. However, taking the apparently larger Neanderthal visual system and body sizes into account suggests that Neanderthals may have had less neural tissue to dedicate to social cognition and therefore had smaller active networks than previously supposed (Chapters 4 & 5). This would decrease the proportion of artefacts that would fall within the smaller active network area radius. In turn this would imply that Neanderthals may have been maintaining contact within layers beyond their active networks. I test this hypothesis below.

Chapter outline

The first part of this chapter aims to test whether there is a relationship between absolute latitude, group size and associated home range size. In the second section of this chapter I compare recent and archaeological hunter-gatherer ranges to identify the maximum social layer in which social interaction took place. In the third and final section, I work towards quantifying the time costs involved in social network maintenance for higher latitude humans. Rather than reporting the results of specific hypothesis testing, this chapter explores questions surrounding the maintenance of social networks at high latitudes and aims to provide a framework for future research.

Method

Recent hunter-gatherers

Issues

I follow a number of other authors (Grove 2009, Grove 2010a, Grove, Pearce, and Dunbar 2012, Layton and O'Hara 2010, Layton, O'Hara, and Bilsborough 2012, Shuttleworth 2013) in using recent human hunter-gatherer societies to examine the behavioural variation that could be expected for hominin groups in particular ecologies. Recent societies are not taken as ‘living fossils’ but rather the range of behaviour they express provides a baseline ‘best guess’ that can be tested against independent evidence from the archaeological record (Kelly 1995, Kuhn and Stiner 2001, Layton 1986). However, many quantitative analyses, including those presented here, use data inferred from qualitative ethnographic accounts, which are often ambiguous and thus make inter-group and inter-observer comparisons extremely challenging. Nonetheless, by using data collated by a single author (Binford 2001), I hope that data collection, though far from ideal, was as consistent as possible. In addition, the available sample of hunter-gatherer societies is geographically biased, with large numbers in North America but none in Europe. However, for ease of comparison with Pleistocene environments without requiring detailed historical- and palaeo-climate data, I follow Layton and colleagues (Layton and O'Hara 2010, Layton, O'Hara, and Bilsborough 2012) in presenting the majority of analyses split by biome, which are taken to be analogous irrespective of continent.

Phylogeny

A recurrent problem in comparative analyses is lack of true independence between data-points, which are likely to be related to each other to differing extents due to shared history (Marlowe 2005). The most reliable method for accounting for such dependence is phylogenetic analysis (Chapter 2), but for hunter-gatherer societies no reliable language- or genetic-based global tree so far exists. To test whether findings held independently of shared history between groups, I therefore followed Hamilton et al (2007a) in using multi-level models to control for spatial relatedness, assuming that societies near each other geographically are more likely to be related genetically and/or culturally. To do this I nested my regression analyses using individual hunter-gatherer societies within biome categories and allowed intercepts and slopes to vary across these biome groups. Although this does not account for differential relatedness within biomes (i.e. branching structure), without a well-resolved tree this is currently the best way of taking into account the nested structure and thus possible dependence of the data.

Sample

I use data collated by Binford (2001), since this is the largest quantitative database of hunter-gatherer societies currently available. I used societies that were classified as 'normal' (that is, not of suspect hunter-gatherer status, according to Binford), mobile[50] and non-mounted, since horses were domesticated after the time period under study and such transportation would have greatly increased the distances groups could cover easily. Although other societies still included in the sample may have possessed transportation devises (e.g. sleds pulled by dogs in the Arctic), the data required to code this information would require examination of original ethnographic accounts for 178 different societies. The areas reported here may therefore be considered the upper limits of distances comfortably covered by hominins without transportation devices.

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[50] Although Hayden (Hayden, B. 2012. Neanderthal social structure? *Oxford Journal of Archaeology* 31:1-26.) suggests that localised differences in behaviour indicated by the archaeological record between Neanderthals and AMH could be due to some AMH groups developing more sedentary lifeways, with greater reliance on storage and higher population densities, reminiscent of societies in the Northwest Coast of America, there is currently no direct archaeological evidence to support this.

Biomes

By looking at the simulated reconstructions of Pleistocene biome distributions in Europe produced by the Stage 3 Project (van Andel and Davies 2003), it is possible to infer the recent hunter-gatherer societies that might be most representative of fossil hominin groups inhabiting similar environments. Although the distributions vary over time, the dominant biomes in Europe in both cold and warm phases (note that these phases are not tied to particular time periods, but instead are general representations of climatic fluctuations), as well as during the Last Glacial Maximum (LGM), are evergreen taiga/montane forest in the North and temperate grassland in the South around the Mediterranean, with the switch occurring at ~45° latitude. This suggests that recent hunter-gatherers from the Subarctic/Mid-latitude Continental Forest and Grassland Plains should show the closest correspondence with Pleistocene hominins in Europe. Unfortunately, the groups inhabiting the Plains of North America are mounted and therefore removed from this analysis. The recent Subarctic/Continental Forest groups therefore provide the closest analogy with Pleistocene Europeans, but I also present the data associated with other biomes for comparison. North American societies in particular may be the most representative of the mosaic of biomes evidenced in Europe during Marine Isotope Stage 3 (60-20kya). These Stage 3 simulations cover the crucial period of overlap between Neanderthal extinction and AMH occupation of Europe.

Layers of the social network (see Table 1.1)

Binford (2001) gives data on a number of different grouping levels. Although these groups are not presented as necessarily nested, averaged across different biomes their median values are fairly similar to the stable concentric layers of living human social group/network organisation: 5, 15, 50, 150, 500, 1500 (Binford 2001, Pearce et al. in press, Zhou et al. 2005). Binford provides data on the size of the (i) Family (I have taken the mean during aggregated and dispersed phases of the seasonal cycle combined and equate this with the ~5-layer: *M*=4.80, *median*=4.51, *range*=3-8, *N*=64), (ii) Group 1 (residential group/band size during the most dispersed phase of the seasonal round and here taken as equivalent to the 15-layer Sympathy group: *M*=14.15, *median*=13.50, *range*=6-32, *N*=139), Group 2 (residential group/band size during the most aggregated phase of the seasonal round and here taken as equivalent to the 50-layer band or Affiliation group: *M*=41.02, *median*=36.50, *range*=20-134, *N*=148), Group 3 (size of periodic aggregations and here taken as roughly equivalent to the active network[51]: *M*=170.47, *median*=150.00, *range*=42-438, *N*=127) and Population (the total number of individuals belonging to a particular named hunter-gatherer society and here taken as equivalent to the ethnolinguistic tribe[52]: *M*=1074.97, *median*=550.00, *range*=23-9000, *N*=178) (see Chapter 1: Figure 1.1).

Table 6.1 shows the results of one-sample Wilcoxon signed rank tests for each biome to test whether the median size of the Family, Group 1, 2, 3 and Population differed significantly from the idealised group/network layer sizes given above: see Appendix 4 (Table A11) for the accompanying data. Overall the observed group sizes in the Subarctic biome (the closest analogy for Pleistocene Europe) correspond fairly well to the idealized social layers, except that Group 3 was significantly different from both 150 (active network) and 500 (endogamous megaband) individuals (*median*=188, *range*=105-438).

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[51] On average Group 3 is the same size as the active network but the maximum is more inline with the megaband.

[52] Although in some societies Population size is more inline with the size of the megaband.

Table 6.1: Significance (p-values) of one-sample Wilcoxon signed rank tests testing for differences between observed hunter-gatherer group sizes and the size of 'idealised' network layers. ns=no significant difference.

Binford's Groups:	**Family**	**Group 1**	**Group 2**	**Group 3**		**Population**		
Idealised Layers:	**5**	**15**	**50**	**150**	**500**	**150**	**500**	**1500**
(Sub)Tropical Asia	ns	ns	ns	ns	ns	.043	ns	ns
(Sub)Tropical South America	ns	ns	ns	ns	.043	.036	ns	ns
(Sub)Tropical Africa	ns	.046	.028	.043	.043	ns	ns	.018
Australia	.001	<.0001	<.0001	<.0001	<.0001	<.0001	.014	<.0001
California and Northern Mexico	ns	ns	.015	ns	.005	.001	.007	ns
North American Desert/Scrub	.028	.001	<.0001	ns	<.0001	<.0001	ns	<.0001
Subarctic/Continental Mid-latitude Forests	.016	ns	ns	<.0001	<.0001	<.0001	<.0001	ns
Arctic	.021	ns	ns	.009	.002	.001	ns	ns

In order to calculate the approximate area associated with different grouping levels below the Population layer, I (i) calculated the area per individual by dividing the total Population area by the Population size and (ii) multiplied this by the number of individuals in the Family, Group 1, Group 2 and Group 3 of each society[53] (in order to simplify matters I ignored the relationship between area per individual and group size (Hamilton et al. 2007a)). I calculated the radius of each area modelled as a circle, for comparison with transfer distances and to estimate corresponding travelling times. I also calculated the theoretical area for the 'ideal grouping layers' listed above using population densities.

Data distributions

Since most variables showed non-normal distributions, for comparisons with archaeological transfer distances and in calculating travelling time I calculated the median, minimum and maximum values per biome. In regression and multi-level model analyses I

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[53] Alternatively, total Population area divided by the number of each type of group in the total Population.

used $\log_{10}$-transformed data, in order to fit linear models, since plots of raw data suggested curvilinear or 'broken-stick' relationships in a number of cases.

Archaeological record

I used the upper limit on obsidian transfer distances to represent the maximum distance over which social relationships were maintained. These data are from Moutsiou (2011) and cover Central and Southeastern Europe, the Middle East and East Africa during the Early Stone Age/Lower Palaeolithic (ESA/LP), Middle Stone Age/Palaeolithic (MSA/MP) and Late Stone Age/Upper Palaeolithic (LSA/UP). Moutsiou argues that obsidian is a particularly salient marker for social interaction due to its high functional and aesthetic value. It should be noted that although I used the maximum transfer distances inferred from histogram distributions of frequencies, the data collected by Moutsiou were minimum transfer distances to known sources and may thus underestimate actual transfer distances to some degree.

Time allocation

Data on time allocation to social interaction in traditional societies including hunter-gatherers are very limited, but I collated available data from the literature (see Table A17 in Appendix 4 for references and the definitions used in determining social time). These data probably underestimate social time because socialising may be concurrent with another activities and usually only 'primary activity' is recorded. The available hunter-gatherer data only relate to (sub)tropical groups living <30 degrees latitude. Due to the paucity of data, I ignored sex differences.

Travel time estimates

I modelled hunter-gatherer areas for each grouping level as circles[54], where $radius=\sqrt{(Area/\pi)}$. Using the radius I calculated the time taken to traverse it at a particular speed. This outputs the time taken for an individual/group to walk continuously from their home base at the centre of their associated 'territory' to meet an individual or group at the boundary of the neighbouring territory. In the case of Population areas, the travel times can be envisioned as peripheral groups around the boundary travelling to gather at a central location. These times are likely to be underestimated because individuals would probably need to stop to rest and/or forage during their journey. I assume that no transport aids are used.

According to ethnographic data collated by Binford (2001), hunter-gatherer walking speeds vary from ~2-4km/hour, with a single male-only hunting pair reaching 4.89km/hour (Binford 2001: Tables 7.10 – 7.13, pages 235 – 238). Although these data refer to foraging parties rather than residential or visiting moves *per se*, I take them as representative of average walking rates. Rodman & McHenry (1980) cite an average human walking speed of 4.5km/hour. I thus used walking speeds of 2, 3, 4, and 5km/hour in my time estimations (Appendix 4: Tables A13-A16), but present only the most conservative time estimates using a speed of 5km/hour here.

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[54] The circle models used here assume exclusive territories for groups within the ethnic population. However, across recent hunter-gatherer societies territories are not universal (Cashdan, E. 1983. Territoriality Among Human Foragers: Ecological Models and an Application to Four Bushman Groups. *Current Anthropology* 24:47Dyson-Hudson, R., and E. A. Smith. 1978. Human Territoriality: An Ecological Reassessment. *American Anthropologist* 80:21-41.). Moreover, the model assumes that there is no buffer zone between the home ranges of different groups: each group travels from the centre of their respective home ranges to the boundary, where they find their neighbouring group. The structuring of space within an ethnic population home range and how this impacts on the ease of social network maintenance is a matter for future consideration.

Results

Latitudinal trends in recent hunter-gatherers

OLS regression analyses revealed significant positive relationships between most area/group size variables and absolute latitude (NB family size showed a significant negative relationship and the size of periodic aggregations showed no significant relationship with latitude). However, once the hierarchical structure of the data was taken into account, only total home range Area and Population size show significant positive relationships with absolute latitude.

A mixed model fitted to $\log_{10}$ Area regressed against absolute latitude found that even when both fitted slopes and intercepts are allowed to vary between biome groups, a significant main effect of absolute latitude on Area remains[55]: $t_{15.692}=6.427$, $p<0.0001$, Figure 6.1. The same is true for $\log_{10}$ Population (ethnolinguistic tribe) size regressed on absolute latitude[56]: $t_{21.056}=2.793$, $p=0.011$, Figure 6.1. Group 3 (periodic aggregation size) did not show any significant relationship with absolute latitude, regardless of the model fitted.

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[55] A log-likelihood ratio test found a significant improvement in fit for the random slope and intercept model compared to the null model in which neither were allowed to vary between groups: $X^2=19.928$, $df_{change}=2$, $p=4.706e^{-5}$. However, the different intercepts and slopes across the different biome groups did not significantly differ from the parameters of a single regression model ignoring the nested groups ($p=0.523$ and 0.657 respectively). This may be because slopes/intercepts differed between some biomes, but not all.

[56] The random intercept term was redundant but the model allowing slope to vary across biome groups produced a significantly better fit to the data ($X^2=11.354$, $df_{change}=1$, $p=0.0008$), although the different group slopes did not show significant variance around a single slope fitted to the whole dataset and ignoring the nested structure (Wald test $p=0.186$).

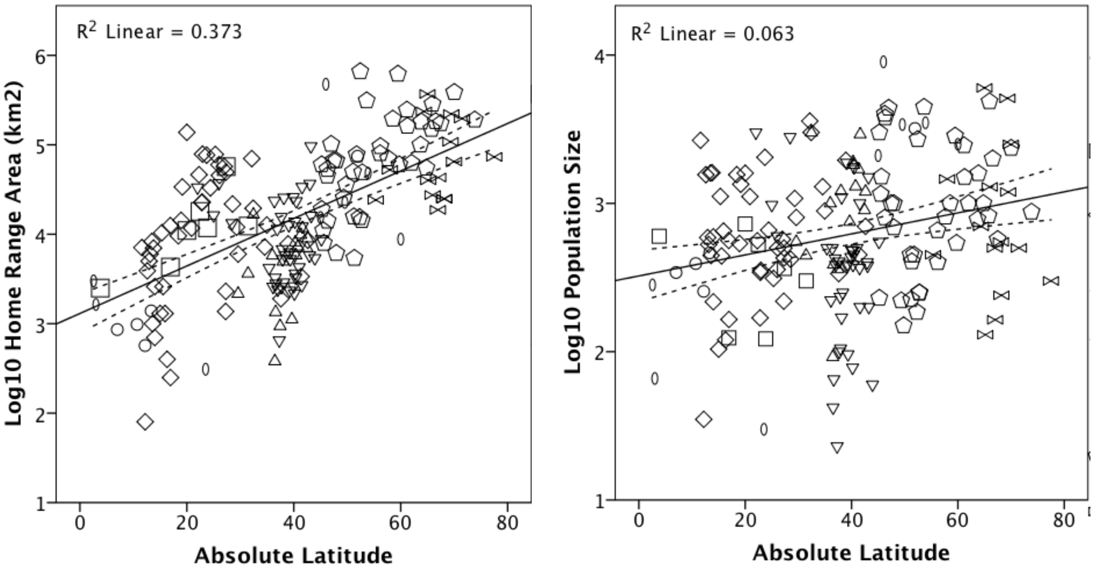

Figure 6.1: Log$_{10}$ Area (LEFT) and Population (i.e. ethnolinguistic tribe) size (RIGHT) plotted against absolute latitude, labelled by biome. The dashed lines show 95% confidence intervals of the regression lines. Circles=Asia, ovals=South America, squares=Africa, diamonds=Australia, mountain-peak triangle=California & Northern Mexico, inverted triangle=North American desert/desert scrub, pentagon=subarctic and continental forests and bow=arctic.

Recent hunter-gatherer ‘social distances’ at low latitudes

To gain an idea of the baseline distance over which social networks are maintained I investigated lower latitude hunter-gatherers. Wiessner (1981, 1982) describes hxaro exchange between !Kung individuals in adjacent bands up to 30km apart, with 70% of partners living <50km from ego. Partners >30km away are contacted less frequently, meeting face-to-face every 2-7 years. She notes that each family has at least one partner 150-200km away. Aka visiting distances in a tropical forest environment are fairly similar but somewhat shorter: 99% confidence interval maxima estimated from the mean and standard deviation values provided distances of 91.8km for family visits, 67.8km for hunting, 58.8km for dancing/ceremonies and 122.1km for trade (average data from Hewlett, Koppel, and Cavalli-Sforza 1982)[57]. The maximum distance over which social

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[57] Average distances were 47.6km for family visits, 22.8km for hunting, 17.6km for dancing and ceremonies and 34.8km for trade.

contact is maintained at low latitudes therefore seems to be in the region of 100-200km. I take 200km as the maximum.

However, given decreasing population densities at higher latitudes, the distance over which ties are maintained is expected to increase nearer the poles. Using population densities at low and high latitudes[58], one can estimate the high latitude equivalent of the maximum social (hxaro exchange) distances seen at low latitudes (Table 6.2). Given a maximum social area radius of 200km in subtropical Africa, the maximum area associated with that 'social distance' is 125,663.71km^2. At the median African density of 0.03 individuals/km^2, an area with a radius of 200km would contain ~3770 individuals. At the median higher latitude median densities, 3770 individuals would take up 377,000km^2 in the subarctic and 188,500km^2 in the arctic, giving radii of 346 km and 245 km respectively. At the lowest (sub)tropical African density of 0.01 individuals/km^2 there would be ~1257 individuals in an area with a 200km radius. At the minimum high latitude density of 0.003 individuals/km^2 1257 individuals would require 419,000km^2, giving a radius of 365km. These predictions are in-line with (i) maximum UP AMH obsidian transfer distances in Europe and (ii) the maximum ethnolinguistic tribe range radii of high latitude recent hunter-gatherers (Table 6.3).

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[58] According to the Binford (2001) database the median population density for the subtropical African hunter-gatherer societies as is 0.029 (*range*=0.01-0.24, *N*=7), whereas for the subarctic and mid-latitude forest groups the median density is 0.011 (positive skew; *N*=40, *range*=0.003-0.27) and for arctic groups the median is 0.016 (positive skew; *N*=15, *rang*e=0.003-0.05) (the higher arctic median may be an artefact of the smaller sample size).

Table 6.2: Using maximum low latitude exchange distances to predict equivalent distances in the high latitude Subarctic biome.

	(Sub)tropical African Biome				**Subarctic Biome**		
	Observed		**Predicted**		**Observed**	**Predicted**	
	‘Social distance’ (km)	**Population density (indiv/km)**	**Area (km^2)**	**Population size**	**Population density (indiv/km)**	**Area (km^2)**	**‘Social distance’ (km)**
Median densities	200	0.03	125,664	3770	0.01	377,000	346
Minimum densities	200	0.01	125,664	1257	0.003	419,000	365

Comparisons between recent and archaeological hunter-gatherers

Actual grouping levels

I calculated the areas and corresponding radii required for recent human hunter-gatherers in different biomes according to observed group sizes: Group1s (dispersed bands or 15-layer), Group 2s (fused bands or 50-layer), Group 3s (periodic aggregations) and ethnolinguistic Populations (tribes). This allowed me to identify which social layer maximum archaeological obsidian transfer distances most closely match: namely, the ethnolinguistic tribe radii (Table 6.3, Figure 6.2). The maximum radii for the smaller groupings are too low to match the maximum obsidian transfer distances in all biomes. At lower latitudes recent hunter-gatherer Population radii generally do not exceed 200km (with one exception in Australia, which lies just beyond that limit, and an extreme outlier in South America). At higher latitudes in the Subarctic and Arctic biomes the maximum Population radii exceed 200km. In the Arctic one society exceeds the MP maximum, but all Arctic radii lie below 400km (the UP maximum). However, the Subarctic seems to match the European habitat during Marine Isotope Stage 3 most closely and in this biome the maximum Population radii exceed the MP maximum of 300km, but match the UP maximum of >400km: Table 6.3, Figure 6.2.

Table 6.3: The rounded radii of the geographic areas associated with different grouping levels (see Table 1.1 for the equivalents in other classification systems) for recent hunter-gatherers, divided by biome, with archaeological transfer distances for comparison. Population maxima are shown in bold.

Biome	**Median (range) radius (km)**				**Archaeological transfer distances (Moutsiou 2011)**		
	Group 1	**Group 2**	**Group 3**	**Population**	**Obsidian**	**Other lithics**	**Shells**
Subtropical Asia (N=5)	3 (2-12)	5 (4- 21)	8 (7- 44)	18 (13 -**154**)			
Subtropical America (N=8)	8 (4 - 21)	13 (5 - 36)	23 (17 – 62)	61 (10 – **389**)			
Subtropical Africa (N=7)	9 (5 – 21)	18 (7– 41)	30 (20– 62)	61 (28 – **135**)	Maximum 150-200km		
Australia (N=46)	6 (3 – 30)	10 (4 – 45)	23 (6– 117)	54 (5 – **209**)			
California & Northern Mexico (N=16)	5 (4 – 7)	8 (6 – 13)	15 (9 – 23)	43 (11– **73**)	Central & Southeastern Europe Maximum **>400km** in UP (MP: max=250-300km)	By the late MP maximum distance exceeded 100km in Western Europe and was up to 300km in Central Europe. In the UP in Central Europe the maximum rose to 450km, occasionally exceeding 800km by the Magdalenian	Western Europe maximum ~300km throughout UP with a maximum of 800km in Central Europe across the same time period (although really Gravettian onwards).
Desert & desert scrub (N=41)	9 (4 – 21)	15 (8 – 43)	29 (11 – 64)	43 (14– **175**)			
Subarctic & mid-latitude forest (N=40)	24 (9 – 42)	40 (12 – 86)	74 (19 – 143)	146 (41– **458**)			
Arctic (N=15)	19 (10 – 53)	29 (15 – 103)	51 (25 – 137)	129 (77– **343**)			

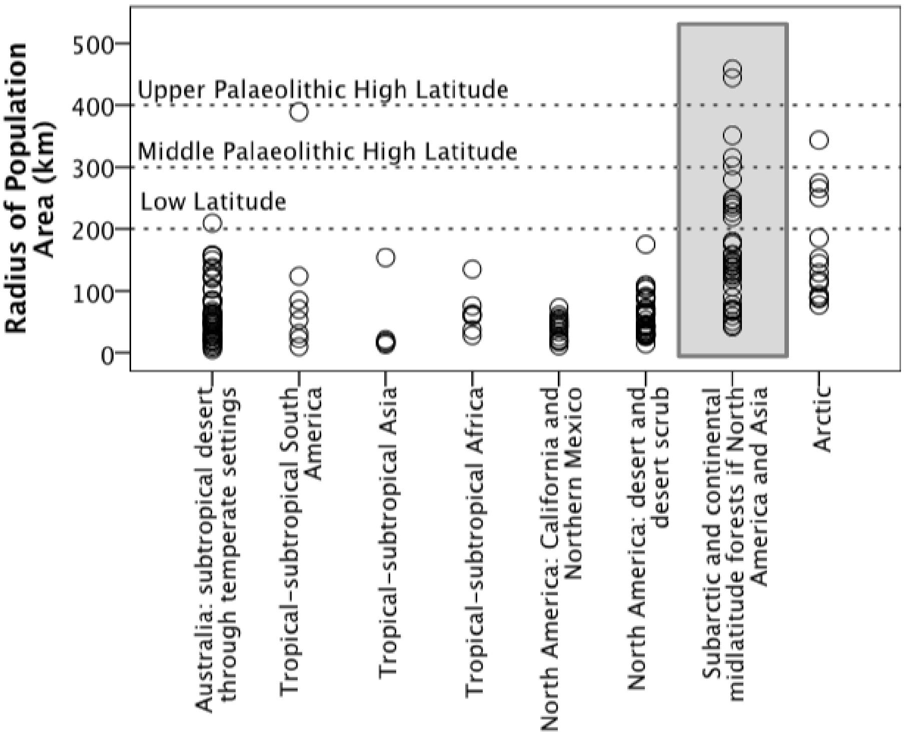

Figure 6.2: The radii of the total home range areas associated with recent hunter-gatherer societies for different biomes (calculated using data from Binford 2001). Horizontal dashed lines indicate maximum archaeological obsidian transfer distances during different time periods at different latitudes (Moutsiou 2011). The Subarctic biome is the closest analogue of Pleistocene Europe (grey box).

From Figure 6.3 it can be seen that the maximum radius for recent hunter-gatherer home range areas (associated with the whole tribe/Population) is ~200km nearer the equator, but this is associated with a single case at 20 degrees latitude. However, a number of societies have range radii that fall around 150km at this latitude. The apparently lower radii below 20˚ may be an artefact of the small sample size near the equator.

In contrast, between 45 and 60 degrees latitude the range radii of three societies approach and exceed 400km. However, from 50 degrees onwards a maximum of 350km seems more representative, in that it lies within the 95% prediction intervals of the data. Either way, the recent hunter-gatherer radii exceed the transfer distances observed in Europe during the MP. Overall, UP obsidian maximum transfer distances seem to match the radii of biome-matched ethnolinguistic Population areas observed in recent human hunter-gatherers.

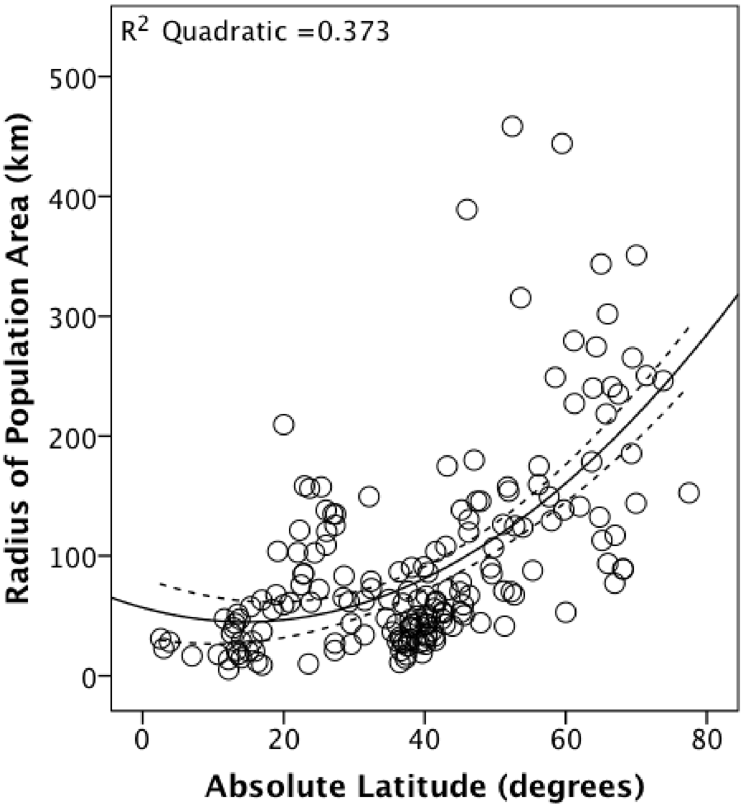

Figure 6.3: Radii of the home range area associated with 178 recent hunter-gatherer societies plotted against absolute latitude (calculated using data from Binford 2001). The dashed lines show the 95% confidence intervals for the quadratic regression line.

The rare occurrences of non-obsidian transfers of up to ~800km in the AMH record from the Gravettian onwards (Moutsiou 2011) may represent the entire span between the most distant boundaries of the home range: the diameter rather than the radii apparently represented by the other transfer distances (Table 6.3). Alternatively, such extended transfer distances could span the home ranges of adjacent Populations, indicating inter-tribal interaction.

Idealised grouping levels

Using recent hunter-gatherer population densities it is possible to estimate the area required for certain numbers of individuals and thus predict the areas expected for the average or 'idealised' social network layers (Zhou et al. 2005), see Appendix 4 (Table A12). Minimum population densities predicted maximum radii of ~400km for the 1500-strong ethnolinguistic Population/tribe layer in the Subarctic/Continental Forest and Arctic biomes, matching maximum UP obsidian transfers: Figure 6.4. For the African biomes the maximum radius (based on minimum population density) was ~200km (219km).

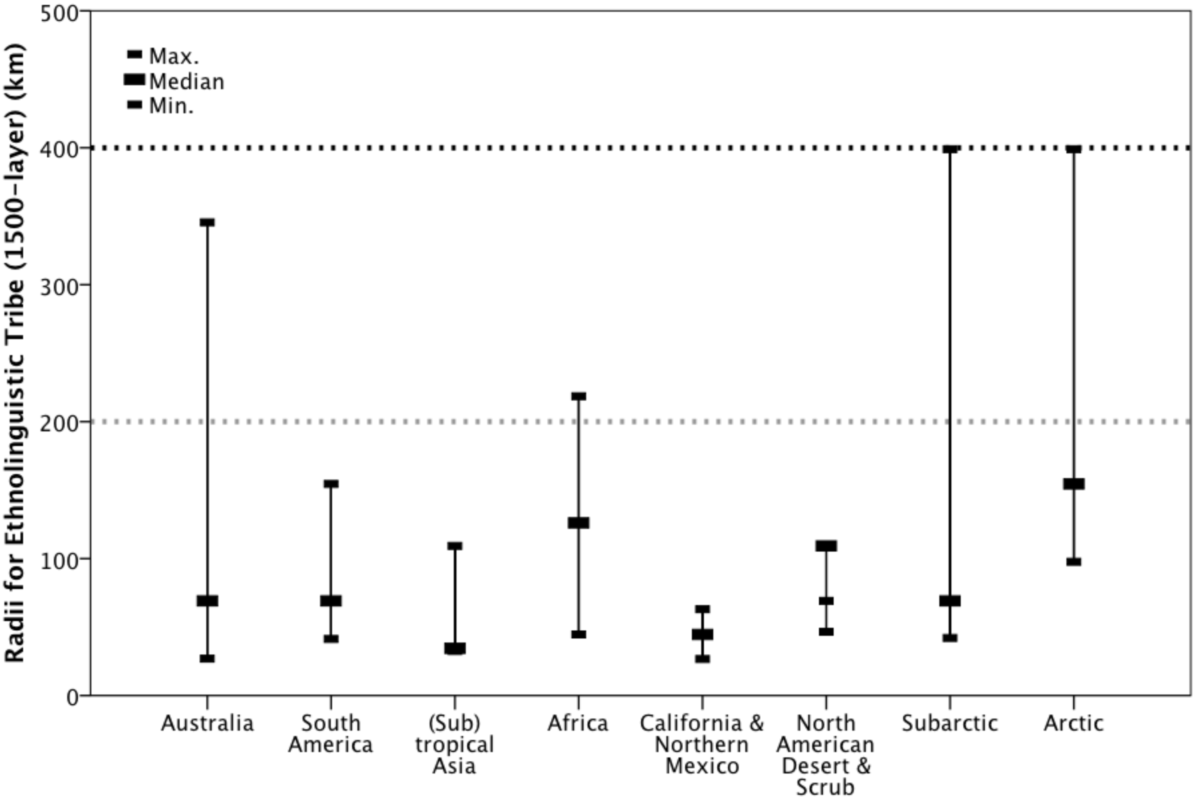

Figure 6.4: The maximum, median and minimum radii estimated for the idealised 1500-strong ethnolinguistic tribe social layer using recent human hunter-gatherer population densities (calculated using data from Binford 2001). The black dashed line indicates the maximum high latitude obsidian transfer distance and the grey dashed line the low latitude maximum obsidian transfer distance.

Social network area comparisons between Neanderthals and AMH

Archaeological signatures

In East Africa the maximum obsidian transfer distance for Early, Middle and Late Stone Age remains constant at 150-200km (for MSA McBrearty and Brooks 2000, for all: Moutsiou 2011). However, Marwick (2003) notes distances of up to 320km in MSA Tanzania dated 100-130kya compared to a maximum of 80km in LP Europe and 120km in early MP Europe for other lithics. Furthermore, silcrete transfer over 220km has recently been reported in MSA levels in Botswana (Nash et al. 2013). In comparisons with recent hunter-gatherers I focus on obsidian data, since transfer distances collated for a single type of raw material by a single author may be more consistently comparable, but it is worth noting that maximum distances differ between materials and that the obsidian data did not rely on chemical signatures but closest primary deposits.

In the Near East the maximum obsidian transfer in the Middle and Upper Palaeolithic is 200-250km (whereas during the LP it is only 100-150km) (Moutsiou 2011). However, it is unclear which hominins are associated with which instances of obsidian transfer in the this area, due to interspersed Neanderthal-AMH habitation.

In Europe there is no obsidian record for the LP. However, in the MP (Neanderthals) the maximum obsidian transfer distance is in the 250-300km range in Central and Southeastern Europe. The longer distance compared to the MSA AMH African record can probably be accounted for by the latitudinal difference between East Africa and Central/Southeastern Europe.

During the UP the maximum obsidian distances are >400km in the same European regions (Moutsiou 2011). These match the data reported by Féblot-Augustins (2009). This suggests that UP AMH transferred obsidian over greater distances than did MP Neanderthals; however, one does have to bear in mind the temporal and therefore climatic differences between these periods. For instance, Moutsiou (2011) found a positive relationship between periods of climatic deterioration and longer obsidian transfer distances. The larger AMH distances might thus reflect the downturn into the LGM. However, regardless of why AMH distances are larger than those recorded for

Neanderthals, the central conclusion here is that AMH seem to have been capable of maintaining their social networks over greater distances.

Estimated areas using standardised endocranial volumes and recent hunter-gatherer population densities

In order to further compare the areas over which social networks were maintained by Neanderthals and contemporary AMH, I used the active network sizes estimated from standardised endocranial volumes (Chapter 5). The size of the other network layers were estimated from these active network sizes using the scaling factor of ~3 between successive nested network layers/grouping levels (Hamilton et al. 2007b, Hill, Bentley, and Dunbar 2008, Zhou et al. 2005) (see Chapter 1). I then used recent hunter-gatherer population densities (Binford 2001) to estimate the geographic range for each layer.

For fossil AMH dated 27-75ky the mean cognitive group size of 164 from Chapter 5 gives a community of 492 and an ethnolinguistic Population layer of 1476. For Neanderthals the mean group size of 144 from Chapter 5 yields a community of 432 and an ethnoliguistic Population of 1296. At the minimum Subarctic/Continental biome population density of 0.003 individuals/km, this yields an ethnolinguistic tribe radius of 396km for AMH (i.e. ~400km as expected) and 371km for Neanderthals. The maximum estimated megaband (~500 layer) radii of 228km for AMH and 214km for Neanderthals lie below the maximum obsidian transfer distances observed for these hominins. This suggests that both taxa were maintaining connectivity within the outermost tribal layer of their respective social networks.

The fact that the Neanderthal radii estimated from standardised endocranial volume exceed the observed 300km transfer limit implies that standardised endocranial volumes overestimate Neanderthal active network size, or that Neanderthal population densities were higher than the recent hunter-gatherer minimum in similar habitats. The larger Neanderthal body mass and consequently higher energetic requirements suggest that the latter is unlikely (e.g. Aiello and Wheeler 2003, Hayden 2012, Kuhn and Stiner 2006, Mellars and French 2011, Sorensen and Leonard 2001, Stiner and Kuhn 2006). This implies that the active network size estimated from endocranial volume using an anthropoid equation may be an overestimate (Chapter 5). The lower active network estimates derived from standardised brain (versus endocranial) volume using an ape (versus anthropoid) equation (Appendix 3: Table A10) may thus be more accurate: a Neanderthal active network of 107 individuals yields a tribe of 963 and an associated home range radius of 319km. This is closer to the observed maximum transfer distance of 300km than the estimates derived from standardised endocranial volume.

An alternative way to approach this is to reverse the estimation process by using the maximum Neanderthal transfer distance and recent hunter-gatherer population densities to estimate Neanderthal group size. A transfer radius of 300km gives an area of ~282,743km^2. At the Subarctic density of 0.003 individuals/km this yields a population of 848 individuals[59]. Scaling this estimate down by ratios of three gives an average Neanderthal mating community/megaband of 283, a community/active network size of 94 (closer to the standardised-brain-derived estimate of 107 individuals: see Appendix 3), a band of 31 (which is supported by the estimates from floor areas and faunal assemblages: see Chapter 5), a foraging group of 10 and family size of 3. In contrast, for contemporary AMH a maximum transfer radius of 400km, gives an area of 502,655km^2. In turn at a density of 0.003 individuals/km this yields an ethnolinguistic population size of 1508

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[59] At a density of 0.05 individuals/km (the recent human hunter-gatherer maximum for the arctic biome), this area would support 14,137 individuals. Given the suggestion that Neanderthals would have been forced to live at lower population densities than AMH and furthermore because no recent hunter-gatherer societies in the Binford database number more than 6000 individuals (although this may be due to historical depletion), the 848-strong population size is probably more realistic.

individuals[60]. The inter-social-layer ratio of three yields nested group sizes of 1508, 503, 168 (note the estimation of 164 from mean standardised endocranial volume), 56, 19 and 6 individuals.

Possible time constraints on network maintenance

Primates, including modern human hunter-gatherers, have finite time to spend maintaining their social relationships. In order to investigate the limits on the size of social network that can remain cohesive at high latitudes I examined the time spent in activities associated with sustaining social bonds: face-to-face interaction, the travelling time necessary in order to meet social partners in other bands face-to-face and the time spent manufacturing objects to act as proxies for face-to-face interaction.

The majority of face-to-face social time is spent on the inner layers of ego's social network (Sutcliffe et al. 2011). Since band size does not vary significantly over latitude (see above), this allocation to face-to-face social time should remain fairly constant as well. As networks spread over greater distances at higher latitudes, more time in addition to this face-to-face 'social time' baseline is probably required to ensure contact is maintained with more distant social partners: ego needs to travel further to meet them and may need to invest time in supplementary methods of cohesion to make up for less frequent face-to-face interaction. From the findings presented above it seems that recent hunter-gatherers maintain connectivity across their tribal ranges at all latitudes, regardless of the progressive increase in the distances involved nearer the poles. However, it is unclear whether they are able to sustain tribal cohesion through social visits and periodic gatherings at the level of the whole tribal network. Examining the travelling times involved might allow an assessment of the feasibility of visiting and aggregating in order

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[60] A density of 0.05 individual/km gives a population of 25,133 individuals.

to in keep contact. If travelling times become excessively high, other mechanisms, such as the exchange of symbolic artefacts to represent social relationships and affiliations, may come into play. However, such artefacts require time for manufacture and this may create an additional limit, beyond that associated with travelling times, on the number of relationships that can be sustained *in absentia*.

Face-to-face interaction time

Hunter-gatherer and non-hunter-gatherer groups for which social time data were available show similar distributions, in that the modes coincide: Figure 6.5. These data give a median of 1.12 (*range*=0.77–1.42, *N*=3) hours for hunter-gatherers and 1.08 (*range*=0.23 – 2.80, *N*=12) hours for non-hunter-gatherers. Although the averaged hunter-gatherer data suggests a lower maximum than for other societies, adult male Ache average 2.13 hours socialising a day (Hill et al. 1985). This might indicate that a higher maximum would be observed for hunter-gatherers if a larger sample were available.

Since the median for hunter-gatherers closely matches the value for non-hunter-gatherers it seems reasonable to assume a similar maximum for hunter-gatherers as for societies using different subsistence methods. This assumption seems particularly warranted given the similarity in the time spent in subsistence activities, regardless of different resources and procurement strategies: for hunter-gatherers the *median*=3.42 (*range*=1.79-6.45, *N*=12) and for non-hunter-gatherers the *median*=3.81 (*range*=1.60-6.51, *N*=11), Figure 6.5. Assuming general similarity in social time regardless of subsistence activity, as a percentage of a 12-hour day humans seem to spend a maximum of 20-25% of their daylight time budget (2.5-3 hours) in social activities, with a median of ~8%. The ~20% figure has previously been reported by Dunbar using a range of traditional subsistence groups (Dunbar 1998a) and matches the maximum grooming time of non-human primates (Dunbar 1991, Dunbar 1993).

Compared to time spent primarily in subsistence, socialising seems to take up only a small proportion of hunter-gatherers' day-light hours. This is likely because much gossiping, singing and so on occurs after dark around the fire (Dunbar and Gowlett in press). However, this means that in terms of time constraints on maintaining social networks, face-to-face interaction with the inner layers of ego's network during the day does not seem to be a limiting factor, at least in modern humans. Since band size does not vary greatly with latitude, nor should daily face-to-face social time. Time constraints on network maintenance at high latitudes are more likely to be associated with activities other than face-to-face interaction *per se*, such as travelling in order to meet social partners in person.

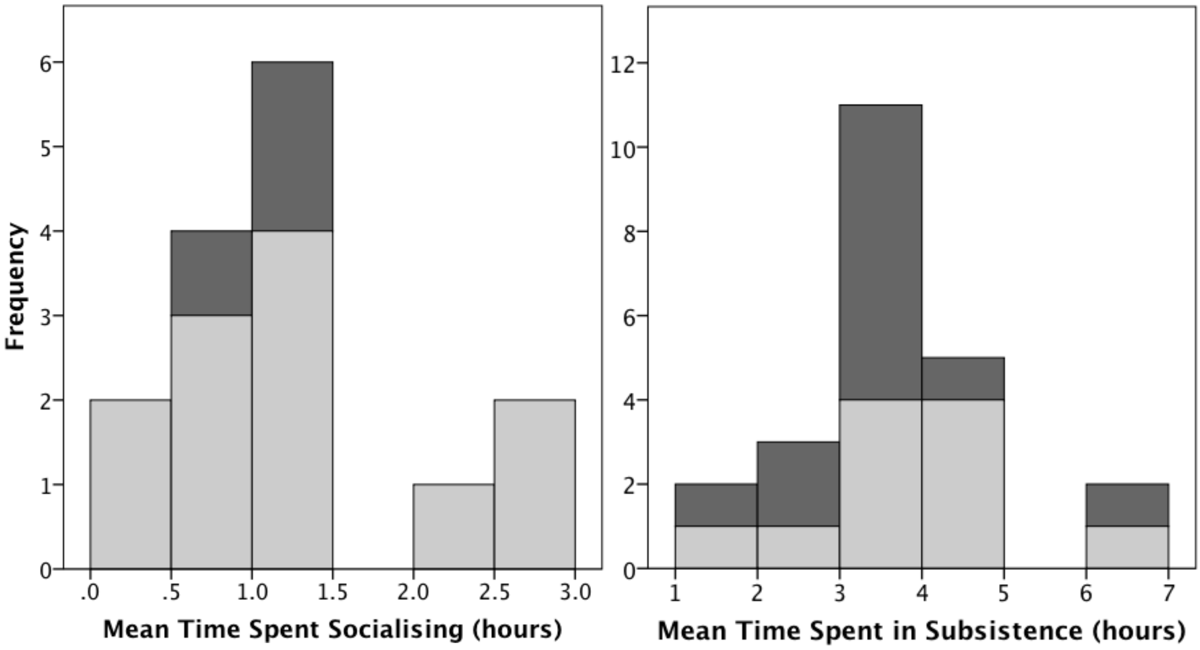

Figure 6.5: The distributions of time allocated to socialising (LEFT) and subsistence (RIGHT) by hunter-gatherers (dark grey) and traditional subsistence non-hunter-gatherers (light grey) (see Table A17 in Appendix 4 for data sources).

Travel time

I calculated the walking times required to cover the distances associated with Groups 1, 2, 3 and Population for different biomes (Appendix 4). Assuming a walking speed of 5km/hour, the area associated with the ethnolinguistic Population breaches the point where its radius can be walked in 12 hours at ~30 degrees latitude and cannot be covered in less than 8 hours at any latitude (see Figure 6.6). In contrast, the radii of areas associated with periodic aggregations (Group 3) breach a walking time of 12 hours at ~55 degrees latitude and a walking time of 8 hours at ~40 degrees latitude. Traversing Group 3 radii in order to periodically aggregate with other bands thus only exceed a day of walking in the Subarctic/Forest and Arctic biomes.

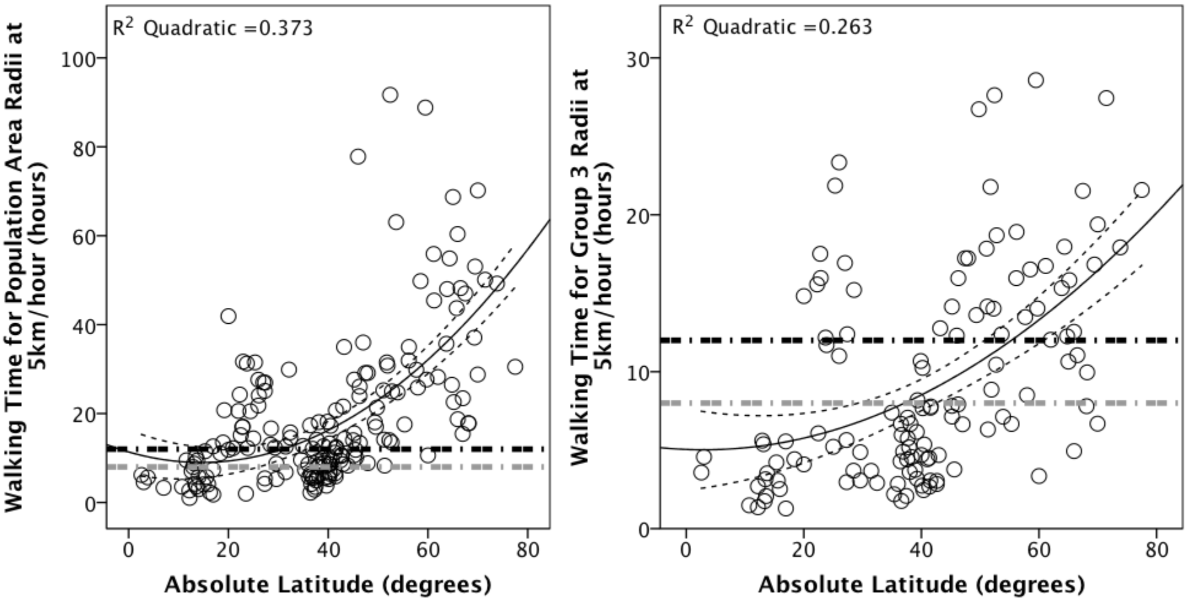

Figure 6.6: The walking time for radii associated with the Population (LEFT) and Group 3/periodic aggregations (RIGHT) in recent human hunter-gatherers (calculated from group size and area data from Binford 2001). The horizontal dashed lines represent 12 (black) and 8 (grey) hour limits. The curvilinear dashed lines indicate 95% confidence limits for the quadratic regression lines. The walking times are given in absolute hours.

Exchange object manufacture time

Unfortunately there is little published data on manufacture times for different artefacts, either from the ethnographic literature or from experimental archaeology. In the

!Kung hxaro exchange system arrows are often exchanged, and McBrearty and Brooks (2000) reference work suggesting that geometrics (small lithics) require 10-20 seconds to manufacture once the raw material has been obtained. However, hafting is a fairly convoluted process, which involves the sourcing and combining of multiple resources such as the whittled haft, the fire-treated adhesive and the binding cord, in addition to the stone tip (Wilkins et al. 2012) and is therefore likely to take much longer than a few seconds in total. Experimental reconstructions of Aurignacian beads suggests a manufacture time of 1-3 hours per bead and the modern recreation of the Hohlenstein-Stadel Lion Man took ~400 hours (Ice Age Art exhibition, British Museum, February 2013). Furthermore, the acquisition of raw materials might also create high time costs.

Even so, once such artefacts are created, they are often curated and therefore have a long use-life[61]. Consequently, the time cost of manufacture, and even of raw material procurement, may be 'worked off' over the long term. In addition, manufacture may be completed over a series of sittings, as suggested by the paucity of complete core re-fits in archaeological contexts (Hallos 2005). Other ways of mitigating time costs could be by having specialist manufactures, similarly to women in the Arctic producing and maintaining crafts and equipment while the men hunt (Kuhn and Stiner 2006). Despite time demands in terms of manufacture, these objects should reduce the time required for travelling to maintain relationships face-to-face. These objects retain utility as long as the 'social' travel time saved outweighs manufacture and procurement time. In any case, the latter might be subsumed within subsistence and residential mobility.

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[61] Although note that thousands of beads were taken out of exchange circulation through their incorporation into Gravettian burials, such as at Sungir. Furthermore, the Lion Man seems too large to be mobiliary art but was rather deposited in a cave where is was finally rediscovered ~40ky later.

Discussion

As predicted and previously noted, home range area increases with absolute latitude in recent hunter-gatherers. The same is true for archaeological transfer distances (Moutsiou 2011). Whether or not a proxy for shared history is taken into account, ethnolinguistic population size increases nearer the poles, whereas the size of periodic aggregations (Binford's Group 3) is constant across latitude. Band size is also similar in different biomes[62]. Together, these analyses suggest that higher latitude hunter-gatherers have a slightly larger pool of potential social partners comprising their ethnolinguistic tribe and yet the tribe is spread over a much wider area. The slopes suggest that areal increase with latitude is more pronounced than that of tribal network membership size (Figure 6.1): for each unit increase in absolute latitude, $\log_{10}$ Area increases by 0.611 units whereas $\log_{10}$ Population size only increases by 0.250 units. Thus, although social information and aid may become increasingly imperative nearer the poles, the opportunity to create and sustain social bonds face-to-face declines as the network becomes dispersed over greater distances.

Maximum UP obsidian transfer distances match both the radii of recent hunter-gatherer Population areas in the Subarctic biome and the maximum hxaro distance expected for high latitudes, suggesting that UP modern humans at all latitudes maintained contact across their tribal home ranges. Since recent hunter-gatherers may use transport aids, this close correspondence between archaeological and recent range distances might suggest that at least UP AMH might have already been using such technology to reduce travel times at the highest latitudes.

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[62] However, note that since biome distributions are partly based on latitude, the lack of a significant relationship between band size and absolute latitude taking biome nesting into account may not be surprising. Nonetheless, area and population size did remain significantly associated with absolute latitude regardless of the hierarchical structure of the data. Still, once a hunter-gatherer phylogenetic tree is available, these analyses should be re-tested.

Areas inferred from the active network sizes based on standardised endocranial volumes (Chapter 5) suggests that similarly to AMH, Neanderthals were maintaining contact within ethnolinguistic tribes. This is supported by the work of Ruebens (2012), who has demonstrated regional variation in late MP Neanderthal-associated bifacial tools, perhaps suggesting cultural differentiation over substantial areas of Western (Mousterian of the Acheulean Tradition: MTA) versus Central/Eastern Europe (Keilmessergruppe: KMG), with a large contact zone in between (Mousterian Bifacial Tools: MBT). Population estimates for the KMG tradition are in-line with the modern human ~1500 layer (1240-1940 individuals), although for the MTA in the West, the numbers are more similar to the AMH ~500 strong endogamous community (470-750 individuals) (Ruebens, 2012). Furthermore, Ruebens (2012) notes further subdivisions within the MTA 'culture', with classic, triangular and bout-coupé handaxes being confined to particular geographic regions within the total MTA range. It could be that these 'subcultures' might represent social structures nested within the ethnolinguistic tribe, such as megabands.

Although the areas covered by Neanderthal technocomplexes suggest slightly larger 'social distances' than the obsidian transfer distances (Table 6.4), there are no similar AMH data for direct comparison. Further work comparing these Neanderthal 'cultural' areas to those covered by MSA industries made by AMH in Africa, as well as with UP regional traditions in Europe, could potentially elucidate whether AMH technological cultures covered greater geographic areas than industries affiliated with Neanderthals. Once a database of well-dated and typologically well-understood sites is collated, it would be fairly straightforward to analyse the geographical coverage of different material 'cultures' using a geographical information system (GIS), along similar lines to Vanhaeren & d'Errico's (2006) examination of Aurignacian beads. Pending a more in-depth analysis, initial visual inspection suggests that the AMH Gravettian (30-

20kya)[63] spans the whole range of the separate MTA and KMG cultures identified in the Neanderthal record by Ruebens (2012), excluding Britain (Svoboda 2007): Figure 6.7. This observation seems to warrant further exploration, although it should be borne in mind that these technocomplex ranges manifest the maximum extent of the use of these technologies amalgamated across their entire date-spans, rather than the extent of the combined social network for a particular generation of hominins.

Table 6.4: Comparison between the areas and radii associated with obsidian transfer distances (Moutsiou 2011) and Neanderthal technocomplexes (Ruebens 2012).

	Obsidian (Maximum)		**MP 'Technocomplexes'**					
	Areas (km^2)	**Radius (km)**	**MTA (Western Europe)**		**MBT (Western Europe)**		**KMG (Central Europe)**	
			Area (km^2)	**Radius (km)**	**Area (km^2)**	**Radius (km)**	**Area (km^2)**	**Radius (km)**
Africa	123,101	198						
Europe – UP	750,840	>400						
Europe - MP	282,743	300	450,000	378	320,000	319	>36,000	>107
NB Lithic transfer distances have consistently been found to be greater in central versus Western Europe (Féblot-Augustins 1993, Féblot-Augustins 2009, Moutsiou 2011) so the fact that the radius of the KMG is only 107km compared to a maximum of 300km for obsidian movement suggests that the KMG may subsequently be found to have a greater geographic range than hitherto appreciated.								

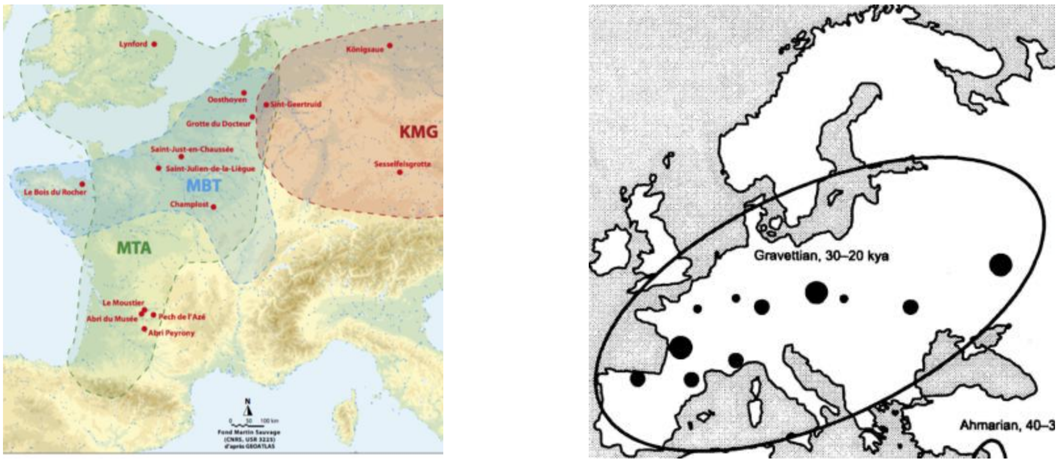

Figure 6.7: The geographic ranges of the Neanderthal MTA and KMG technocomplexes (LEFT) (Ruebens 2013, permission given. NB the site names are not important, the point is to see the areas covered by MTA and KMG and the overlap zone MBT) and the AMH Gravettian industry (RIGHT) (Svoboda 2007, permission for use granted).

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[63] The Gravettian chronologically follows the Aurignacian dispersal and is thus the most contemporaneous 'colonised/settled' culture to those of the European Neanderthals, rather than reflecting large-scale population movement.

Even though the transfer distance data suggest that both Neanderthals and AMH were maintaining contact within their ethnolinguistic Populations, the infrequent instances of AMH transfer distances of up to 800km (Féblot-Augustins 1997, Moutsiou 2011) suggest that unlike Neanderthal tribes, those of AMH did interact on occasion. Moreover, the frequencies of longer transfer distances are higher for AMH than Neanderthals (Moutsiou 2011), suggesting that although Neanderthal endogamous megabands within the same ethnic Population did interact, they perhaps did so less often than AMH megabands.

Comparison between the average active network size estimates made (i) from standardised endocranial or brain volumes and (ii) from obsidian transfer distances suggested that for Neanderthals, the endocranial-derived prediction (144 individuals) was an overestimate whereas the lower brain-derived prediction (107 individuals) was closer to the prediction based on maximum transfer distance (94 individuals). In contrast, for AMH the endocranial-derived prediction (164 individuals, versus 152 individuals estimated from the brain equation) matched the transfer-derived estimate (168 individuals) very well. This discrepancy may indicate that the difference in social network size between these taxa was greater than predicted in Chapter 5. The anthropoid equation used in Chapter 5 has a lower slope than the ape regression model used in Appendix 3. Furthermore, using absolute endocranial volume adds variance to the primate relationship with group size and this will also lower the slope. For a given difference in endocranial/brain volume, a lower slope will predict smaller differences between the associated active network sizes. Estimates of active network size based on neocortex volume should be closer to reality for both taxa, especially if visual areas beyond just V1 and V2 were taken into account. Overall, it seems that any social cognitive difference, and thus any underlying difference in brain organization between Neanderthal and AMH may have been even more substantial than proposed in Chapters 4 & 5.

On the other hand, the apparent discrepancy between cognitive and realized group sizes might be due to time as well as cognitive constraints, for instance associated with low population densities linked to high energetic requirements. Alternatively, Neanderthals may have been limited to smaller home ranges due to their robust physiology impeding long-distance travel (Burke 2012, Finlayson 2004). Either way, the apparent difference between Neanderthals and AMH in the distances over which social connections were maintained seem to be a matter of degree rather than qualitatively distinct. Any mechanisms for maintaining networks *in absentia* may therefore be found associated with Neanderthals, but to a much lesser extent and perhaps in fewer different forms than associated with AMH.

Rather than face-to-face interaction or manufacture time, the strongest constraint on the maintenance of social networks over larger areas seems to be travelling time. This seems to gel well with previous work showing that travelling time is the limiting factor on population-specific community size in extant apes as well as *Australopithecines* (Bettridge 2010). According to the models presented here, travelling for periodic aggregations at a walking pace of 5km/hour exceeds 12 hours for recent hunter-gatherers in the Subarctic biome (above 45 degrees latitude) even without stops for resting or foraging. This may be one reason that Group 3 aggregation size does not increase with latitude: the necessary time involved becomes unmanageable (probably in conjunction with carrying capacity constraints). Additional costs associated with aggregating in winter are likely to accrue at higher latitudes because day-length is extremely short and travel conditions are particularly difficult.

In both Subarctic and Arctic biomes, walking the radii of Population home ranges could take several 12-hour days of solid walking. It is therefore likely that travelling times place a limit on the distance that individuals can cover and thus on the number of individuals that can aggregate at any one time. This means that at higher latitudes the outer layers of a social network cannot be bonded during intermittent physical gatherings and consequently, tribal cohesion requires alternative support. For instance, mobility for subsistence needs could inadvertently increase the chance of encountering and maintaining bonds with neighbouring groups. Thus ‘social’ travel costs might be mitigated by incorporating them into residential and subsistence mobility. In order to investigate this, in Chapter 7 I take a gas modelling approach to look at predicted contact frequencies in different biomes and at different levels of group fissioning. Where subsistence mobility is insufficient to sustain intergroup connectivity for all layers of the social network, additional mechanisms of maintaining bonds over space and time are expected.

Chapter 7 Gas models, subsistence mobility and social network maintenance

Higher latitude hominins need to maintain their social networks over increasingly greater geographic distances. This suggests that as latitude increases, face-to-face interaction becomes progressively less frequent for the outer layers of a network. Given this, additional mechanisms for maintaining social relationships in absentia should become imperative. However, it may be that daily travel for subsistence provides opportunities for neighbouring groups to meet each other sufficiently frequently to sustain connectivity. Here I model mobile groups as moving gas particles in order to investigate whether subsistence mobility on its own allows the members of a group to maintain contact with all individuals in their total social network. I look at the movement of Families and bands at both the most dispersed (Binford's Group 1) and fused (Binford's Group 2) stages of the seasonal cycle in order to see the effect of varying degrees of fission-fusion on intergroup encounter rates. The gas model predicts that only in the highest latitude Subartic/Continental Mid-latitude Forest and Arctic biomes is subsistence movement insufficient to facilitate adequate contact between members of the mating community (megaband/500-layer) and ethnolinguistic tribe (~1500-layer). This suggests that special mechanisms for maintaining the outer layers of the social network in absentia should be expressed in these types of environments in particular. Although the gas models reported here are productive first steps, I propose that agent-based models are necessary in order to develop this investigation further.

Introduction

In Chapter 6 I argued that although high latitude recent hunter-gatherers may not have to maintain much larger social networks than hunter-gatherers living in the (sub)tropics, individuals living nearer the poles have to contend with their social networks being spread over greater geographic distances. If they are to reap the benefits of wider networks, such as reproductive opportunities and insurance against ecological risk, high latitude individuals require the means to sustain social bonds over separations in space and time. Travelling to visit more distant groups or to take part in periodic aggregations is time-costly (Chapter 6). However, one way of absorbing these potential time costs is to embed social activities within more purely subsistence-based ones. In recent hunter-gatherers residential mobility increases with latitude: $\log_{10}$ total annual distance moved is significantly positively associated with absolute latitude, even when the grouping of hunter-gatherer societies within biomes is taken into account ($t_{10.348}$=3.334, p=0.007)[64] (data from Binford 2001). Higher mobility primarily linked to tracking resources may allow social networks to remain connected as neighbouring groups are coincidentally encountered. My aim here is to examine whether the movement of groups around a given area creates a sufficient number of encounters between those groups for each individual member to maintain their social network. In other words, to investigate whether the normal movement of groups around the landscape for resource gathering inadvertently allows neighbouring groups to stay connected, without having to resort to special social visiting trips or other mechanisms of contact and cohesion.

Compared to groups nearer the equator, higher latitude groups may need to fission into greater numbers of foraging units in order to accumulate sufficient resources and simultaneously maintain manageable day journey lengths (Grove, Pearce, and Dunbar 2012, Pearce et al. in press). There are several implications of greater numbers of mobile groups: (i) coordination becomes more complex and cognitively demanding (although agreed home bases might mitigate this to some extent) and (ii) the encounter rate between groups is increased so that individuals may not have to rely solely on specifically social visits to maintain social contact, but may rather meet members of their neighbouring bands during foraging and other resource procurement journeys. However, it remains to be

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[64] The biome model provided a significantly better fit than the null model: X^2=14.903, df_{change}=2, p=0.0006.

empirically tested whether the higher encounter rate associated with fissioning can counteract home range area increase with absolute latitude, and furthermore, at which social grouping layer this kind of opportunistic mechanism for network maintenance might break down. I test this here using the ideal gas model equation (Grove, Pearce, and Dunbar 2012, Harcourt and Greenberg 2001, Hutchinson and Waser 2007). This treats each group as a gas particle moving independently and randomly around a two-dimensional space and for a focal group outputs either (i) the encounter rate per unit time or (ii) the number of encounters during a particular period.

To investigate the influence of varying degrees of fissioning, I model mobility at three grouping levels (see Chapter 1): Binford's (2001) (i) Family (~5-layer), (ii) Group 1 (the band at the most dispersed phase of the seasonal cycle and equivalent to the ~15-layer sympathy/foraging group) and (iii) Group 2 (the band at the most fused phase of the seasonal cycle and equivalent to the ~50-layer affiliation group). Bands will normally split for foraging purposes, into a single female gathering group and several male hunting parties, as well as some individuals staying behind in camp. These foraging groups will have different mobility strategies and be of different sizes, but these details are ignored here. Instead, for the purposes of the model presented in this chapter, the ~5-strong 'Family' unit could represent either (i) the basal unit of band social organisation i.e. the nuclear family or (ii) foraging parties linked to division of labour. I concentrate here on daily subsistence/foraging movement, which generally involves subsections of the band moving together, rather than residential movement, where the band would usually move as a more aggregated unit. More complex models could take both types of mobility into account, as well as variation in both over season and latitude. Since splitting into the smallest units (a Family) increases the density of groups within a particular area[65], the modelled encounter rate for a Family unit will be highest and thus most likely to yield adequate contact frequencies between components of a social network compared to more fused groups. If not even Families experience sufficient encounters with neighbouring groups, it is likely that the encompassing network could not be maintained through subsistence movement alone. The Family-level outputs of the gas models thus act as a conservative test of the feasibility of network maintenance under the model assumptions.

In order to ascertain how realistic these modelled 'expected' encounter rates are, I compare them to observed face-to-face contact frequencies from an industrialised society (data from Roberts et al. 2009, recalculated following Sutcliffe et al. 2011). Such studies of modern data assume that face-to-face contact at least once a year is required in order to keep a relationship 'live'. Since hunter-gatherer networks are known to possess similar attributes to 'modernised' networks (Apicella et al. 2012), I take a yearly cycle as the unit of analysis here as well. I compare the encounter rates predicted by the gas model for mobile hunter-gatherer groups during a single seasonal cycle with the observed rates of contact obtained for individuals living in an industrialised society where membership of their network required contact at least once a year.

These empirical data are given as the time from last contact but can be reconfigured to give the frequency of interaction within each network layer per day and per year (Sutcliffe et al. 2011): Figure 7.1. The assumption is that due to competing demands on their time and energy, individuals will invest the minimum amount of effort required to service each relationship so that it remains active. These observed rates of contact will therefore indicate the baseline frequency of interaction that is necessary to

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[65] Although perhaps also decreasing the ability to detect such groups to some extent (see the Gas Model equation below).

maintain a relationship at a particular degree of intimacy. I therefore take these observed data as the lowest benchmark number of interactions between individuals required in order to maintain a relationship within a particular social layer. If expected encounter rates from the gas models exceed these observed rates, then relationships within the associated network layer could be maintained. In contrast, if the encounter rates predicted by the gas model fall below the observed contact rates, the corresponding social relationships would dissolve due to insufficient interaction. As can be seen from Figure 7.1, the necessary encounter rate drops steeply beyond the most intimate support clique of 5 individuals, here equated with the Family. Since the Family is the basal unit in the models presented here, interaction between family members is constant and contact frequency within the 5-layer is redundant. I therefore concentrate on the frequency of interaction required for the subsequent social layers.

A caveat to these comparisons is that necessary contact frequencies are likely to differ between kin and non-kin, since relationships between the latter seem to decay more quickly in the absence of frequent interaction (Roberts and Dunbar 2011a, Roberts and Dunbar 2011b). However, the mean encounter rates used here act as guidance to (i) whether the gas model produces realistic estimates and (ii) whether the predicted encounter/contact rates for hunter-gatherer societies in all biomes at least match these observed rates and thus imply the ability to maintain adjacent network layers, given the model parameters.

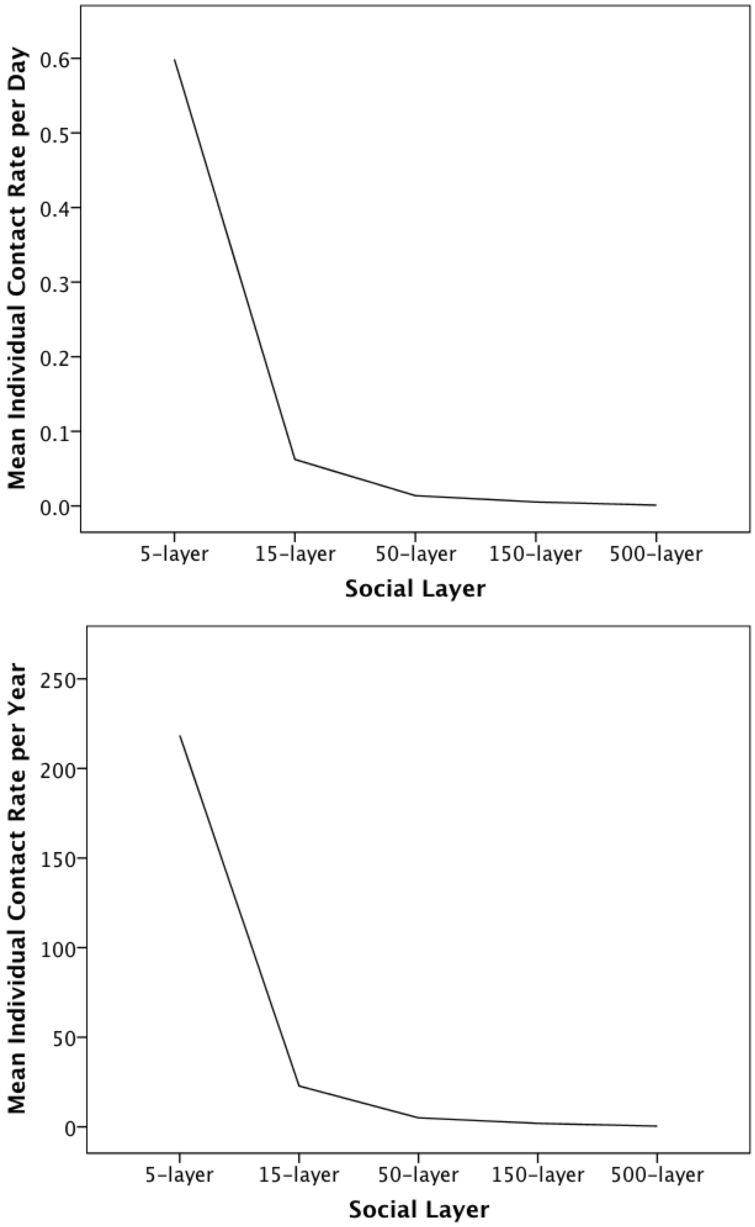

Figure 7.1: Observed mean contact rates between ego and an average individual in each of ego's social network layers, per day (TOP) and per year (BOTTOM) (data from Roberts et al. 2009, recalculated by R. I. M. Dunbar following Sutcliffe et al. 2011). The frequency of contact per day is calculated as the reciprocal of days since last contact and converted to the rate per year through multiplying by 365 days. The figures are based on Sutcliffe et al (2011) but redrawn with corrected data.

A complementary approach is to calculate the number (versus the rate) of encounters during a particular period and compare this with the number of encounters that would be required to maintain successive social layers. For instance, a Family unit already encompasses the 5-layer but would need to interact with at least two other families in order for its members to each maintain their 15-layer. Fewer than two encounters within a given time period indicates that the 15-layer could not be sustained. Here I present both encounter rate and number outputs.

Since the area over which networks are maintained increases with latitude, I expect encounter rates to decrease nearer the poles and for subsistence movement to become insufficient to sustain network connectivity. The model should yield testable predictions regarding the types of environments in which evidence for extra mechanisms to bond extended networks *in absentia* can be expected. Although it is the distribution of resources and network members that is important regarding cohesion, rather than the environmental typology *per se*, for simplicity I present the gas model output per biome.

Methods

The ideal gas model predicts how frequently another group encounters a focal group within a particular area. The model presented here can be interpreted one of two ways: (i) groups moving across the entire home range of their tribe or (ii) groups moving within an habitual home range associated with a number of bands that periodically aggregate together (i.e. the area associated with Binford's Group 3: a sub-section of the total tribal home range) (Figure 7.2). This is because the encounter rates are identical in both scenarios. Since the calculation of the area associated with a Group 3 unit depends on the number of Group 3 units per Population and total Population area, the relative group densities and thus encounter rates are identical regardless of whether the area within which the mobile units are contained is associated with the total Population or the average Group 3 unit. Although I report the method of using groups moving within the area associated with periodic aggregations, theoretically representing some sub-structuring within the total tribal home range (Figure 7.2), the model outputs could be interpreted either way.

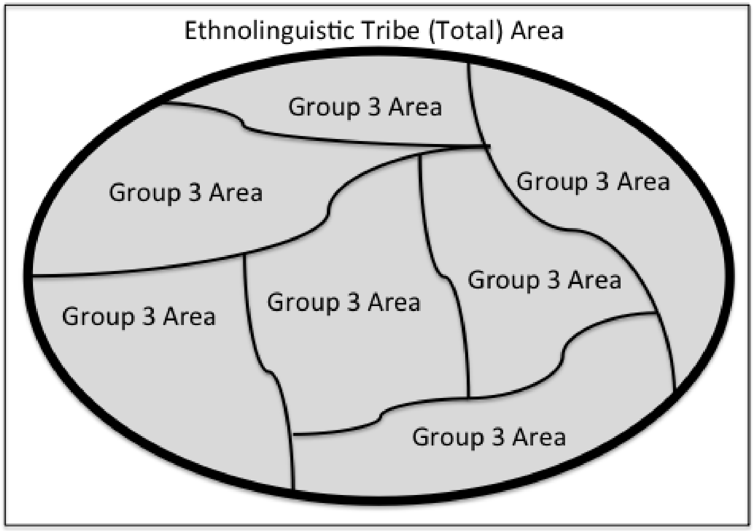

Figure 7.2: In the gas models presented here, groups move within the average area associated with periodic aggregations of bands (the Group 3 areas, in Binford's terminology).

For each grouping level I calculated the number of encounters between like-groups: a Family unit encountering another Family unit, a Group 1 unit encountering another Group 1 unit and a Group 2 unit encountering another Group 2 unit. The Family unit is taken to represent the ~5-individual level of the social network, so interaction frequencies between Family units are seen to be at the 15-layer level: three Families interacting creates the 15-individual social network layer. The Group 1 or most dispersed band unit is assumed to equate with the 15-individual layer of the social network (Sympathy group), so interactions between Group 1 units are at the 50-layer (Affiliation group) level. Lastly, the Group 2 or aggregated band unit is assumed to represent the 50-layer, meaning that interactions are between Group 2 units are at the 150-layer level. I assume that bands are the highest level of grouping travelling as an integrated unit. I therefore ignore the frequency of interactions between Group 3 units: these groupings are the result of band aggregations rather than mobile groups themselves. All calculations were run using code written in R.

I followed Hutchinson & Waser (2007) to calculate the number of encounters for an individual focal group using the ideal gas model equation:

Individual rate of encounter = $8\rho Dv/\pi$

where ρ is the density of groups, D is the detection distance (see below) and v is velocity, which I assumed to be 25km/day (Binford 2001: Table 7.11 for Nunamiut men). This is also the maximum foraging radius for a sample of hunter-gatherers given by Layton et al (2012), which suggests that for an estimate of the distance covered in a day this value should be doubled, assuming hunter-gatherers avoid redundancy by not retracing their steps exactly. In order to take this into account I also ran the models with a velocity of 40km/day following Grove et al (2012). This is the total foraging distance suggested by the median foraging radius given by Layton et al. (2012: range 15-25km). Overall the patterns produced are similar regardless of the velocity used, and in general I present only the output of the 25km/day velocity model while commenting on predictions produced by the 40km/day model.

Detection distance can be understood as the distance within which two groups need to come of one another in order for an ‘encounter’ to have taken place. Hutchinson & Waser (2001) explain that if the diameter of a social group is s and the maximum detection distance between individuals is d, the members of the group travelling at the periphery of the group may detect each other when the group centres are less than or equal to $d+s$ apart[66]. The detection distance D equates with $d+s$. The authors specifically state that D is not the distance between the edges of groups (which is actually just d). I calculated the diameter of Family, Group 1 and 2 for each hunter-gatherer society (mobile, non-mounted, non-suspect) in the Binford (2001) compendium for which such groupings exist, by first assuming a circle with a radius of 0.5 meters for each individual: each individual moves within a one meter diameter circle of space. I then multiplied this area by the size of

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[66] The detection distance between the periphery of the group (d) plus the radii of both groups (s).

Family/Group 1 or 2 and from this calculated the overall diameter of the physically aggregated group, as opposed to their geographic range, in km (*s* above). For the largest grouping level, Group 2, the diameter was <11m and mostly <8m. I then assumed an average detection distance between group edges (*d* above) of 0.5km, following Grove et al (2012). Summing these gave the overall detection distance *D* (km) for each specific grouping level for each hunter-gatherer society.

To calculate the mean geographic area associated with each Group 3 unit I calculated the number of Group 3s (periodic aggregation groups) per Population and divided the total area associated with the Population by this number. To calculate the density of Family, Group 1 and Group 2 units within the Group 3 area, I first calculated the number of Family, Group 1 and Group 2 units per Group 3. I then divided the number of each group by the area associated with the Group 3 unit of each society that has periodic aggregations to give the respective densities.

In addition, I converted rate to number of encounters within a specified time period by multiplying the numerator of the above expression by time *t*, yielding the equation:

Individual number of encounters = $8\rho Dvt/\pi$.

where *t* is the time period systematically varied from 1 to 365 days. For each biome I calculated the maximum, median and minimum number of encounters over time period *t* (days) for the focal group. Rather than giving the number of encounters per day, this gives the total number of encounters for the cumulative number of days: during a single day, during two days, during three days and so on. The maximum number of encounters relates to groups with the highest detection distances and densities in the biome, whereas the minimum number of encounters relates to groups with the lowest detection distances and densities. I chose 365 days as the cut-off to test whether units at each fission-fusion level would encounter sufficient other units of the same social level to maintain their social network without purposeful directed travel during one seasonal cycle. However, this does not take into account seasonal differences in group fission/fusion, mobility strategy or residential pattern.

For the ‘number of encounters’ output, I concentrate on the North American biomes, for which there are most data. I assume that the Californian/Northern Mexico biome is similar to the European Mediterranean biome, that North American Desert/Scrub represents savannah-like/grassland environments and that the Subarctic biome is the closest proxy for Late Pleistocene Europe (Chapter 6, this thesis; Layton, O'Hara, and Bilsborough 2012). I also include the (Sub)Tropical African and Arctic biomes.

Results

Encounter rates

Overall the encounter rates predicted by the gas model are fairly similar to contact rates observed for individuals living in a modern society, indicating that the model estimates are realistic. In all biomes predicted encounter rates lie above the observed rate per day for each grouping layer: the parameters of the gas model allow encounter rates to be greater than the minimum necessary for the cohesion of the corresponding social layer (Figure 7.3). Wilcoxon rank tests found no significant differences between the median daily encounter rate and the observed rate for any biome. Nonetheless, the rates for the Subarctic and Arctic biomes fall on or closest to the baseline whereas the rates for the other biomes are predominantly higher. However, although the minimum modelled encounter rates for the Subarctic and Arctic biomes fall below the observed contact frequencies, on average even mobile groups in the highest latitude biomes seem able to maintain contact with other units in their adjacent encompassing layer.

The minimum expected encounter rate for Australia also falls below the observed contact frequencies, that is, below the minimum rate that allows each social layer to be maintained. This is likely to be because some of the hunter-gatherer societies in this biome inhabit harsh environments that necessitate low population densities, even though they are relatively near the equator. For instance, low latitude deserts may produce similar constraints on social network maintenance to those found in high latitudes, due to the geographic spread of network members (Layton, O'Hara, and Bilsborough 2012, Pearce et al. in press). Indeed, it may be similarly harsh low latitude African environments that initially forced AMH to develop the bonding mechanisms necessary to maintain social networks over even greater areas at higher latitude as they dispersed out of Africa.

The above patterns are also evident in the number of encounters per year (Table 7.1). These annual encounter rates again pertain to the 15-layer (encounter rate for a Family/~5-layer), the 50-layer (encounter rate for a Group 1/dispersed band/foraging group unit) and the 150-layer (encounter rate for a Group 2/band unit). When the velocity of groups is increased from 25km/day to 40km/day, the patterns of expected/modelled encounter rates do not differ markedly in relation to the observed baselines.

Overall, in all biomes the modelled encounter rates resulting purely from daily subsistence movement are at least equal to the frequency expected for the maintenance of social bonds. Thus, for each level of mobile grouping (Family, Group 1/dispersed band, Group 2/fused band), subsistence movement seems sufficient to allow the subsequent encompassing network layer to be sustained. However, this analysis does not convey the limit on the total number of social layers or identify the outermost social layer that can be maintained in each biome through subsistence mobility alone. To investigate this question, I turn to the total number of encounters accumulated over a year.

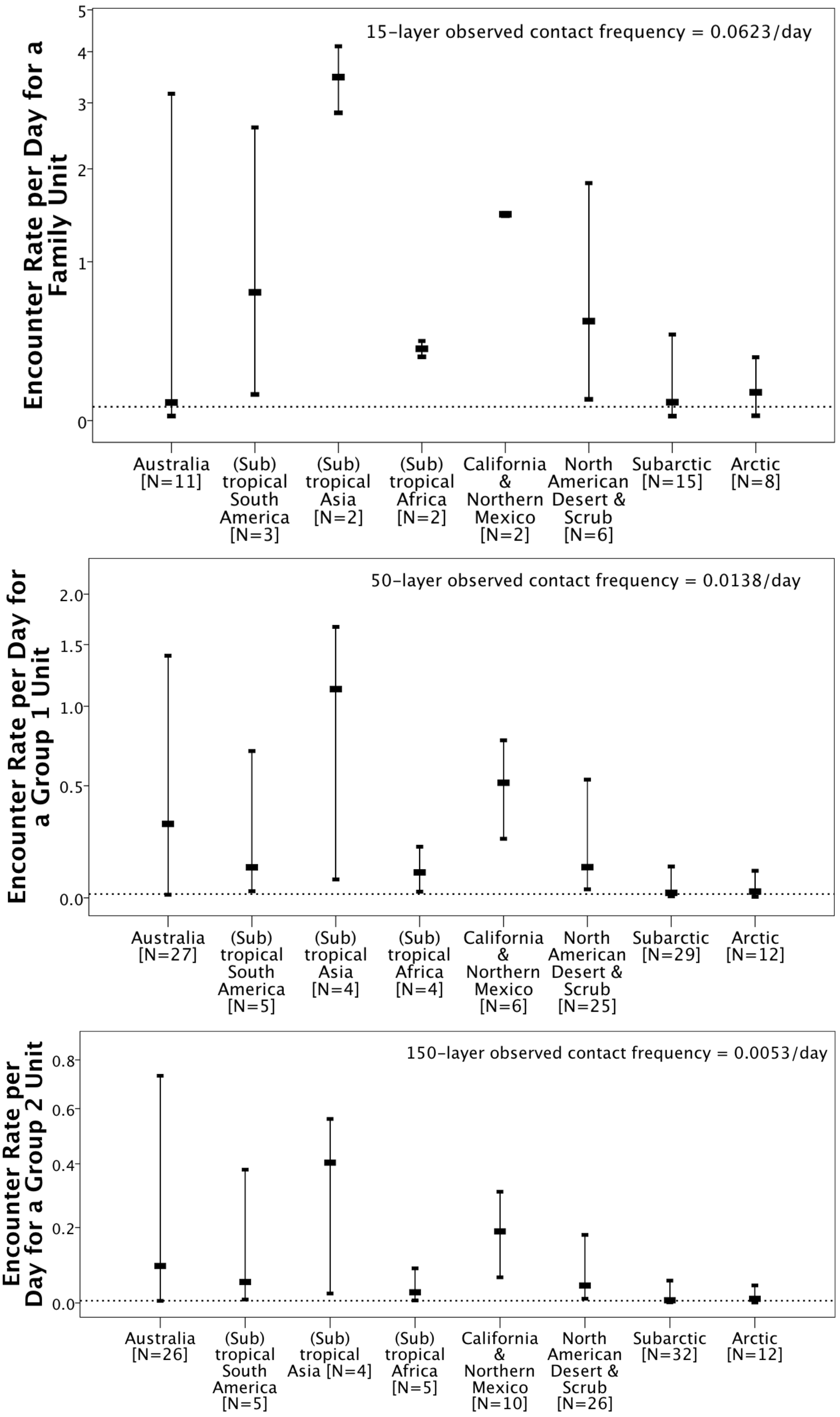


Figure 7.3: The maximum, median and minimum modelled daily encounter rates (log$_{10}$ scale) for a Family (TOP), Group 1/dispersed band (MIDDLE) and Group 2/fused band (BOTTOM) compared to observed contact frequencies (dashed lines) (observed data from Roberts et al. 2009, recalculated following Sutcliffe et al. 2011).

Table 7.1: Annual encounter rates per biome for a Family, Group 1/dispersed band unit and Group 2/fused band unit, predicted from the gas model at velocities of 25km/day and 40km/day. Observed rates are given in [ ] for comparison (data from Roberts et al. 2009, recalculated following Sutcliffe et al. 2011). Grey cells indicate that the modelled encounter rate falls below the observed encounter rate required for relationship maintenance within a particular network layer.

Biome		**25km/day**			**40km/day**		
		Annual encounter rate for:			**Annual encounter rate for:**		
		Family unit [observed contact frequency = 22.8]	**Group 1 Unit [observed contact frequency = 5.05]**	**Group 2 Unit [observed contact frequency = 1.94]**	**Family unit [observed contact frequency = 22.8]**	**Group 1 Unit [observed contact frequency = 5.05]**	**Group 2 Unit [observed contact frequency = 1.94]**
Australia	Median	30.00	112.04	34.14	48.00	179.26	54.63
	Min.	7.56	4.25	1.88	12.09	6.80	3.00
	Max.	1153.8507	511.52	267.26	1846.16	818.43	427.62
Subtropical South America	Median	273.90	42.61	19.02	438.23	68.18	30.44
	Min.	44.20	8.89	2.98	70.71	14.22	4.77
	Max.	946.57	255.73	138.87	1514.52	409.16	222.12
Subtropical Asia	Median	1268.07	411.89	147.44	2028.92	659.02	235.91
	Min.	1032.73	25.21	8.46	1652.37	40.33	13.53
	Max.	1503.41	607.92	204.52	2405.46	972.68	327.23
Subtropical Africa	Median	134.37	35.23	9.58	214.99	56.36	15.33
	Min.	117.11	8.29	2.26	187.38	13.27	3.61
	Max.	151.63	74.21	31.88	242.60	118.73	50.99
California & Northern Mexico	Median	532.65	188.52	68.92	852.24	301.63	110.27
	Min.	527.82	86.99	23.27	844.50	139.18	37.23
	Max.	537.48	280.32	112.65	859.97	448.52	180.23
North American Desert & Scrub	Median	198.48	42.93	15.71	317.57	68.69	25.13
	Min.	35.66	11.44	3.68	57.05	18.30	5.89
	Max.	663.61	194.86	65.25	1061.78	311.78	104.40
Subarctic	Median	30.60	6.76	2.42	48.96	10.81	3.87
	Min.	7.24	2.13	.51	11.58	3.40	.82
	Max.	166.60	43.96	20.28	266.56	70.33	32.44
Arctic	Median	48.10	8.50	3.62	76.95	13.60	5.79
	Min.	7.92	1.35	.35	12.66	2.16	.57
	Max.	116.19	37.50	15.79	185.91	59.99	25.26

Number of encounters & network layers

Figures 7.4-7.6 show the minimum, median and maximum cumulative number of encounters over one year for each biome (velocity=25km/day). Superimposed on these are horizontal lines indicating the number of encounters required for the maintenance of each layer of the social network. These are the total number of social units comprising a particular layer minus one: the focal group needs to maintain contact with *N-1* other groups to maintain a particular social network layer, where *N* is the total number of subunits within a particular network layer.

The output of the gas models indicates that at each grouping level the expected number of encounters during a year in the Subarctic and Arctic biomes cannot facilitate the maintenance of as many social layers as in other biomes. This is the case even when the velocity parameter of the gas model is increased from 25km/day to 40km/day.

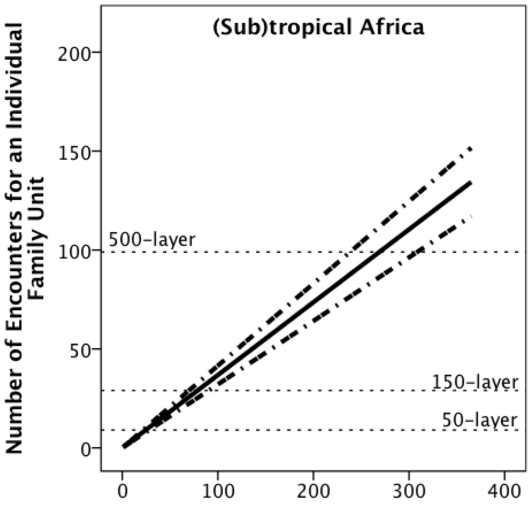
Concentrating on the median number of encounters, if hunter-gatherers split themselves into Family units of ~5 individuals, in Subarctic and Arctic biomes they are able to maintain the 150-layer, whereas in other biomes at least the 500-layer can remain connected. In the California & Northern Mexico (Mediterranean-like) biome, on average the 1500-layer can be bonded. Even though the number of encounters in a year increases when the velocity is increased from 25km/day to 40km/day, the Subarctic and Arctic biome groups still fail to reach the number of encounters required to bond the 500-layer. In contrast, when Families move 40km/day, societies in the North American Desert & Desert Scrub biome join those in the California & Northern Mexico biome in achieving contact between units within the 1500-layer.

In the Subarctic and Arctic biomes mobile Group 1s (bands during the dispersed part of a seasonal cycle) are able to achieve contact within the 50-layer at a velocity of

25km/day whereas at a velocity of 40km/day they are able to connect units within the 150-layer as well (Figure 7.5). In all other biomes the median number of encounters ensures that at least the 500-layer can be maintained, and in the California/Northern Mexico biome the 1500-layer can remain connected even at a velocity of 25km/day.

When Group 2 units are considered (~50-strong units), at least the 500-layer can be maintained in all biomes except the Subarctic and Arctic, even when the velocity is 25km/day (Figure 7.6). A velocity of 40km/day does not alter the median number of encounters in relation to the social layers that can be maintained.

Overall, the gas models predict that in the Subarctic/Continental Forest and Arctic biomes individuals in mobile groups at all degrees of fissioning are capable of maintaining their active networks (150-layer) through encountering other mobile groups during daily subsistence. In contrast, individuals at lower latitudes (African, California/Northern Mexico and North American Desert/Scrub biomes) are capable of maintaining contact with the members not only of their active network but also members of their mating community (500-layer) and in some cases even their ethnolinguistic tribe (1500-layer), solely through daily subsistence mobility.



Family units comprising ~5 individuals require 2 other family units to make up their 15-layer (total: 3 families), 9 other units to make up their 50-layer (total: 10 families), 29 other families to make up their 150-layer (total: 30 families), 99 other families to make up their 500-layer (total: 100 families) and 299 other families to make up their 1500-layer (total: 300 families).

When velocity is increased from 25km/day to 40km/day, the median encounter rate for the North American Desert/Scrub exceeds the 1500-layer. For other biomes the pattern is unchanged.

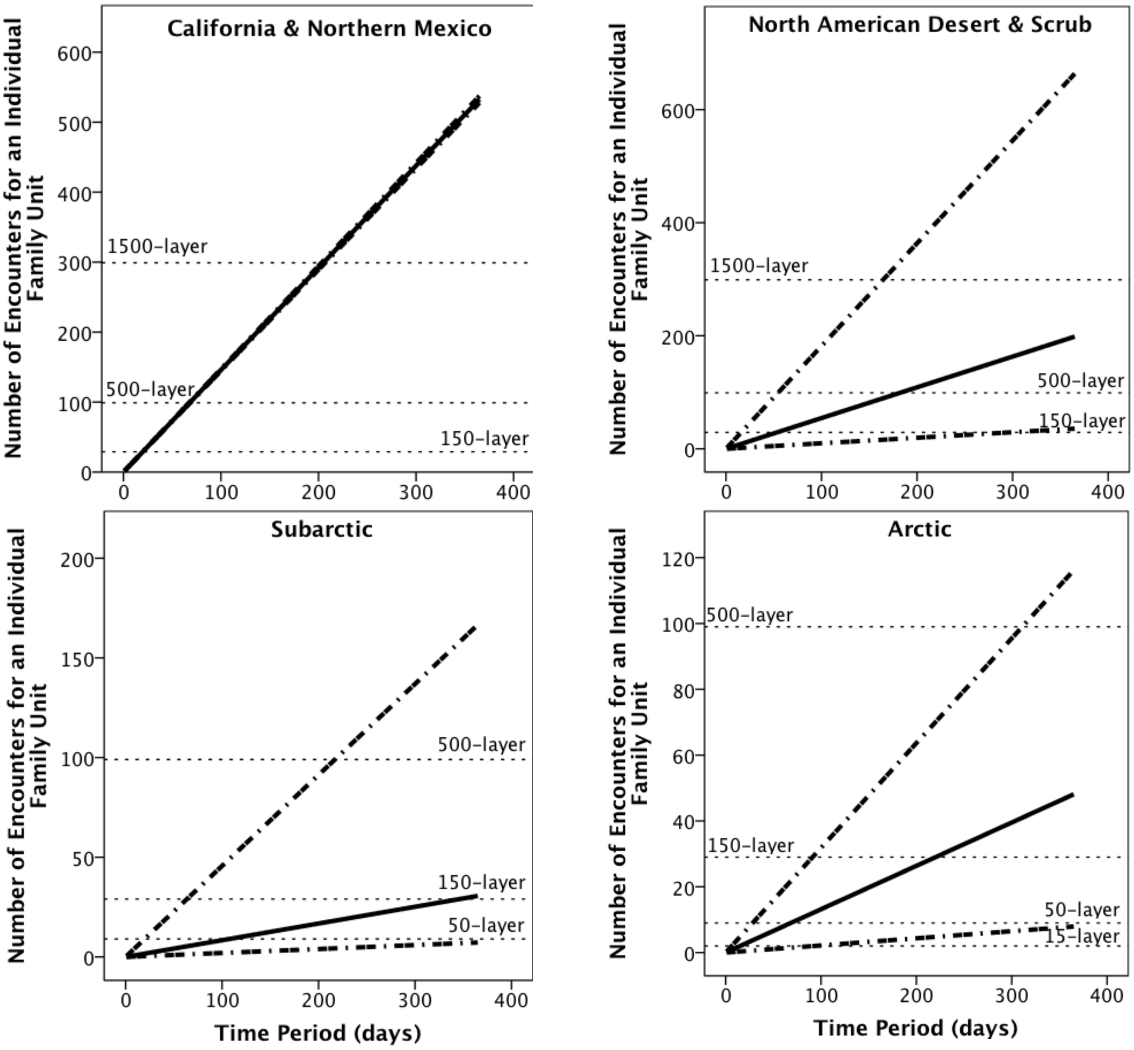
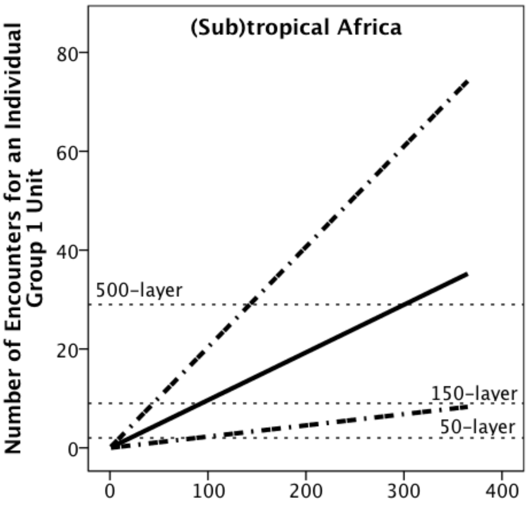


Figure 7.4: The median (solid line), minimum and maximum (dashed lines) number of encounters for an individual hunter-gatherer Family unit, plotted against the cumulative number of days elapsed, split by biome. The horizontal dashed lines represent social network/grouping layers.

Assuming that Group 1 units represent the 15-layer of an individual's social network, each Group 1 unit requires 2 other Group 1 units to make up their 50-layer (total: 3 Group 1s), 9 other Group 1 units to make up their 150-layer (total: 10 Group 1s), 29 other Group 1 units to make up their 500-layer (total: 30 Group 1s) and 99 other Group 1 units to make up their 1500-layer (total: 100 Group 1s).

When velocity is increased to 40km/day, the median encounter rate for the (Sub)Arctic biomes exceeds the requisite number of encounters to bond the 150-layer.



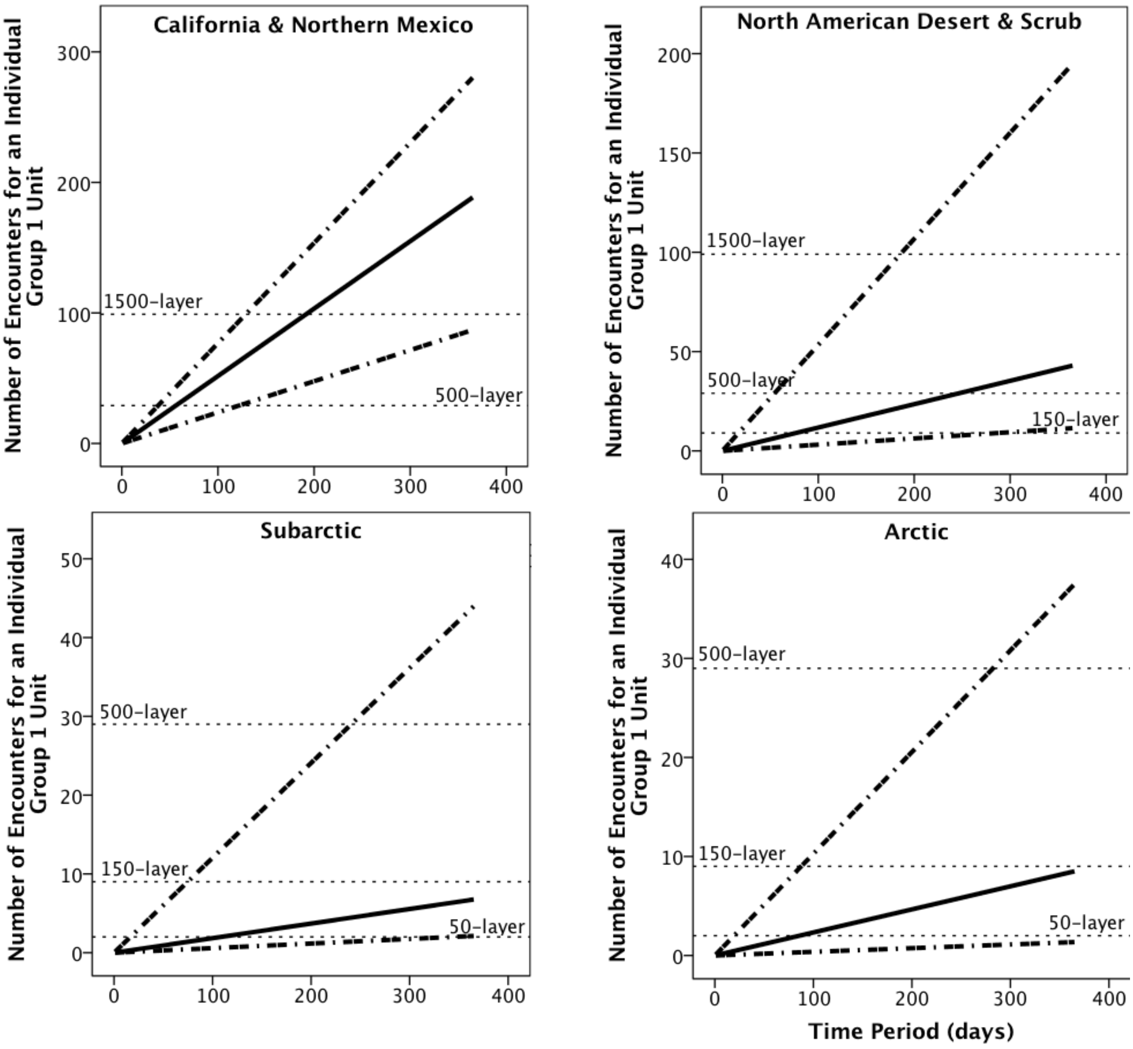
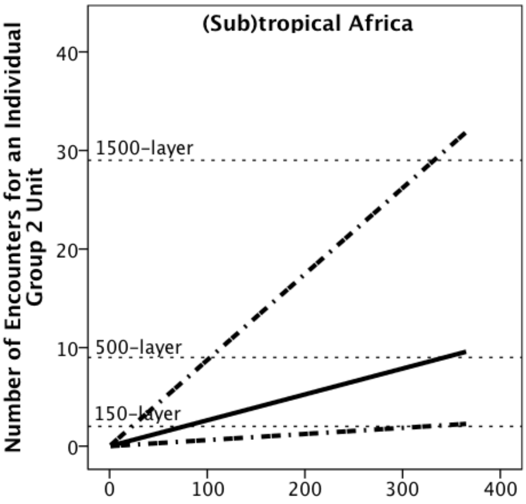


Figure 7.5: The median (solid line), minimum and maximum (dashed lines) number of encounters for an individual hunter-gatherer Group 1/dispersed band unit, plotted against the cumulative number of days elapsed, split by biome. The horizontal dashed lines represent social network/grouping layers.

Assuming that a Group 2 unit approximates the ~50-layer of a social network, each Group 2 unit requires 2 other units to make up the 150-layer of the members' social network (total: 3 Group 2s), 9 other units to make up the 500-layer (total: 10 Group 2s) and 29 other units to make up the 1500-layer (total: 30 Group 2s).

*When velocity is increased from 25km/day to 40km/day, these patterns remain the same, although the North American Desert/Scrub biome almost reaches the 1500-layer: 25 versus the necessary 29 encounters (*Table 7.1*).*



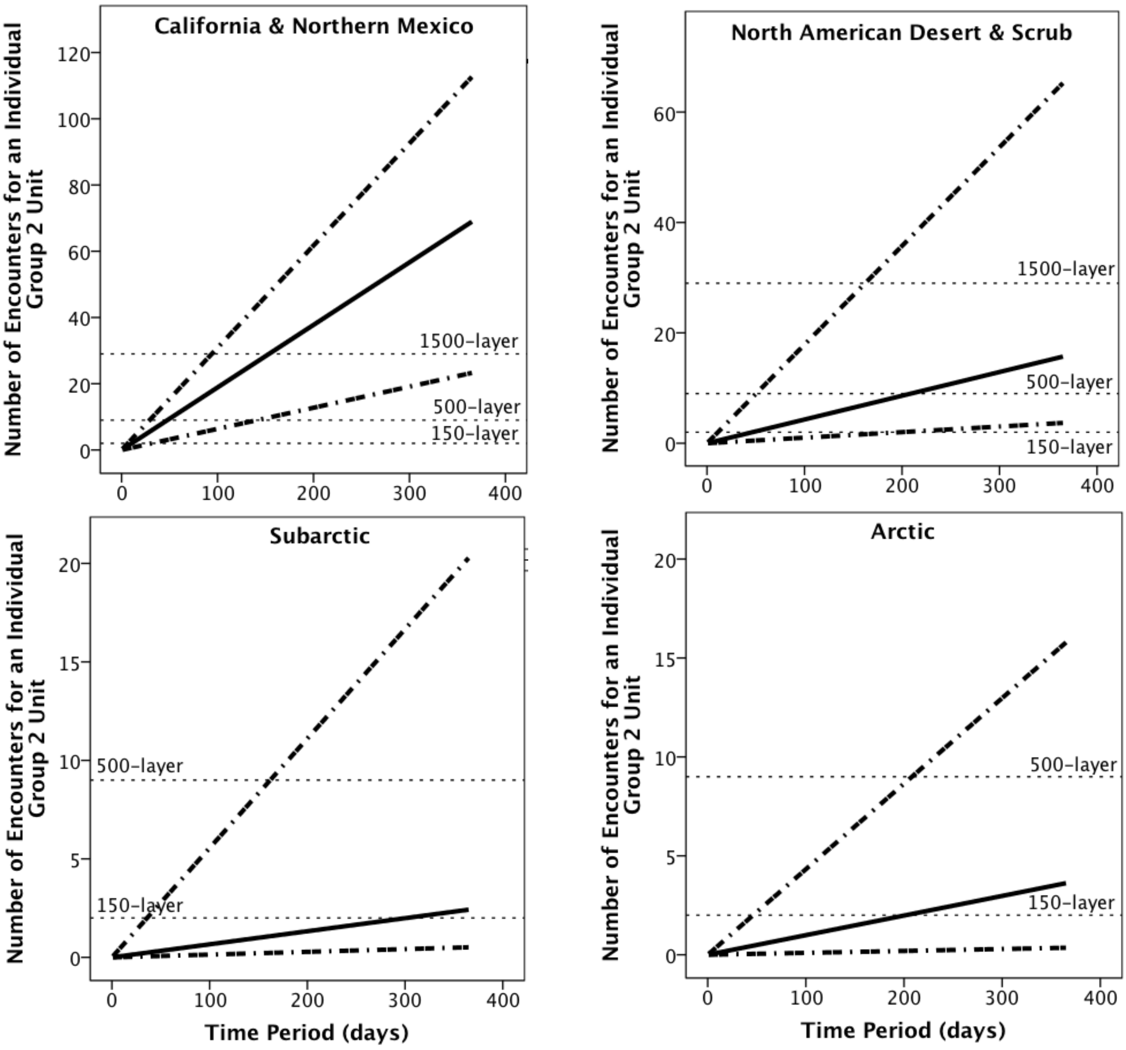


Figure 7.6: The median (solid line), minimum and maximum (dashed lines) number of encounters for an individual hunter-gatherer Group 2/fused band unit, plotted against the cumulative number of days elapsed, split by biome. The horizontal dashed lines represent social network/grouping layers.

Discussion

The number of encounters experienced by focal groups generally (i) declines with increasing latitude and (ii) increases with the degree of group fissioning, being highest for Family units. Comparisons with observed contact frequencies suggest that the encounter rates predicted by the gas model are realistic. In all biomes subsistence mobility allows a sufficient rate of intergroup contact to maintain the adjacent encompassing layer at all grouping levels. However, in most cases the encounter rates for the Subarctic/Continental Forest and Arctic biomes are only just sufficient. Moreover, although the number of encounters implies that contact could be maintained within an individual's entire active network (150-layer) in all biomes, in the Subarctic and Arctic biomes subsistence mobility fails to ensure encounters with all subgroups in the mating community (500-layer) or ethnolinguistic Population (1500-layer). The data presented in Chapter 6 indicated that populations of both recent and fossil hunter-gatherers maintained contact across the entire area associated with their ethnolinguistic tribes. This implies that higher latitude individuals are able to maintain these outer social layers, but must rely on some means other than subsistence mobility.

The gas model predictions suggest that in the highest latitude regions extra mechanisms for social cohesion over larger geographic areas are required in order to sustain the outermost social network layers. This might explain the appearance of symbolic and figurative art in Europe at the start of the Upper Palaeolithic: although some low latitude environments might require mechanisms to ensure social cohesion in the absence of face-to-face interaction, the need would vastly increase as the geographic ranges of AMH progressively increased during dispersals into higher latitudes. Although an explosion of artistic expression is commonly reported during the Gravettian, which is some time after the initial AMH dispersal into Europe, accumulating evidence suggests that such non-utilitarian artefacts are present from the earliest Upper Palaeolithic, at least in some regions (Conard 2003, Conard 2009, Higham et al. 2012, Kuhn and Stiner 2007, Stiner, Kuhn, and Güleç 2013). Incidentally, the emergence of the earliest examples of symbolic artefacts and ornamentation also seems to occur in the highest latitudes at either end of Africa, rather than in tropical regions (Bouzouggar et al. 2007, d'Errico et al. 2005, Henshilwood et al. 2011, Henshilwood et al. 2002)[67]. Similarly, the appearance of symbolism in the Australian record might be associated with the harshest desert environments. Although rock art and ornamentation enters the record from ~40kya, about 15ky after the earliest dates of AMH habitation, preservation and dating issues may mask earlier evidence (Langley, Clarkson, and Ulm 2011) and makes this hypothesis difficult to test.

It is worth pointing out that the gas models make several simplistic assumptions, including that (i) groups move independently of each other, (ii) groups move randomly around a range rather than to and from more temporally stable base camps, (iii) groups do not spend any time interacting when they meet and indeed only need to come within 0.5km of each other for an ‘interaction’ to have taken place. In reality, even if distinct territories are not physically defended, certain groups may have habitual areas through which they travel that might not overlap the habitual ranges of all other groups. Furthermore, there might be ‘anchors’ in the landscape, which groups are attracted to (or avoid) and which could skew the probability of encountering another group. Indeed, rather than following a random path (Brockmann, Hufnagel, and Geisel 2006), individuals return frequently to a few places, at least in industrialised societies (Gonzalez, Hidalgo, and Barabasi 2008). The emergence of nightly returns to band camps is considered an important development

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[67] Although this patterning might be associated with coastal habitats allowing higher population densities, which might necessitate social boundary maintenance, rather than the maintenance of dispersed networks.

in hominin evolution, which enabled the sharing of risky resources such as meat (e.g. Layton, O'Hara, and Bilsborough 2012). Although places of repeated aggregation might initially correspond to locations of especially abundant resources or where alternative options are limited, these places might take on social meaning as a place of gathering so that the landscape is transformed from purely physical to being socially constructed (Gosden 1994, Greider and Garkovich 1994, Grove and Dunbar in prep, Richards 1996). This can be seen in the need for Australian Aboriginal men to conceive and die on their lineage’s sacred site, which makes it necessary to revisit particular locations periodically, thus increasing the chance of meeting others in their network (Layton, 1986).

Furthermore, groups that share alliances may settle and camp together overnight before moving on, thus reducing the chance of encountering further groups on the same day as encountering the first group. Moreover, gas models do not attach identity to different groups, so the number of encounters accumulated over days does not necessarily equate with the total number of different groups encountered: nearest neighbours may be re-encountered multiple times. This means that the reported encounter rates/numbers might overestimate actual contact frequencies. If so, all encounter rates in Figure 7.3 should be pulled downwards, putting the rates of most biomes on the observed baseline and those of the Subarctic and Arctic biomes below, implying an insufficient contact frequency to ensure connectivity in these higher latitude biomes.

In addition, it is possible that not all members of an encountered group share a meaningful relationship with ego. One might expect that at higher latitudes individuals would maintain links with a smaller proportion of each band but with a greater number of different bands, so that they would have a greater number of independent options under higher-risk conditions. That might mean that higher latitude networks overlap less between individuals, at least at the outer layers, with greater emphasis on incorporating individuals into the insurance pool through indirect ties. Incomplete network/group overlap would mean that encounter rates would have to be even higher: a fused band might need to meet more than two other bands for all its members to maintain their ~150-strong active network layer. Both repeated encounters and partial network matching might create a disparity between predicted and actual encounter rates: the gas model may overestimate the ability to maintain network connectivity through daily subsistence mobility.

Future work could use agent-based modelling to develop the outcomes of this exploratory analysis. For instance, modelling of identifiable groups moving within an environment containing resource 'anchors' might provide a way of overcoming the issues listed above and thus develop a more realistic picture of the relationship between subsistence mobility and group interaction. For instance, such models could allow the exploration of network cohesion in relation to (i) varying degrees of overlap between individual active networks, (ii) antagonistic as well as friendly group interaction, (iii) fluid group composition, (iv) territoriality or home range sub-structuring, which would expand upon the modelling work of Wobst (Williams and Wobst 1974, Wobst 1974, Wobst 1976) by incorporating group movement, (v) increasing mobility with latitude, (vi) the time period required to accumulate a sufficient number of encounters to bond the tribe in different biomes (i.e. allowing *t* to increase beyond 365 days) and (vii) variations in the temporal and spatial fluctuations of resource 'anchors', for example representing rich resource patches where groups might seasonally aggregate. The spacing of members of a social network and thus the degree of difficulty in maintaining that network ultimately depends on resource distribution. Thus, similarities might occur between biomes where different kinds of climates produce similar resource distributions, resulting in similar social network spacing, such as with low latitude deserts and the arctic. However, the analogous-biome approach provides a benchmark from which to develop more precise models incorporating historical climate data and palaeoclimate data (e.g. from the Cambridge Stage 3 Project) to predict resource landscapes.

Observational data on hunter-gatherer group encounter rates from a range of habitats are still required, but the simulations presented here serve as a simplified baseline model in order to generate verifiable hypotheses. Overall the gas model predicts that in (Sub)Arctic hunter-gatherer societies extra mechanisms over and above purely subsistence-based mobility may be required to maintain social ties beyond the active network. Cultural supports for network maintenance and group identity such as exchange of symbolic artefacts and the extension of kinship terminology should thus become particularly marked above ~45 degrees latitude. The same might be true of time-saving devices such transport aids and more efficient, reliable and unsupervised subsistence technologies, which would free up time to spend in social bonding activities. I explore such mechanisms further in the course of my general discussion in Chapter 8.

Chapter 8 Discussion: Social network maintenance at high latitudes

In order to take advantage of the opportunities afforded through membership of a wider social network, hominins at higher latitudes need to maintain their ethnolinguistic tribes across progressively larger geographic ranges. The mechanisms for achieving cohesion have to overcome both cognitive constraints and time costs. Since Neanderthals seem to have had smaller networks than AMH, they would not have required mechanisms to support network cohesion to the same extent as high latitude AMH. Here I summarise the main findings of my thesis before discussing potential mechanisms for the maintenance of large, dispersed networks at higher latitudes.

Summary of thesis findings

The first part of this thesis explored the impact of latitude on brain organisation and possible associated implications for social cognition. I hypothesised that low temperatures and light levels would select for larger bodies and visual systems, respectively, leading to larger somatic and visual brain areas at higher latitudes. Since orbit size can provide information about the size of the visual cortex independently of overall brain and body size (Chapter 2), the significant positive relationship between absolute latitude and orbit volume in recent historical humans (Chapter 3) implies that individuals living at higher latitudes have larger eyes and visual cortices compared to their equatorial counterparts. I argued that larger visual cortices (and somatic areas) translate into larger brains overall in *H. sapiens* living nearer the poles.

Although Neanderthals have significantly larger orbits than contemporary AMH, on average Neanderthals and AMH dated 27-75kya have almost identical endocranial volumes (Chapter 4). Thus, in contrast to recently living humans, apparently larger

Neanderthal visual cortices do not translate into larger brains than those of contemporary AMH. I argued that if a larger proportion of the Neanderthal brain was used for controlling their larger bodies and for visual processing, less neural tissue would have been available for other brain functions. For instance, given the well-known relationship between particular brain areas and the degree of social complexity that an individual can track, I proposed that Neanderthals might have been limited to smaller social networks than AMH (Chapter 5). In contrast with previous estimates of Neanderthal community size based on absolute endocranial volumes, taking account of possible differences in brain organisation brings estimates of active network size in line with archaeological indicators that Neanderthals had smaller and less geographically extensive social networks compared to AMH.

The second part of the thesis focused on time constraints on social network size and how these change with latitude. In Chapter 6 I argued that hunter-gatherer networks are spread over larger geographic distances nearer the poles, exacerbating the challenge of maintaining cohesion. Comparisons between the radii of recent hunter-gatherer range areas and maximum obsidian transfer distances from the archaeological record suggested that AMH hunter-gatherers maintained contact across the entire range of their ethnolinguistic tribes at all latitudes. For AMH, but not Neanderthals, there is evidence of infrequent interactions between tribes. Although Neanderthals seem to have added the outermost ethnolinguistic tribe layer to their networks, assuming similar population densities their shorter and less frequent maximum transfer distances (300km versus >400km) suggest that compared to AMH their tribes comprised fewer individuals.

I conservatively estimated that at the highest latitudes it would take AMH several days of continuous walking to travel from the periphery of their tribal home range to a meeting point at the centre. Consequently, journey times may have constrained the proportion of the tribe that could take part in periodic aggregations and this would have limited their ability to maintain tribal connectivity through face-to-face contact. However, one means of mitigating social time costs would be to nest ‘social’ travel within subsistence movement. A gas modelling approach suggested that groups in lower latitude biomes have sufficient intergroup encounters arising purely from daily subsistence movement to remain connected with all groups within their mating community and sometimes even their ethnolinguistic tribe (Chapter 7). In contrast, groups in the Subarctic/Continental Forest and Arctic biomes are only able to maintain layers up to their active network through daily subsistence mobility. Given this, it is at higher latitudes in particular that we should expect to find supplementary mechanisms for maintaining contact within the two outermost social layers, such as symbolic artefacts for exchange and time-saving devices for non-social activities that would free up social time.

Overcoming time costs

One way of reducing the time costs incurred when travelling to meet members of one’s social network is scheduling: either spreading the costs across a prolonged period of time, as in the manufacture of exchange objects, or clustering social time into a ‘social season’. The most obvious means of doing this are periodic aggregations, for instance where resource acquisition and processing requires cooperation, as in the case of seal breathing-hole hunting. At the level of the band this is straightforward for the most part and consists of nightly returns to a home base, where meat and other high-risk food can be shared (e.g. Hames 1990, Kaplan, Hill, and Hurtado 1990, Low 1990, Winterhalder 1986). However, at the level of the whole community the opportunity to aggregate is limited by resource abundance, and possibly travelling times (Chapter 6). Only in a few exceptional hunter-gatherer societies, such as in the Northwest Coast Native Americans' winter villages, could sufficient resources be accumulated to feed the entire community (Layton and O'Hara 2010).

A major difference between Northwest Coast America and other regions is that societies in the former practised large-scale storage associated with fishing gluts. Hayden (2012) has suggested that AMH practised storage in the Upper Palaeolithic and that in some regions this allowed them to support more frequent and larger scale aggregations of their social networks compared to Neanderthals, whose archaeological record shows no indicators of storage. A more sedentary life-style associated with large-scale storage might have further increased the importance of social networks for AMH to replace high mobility as insurance against ecological risk (Nettle 1999). Lower latitude recent hunter-gatherers do not often practise large-scale storage, partly due to higher temperatures inhibiting preservation and perhaps partly because seasonality is less severe and storage is thus not required (Binford 2001). Lack of storage may partly explain why periodic aggregations do not tend to be much larger at lower compared to higher latitudes (Chapter 6): Figure 8.1. In most hunter-gatherer cultures outside the harshest conditions, the frequency of aggregations ranges from annually to every few years, but generally these gatherings incorporate only a fraction of the total megaband and roughly correspond to the size of an average individual's active network (Figure 8.1) (Layton and O'Hara 2010, Layton, O'Hara, and Bilsborough 2012).

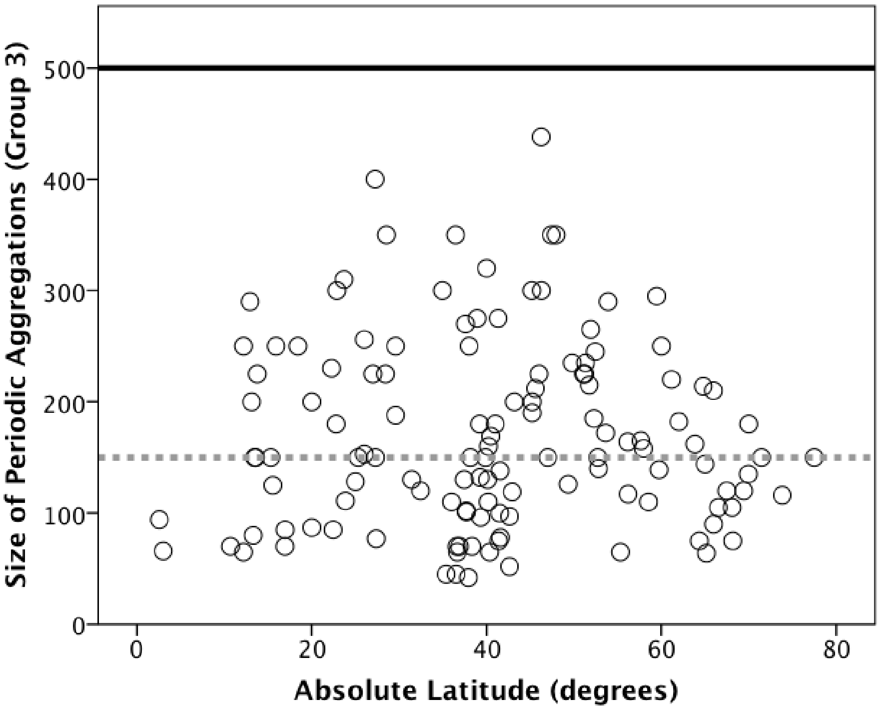

Figure 8.1: The size of periodic aggregations plotted against absolute latitude for 127 hunter-gatherer societies (data from Binford 2001, redrawn from Pearce et al. in press). The solid line represents the size of the average endogamous mating community (500 individuals) and the dashed line represents the average size of a modern human active network (~150 individuals).

At lower latitudes intergroup encounters linked to daily subsistence mobility may compensate for the apparent limits on aggregation size (Chapter 7, see below). Moreover, perhaps the fluidity of personnel in hunter-gatherer groups means that individuals can sustain sufficient contact with all members of the same megaband or ethnolinguistic tribe without having to resort to huge aggregations comprising the entire network: individuals or nuclear families may meet with different 'sections' of their combined network at different gatherings. If so, high latitude aggregations might be expected to be more frequent than nearer the equator, but the travel times involved nearer the poles may inhibit this. During aggregations *en masse* bonding activities usually predominate, for instance singing, dancing, rituals and feasting, as well as alliance creation through marriage brokering. Nonetheless, for the majority of modern hunter-gatherers, the size of gatherings is restricted and, although periodic aggregations can help sustain individual active networks, it appears that they cannot provide the only means for megaband and tribe maintenance.

The same would be true of other high latitude hominins once the megaband emerged through reduced overlap between individual active networks, particularly in the absence of large-scale storage (other than perhaps opportunistic freezing) (Pearce et al. in press).

Other types of scheduling to reduce possible social time costs include gossiping whilst engaged in productive activities, which may themselves elicit neurochemically-mediated bonding through shared attention and synchrony. Alternatively, social maintenance time could be outsourced to 'representatives': for instance in the Arctic women manufacture objects that can be used in exchange while men hunt (Kuhn and Stiner 2006) even though exchange partnerships tend to be maintained at the individual level (Hennigh 1971).

Another strategy could be to reduce the time spent on other, 'non-social' activities, for example by increasing the use of unsupervised trapping technologies and the reliability of hunting tools, as is reported for higher latitude modern human hunter-gatherers (Stiner and Kuhn 2006, Torrence 1983, 2001). The use of traps might be one reason why AMH seem to have been much better than Neanderthals at exploiting fast moving and reproducing small game such as rabbits (Fa et al. 2013, Stiner and Kuhn 2006). Moreover, unsupervised trapping would have allowed AMH sufficient 'spare' time in which to manufacture symbolic exchange objects. In addition, transport aids would substantially decrease travel times and increase encounter rates between mobile groups, aiding network connectivity.

The rates of encounter with foraging groups from other bands or megabands could also be increased through fissioning into highly mobile, small, logistic (specific task force) groups, assuming non-exclusive ranges rather than physically defended territories (Grove 2010a). This is demonstrated by the higher frequencies of encounters for Family versus

Group 2 (fused bands/~50-layer) units (Chapter 7). As with periodic aggregations, each encounter provides an opportunity for the group composition to change: individuals can switch into another group that may move in a different section of the tribal home range and therefore encounter groups not met otherwise. Moreover, intergroup encounters can provide an opportunity for information exchange about mutually known third parties, so that the informational (as opposed to the neurochemical: see Machin and Dunbar 2011) aspect of face-to-face social bonding facilitated by group encounters is amplified throughout overlapping active networks.

However, as demonstrated in Chapters 6 and 7, at progressively higher latitudes, declining population densities rapidly increase the cost of travelling between residential groups and reduce the encounter rate. Nonetheless, it is possible that visual displays of presence in terms of assemblages of artefacts might act as a proxy for contact (e.g. the Visual Display Hypothesis: McNabb 2012). For instance, shared spaces such as caves could act to reinforce group membership so that even if groups do not meet, they bond through using the same sites, which may be marked by paintings or carvings. Moreover, detection is not necessarily only visual. Auditory detection might increase the distance over which separate groups can be aware of each other’s presence, as in the case of !Kung groups hearing the sound of mongongo nut processing ('mortar speech': Lee 1979). Furthermore, on detecting another group, agents can manipulate the encounter rate by purposefully changing the direction of travel to cause convergence (or divergence). Strategies for inflating the chance of encountering other groups seems to fit the observation that hunter-gatherers often move further than is necessary for purely foraging requirements alone (Hewlett, Koppel, and Cavalli-Sforza 1982).

Alternative strategies for maintaining contact when partners are separated in space and time are purposeful individual or family visits to other residential groups, often for extended periods (Apicella et al. 2012, Lee 1972, Lee 1979, Wiessner 1982, Wiessner 2002). Social visiting can also be timetabled to reduce time costs: the most distant members of one's network may only be contacted every couple of years, as with hxaro partners 50km away being visited every 2-7 years (Wiessner 1981). As social networks become more geographically dispersed nearer the poles, such frequencies of contact may decline rapidly. However, in order for the frequency of face-to-face contact to be so low and yet a social bond remain 'active' in the sense that one could call upon that partner for help in a crisis, mechanisms to overcome cognitive limits on remembering that connection may be required.

Overcoming cognitive costs

Other means of maintaining ties with specific partners or regional groups can be subsumed under the category of 'cultural scaffolding' and are likely to be particularly important in maintaining the outer megaband and ethnolinguistic network layers. As a whole, these cultural scaffolds lessen the cognitive demands of having to actively track a social partner's interaction history and whereabouts. Such demands are likely to increase as networks disperse and the frequency of face-to-face interaction declines nearer the poles. The use of narrative and external storage of information, for instance in stylised objects, reduces the cognitive load of remembering which group is friendly and which is the enemy, as well as the obligations owed to or by specific individuals. For instance, reciprocal gift-giving creates exchange networks where material artefacts come to stand for individuals with whom one maintains relationships *in absentia*, thereby obviating the need for daily face-to-face maintenance of social bonds (e.g. Gamble 1982, Gamble 1998, 1999, Gamble 2010, Wiessner 1983). In addition, regularities in the structure of relationships within a network and schema such as triadic connections and kinship categories can aid memory of network content (Brashears 2013) and thus the mental manipulation of that information.

Furthermore, collective identities can generate bonds to a group that will permeate to all recognised members, rather than to specific individuals within that group. Thus, particularly in the layers beyond the active network, material objects representing group identity can obviate the need for pre-existing personal relationships: signals of membership are sufficient to foster cooperation. Affiliation may be marked by, for instance, ornamentation such as shell beads, which appear early in the Upper Palaeolithic record (e.g. Stiner, Kuhn, and Güleç 2013). Languages or dialects and kinship classifications such as namesakes are non-material equivalents of such visual markers (Cohen 2012, Nettle and Dunbar 1997).

Kinship terminology invariably incorporates marriage partners and their consanguinal kin, thus widening the kin-based network of mutual help without having to maintain strong ties with individual members. In other words, marriage extends obligations associated with biological kinship to affines. Marriage rules about who should or should not marry can allow individuals and families to strategically create advantageous sets of social bonds. Such culturally structured mating arrangements likely appeared when the endogamous megaband became part of the social network structure as overlap between individual active networks lessened (Pearce et al. in press). Descent groups also allow networks to be extended through increasing the number of peers that can be counted as kin via shared relationships to ancestors (Foley and Gamble 2009) and who share interests in terms of inclusive fitness via the high reproductive value of adolescents in subsequent generations (Hughes 1988). Increasing the generations through which ancestors are traced (which may be under cognitive constraint in terms of recursion), or identifying kin bilaterally rather than by descent through either the matriline or the patriline, can both extend the pool of kin from which help can be expected.

Cultural scaffolding can reduce the cognitive load of incorporating many more individuals into the less intimate layers of one’s network, because one no longer has to take account of every mind in the group, but merely the group consensus, thus reducing the mentalising demands of a particular situation. The larger the group that needs to be bonded and the greater the distance over which its members are spread, the further social markers should be extended throughout the social layers and the less specific they should become. However, it may be that the number of such traits that are shared acts as a ‘meta-marker’ for where an individual fits into the layered network and thus proportionally how much trust should be placed in them (e.g. Curry and Dunbar 2013, Curry and Dunbar in press).

Additional avenues for research include more extensive study of the ethnographic literature, which may allow the connection of particular mechanisms of social cohesion with particular resource profiles and/or topographies (relating to the ease of travel). For instance, looking at whether kinship terms tend to be extended further through the outer social network layers in regions where social networks cover larger areas. However, Layton (1986) cautions that cultural variation cannot be reduced to ecology alone: although it seems that modern humans often respond to ecological challenges in social ways, there is variation in the exact form such responses take. If different mechanisms of social network maintenance can be distinguished, it might be possible to use phylogenetic analysis to reconstruct ancestral forms of cultural scaffolding. However, categorising such traits is inherently problematic and so far a reliable phylogenetic tree for hunter-gatherer groups has not been produced. Global positioning system (GPS) tracking of individual hunter-gatherers combined with geographic information system (GIS) analysis over large regions would allow the detailed construction of the process of social network creation and maintenance over space and time. To date network analysis has been conducted for only two hunter-gatherer groups (Apicella et al., 2012; Schweizer et al., 1997), but such studies need to become more widespread in order to be useful in an evolutionary framework that uses hunter-gatherer variation, rather than single-society analogues, to inform scenarios of hominin evolution.

If cultural means of social cohesion become increasingly important as network connections (edges) are stretched over longer distances, there should be an increase in these kinds of cultural behaviours at higher latitudes. The gas model presented in Chapter 7 predicts that in most lower latitude biomes (tropical, Mediterranean or desert/desert scrub) subsistence mobility alone allows sufficient numbers of encounters for the megaband and encompassing ethnolinguistic population to remain connected. However, according to the model this is not the case in Subarctic/Mid-latitude Continental and Arctic biomes above ~45 degrees.

Intriguingly, there are several changes at ~40 degrees latitude which may relate to the apparent shift in the difficulty of maintaining social networks from ~45 degrees upwards: (i) although societies relying predominantly on aquatic resources are found at all latitudes, at ~40 degrees a switch occurs from societies depending primarily (>50%) on plants to societies obtaining >50% of their diet from terrestrial animals[68], even though the number of different mammal species starts to decline (Cordain et al. 2000, Mace and Pagel 1995, Pearce et al. in press), and (ii) after 40 degrees latitude the number of different languages and speakers per language starts to decline (Mace and Pagel 1995). In addition, Figure 8.1 suggests that the maximum size of periodic aggregations (Group 3) might also have an inverse-U distribution with a peak around 40 degrees latitude, although unequal sample sizes across the latitudinal range makes this difficult to test. These humped distribution patterns seem to reflect a pressure to increase megaband/ethnolinguisitic tribe size in order to provide insurance against ecological risk further from the equator, which hits a limit at very high latitudes because greater population dispersion reduces contact rates and consequently increases the difficulty of sustaining network cohesion.

Extra mechanisms for social bonding of the kind mentioned above should thus become particularly pronounced above ~45 degrees latitude. For instance, in riskier environments formalised non-kin exchange partners may be recruited in addition to a core of close kin (Guemple 1971, Wiessner 1982, 2002, Wiessner and Schweizer 1998). Moreover, whereas the lower latitude !Kung predominantly connect through hxaro exchange (Wiessner 1982, 2002, Wiessner and Schweizer 1998), polar Inuit use many different kinds of bonding mechanisms including exchange of crafted goods, communal rituals, dances, spouse exchange and food-sharing partnerships (Guemple 1971) (although

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[68] Pearce et al (in press) found that hunter-gatherer societies depending primarily (>50%) on aquatic resources exist at all latitudes and that at ~40 degrees latitude a switch occurs from >50% of the diet being plant-based to >50% relying on terrestrial animals (data from Binford 2001). However, Cordain et al (2000) found that subsistence supplied by hunted animals remains fairly constant at 26-35% across latitudes, whereas reliance on plants decreased after 40 degrees latitude and reliance on fishing increased in line with absolute latitude. Either way, plants no longer make up more than 50% of the diet after ~40 degrees latitudes. However, whether reliance is then primarily on aquatic or hunted food has an important implication for population densities, since societies relying more on aquatic resources can be more sedentary and live at higher densities. The apparent discrepancy arises because Cordain et al deal with average dependence at each latitude whereas Pearce et al categorise groups according to dominant subsistence resource type: below ~40 degrees no societies depend on more than 50% animal products, but greater variance at higher latitudes (i.e. the maximum percentage of hunting increases with latitude: Binford, 2001 data) keeps the mean fairly constant across latitudes.

whether this is the summation of all practices in such environments rather than the case for each specific society is unclear from the ethnographic literature surveyed).

The fact that *in absentia* social bonding mechanisms are expected specifically in the Subarctic/Taiga biome but perhaps not in the more southerly Temperate Grassland biome might explain why the distribution of Venus figurines in the Aurignacian (~45-30ky) and particularly the Gravettian (~30-20kya) seems to be predominantly in the former biome (Figure 8.2). It has been argued that such artefacts communicate group identity and were exchanged to bond large-scale networks (e.g. Gamble 1982). However, raw material transfer distances are generally longer in continental Central versus oceanic Western Europe, suggesting that social networks were maintained over larger areas in the former (Féblot-Augustins 1993). Given this, it is surprising that the Venus distribution continues from Central Europe down to Southwestern France and Northern Spain, where cave art also happens to be disproportionately abundant: the smaller home range areas indicated by the shorter transfer distances should have necessitated fewer mechanisms of social cohesion across the ethnolinguistic social layer in these more southerly regions. However, examination of the biome distributions produced by the Stage 3 Project suggests that Southwestern France/Northern Spain fluctuated between Taiga Forest and Temperate Grassland (Figure 8.2). If higher resolution, precisely dated transfer distance data could be collected, it may be shown that the appearance/absence of Venus figurines track these large-scale ecological changes.

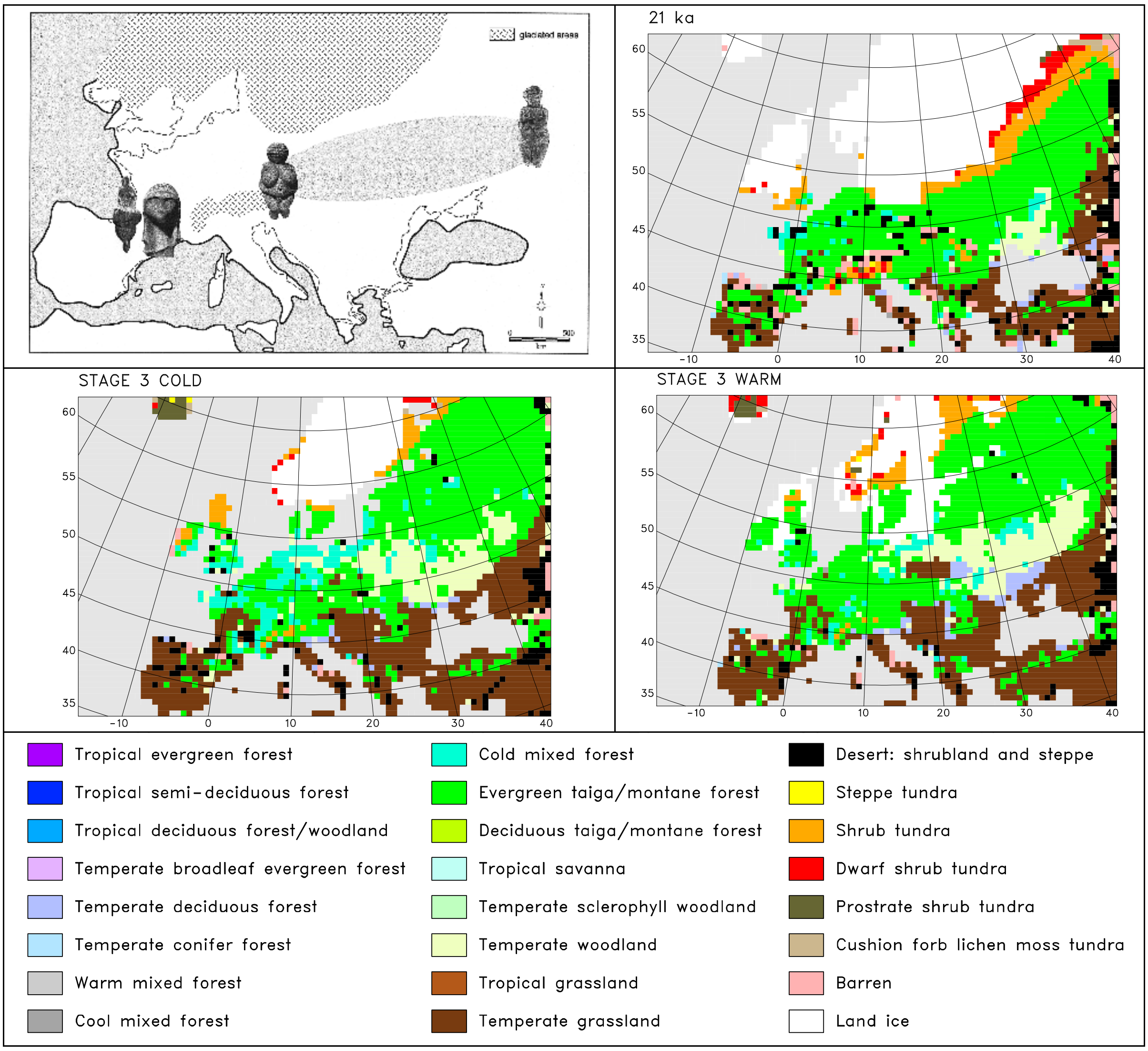

Figure 8.2: Comparison of the distribution of Venus figurines (O. Soffer, J. M. Adovasio, and D. C. Hyland 2000) (TOP LEFT) with Pleistocene biome distributions from the Stage 3 Project (van Andel and Davies 2003) for the LGM (TOP RIGHT) and cold (BOTTOM LEFT) and warm (BOTTOM RIGHT) climatic phases. Although the distribution depicted by Soffer et al (2000) refers explicitly to 'clad' figurines (those showing evidence of garments), this reflects the distribution of the Venus figurines more generally, although examples have also been found in Northern Italy (Gamble 1982: Figure 2).

Alternatively, it has been argued that higher population densities associated with population retraction into refugia as the climate deteriorated towards the LGM could explain the preponderance of cave art in the Southwestern region: contraction of social networks and the creation of more rigid social boundaries in the face of increasing competition for resources (Barton, Clark, and Cohen 1994, Jochim 1983). However, these explanations are not mutually exclusive. Different social phenomena could explain the presence of symbolic artefacts in different areas of their distribution: bonding of dispersed networks in Central Europe and enhanced group solidarity to counter intergroup conflict in the Southwest. Equally, population movement into southern refugia from further north might mean that groups brought their Venus figurines with them even though such material cultural supports for the cohesion of dispersed networks were less imperative below ~45 degrees latitude. Comparing the dates of the figurines would provide a test of this hypothesis. In any case, in light of the gas model predictions it is interesting that the Venus distribution seems to remain at and above ~45 degrees latitude (Figure 8.2), where the gas model predicts additional social bonding mechanisms via proxy are particularly crucial.

Additional support for increasing mechanisms for social cohesion in recent hunter-gatherers living at higher latitudes is provided by Shuttleworth (2013). He used a principal component analysis to define a ‘social control’ variable in terms of the appearance and strength of (i) social hierarchy, (ii) taboos, (iii) tension relief ceremonies, (iv) a code of honour and (v) ritual violence in a sample of recent hunter-gatherers, and found that ethnographic expressions of social control in contemporary hunter-gatherers are positively associated with latitude. This factor can also be interpreted as combining strategies of conflict avoidance: preventing conflict would negate group fission and is thus a form of social cohesion. This assessment is supported by the fact that, within the Gravettian and Aurignacian (both Pioneer and Developed: Davies 2001) periods, social cohesive signatures in the archaeological record (such as evidence of cooperative hunting and artefacts including beads and tool engravings, which might communicate kin affiliations or societal roles) are positively associated with signatures of social control (for instance, ritual violence such as evidence of cannibalism and spiritual expressions, for example manifested through burial). This is more the case in the Gravettian than in the

Aurignacian, in line with increasing maximum lithic transfer distances (Moutsiou 2011), suggesting that cohesion behaviours developed throughout the Upper Palaeolithic as social networks expanded (Shuttleworth 2013).

Within the ethnographic data there are also positive relationships between Shuttleworth's 'social control' factor and expressions of spiritualism, material symbolism and social ceremonies and rites, including ceremonial artefacts and clothing. Social ceremonies are considered to be mechanisms for social bonding (Dunbar 2008, Dunbar 2012a) and symbolic artefacts have been associated with exchanges used to maintain social insurance networks (Gamble 1999). It therefore seems that, within AMH hunter-gatherers from the Upper Palaeolithic to the present, material and non-material culture supports enhanced social control as a form of social cohesion at higher latitudes, where social networks are spread over larger areas. The same may be true to a certain extent in low latitude deserts (Layton, O'Hara, and Bilsborough 2012, Pearce et al. in press). Indeed, the latter might be where AMH developed the forerunners of such mechanisms before dispersing into higher latitudes. This would account for the early emergence of symbolic artefacts in Africa. Nonetheless, contrary to widespread opinion (following McBrearty and Brooks 2000), the Upper Palaeolithic 'revolution' may be a real phenomenon associated with the emergence of cultural scaffolding to support network cohesion as AMH dispersed into higher latitudes, where daily subsistence movement no longer provided sufficient intergroup contact.

Neanderthals and AMH

Smaller proposed cognitive active network/community sizes (Chapter 5) and shorter maximum transfer distances (Chapter 6) suggest that Neanderthal social networks incorporated fewer members and were maintained over smaller geographic ranges than those of AMH. This is surprising given that the positive relationship between body size and home range area (e.g. Antón, Leonard, and Robertson 2002) would predict the opposite: larger home ranges for Neanderthals versus AMH. If Neanderthals did not have as large social networks spread over as large areas as AMH, then they would have had less need for cultural scaffolding to assist their network maintenance: smaller areas would necessitate lower travel times and might increase encounter rate (unless population density was also much reduced). In turn, a lack of cultural scaffolding may have limited their capacity to increase social network size.

However, the difference between Neanderthal and AMH maximum transfer distances is 100km (a ~33% increase over the Neanderthal 300km maximum distance), which implies a quantitative rather than a qualitative difference in the requirement for *in absentia* bonding mechanisms, similar to the quantitative social cognitive difference suggested in Chapter 5. For instance, Neanderthals have been purportedly associated with possible symbolic activity: there are examples of ornamentation at some Châtelperronian sites (Hublin et al. 2012) as well as two apparent shell beads from caves in Spain dating back to 50kya (Zilhão et al. 2010), extensive examples of ochre use (which alternatively could have medicinal, skin preparation or more simple aesthetic functions) (e.g. Roebroeks et al. 2012) as well as apparent raptor feather accessories (Finlayson et al. 2012) and even some cave art with dates overlapping the last Neanderthals and the earliest European AMH (Pike et al. 2012). Still, compared to the many shell beads recovered from North and South African, Near Eastern and European MSA sites associated with AMH (Bar-Yosef Mayer, Vandermeersch, and Bar-Yosef 2009, Bouzouggar et al. 2007, d'Errico et al. 2005, Henshilwood et al. 2004, Kuhn and Stiner 2007, Stiner, Kuhn, and Güleç 2013, Vanhaeren and d'Errico 2006) as well as the figurative art and evidence for music recovered from the earliest Aurignacian strata onwards (Anikovich et al. 2007, Conard 2009, Higham et al.

2012, Nelson 1990), the Neanderthals do not seem to have made much use of symbolic artefacts. Thus, Neanderthals may have been capable of executing mechanisms for *in absentia* social bonding, but expressed (required) them to a far lesser extent than did contemporary AMH due to smaller networks in terms of both membership and geographic spread.

In living humans larger V1 areas have been associated with both higher visual acuity (Duncan and Boynton 2003) and decreased susceptibility to two visual illusions (Schwarzkopf, Song, and Rees 2011). The latter finding implies that the number of neurons in V1 can help explain individual differences in the conscious perception of seemingly physically identical stimuli (Bakken et al. 2012). A fascinating, if highly speculative, possible implication of this is that the larger Neanderthal V1s meant that these hominins were less likely to, for example, see faces in natural phenomena or the ambiguity of perceptual illusions such as faces/vase or rabbit/duck. This might help explain why Neanderthals do not seem to have been drawn to making figurative art, particularly the apparent chimera-type images such as the ‘sorcerer’ from Les Trois Frères and figures that incorporate natural rock formations, as in the case of Altamira bison. It might be that unlike AMH, Neanderthals were not attracted to visual experiences that to them were unambiguous. AMH, on the other hand, might have been more susceptible to visual ‘tricks of the mind’, leading them to see faces and other living forms in the physical world around them. It is therefore possible that in addition to weaker requirements for material representations of social relationships and identities in the form of art, due to their smaller social networks, Neanderthals were not as cognitively predisposed to making art as AMH.

Even if Neanderthals did produce some symbolic artefacts, they may not have used them in the same way as AMH did. For instance, rather than Neanderthal symbolism being linked to the maintenance of extended networks, it could have been linked to the identity/status of individuals or bands. The latter may be particularly pertinent given that Neanderthal social cohesion practices seem to be associated mainly with cooperative large game hunting rather than the outer layers of the social network (Shuttleworth 2013). This suggests that the hub of Neanderthal cohesion was the residential unit (band) within which, according to recent hunter-gatherer ethnography, hunting tasks and meat sharing would have taken place. Although their respective maximum transfer distances suggest that both Neanderthals and AMH interacted throughout their ethnolinguistic tribes, the weighting of social tie strength across the different component layers of their tribes may have differed. For instance, under stressful high latitude conditions Neanderthals may have contracted their networks, similarly to the constriction of grooming cliques in stressed monkeys (Wittig et al. 2008), thus enhancing trust and cooperation within the inner layers of their networks. In contrast, AMH seem to have responded by expanding their social networks and perhaps spreading the strength of ‘weak ties’ more evenly across their outer layers through cultural scaffolding, thus optimising information-flow by minimising network redundancy. This fits with the implication that only AMH sometimes interacted between ethnolinguistic tribes, accounting for transfer distances of up to ~800km (Chapter 6). Larger-scale cohesion within and between ethnolingusitic populations to the degree that eventually shows up clearly in the archaeological record may thus have been a hallmark of the AMH niche.

A difference in social cognition does not necessarily mean that Neanderthals were less cognitively competent in other domains: they were capable of hunting large game and their tools seem to be different but arguably equally complex compared to those of AMH, for instance both used composite tools. The fact that Neanderthals show no evidence for bow and arrow technology and do not seem to have exploited fast moving small prey may be due to their low population densities and a lack of need because of abundant megafauna, rather than a cognitive inability to do so. Whereas Neanderthals seem to have adapted to harsh Eurasian environments physically, increasing the size of their bodies and visual systems, AMH may have taken a more social strategy, including larger networks to buffer risk and spread cultural innovations. This is not to say that AMH did not also evolve physically or that Neanderthals showed no cultural adaptations and lived in isolation. Rather, I am proposing that the difference is a matter of the relative weighting of these strategies, which was not a conscious decision and theoretically could have manifested in the opposite direction.

However, since both body mass (Blackburn, Gaston, and Loder 1999, Katzmarzyk and Leonard 1998) and visual system sizes (Pearce and Dunbar 2012) are enlarged at higher latitudes in living humans, it may be the fact that AMH evolved in low-latitude Africa that allowed these social adaptations to take-off in AMH but not Neanderthals. That is, evolving at lower latitudes might have given AMH the advantage of lighter environments and bodies, reducing somatic and visual requirements for brain tissue and thus allowing their social brain areas to increase while maintaining manageable energetic costs. AMH may have been under strong selection to evolve additional sociocognitive competences and develop cultural supports when they inhabited open environments with more fluctuating resources (Finlayson 2004), where social insurance against risk would be paramount (e.g. Cashdan 1985, Dirks et al. 1980, Low 1990, Wiessner 1982). In contrast, Neanderthals seem to have preferred (or were limited by their robust physiology to) heterogeneous environments which would have allowed easier diet switches if necessary, as well as more manageable resource monitoring, thus reducing the importance of information exchange between social units moving independently around the landscape (Finlayson 2004). The idea that Neanderthal brains are large due to large somatic and visual areas whereas AMH brains are large at least partly due to large areas to cope with social complexity fits well with the idea that Neanderthals and AMH brains enlarged relative to those of their common ancestor along divergent developmental and evolutionary trajectories (Bruner, Manzi, and Arsuaga 2003, Gunz et al. 2012).

The historical accident of where Neanderthals and AMH evolved may have influenced other aspects of social organisation, such as division of labour. For instance, Kuhn & Stiner (2006) argue that cooperative economies with complementary subsistence roles are more likely to develop at low latitudes because suitable smaller prey and plant resources to supplement larger game hunting are more abundant and diverse than nearer the poles. They argue that AMH practised division of labour whereby adult females and children manufactured elaborate technologies and foraged for plant food[69] as well as smaller sessile and faster moving prey, while adult males embarked on smaller group or individual pursuit of larger game. In contrast, they posit that the Neanderthal concentration on medium/large herbivores necessitated that all group members were involved in the hunt, either through close-quarter killing or beating/herding/blocking and that consequently division of labour was not practised (e.g. Kuhn and Stiner 2006, Layton, O'Hara, and Bilsborough 2012, Pearce et al. in press). If Neanderthals did not engage in division of labour, their bands may have undergone fission less frequently than those of AMH, meaning that coordination of subgroups was not often necessary for Neanderthals. Although AMH would have needed to meet the cognitive demands of more complex coordination of foraging groups, division of labour may have facilitated the existence of specialist manufacturers of time-costly symbolic objects to mark tribal affiliation and for exchange, aiding network cohesion.

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[69] Recent hunter-gatherers in the Subarctic biome still obtain a median of 10% of their subsistence from plants, 58% from hunting and 35% from fishing (Binford 2001). In the Arctic 30% is from hunting, 69.99% from fishing and 0.1% from plants (ibid.)

As well as larger bodies and visual system sizes, higher latitudes and the associated greater seasonality of resources may select for greater cognitive flexibility, as in birds (Sol 2009). The supposed common ancestor of Neanderthals and AMH, *H. heidelbergensis*, already seems to show a high degree of behavioural flexibility by apparently surviving in boreal zone environments (Parfitt et al. 2010), probably through projectile technology (Thieme 1997) and controlled use of fire (Roebroeks and Villa 2011). Once body and visual system size is taken into account, Neanderthals do not have endocranial volumes outside the range of *H. heidelbergensis*, whereas AMH brains are still larger (Chapter 4: Figure 4.6). This might imply that the majority of latitudinal (or otherwise) selection for cognitive flexibility, at least in terms of technical ability, long-term planning and extractive foraging, had already taken place by the time that Neanderthals and AMH evolved. Any difference between the descendant taxa might thus rest predominantly in the relative size of somatic, visual and 'social' brain areas, although parietal differences hint at further discrepancies. If AMH had larger extended networks this would have (i) given individuals greater numbers of alternative sources of help if local resources failed, (ii) reduced vulnerability to demographic fluctuations and (iii) ensured greater conservation of cultural knowledge and innovations for cumulative development, perhaps enabling further AMH expansion towards the poles. As such, larger social networks may have given AMH the edge in direct competition and/or the ability to cope with demographic fluctuations and resource variability, so that they did not go extinct along with Neanderthals as the climate deteriorated into the LGM.

Conclusion

In this thesis I have examined the additional challenges faced by hominins as their social networks became spread over progressively greater distances at higher latitudes.

For instance, competing demands on the allocation of brain tissue may have limited the social complexity that could be cognitively supported. Specifically, I have proposed that the lower light levels of higher latitudes select for larger eyes and thus larger visual brain areas. Due to overall energetic constraints on brain size, larger eyes (and larger bodies) may mean that other areas of the brain, such as those underlying the processing of social complexity, cannot be enlarged as well. This seems may have been the case for Neanderthals. I have also shown that at all latitudes, both Neanderthals and AMH appear to maintain social networks across the geographic area associated with their ethnolinguistic tribes. Only AMH seem to have occasionally interacted between tribes. Taking a modelling approach, I predicted that although at lower latitudes tribal coherence can be achieved through daily subsistence movement alone, at higher latitudes additional mechanisms are required for bonding over separations in time and space. This specific hypothesis can be tested against hunter-gatherer ethnographic and archaeological evidence and has widespread implications for explaining the geographic distribution and temporal appearance of, for instance, abstract and figurative art during the global AMH diaspora. Overall I have demonstrated that latitude can influence brain organisation and cultural expression and have argued that both can substantially impact on the maintenance of social networks, which are vital for hominin reproduction (mating opportunities, cooperative child-rearing) and survival (insurance against ecological risk, cultural knowledge).

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Appendix 1: Visual system scaling

Orbits and visual cortex surface area in diurnal primates, controlling for overall neocortex size

A PGLM analysis of $\log_{10}$ total visual surface area regressed against $\log_{10}$ orbital diameter and $\log_{10}$ rest-of-neocortex surface area yielded a model where neither covariate showed a significant partial relationship with visual cortex volume (p=0.241 and 0.110 respectively). Overall the model was significant (F=176.039, p=0.0056), with an overall *adjusted* R^2 of 0.994. The optimised lambda value for the model (6.611e^{-5}) was not significantly different from either 0 (χ^2=-0.0002, p=1) or 1 (χ^2=3.723, p=0.054). The lack of significance may be due to insufficient sample size, which provided too few degrees of freedom once additional covariates were added.

PGLM analysis revealed that $\log_{10}$ orbital diameter is significantly and positively related to $\log_{10}$ rest-of-neocortex surface area: t_3=7.217, p=0.005, R^2=0.946, *adjusted* R^2=0.927. The optimised lambda for the model (6.611e^{-5}) was not significantly different from either 0 (χ^2=-0.0001, p=1) or 1 (χ^2=1.771, p=0.183). This suggests that multicollinearity might be a problem, so I calculated relative visual surface area and orbital diameter as ratios against non-visual neocortex surface area. However, relative total visual surface area was not significantly associated with relative orbital diameter independently of phylogeny (p=0.235). Figure A1 suggests a more quadratic than linear relationship, but this is probably due to small sample size and the variance in the data. In addition the optimised lambda (6.611e^{-5}) is very low yet chi-squared tests failed to show that it was significantly different from one (χ^2=1.843, p=174), again suggesting inadequate sample size.

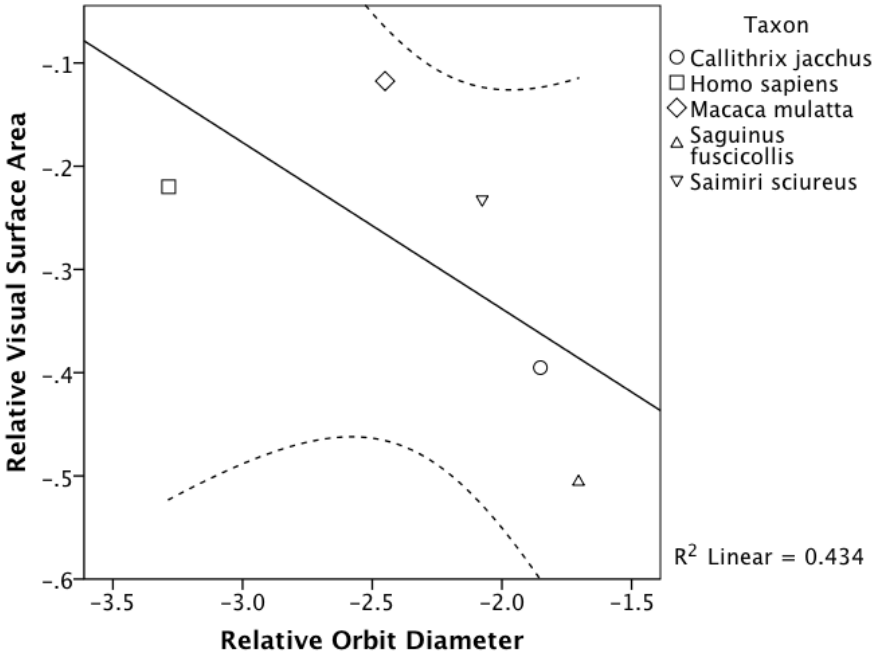

Figure A1: Relative visual surface area plotted against relative orbit diameter for 5 diurnal anthropoids. The dashed lines give 95% confidence intervals for the non-significant regression line.

Higher quality MRI scan sample (*N*=40): Scaling between orbital and eye volume in living humans

For the higher quality subset sample, OLS regression revealed that mean orbital volume was significantly positively associated with mean eyeball volume (Figure A2): t_{38}=5.397, p=3.815x10^{-6}, R^2=0.434. This relationship remained significant when a high outlier was excluded from the analysis. Orbital volume remained significantly associated with eyeball volume (t_{37}=5.847, p=1.011x10^{-6}) independently of brain-minus-visual-cortex-grey-matter volume, which itself failed to show a significant partial relationship with eye volume (p=0.071): overall adjusted R^2=0.454. Controlling for rest-of-grey-matter (i.e. non-visual) cortical volume, cerebellum plus brainstem or subcortical grey matter volume yielded similar patterns.

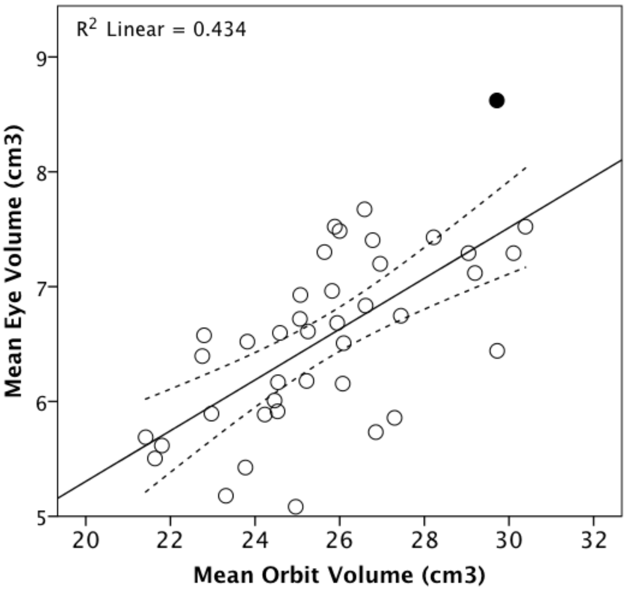

Figure A2: Mean eye volume plotted against mean orbital volume for the higher quality image sample of 40 living humans. The outlier is shaded (see main text). The dotted lines represent 95% confidence intervals for the regression line.

Scaling between eye and V1 volumes in living humans

OLS regression revealed that mean eyeball volume was significantly positively associated with total V1 grey matter volume: t_{86}=3.523, p=0.001, R^2=0.126. Removing the outlier (Figure A3) did not alter the results. The partial relationship between eyeball volume and V1 grey matter volume remained independently of overall brain size measures (Table A1). In the full sample eyeball volume is related to V1 grey matter volume when rest-of-grey-matter, motor or somatosensory cortex volumes are separately controlled for, whether or not the outlier included. These significant partial relationships between eyeball and V1 grey matter volumes remain when the models also include sex whether or not the outlier is excluded (except for the motor/somatosensory full models when the outlier is removed).

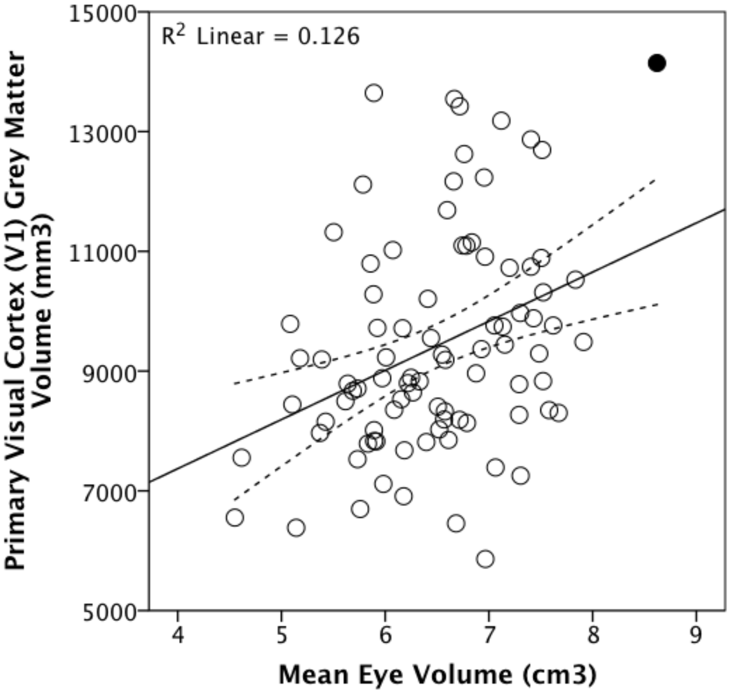

Figure A3: Total V1 grey matter volume plotted against mean eyeball volume for a sample of 88 living humans. The outlier is shaded (see main text). The dotted lines represent 95% confidence intervals for the regression line. Note that an RMA regression with a steeper slope through the middle of the data would produce a better fit.

Table A1: OLS regression statistics for partial relationship between eyeball volume and V1 grey matter volume, controlling for various measures of overall brain size.

Eyeball volume predicting V1 volume, separately controlling for:	**OLS Regression Statistics**					
	t	**df**	**p**	**Partial R^2**	**Overall R^2**	**Overall adjusted R^2**
Total brain volume	3.598	85	0.001	0.132	0.214	0.195
Brain volume minus total visual grey matter volume	3.607	85	0.001	0.133	0.203	0.185
Subcortical grey matter volume	3.680	85	$4.082e^{-4}$	0.137	0.198	0.179
Cerebellum + Brainstem	3.670	85	$4.230e^{-4}$	0.137	0.183	0.163
Non-visual cortical grey matter volume	3.316	85	0.001	0.115	0.248	0.230
Motor cortex grey matter volume	2.796	85	0.006	0.084	0.215	0.196
Somatosensory cortex grey matter volume	2.732	85	0.008	0.081	0.252	0.235

Scaling between visual brain areas in living humans

Hypothesis: V1 grey matter volume is associated with V2 grey matter volume, and V2 (left and right) grey matter volume is in turn related to V5/MT grey matter volume (see Figure A5 for connections between visual areas)

OLS yielded a significant positive relationship between V1 and V2 grey matter volumes (Figure A4): t_{97}=11.468, p<e^{-36}, R^2=0.576. Furthermore, V1 remained significantly associated with V2 independently of rest-of-cortex grey matter volume: t_{96}=9.348, p=3.7041e^{-15}, overall R^2=0.685, overall *adjusted* R^2=0.678. This significant partial relationship between V1 and V2 was maintained when heteroscedasticity corrections were performed using the HCREG macro (Hayes and Cai 2007) (p<0.00001). Similar results are obtained when controlling for the various other measures of overall brain volume (see Chapter 2 Methods).

OLS regression yielded a significant positive relationship between V2 and V5/MT volumes (Figure A4): (t_{97}=5.742, p<e^{-36}, R^2=0.254). Moreover, V2 showed a significant partial relationship with V5/MT independently of rest-of-cortex grey matter volume, which itself did not show a significant partial relationship: t_{96}=3.640, p=4.411e^{-4}, overall R^2=0.267, overall *adjusted* R^2=0.252. When an outlier was removed (Figure A4) both V2 (t_{95}=3.495, p=0.001) and rest-of-cortex grey matter volumes (t_{95}=2.396, p=0.019) were significantly partially associated with V5/MT grey matter volume (overall R^2=0.336, overall *adjusted* R^2=0.322). Similarly significant results are obtained when controlling for the various other measures of overall brain volume.

Furthermore, V1 was significantly positively associated with V2 volume independently of motor (t_{96}=9.511, p=1.672e^{-15}, overall R^2=0.686, overall *adjusted* R^2=0.680) and somatosensory (t_{96}=8.852, p=4.338e^{-14}, overall R^2=0.667, overall *adjusted* R^2=0.660) grey matter volumes. In turn, V2 was significantly positively associated with MT volume independently of motor (t_{96}=3.808, p=2.469e^{-4}, overall R^2=0.263, overall *adjusted* R^2=0.247) and somatosensory (t_{96}=2.823, p=0.006, overall R^2=0.313, overall *adjusted* R^2=0.298) grey matter volumes.

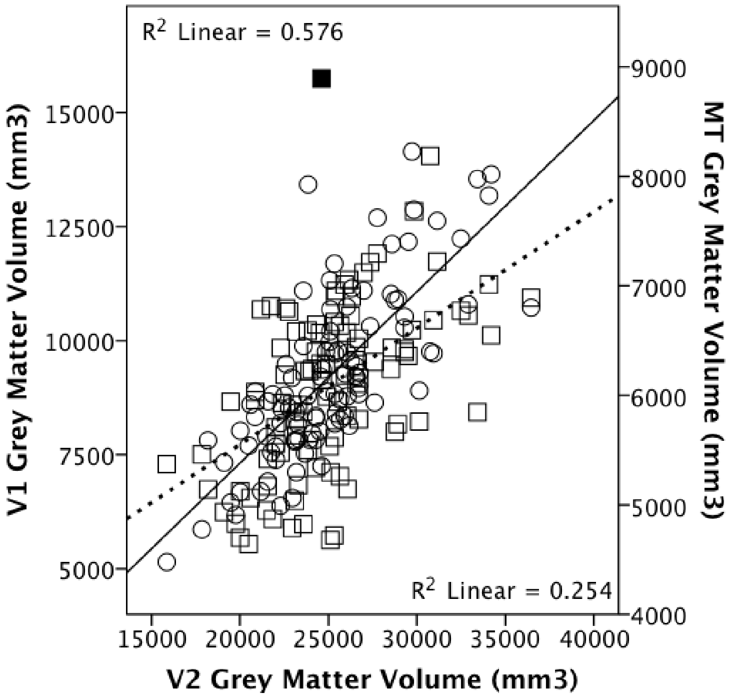

Figure A4: V1 (circles, sold regression line) and V5/MT (squares, dashed line) grey matter volume plotted against V2 grey matter volume (N=99). The outlier is shaded.

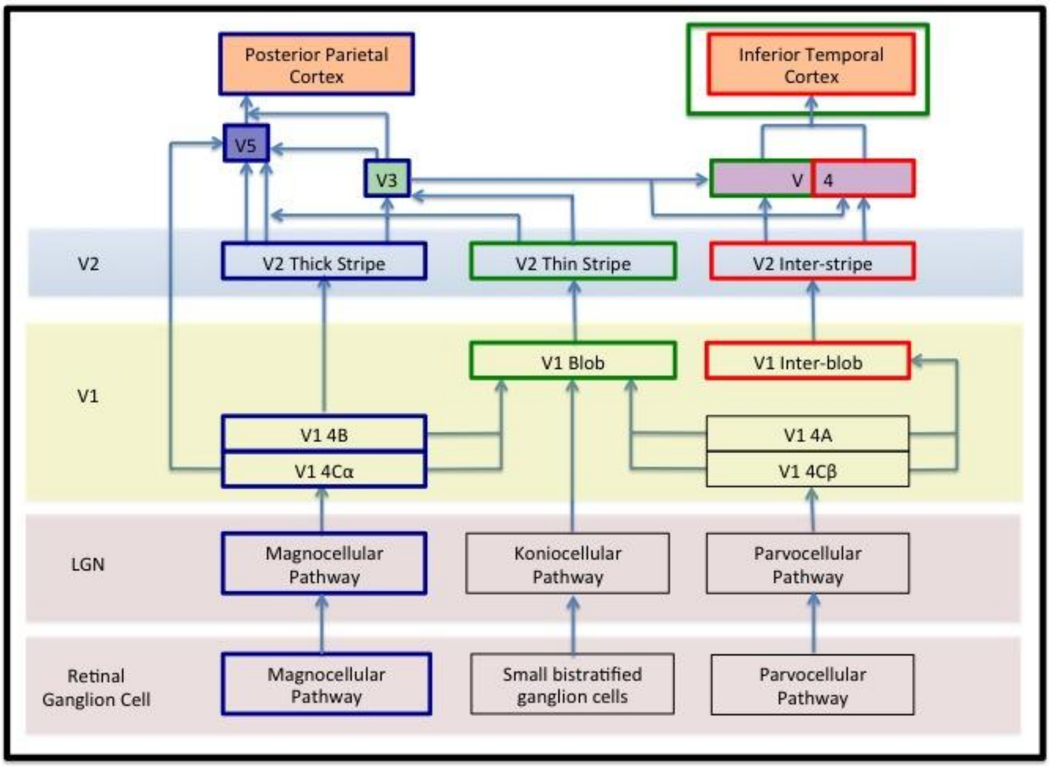

Figure A5: The main subcortical and cortical visual pathways in the macaque redrawn from Tovee (2008: Figure 4.4 page 66). The Magnocellular (movement) pathway is shown by the boxes outlined in blue (left), and the Parvocellular (colour and detail) pathway in green (colour pathway: centre) and red (details pathway: right).

Scaling between eye/orbit and non-visual brain areas in living humans

Eye volume is not significantly related to non-visual cortex grey matter volume, subcortical grey matter volume, non-visual brain volume or brain stem + cerebellum volume. However, eye volume is significantly positively related to both somatosensory (t_{86}=2.367, p=0.020, R^2=0.061) and motor (t_{86}=2.412, p=0.018, R^2=0.063) cortex grey matter volumes. With or without outliers excluded, orbital volume is also associated with all these variables: Table A2. Similarly, significant relationships were found between visual cortex grey matter volume and these same brain regions (all p<0.0001 and with visual cortex explaining ~30-40% of the variance, except brainstem+cerebellum, where p=0.06). The lack of a relationship between these brain regions and eyeball volume may thus be due to measurement error rather than actual lack of scaling.

Table A2: OLS regression statistics for relationships between orbital volume and 'non-visual' brain regions. Outliers have been removed.

Orbital volume predicting:	**t**	**df**	**p**	**R^2**
Non-visual cortex grey matter volume	4.292	83	4.763×10^{-5}	0.182
Subcortical grey matter volume	2.366	83	0.020	0.063
Non-visual brain volume	4.508	83	2.131×10^{-5}	0.197
Brain stem + cerebellum	2.138	83	0.035	0.052
Somatosensory area	3.598	83	0.001	0.135
Motor area	2.959	83	0.004	0.095

Inter-relations between different measures of orbit and eye size

Table A3: Statistics for simple OLS regressions between different measures of orbital size – volume, area, height, width – for 40 living humans, giving R^2 values and significance levels for each association. Where obvious outliers occurred, the statistics for models either including or excluding them are presented.

		Independent Variable		
		Orbit Volume	**Orbit Area**	**Orbit Height**
Dependent Variable	**Orbit Area**	0.449***		
	Orbit Height	0.188* (with outlier excluded 0.303***)	0.472*** (with outlier excluded 0.423***)	
	Orbit Width	0.214**	0.582***	0.245**

***p<0.0001, **p<0.005, *p<0.05

Table A4: Statistics for simple OLS regressions between different measures of orbital and eye size – volume, area, height, width – for 40 living humans, giving R^2 values and significance levels for each association. Where obvious outliers occurred, the statistics for models either including or excluding them are presented.

		Independent Variable			
		Orbit Area	**Orbit Height**	**Orbit Width**	**Orbital Volume**
Dependent Variable	**Eye Volume**	0.385***	0.228**	0.151* (when 2 outliers are excluded 0.301***)	.434***
	Eye Area	0.211**	n.s.	n.s	.274**
	Eye Height	0.180**	n.s.	0.148*	.139*
	Eye Width	0.129*	n.s.	n.s.	.130*

***p<0.0001, **p<0.005, *p<0.05

Appendix 2: Recent humans

Data

Table A5: The 12 populations for which 3 or more skulls were sampled for the original study (Pearce and Dunbar 2012). I give sample size per population, the source (OUM: Oxford University Museum of Natural History; Duckworth: The Duckworth Collection at the University of Cambridge) and the latitude, cranial capacity and orbital volume data used in the mean population analyses. Where relevant standard deviations for these means are given in parentheses.

Country	Mean (SD) Latitude	Sample Size (N) per Country	Source of the Skulls Measured	Mean (SD) Cranial Capacity (ml)	Mean (SD) Orbital Volume (ml)	Mean (SD) Intercondyle Foramen Magnum Area (mm^2)
Australia	-22.89 (11.38)	5	Duckworth	1282 (85.85)	24.85 (1.46)	560.52 (62.95)
Canary Islands	28.51	4	1 Duckworth, 3 OUM	1435 (134.04)	24.66 (3.00)	747.99 (130.20)
China	37.37	3	OUM	1492 (186.57)	24.46 (3.14)	685.24 (44.80)
England	51.90 (0.42)	7	OUM	1416 (106.28)	26.22 (3.25)	660.96 (84.64)
France	47.65 (1.01)	6	4 Duckworth, 2 OUM	1462 (140.63)	26.27 (2.81)	633.23 (62.56)
India	17.63 (8.56)	3	OUM	1270 (130.77)	24.25 (3.27)	567.68 (40.53)
Kenya	-0.02	5	Duckworth	1280 (107.703)	22.58 (2.13)	542.65 (90.90)
Micronesia	4.06 (2.36)	3	OUM	1200 (100.00)	21.83 (0.76)	619.01 (31.03)
‘Scandinavia’	64.21 (1.12)	5	3 Duckworth, 2 OUM	1484 (100.15)	26.83 (1.01)	642.39 (118.81)
Somalia	10.10 (0.71)	5	Duckworth	1378 (162.85)	23.33 (2.45)	604.09 (115.62)
Uganda	1.36	5	4 Duckworth, 1 OUM	1340 (91.65)	23.98 (1.39)	661.29 (153.60)
Native American	40.74 (1.49)	4	OUM	1342.5 (117.86)	26.63 (1.97)	597.79 (89.14)

Table A6: The populations and data used in the visual acuity analyses (data from Myers 1902, Rivers 1898). Standard deviations are given in parentheses where possible, but the data presented by Myers (1902) and Rivers (1898) prevented these being calculated in some cases.

Population	**N**	**Mean Visual Acuity (SD)**	**Reference**	**Subset Using Same Method***
Arabs	13	2.27	Referenced in Rivers	E
Bakairi & Trumai	5	1.58 (0.319)	Referenced in Rivers	
Chippeway	6	1.42 (0.129)	Referenced in Rivers	
Cossaks		2.65	Referenced in Rivers	
German navy	100	2.10	Referenced in Rivers	E
Heligoland Men	100	1.77	Referenced in Rivers	E
Kalmuks	17	2.70	Referenced in Rivers	E
Kiwai	19	2.06	Rivers	E
Mabuiag	36	2.32	Rivers	E
Murray Island	115	2.06	Rivers	E
Osset soldiers	142	2.40	Referenced in Rivers	
Sarawak	24	1.80	Myers	E
Sinhalese & Hindus	23	2.15	Referenced in Rivers	E
Torres Straits and Fly River	170	2.12	Rivers	E

*The E method requires subjects to indicate the orientation of the E shape being presented.

Phylogenetic analyses (Pearce and Dunbar 2012: supplementary online material)

Main orbital (bead) database phylogenetic analyses

Mesquite (Maddison and Maddison 2010) was used to both create the tree structure and assign branch lengths, which I calculated using the method outlined below. I obtained global F_{ST} genetic distances (x10,000) from Cavalli-Sforza et al (1994) Table 2.3.1A (page 76), with some regional distances within Europe from Table 5.5.1 (page 270). Since the orbital volume data are low resolution country-level, rather than consisting of specific ethnic groupings within national boundaries, I matched the orbital countries to equivalent groupings in the Cavalli-Sforza et al database. I took Cavalli-Sforza et al's Berber data to correspond to the Canary Island Guanche (Maca-Meyer et al. 2003) and their East African data for our Somalians, as well as matching their Nilo-Saharan data to our Kenyans and Ugandans (Lynch and Robbins 1979, Scotton 1981), although I could alternatively have used the single Bantu datum. Although Cavalli-Sforza et al's (1994) regional African Table 3.6.1 (page 172) gives distance data for Cushitic people and these are the closest fit for representing our Somalian sample (Lewis 2009), since distances were only available *within* Africa rather with other world populations, I used the East African data for calculating genetic distances between the Somalians and other populations. I obtained the French-English distance from Table 5.5.1.

The global Table 2.3.1A gives data for both Lapps and Uralic (the language family containing Finnish and Saami (Lewis 2009)) peoples and I calculated the mean of these for each of the Scandinavian comparisons, since the exact genetic composition of the sample was unknown. I also calculated the mean between genetic distances for South China and the Northern Turkic, which was the closest sample to Northern China, since the specific location of where our Chinese skulls originated is unknown. Although Northern Chinese distances were available in a regional Asian table (4.12.1, page 230), no data for comparisons with worldwide populations were provided.

I based the structure of our tree on the average linkage tree presented by Cavalli-Sforza et al (1994) in their Figure 2.3.2.B (page 78), which was based on 120 allele frequency differences between 42 populations. I then calculated branch-lengths from the genetic distances outlined above. For the branch-lengths between Kenya and Uganda I assigned an arbitrary value of one, since I treated these populations as the same Nilo-Saharan group when identifying genetic distances with other populations, but needed to delineate them as separate populations regarding the orbital volumes analyses. Global comparative genetic distance data was unavailable for France, so I took the genetic distances to all other populations to be equivalent to the distances recorded for the English population, which was the most closely related to the French in the European-only table (see above).

To calculate the branch-lengths between a pair of tips and their common node, I halved the genetic distance between them and this was the branch length either side of the node. For the subsequent nodes I calculated the mean distance between the two sides of the bifurcation and halved this to find the total branch length from the terminal tips to that internal node. For instance, for the branch-length between Somalia and Kenya/Uganda, I summed the geographic distances between Somalia and Kenya with that between Somalia and Uganda, divided this by 2 (i.e. by the number of pair-wise genetic distances) to get the mean distance, and by 2 again to get the total branch length either side of the splitting node. Since some of this total branch length is taken up by the branch-lengths between Uganda and Kenya, to find the residual branch-length between the split with Somalia to the split between Kenya and Uganda, I subtracted the branch-length between Kenya/Uganda and their common ancestral node from the total branch length from the tips of Uganda/Kenya/Somalia and their common node. I applied this to all the other nodes in the tree, with nodes between clades requiring the mean distance of all the combinations of population pairs between the two clades to be calculated, for example USA-England, USA-France, USA-India, USA-Canary Islands, USA-Scandinavia, China-England, China-France, China-India, China-Canary Islands, China-Scandinavia. In calculating mean genetic distances between the England/France clade and others nodes/clades, I treated the former populations as separate data points, thus incorporating identical values (derived from the English) into the equations twice, to represent the distances to both France and England. Note that the 'USA' sample comprises native Americans only.

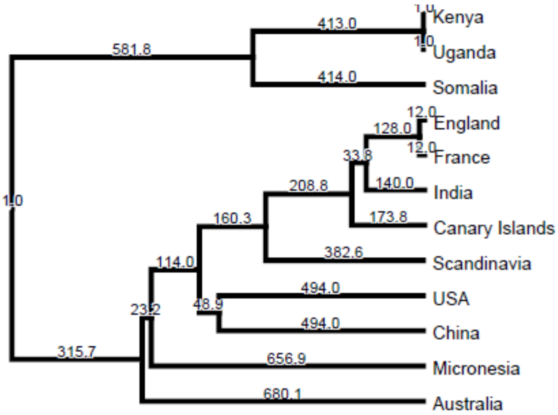

Figure A6: Human population tree for the orbital volume analyses, based on Cavalli-Sforza et al (1994) Figure 2.3.2.B, with branch lengths based on genetic distances given in Tables 2.3.1A and 5.5.1 of the same publication.

Method: Visual Acuity Phylogenetic Analyses

I followed the above method to produce the tree shown in Figure A7. I used Cavalli-Sforza et al's Indians to represent our Sinhalese/Hindus, their Iranians to represent our Georgian Ossets, their Near Easterners to represent our Egyptian Arabs, their North and Southern Americans to represent our Chippeway and Bakairi/Trumai (Brazil) samples, the mean of the distances associated with their English, Greek and Italian samples to represent our Indo-European Slavic Cossaks, their Northern Turkics to represent our Mongolian Kalmuks and their Danish sample to represent our German navy and Heligoland samples (because the European regional table (see above) showed this to be the closest match). The New Guinean Kiwai, Australian Mabuiag, Murray Islanders and Torres Strait samples, as well as the Malaysian Sarawak sample, could be matched to these broad regional categories in Cavalli-Sforza et al's worldwide genetic distance table (see above). In order to maintain structure within the Australian clade in the face of missing genetic distance data, arbitrary branch lengths of 1 were assigned between Mabuiag and Murray Island and 1.5 between this clade and Torres Straits, so that the resulting tree was resolved and because the latter is geographically closer to New Guinea. Arbitrary branch lengths of 1 were also added between Heligoland and Germany and their ancestral node, for the same reason.

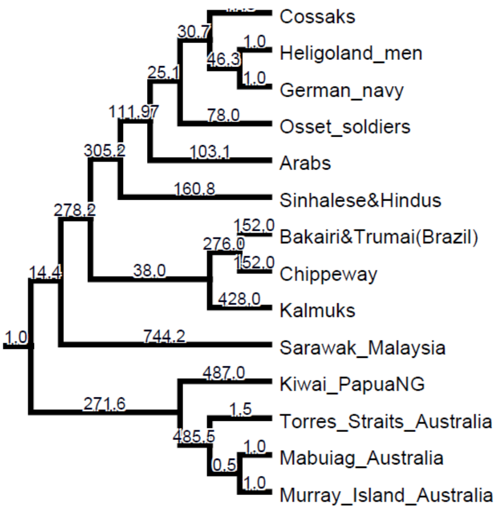

Figure A7: Human population tree for the visual acuity analyses, based on Cavalli-Sforza et al (1994) Figure 2.3.2.B, with branch lengths based on genetic distances given in Tables 2.3.1A of the same publication. Branch lengths are shown as whole numbers.

Method: Partial (CT) Orbital Volumes Phylogenetic Analyses

I first created a tree using Mesquite, basing the structure on the global human tree provided by Li et al (2008): Liberians represented Africans, the Germans and Lithuanians represented Europeans, I took Indians to be positionally equivalent to Pakistanis in Li et als' tree. Since native Australians, Papuans and Melanesians are closely related genetically and Micronesians are closely related to Melanesians (Lum and Cann 1998, Lum, Jorde, and Schiefenhovel 2002), I regarded Australians and Micronesians as a clade, which is most closely related to the Asian and Native American clade, following Li et al (2008). Greenlanders are most closely related to native Americans (Derenko et al. 2007, Dillehay 2009, Zegura et al. 2004), so I took the form to fill the position of Li et al's South Americans. I used the Li et al tree rather than the Cavalli-Sfroza et al tree used above because the former is more recent. In the other phylogenetic analyses I used the Cavalli-Sforza tree because I was using their corresponding genetic distances. However, in the partial orbital analyses I relied on geographic rather than genetic distances (see below) so I was not limited to using the Cavalli-Sforza tree.

I calculated branch-lengths from pairwise geographic distances, since genetic distances between all the populations were unavailable, namely with regard to Lithuania and Liberia (Cavalli-Sforza, Menozzi, and Piazza 1994). I used http://www.movable-type.co.uk/scripts/latlong.html (Movable Type Scripts Accessed 2010) to calculate distances between each pair of population latitude/longitude coordinates. The criteria were as follows: the shortest straight-line distance between the two points, avoiding large bodies of water such as the Atlantic Ocean and passing through known dispersal points (Suez and the Bering Strait) where necessary. The latter two criteria meant that for some pairs a number of intermediate steps were necessary and the intervening distances were totalled. I set the maximum number of places used per place-pair, including the two endpoints, to six. These allowed me to create a pair-wise geographic distance matrix, from which I could calculate branch-lengths by following the method outlined above. I assigned the branch to the root an arbitrary value of 1. Using geographic-distance-based branch lengths had the problem of creating a negative branch-length between the Australia-Greenland clade and the India-Germany-Lithuania clade. I conducted analyses using both the raw brain-lengths and a tree where the negative branch-length was replaced by very small positive number (1x10^{6}) and these gave results that did not differ significantly and I report only those based on the raw branch-lengths here.

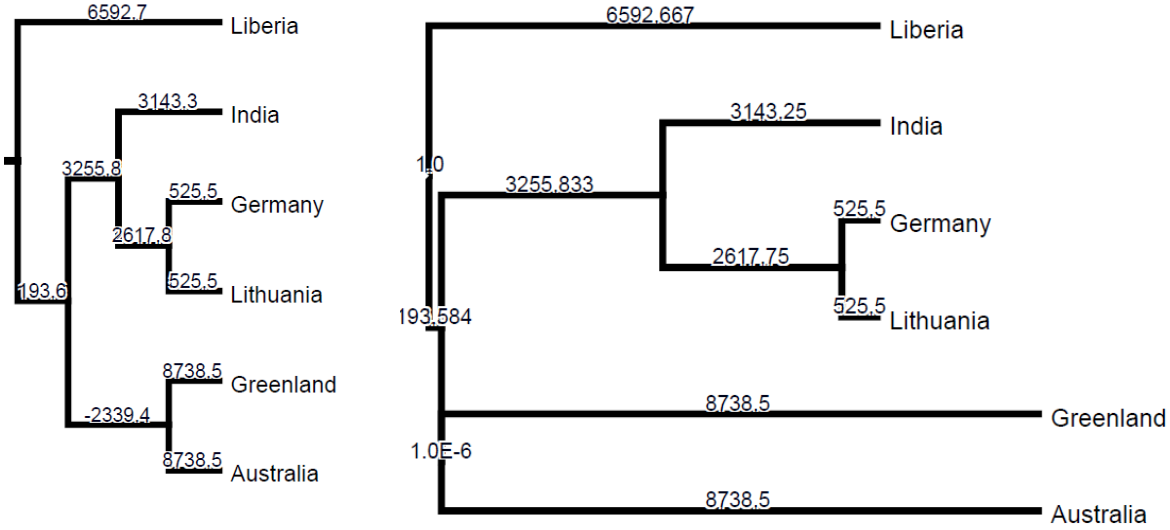

Figure A8: Population trees for the partial orbital volume analyses: LEFT Actual geographic distance branch lengths, including a negative value, branches are not proportional to their length, RIGHT With the negative branch length replaced with a low positive value, branches are proportional to their lengths.

Appendix 3: Neanderthal versus AMH brain organization

Specimens for analyses reported in Chapters 4 & 5 (Pearce, Stringer, and Dunbar 2013: supplementary online material)

Table A7: The sample used in the analyses presented in Chapters 4 and 5 (Pearce, Stringer, and Dunbar 2013), based on the absolute endocast volume dataset from (Holloway 2004). The orbital size comparison samples are also indicated. From the original endocast sample I excluded (i) AMH dated <27ky, (ii) children and infants (Engis 2, La Quina 18, Skhul 1, Qafzeh 11, Atapuerca 6, Sungir 3 (De Miguel and Henneberg 2001, Osaka City University Accessed 2011)). I included the Kostenki and Sungir specimens, now dated to ~35kya (Marom et al. 2012). I also re-classified the Skhul and Qafzeh specimens as AMH rather than Neanderthals. I include 'archaic' specimens for comparison, but these were not included in any analyses.

Assigned taxon	Specimen	Assigned date (mya)	Orbital Dimension
Homo neanderthalensis	St Césaire	.040	OBH, OBB
Homo neanderthalensis	Le Moustier 1 subadult	.040	Area
Homo neanderthalensis	Spy 1	.040	
Homo neanderthalensis	Spy 2	.040	
Homo neanderthalensis	Amud 1	.050	Volume, Area, OBH, OBB
Homo neanderthalensis	Ganovce 1	.050	
Homo neanderthalensis	Gibraltar 1 (Forbes' Quarry)	.050	Volume, Area, OBH, OBB
Homo neanderthalensis	La Chapelle	.050	Volume, Area, OBH, OBB
Homo neanderthalensis	La Quina 5	.050	
Homo neanderthalensis	Feldhofer 1	.050	
Homo neanderthalensis	Shanidar 1	.050	OBH, OBB
Homo neanderthalensis	Shanidar 5	.050	OBH, OBB
Homo neanderthalensis	Monte Circeo (Guattari 1)	.055	Volume, OBH, OBB
Homo neanderthalensis	La Ferrassie 1	.060	Volume, Area, OBH, OBB
Homo neanderthalensis	Saccopastore 1	.120	Area, OBH, OBB
Homo neanderthalensis	Saccopastore 2	.120	OBH, OBB
Homo neanderthalensis	Krapina 3 (C)	.130	OBH, OBB
Homo neanderthalensis	Krapina 6 (E)	.130	
Homo neanderthalensis	Krapina B subadult	.130	
Homo neanderthalensis	Tabun C1	.130	OBH
Homo neanderthalensis	Biache	.170	
Homo neanderthalensis	Lazaret	.170	
Homo sapiens	Zhoukoudian 1	.027	Area
Homo sapiens	Zhoukoudian 2	.027	Area

Homo sapiens	Zhouzoudian 3	.027	Area, OBH, OBB
Homo sapiens	Brno 1	.030	
Homo sapiens	Brno 2	.030	
Homo sapiens	Brno 3	.030	Volume, Area, OBH, OBB
Homo sapiens	Cro-Magnon 1	.030	Volume, Area, OBH, OBB
Homo sapiens	Cro-Magnon 3	.030	
Homo sapiens	Dolní Věstonice 3	.030	Area (specimen number not given), OBH, OBB
Homo sapiens	Dolní Věstonice 14	.030	
Homo sapiens	Dolní Věstonice 18	.030	
Homo sapiens	Dolní Věstonice 20	.030	
Homo sapiens	Dolní Věstonice 21	.030	
Homo sapiens	Grotte des Enfants 4	.030	
Homo sapiens	Grotte des Enfants 5	.030	
Homo sapiens	Grotte des Enfants 6 subadult	.030	OBH, OBB
Homo sapiens	Kostenki 14	035	OBH, OBB
Homo sapiens	Kostenki 2	035	
Homo sapiens	Pavlov 1	.030	OBH, OBB
Homo sapiens	Předmostí 10	.030	
Homo sapiens	Předmostí 3	.030	Area, OBH, OBB
Homo sapiens	Předmostí 4	.030	OBH, OBB
Homo sapiens	Předmostí 9	.030	
Homo sapiens	Sungir 1	.035	
Homo sapiens	Sungir 2	.035	
Homo sapiens	Sungir 5	.035	
Homo sapiens	Mladeč 1	.035	Volume, Area (specimen number not given), OBH, OBB
Homo sapiens	Mladeč 2	.035	
Homo sapiens	Mladeč 5	.035	
Homo sapiens	Nazlet Khater	.037	
Homo sapiens	Liujiang	.040	OBH, OBB
Homo sapiens	Border Cave partial skull	.070	
Homo sapiens	Qafzeh 6	.100	OBH, OBB
Homo sapiens	Qafzeh 9	.100	Area, OBH, OBB
Homo sapiens	Skhul 4	.110	
Homo sapiens	Skhul 5	.110	Volume, Area, OBH, OBB
Homo sapiens	Skhul 9	.110	OBH, OBB
Homo sapiens	Herto 1 / 16	.160	

?Denisovan, Neanderthal clade?	Dali 1	.250	OBH, OBB
?Denisovan, Neanderthal clade?	Yingkou (Jinniushan)	.250	
?Denisovan, Neanderthal clade?	Narmada 1	.300	
Archaic H. neanderthalensis	Ehringsdorf 9	.200	
Archaic H. neanderthalensis	Reilingen	.300	
Archaic H. neanderthalensis	Steinheim 1	.300	Volume, Area
Archaic H. neanderthalensis	Atapuerca 4 (AT600)	.400	
Archaic H. neanderthalensis	Atapuerca 5 (AT700)	.400	
Archaic H. neanderthalensis	Swanscombe 1	.400	
Archaic H. sapiens	LH18 (Laetoli 18)	.150	
Archaic H. sapiens	Singa 1	.150	OBB
Archaic H. sapiens	Omo Kibish 2	.195	
Archaic H. sapiens	Jebel Irhoud 1	.200	Area, OBH, OBB
Archaic H. sapiens	Jebel Irhoud 2	.200	
Homo heidelbergensis	Broken Hill / Kabwe 1	.300	Volume, Area, OBH, OBB
Homo heidelbergensis	Petralona 1	.300	Volume, OBH, OBB
Homo heidelbergensis	Ceprano	.400	
Homo heidelbergensis	Arago 21	.450	OBH, OBB
Homo heidelbergensis	Elandsfontein (Saldanha 1)	.500	
Homo heidelbergensis	Sale 1	.500	
Homo heidelbergensis	Bodo	.600	Area, OBH, OBB
Homo heidelbergensis	Yunxian (Ev9002 skull ii)	.600	

Alternative method, analyses & results

Rather than using endocranial volumes directly, I first estimated brain volumes from endocranial volume and conducted the subsequent body mass and visual system size corrections and analyses on these brain volumes. This method yields the cognitive group size and mentalising competence estimates for Neanderthals and AMH referred to in (Pearce et al. in press).

Methods

I estimated brain volume from cranial capacity for 24 Neanderthals and 30 AMH (Bailey and Geary 2009) dated 30-200ky (Table A10). I excluded AMH younger than 30ky so that the AMH specimens were as close in time to the Neanderthal specimens as possible. I excluded specimens dated earlier than 200kya as being taxonomically arguable. Log_{10} brain volume (mm^3) was estimated from log_{10} endocranial volume (mm^3) using a Phylogenetic Generalised Linear Model (PGLM) equation fitted to data for 36 primate species (Martin 1990, Stephan, Frahm, and Baron 1981), using the CAIC package in R (R-Forge Accessed March 2011) and a corresponding consensus tree from the 10k tree project (Arnold, Matthews, and Nunn 2010): $Log_{10}Brain=0.081(95\%\ CI\ -0.047 - 0.209)+0.981(95\%\ CI\ 0.953-1.009)*Log_{10}CC$, $t_{34}=68.471$, $p=5.117\times10^{-38}$, adjusted $R^2=0.993$. For these analyses, genus was used where species did not match between the databases.

I checked the results of these analyses using a separate published dataset of endocast volumes (De Miguel and Henneberg 2001, Holloway 2004). Although volumes differed between the datasets for some specimens, overall the results remained unchanged regardless of the database used. I present only the results from the most recently published dataset here (Bailey and Geary 2009), which has been used in several other publications (e.g. Grove, Pearce, and Dunbar 2012, Shultz, Nelson, and Dunbar 2012). In Chapters 4 and 5 I used the Holloway dataset following the insistence of reviewers for Pearce et al (2013). I also re-ran the analyses excluding fragmentary specimens, but the results remained unchanged and I report the analysis for the full dataset only.

Body mass corrections were applied using the method presented in Chapter 4. Since sex and latitude are known to influence body mass, I also created sex- and latitude-specific body mass correction factors. However, these refined corrections yielded the same results as the generic ones. Moreover, since sex determination of fossils is somewhat ambiguous and because the relatively small sample sizes in each sex- and latitude-specific category might produce unrepresentative means, I report only the results based on the aggregated body mass corrections, ignoring sex and latitude.

I used the same orbital dimension data as reported in Chapter 4 and the same method of estimating the visual cortex volumes and correction factors.

I used an ape equation of group size plotted against brain size and an anthropoid equation of level of intentionality plotted against brain size to estimate fossil social cognitive competences. Since variance was expected in both x- and y-variables and the relationship is symmetric (Smith 2009), I initially fitted a phylogenetically-controlled reduced major axis (RMA) regression (Ives, Midford, and Garland 2007) using the phytools package in R (Revell 2011 (accessed 2011)) to log_{10} group size ($M=1.321$, $SD=0.763$) against log_{10} brain volume (mm^3) ($M=5.585$, $SD=0.457$) for 4 apes (humans, gorillas, chimpanzees and *hylobates*) (Joffe and Dunbar 1997): $t_2=5.256$, $p=0.034$, $R^2=0.932$, $Log_{10}Group=-8.037+1.674*Log_{10}Brain(mm^3)$, *95% confidence limits of the* *slope=0.459-9.787, intercept=-1.243 - -53.343* (Figure A9). I fitted the regression to the ape data only, rather than including all anthropoids, due to grades evident in the brain-group data (Dunbar 1998b). However, qualitatively similar results are obtained irrespective of the regression model fitted.

The phylogenetic RMA model parameters did not differ from a standard RMA calculated using the lmodel2 (Legendre 2011 (accessed 2011)) package in R (Legendre 2011 (accessed 2011)), in which RMA is termed 'Standard Major Axis' (SMA). Unfortunately the phytools and lmodel2 packages do not provide tests of significance for the SMA method, so I used the method outlined in Chapter 5 to perform significance tests. The intercept (-8.016) and slope (1.672) of an RMA fitted to these data excluding the human datum are almost identical to the parameters of the RMA fitted to the full dataset. I therefore used the full ape dataset equation.

Furthermore, standard and phylogenetically-controlled RMA equations fitted excluding gorillas, a species which has relatively small groups sizes for its brain volume due to a disproportionately large cerebellum and therefore a correspondingly small neocortex (Dunbar 2011a), did not differ significantly from the line fitted to all four apes for which data were available. The confidence intervals for the former equation are much narrower than those for the equation including gorillas. Moreover, RMA lines fitted to a larger sample of anthropoid primates (N=25) (Joffe and Dunbar 1997) yields similar results with respect to the fossil group size estimates.

Although the confidence intervals are fairly wide for the line presented in Figure A9, the consistent results gained using the other equations, which are all associated with narrower confidence intervals, gives me confidence in this approach. Since the aim of this research was to compare group size between AMH and Neanderthals, rather than to estimate exact group sizes *per se*, this method is justified: all equations, regardless of (i) fitting method, (ii) the sample from which they are extracted and (iii) whether or not they are phylogenetically-controlled, produce qualitatively identical results in the AMH-Neanderthal group size comparisons. I used the standard ape RMA equation in predicting fossil group sizes (the phylogenetic control is not well understood and its accuracy has not been verified).

Following (Dunbar 2003a, Dunbar 2009), I fitted an linear regression predicting level of intentionality from raw brain volume (Dunbar 2009, Stephan, Frahm, and Baron 1981) for 12 species of Old World monkeys and great apes (Figure A9), setting modern humans at level 5 intentionality (Stiller and Dunbar 2007), chimpanzees and orang-utans at level 2 (Cartmill and Byrne 2007, O'Connell and Dunbar 2003) and 9 species of Old World monkeys at level 1. A PGLM yielded a significant relationship between brain volume and level of intentionality: $ToM=0.683(95\%\ CIs=0.558 - 0.809)+3.354e^{-6}(95\%\ CIs=3.048x10^{-6} - 3.660x10^{-6})*Brain(mm^3)$, $t_1=24.410$, $p=3.036e^{-10}$, adjusted $R^2=0.982$.

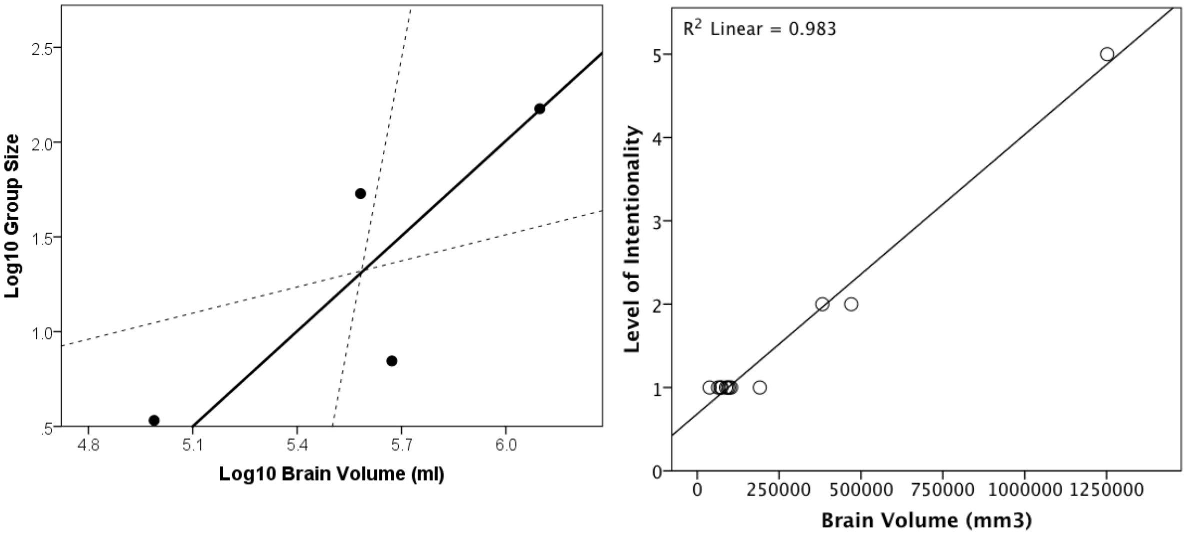

Figure A9: LEFT: Log$_{10}$ group size plotted against log$_{10}$ brain size for 4 apes, with an RMA regression line fitted. The dashed lines indicate 95% confidence limits (see method for calculation below). RIGHT: Level of intentionality plotted against brain size for twelve Old World primate species.

Results

In general the results were the same as those presented in Chapter 4 and 5 (Figure A10, Table A8, Table A9: note that non-parametric analyses were conducted as conservative tests of significance), except that the group size estimates are quantitatively different. Using this alternative method, the primate equations suggest that Neanderthals dated 30-75kya had significantly smaller estimated group sizes (*Median*=107, *range*=70 - 141, *N*=13) than contemporary fossil AMH, whereas fossil AMH (*M*=152, *range*=118 - 196, *N*=23) seem to have group sizes in line with those demonstrated for the mean active network/community sizes of living humans (Figure A10). Similarly, analysis of the intentionality competences predicted from standardised brain volume likewise suggests that Neanderthals had significantly lower competences than AMH (Figure A10). In this respect, Neanderthals once again fall within the range of more archaic hominins.

Table A8: Mann-Whitney U test statistics for comparisons between AMH and Neanderthals for raw and corrected brain volume, split by date group.

Date Groups	**Brain Volume Variables**		**Taxon**		**Mann-Whitney test (two-tailed)**		
			AMH	**Neanderthals**	**z**	**p**	**R^2**
30-76kya	Raw Brain Volume (cm3)	N	23	13	-0.148	0.882	NA
		Median	1395.81	1368.21			
		Range	1202.51 – 1627.28	1132.58 – 1600.3			
	Corrected Brain Volume (cm3)	N	23	13	-4.101	<0.001	0.47
		Median	1269.54	1033.06			
		Range	1093.72 – 1480.07	801.89 – 1220.19			
76-200kya	Raw Brain Volume (cm3)	N	7	11	-3.133	0.002	0.55
		Median	1407.54	1153.64			
		Range	1198.89 – 1458.33	985.89 – 1334.45			
	Corrected Brain Volume (cm3)	N	7	11	-3.217	0.001	0.57
		Median	1289.58	987.83			
		Range	1098.4 - 1336.11	835.33 - 1152.22			

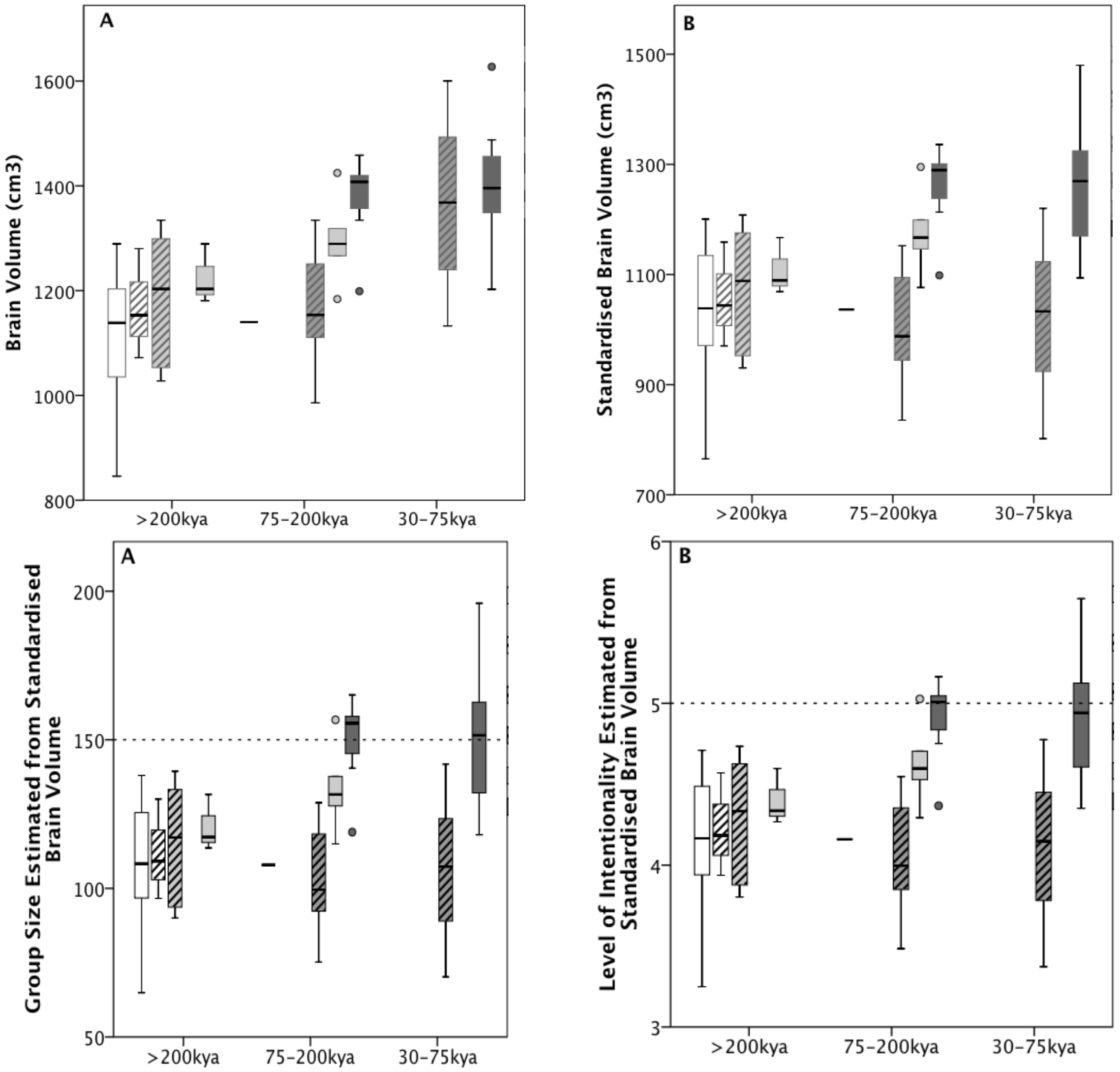

Figure A10: TOP: Boxplots showing the comparison between AMH, Neanderthals and archaic date groups for brain volume (A) unstandardised/raw and (B) standardised for body mass and visual differences. BOTTOM: Boxplots showing the difference between AMH and Neanderthals as well as the similarity between Neanderthals and archaics in (A) corrected group size, with the dashed line indicating the expected community size of living humans: 150 individuals and (B) level of intentionality, with the dashed line marking the expected 5th order level for living humans. The horizontal bars represent the median and the boxes the inter-quartile range. For both top and bottom, the outliers are from left to right across the taxon/date groups, for (A) LH18 (low outlier), Singa 1 (high outlier), Skhul 2 and Grotte des Enfants 4 and (B) Singa 1 and Skhul 2. The single H. heidelbergensis specimen in the 75-200kya date group is Eyasi. White=H. heidelbergensis, white striped=Denisovans, light grey striped=archaic H. neanderthalensis, dark grey striped=H. neanderthalensis, light grey=archaic H. sapiens, dark grey=H. sapiens.

Table A9: Descriptive and Mann-Whitney U test statistics for contrasts between AMH (N=23) and Neanderthals (N=13) dated 30-75kya for brain volumes corrected for vision and body mass differences both separately and together, as well as associated group size and level of intentionality estimates, along with uncorrected values for comparison.

Brain Volume Corrected for:	Variable	AMH	Neanderthal	Mann-Whitney U		
		Median (range)	Median (range)	z	p	R^2
Uncorrected	Brain Volume (mm^3)	1395.81 (1201.51 – 1627.28)	1368.21 (1132.58 – 1600.3)	-0.148	0.882	NA
	Group Size	178 (138 – 230)	172 (125 – 223)			
	Level of Intentionality	5.36 (4.72 – 6.14)	5.27 (4.48 – 6.05)			
Mean body mass	Corrected Brain Volume (mm^3)	1269.54 (1093.72 – 1480.01)	1164.07 (963.60 – 1361.54)	-1.927	0.054*	0.10
	Corrected Group Size	152 (118 – 196)	131 (96 – 170)			
	Corrected Level of Intentionality	4.94 (4.35 – 5.65)	4.59 (3.91 – 5.25)			
Visual differences	Corrected Brain Volume (mm^3)	1395.81 (1202.51 – 1627.28)	1237.21 (970.87 – 1458.95)	-2.882	0.004	0.23
	Corrected Group Size	178 (138 – 230)	145 (96 – 191)			
	Corrected Level of Intentionality	5.36 (4.72 – 6.14)	4.83 (3.94 – 5.58)			
Both body mass and visual differences	Corrected Brain Volume (mm^3)	1269.54 (1093.72 – 1480.07)	1033.07 (801.89 – 1220.19)	-4.101	<0.001	0.47
	Corrected Group Size	152 (118 – 196)	107 (70 – 142)			
	Corrected Level of Intentionality	4.94 (4.35 – 5.65)	4.15 (3.37 – 4.78)			

* When fragmentary specimens are excluded $p=0.048$. Furthermore, using an independent t-test (all variables are not significantly different from a normal distribution and group variances are not significantly different) reveals that the difference in brain volume corrected for body mass only between Neanderthals and AMH dated 30-75kya is significant ($p<0.05$). I chose to present nonparametric test statistics here due to the small sample sizes as a more conservative test of significance.

Table A10: Specimen details for the alternative database and analyses. Endocranial volume (Bailey and Geary 2009), date and both raw and corrected brain volume, level of intentionality and group size estimates for the Neanderthal and AMH specimens used in the analyses presented. I removed a number of specimens from the original database (Bailey and Geary 2009): (i) all AMH dated to less than 30kya (corrected date), (ii) Guattari 1, because it is the same fossil as their Monte Circeo 1, (iii) Paderborn-Sande, because it has been re-dated as Medieval (Street, Terberger, and Orschiedt 2006), and Combe Capelle, since this specimen is now considered Holocene (Bednarik 2009) (iv) pre-adolescents (Teshik Tash, Devil's Tower Gibraltar, Skhul 1, La Quina 18, Engis 2 and Qafzeh 11 (Osaka City University Accessed 2011). However, I included Le Moustier, Grotte des Enfants 6 and Krapina B because these adolescents fell within the taxon-specific cranial capacity ranges. These changes left 24 Neanderthals dated 40-170kya and 30 AMH dated 30-110kya. The corrected variables are the result of body mass and visual cortex standardisation. I also include the 34 'archaic' specimens (Bailey and Geary 2009) used as a comparative sample, but not included in the analyses. I identify a number of fragmentary specimens, the exclusion of which left the results unchanged. I therefore present analyses including all the specimens listed here.

Taxon	Fossil name	Date (my)	Cranial Volume (cc)	Brain Volume (mm^3)	Brain Volume Corrected for Body & Visual System Size (mm^3)	Estimated Level of Intentionality		Estimated Group Size	
						Uncorrected Brain	Corrected Brain	Uncorrected Brain	Corrected Brain
Homo neanderthalensis	Le Moustier 1 subadult	.040	1486.20	1367.12	1032.15	5.27	4.14	172	107
Homo neanderthalensis	Spy 1	.040	1457.50	1341.22	1010.11	5.18	4.07	166	103
Homo neanderthalensis	Spy 2	.040	1487.40	1368.21	1033.07	5.27	4.15	172	107
Homo neanderthalensis	Amud 1	.050	1745.00	1600.30	1220.19	6.05	4.78	223	142
Homo neanderthalensis	Ganovce 1	.050	1320.00	1216.98	904.41	4.76	3.72	141	86
Homo neanderthalensis	Gibraltar 1 (Forbes' Quarry)	.050	1226.75	1132.58	801.89	4.48	3.37	125	70
Homo neanderthalensis	La Chapelle	.050	1626.00	1493.17	1123.38	5.69	4.45	199	123
Homo neanderthalensis	La Quina 5	.050	1345.25	1239.81	923.83	4.84	3.78	146	89
Homo neanderthalensis	Neanderthal 1	.050	1337.75	1233.03	918.06	4.82	3.76	144	88
Homo neanderthalensis	Shanidar 1	.050	1650.00	1514.79	1181.48	5.76	4.65	204	134

Homo neanderthalensis	Shanidar 5	.050	1550.00	1424.67	1079.04	5.46	4.30	184	115
Homo neanderthalensis	Monte Circeo (Guattari 1)	.055	1551.00	1425.58	1090.45	5.46	4.34	184	117
Homo neanderthalensis	La Ferrassie 1	.060	1650.20	1514.97	1181.63	5.76	4.65	204	134
Homo neanderthalensis	Saccopastore 1	.120	1234.33	1139.45	941.86	4.50	3.84	126	92
Homo neanderthalensis	Saccopastore 2 (incomplete)	.120	1295.00	1194.36	1061.37	4.69	4.24	137	112
Homo neanderthalensis	Krapina 3 (C) (incomplete)	.130	1200.00	1108.35	926.82	4.40	3.79	121	89
Homo neanderthalensis	Krapina 6 (E) (incomplete)	.130	1205.00	1112.88	950.78	4.42	3.87	122	93
Homo neanderthalensis	Krapina B subadult (incomplete)	.130	1450.00	1334.45	1152.22	5.16	4.55	165	129
Homo neanderthalensis	Krapina-D (incomplete)	.130	1450.00	1334.45	1152.22	5.16	4.55	165	129
Homo neanderthalensis	Tabun C1	.130	1270.50	1172.19	1020.52	4.61	4.11	133	105
Homo neanderthalensis	La Chaise / Suard 1 (incomplete)	.150	1065.00	985.89	835.33	3.99	3.48	99	75
Homo neanderthalensis	Fontéchevade 2 (incomplete)	.160	1420.00	1307.36	1127.59	5.07	4.46	159	124
Homo neanderthalensis	Biache	.170	1200.00	1108.35	946.66	4.40	3.86	121	93
Homo neanderthalensis	Lazaret (incomplete)	.170	1250.00	1153.64	987.83	4.55	4.00	129	100
Homo sapiens	Brno 1	.030	1600.00	1469.74	1336.78	5.61	5.17	194	165
Homo sapiens	Brno 2	.030	1500.00	1379.58	1254.77	5.31	4.89	174	149
Homo sapiens	Brno 3	.030	1304.00	1202.51	1093.72	4.72	4.35	138	118
Homo sapiens	Cro-Magnon 1	.030	1600.00	1469.74	1336.78	5.61	5.17	194	165
Homo sapiens	Cro-Magnon 3	.030	1590.00	1460.73	1328.58	5.58	5.14	192	164
Homo sapiens	Dolní Věstonice 3	.030	1322.00	1218.79	1108.52	4.77	4.40	142	121
Homo sapiens	Dolní Věstonice 14	.030	1538.00	1413.85	1285.94	5.43	5.00	181	155
Homo sapiens	Dolní Věstonice 18	.030	1481.00	1362.43	1239.17	5.25	4.84	171	146
Homo sapiens	Dolní Věstonice 20	.030	1378.00	1269.41	1154.57	4.94	4.56	152	129

Homo sapiens	Dolní Věstonice 21	.030	1547.00	1421.97	1293.32	5.45	5.02	183	156
Homo sapiens	Grotte des Enfants 4	.030	1775.00	1627.28	1480.07	6.14	5.65	230	196
Homo sapiens	Grotte des Enfants 5	.030	1375.00	1266.70	1152.11	4.93	4.55	151	129
Homo sapiens	Grotte des Enfants 6 subadult	.030	1580.00	1451.72	1320.38	5.55	5.11	190	162
Homo sapiens	Pavlov 1	.030	1522.00	1399.42	1272.82	5.38	4.95	178	152
Homo sapiens	Předmostí 10	.030	1452.00	1336.25	1215.36	5.16	4.76	165	141
Homo sapiens	Předmostí 3	.030	1608.00	1476.95	1343.33	5.64	5.19	195	167
Homo sapiens	Předmostí 4	.030	1518.00	1395.81	1269.54	5.36	4.94	178	152
Homo sapiens	Předmostí 9	.030	1555.00	1429.18	1299.88	5.48	5.04	185	158
Homo sapiens	Mladeč 1	.035	1620.00	1487.76	1353.17	5.67	5.22	198	169
Homo sapiens	Mladeč 5	.035	1500.00	1379.58	1254.77	5.31	4.89	174	149
Homo sapiens	Nazlet Khater	.037	1420.00	1307.36	1112.30	5.07	4.41	159	121
Homo sapiens	Liujiang	.040	1480.00	1361.53	1158.39	5.25	4.57	170	130
Homo sapiens	Border Cave (incomplete)	.070	1510.00	1388.60	1181.42	5.34	4.65	176	134
Homo sapiens	Qafzeh 6	.100	1535.00	1411.15	1292.88	5.42	5.02	181	156
Homo sapiens	Qafzeh 9	.100	1531.00	1407.54	1289.58	5.40	5.01	180	156
Homo sapiens	Skhul 2 (incomplete)	.110	1300.00	1198.89	1098.41	4.70	4.37	138	119
Homo sapiens	Skhul 4	.110	1554.50	1428.73	1308.99	5.47	5.07	185	159
Homo sapiens	Skhul 5	.110	1499.50	1379.12	1263.54	5.31	4.92	174	150
Homo sapiens	Skhul 9	.110	1587.33	1458.33	1336.11	5.57	5.16	191	165
Homo sapiens	Herto 1 / 16	.160	1450.00	1334.45	1213.22	5.16	4.75	165	140
Archaic *Homo sapiens*	LH18 (Laetoli 18)	.150	1283.50	1183.96	1076.40	4.65	4.29	135	115
Archaic *Homo sapiens*	Singa 1	.150	1550.00	1424.67	1295.25	5.46	5.03	184	157

Archaic *Homo sapiens*	Omo Kibish 2	.195	1432.50	1318.65	1198.85	5.11	4.70	161	138
Archaic *Homo sapiens*	KNM-ER 3884	.200	1400.00	1289.29	1167.03	5.01	4.60	155	132
Archaic *Homo sapiens*	KNM-ES 11693 Eliye Springs	.200	1375.00	1266.70	1146.58	4.93	4.53	151	128
Archaic *Homo sapiens*	Jebel Irhoud 1	.200	1305.00	1203.41	1089.29	4.72	4.34	139	117
Archaic Homo sapiens	Florisbad 1 (incomplete)	.260	1280.00	1180.79	1068.81	4.64	4.27	134	114
Archaic *Homo sapiens*	Jebel Irhoud 2	.200	1400.00	1289.29	1167.03	5.01	4.60	155	132
Archaic Homo neanderthalensis	Ehringsdorf 9	.200	1450.00	1334.45	1207.90	5.16	4.73	165	139
Archaic Homo neanderthalensis	Steinheim 1	.300	1111.19	1027.82	930.35	4.13	3.80	106	90
Archaic Homo neanderthalensis	Reilingen	.300	1432.00	1318.20	1193.19	5.10	4.68	161	137
Archaic Homo neanderthalensis	Swanscombe 1 (incomplete)	.400	1305.00	1203.41	1088.46	4.72	4.33	139	117
Archaic Homo neanderthalensis	Atapuerca 4 (AT600)	.400	1390.00	1280.26	1157.97	4.98	4.57	154	130
Archaic Homo neanderthalensis	Atapuerca 5 (AT700)	.400	1125.00	1040.35	940.98	4.17	3.84	109	92
Archaic Homo neanderthalensis	Atapuerca 6	.400	1153.33	1066.05	964.22	4.26	3.92	113	96
?Denisovan (part of Neanderthal clade?)	Dali 1	.250	1160.00	1072.10	970.42	4.28	3.94	114	97
?Denisovan (part of Neanderthal clade?)	Yingkou (Jinniushan)	.250	1390.00	1280.26	1158.85	4.98	4.57	154	130
?Denisovan (part of Neanderthal clade?)	Narmada 1	.300	1249.33	1153.03	1043.69	4.55	4.18	129	109
Homo heidelbergensis	Eyasi	.120	1235.00	1140.05	1036.48	4.51	4.16	127	108
Homo heidelbergensis	Broken Hill / Kabwe 1	.300	1310.00	1207.93	1093.38	4.73	4.35	139	118
Homo heidelbergensis	Petralona 1	.300	1266.56	1168.62	1057.80	4.60	4.23	132	112

Homo heidelbergensis	Verteszollos 2 (incomplete)	.300	1334.57	1230.16	1113.50	4.81	4.42	144	122
Homo heidelbergensis	Zuttiyeh (incomplete)	.300	1400.00	1289.29	1167.03	5.01	4.60	155	132
Homo heidelbergensis	Ceprano	.400	1185.00	1094.76	990.18	4.35	4.00	118	100
Homo heidelbergensis	Arago 21	.450	1138.67	1052.75	952.19	4.21	3.88	111	94
Homo heidelbergensis	Elandsfontein 1	.500	1216.67	1123.45	1016.14	4.45	4.09	123	104
Homo heidelbergensis	Ndutu 1	.500	1100.00	1017.67	920.46	4.10	3.77	105	88
Homo heidelbergensis	Sale 1	.500	911.00	845.84	765.04	3.52	3.25	77	65
Homo heidelbergensis	Bodo	.600	1250.00	1153.64	1155.27	4.55	4.56	129	129
Homo heidelbergensis	Yunxian (Ev9002 skull ii)	.600	1100.00	1017.67	1019.11	4.10	4.10	105	105
Homo heidelbergensis	Tighenif (incomplete)	.800	1300.00	1198.89	1200.59	4.70	4.71	138	138

Appendix 4: Time Constraints

Table A11: Data for group sizes at different social levels and the estimated associated area for each group (data from Binford 2001).

BIOME		**Group 1 Size (individuals)**	**Group 1 Area (km^2)**	**Group 2 Size (individuals)**	**Group 2 Area (km^2)**	**Group 3 Size (individuals)**	**Group 3 Area (km^2)**	**Population Size (individuals)**	**Population Area (km^2)**
Tropical-subtropical Asia	N	5	5	5	5	4	4	5	5
	Median	11	33	31	78	75	207	393	980
	Minimum	9	19	23	57	65	145	255	570
	Maximum	20	465	60	1395	265	6161	3200	74400
Tropical-subtropical South America	N	7	7	6	6	5	5	8	8
	Median	19	201	38	560	225	1640	2300	12095
	Minimum	6	46	24	84	66	880	30	310
	Maximum	25	1320	75	3961	290	11883	9000	475300
Tropical-subtropical Africa	N	6	6	7	7	5	5	7	7
	Median	10	260	24	988	85	2898	364	11800
	Minimum	6	69	21	175	70	1318	122	2500
	Maximum	17	1409	54	5223	111	12058	726	57000
Australia	N	35	35	32	32	28	28	46	46
	Median	10	116	32	327	228	1701	567	9085
	Minimum	7	23	21	44	52	1287	35	80
	Maximum	20	2750	60	6250	400	42762	3589	137800
California and Northern Mexico	N	7	7	13	13	10	10	16	16
	Median	17	67	40	177	130	732	1100	5805
	Minimum	10	42	21	104	70	244	92	380
	Maximum	19	140	62	507	350	1593	3000	16600
North America: desert and desert scrub	N	32	32	34	34	29	29	41	41
	Median	12	283	31	721	128	2596	400	5840
	Minimum	8	60	19	180	42	378	23	650
	Maximum	21	1440	60	5769	320	12800	3000	96000
Subarctic and mid-latitude forests	N	32	32	36	36	34	34	40	40
	Median	17	1807	55	4937	188	17086	938	66600
	Minimum	6	267	25	447	105	1116	150	5400
	Maximum	32	5520	134	23222	438	64113	4863	660000
Arctic	N	15	15	15	15	12	12	15	15
	Median	18	1076	35	2604	113	8335	550	52500
	Minimum	11	312	25	665	64	1915	130	18700
	Maximum	22	8668	85	33490	158	59100	6000	370600

Table A12: Range radii calculated for idealised social network layers from the areas predicted for those group sizes using hunter-gatherer densities (data from Binford 2001).

General Biome	**Statistics from Binford (2001) data**			**Radius (km) for a group size (number of individuals) of:**				
		Absolute Latitude (degrees)	**Density (individuals/km)**	**15**	**50**	**150**	**500**	**1500**
Tropical-subtropical Asia (N=5)	Median	12.19	.40	3.45	6.31	10.93	19.95	34.55
	Min.	7.00	.04*	10.93	19.95	34.55	63.08	109.25
	Max.	51.91	.45	3.26	5.95	10.30	18.81	32.57
Tropical-subtropical South America (N=8)	Median	45.50	.10	6.91	12.62	21.85	39.89	69.10
	Min.	2.56	.02*	15.45	28.21	48.86	89.21	154.51
	Max.	60.00	.28	4.13	7.54	13.06	23.84	41.29
Tropical-subtropical Africa (N=7)	Median	22.46	.03	12.62	23.03	39.89	72.84	126.16
	Min.	3.82	.01*	6.91	39.89	69.10	126.16	218.51
	Max.	31.47	.24	4.46	8.14	14.10	25.75	44.6
Australia: subtropical desert through temperate settings (N=46)	Median	22.53	.10	6.91	12.62	21.85	39.89	69.10
	Min.	11.59	.004*	34.55	63.08	109.25	199.47	345.49
	Max.	42.62	.66	2.69	4.91	8.51	15.53	26.90
North America: California and Northern Mexico (N=16)	Median	38.82	.24	4.46	8.14	14.10	25.75	44.6
	Min.	29.59	.12*	6.31	11.52	19.95	36.42	63.08
	Max.	42.62	.67	2.67	4.87	8.44	15.41	26.70
North America: desert and desert scrub (N=41)	Median	39.19	.04	10.93	19.95	34.55	63.08	109.25
	Min.	22.00	.01*	6.91	12.62	21.85	39.89	69.10
	Max.	45.17	.22	4.66	8.51	14.73	26.90	46.59
Subarctic and continental midlatitude forests if North America and Asia (N=40)	Median	52.75	.01	6.91	12.62	21.85	39.89	69.10
	Min.	45.21	.003	39.89	72.84	126.16	230.33	398.94
	Max.	73.83	.27	4.21	7.68	13.30	24.28	42.05
Arctic (N=15)	Median	66.99	.02	15.45	28.21	48.86	89.21	154.51
	Min.	55.32	.003*	39.89	72.84	126.16	230.33	398.94
	Max.	77.49	.05	9.77	17.84	30.90	56.42	97.72

*Minimum densities used to predict maximum geographic ranges.

Table A13: Walking times calculated for the radii of areas associated with hunter-gatherer Group 1s (dispersed bands/15-layer) in different biomes at different walking speeds.

Biome	**Group 1 Walking Time (hours)**				
	For Median (Range) Radius (km)	**At Walking Speed (km/hour) of:**			
		2	**3**	**4**	**5**
Subtropical Asia	3.24 (2.47-12.17)	1.64 (1.24-6.09)	1.08 (0.8-4.06)	0.81 (0.62 - 3.04)	0.648 (0.49 -2.43)
Subtropical America	7.99 (3.82 -20.50)	4.00 (1.91-10.25)	2.66 (1.27 - 6.83)	2.00 (1.00 - 5.13)	1.60 (0.76 - 4.10)
Subtropical Africa	9.02 (4.68 – 21.18)	4.51 (2.34-10.59)	3.01 (1.56-7.06)	2.27 (1.17-5.30)	1.80 (0.94-4.24)
Australia	6.07 (2.70 – 29.59)	3.04 (1.35-14.80)	2.02 (0.90-9.86)	1.52 (0.68-7.40)	1.21 (0.54-5.92)
California & Northern Mexico	4.61 (3.65 – 6.68)	2.31 (1.83-3.24)	1.54 (1.22-2.23)	1.15 (0.91-1.67)	0.92 (0.73-1.34)
Desert & desert scrub	9.49 (4.37 – 21.41)	4.75 (2.19-10.71)	3.16 (1.46-5.35)	2.37 (1.09-5.35)	1.90 (0.87-4.28)
Subarctic & continental midlatitude forest	23.98 (9.21 – 41.92)	11.99 (4.61-20.96)	7.99 (3.07-13.97)	6.00 (2.30-10.48)	4.80 (1.84-8.38)
Arctic	18.50 (9.97 – 52.53)	9.25 (5.00-26.27)	6.17 (3.32-17.51)	4.63 (2.49-13.13)	3.70 (1.99-10.51)

Table A14: Walking times calculated for the radii of areas associated with hunter-gatherer Group 2s (fused bands/50-layer) in different biomes at different walking speeds.

Biome	**Group 2 Walking Time (hours)**				
	For Median (Range) Radius (km)	**At Walking Speed (km/hour) of:**			
		2	**3**	**4**	**5**
Subtropical Asia	4.98 (4.27-21.07)	2.49 (2.135 -10.54)	1.66 (1.42-7.02)	1.25 (1.07-5.27)	1.00 (0.85- 4.21)
Subtropical America	13.34 (5.19-35.51)	6.67 (2.60-17.76)	4.45 (1.73-11.84)	3.34 (1.30-8.87)	2.67 (1.04-7.10)
Subtropical Africa	17.73 (7.46 – 40.77)	8,87 (3.73-20.39)	5.91 (2.49-13.59)	4.43 (1.87-10.19)	3.55 (1.49-8.15)
Australia	10.20 (3.74 – 44.60)	5.10 (1.87-22.30)	3.40 (1.25-14.87)	2.55 (0.94-11.15)	2.04 (0.75-8.92)
California & Northern Mexico	7.50 (5.77 – 12.71)	3.75 (2.89-6.36)	2.50 (1.92-4.24)	1.88 (1.44-3.18)	1.50 (1.15-2.54)
Desert & desert scrub	15.14 (7.57 – 42.85)	7.57 (3.79-21.43)	5.05 (2.52-14.28)	3.79 (1.89-10.71)	3.03 (1.51-8.57)
Subarctic & continental midlatitude forest	39.64 (11.93 – 85.98)	19.82 (6.00-42.99)	13.21 (3.98-28.66)	9.91 (2.98-21.50)	7.93 (2.39-17.20)
Arctic	28.79 (14.55 – 103.25)	14.40 (7.28-51.63)	9.60 (4.85-34.42)	7.20 (3.64-25.81)	5.76 (2.91-20.65)

Table A15: Walking times calculated for the radii of areas associated with hunter-gatherer Group 3s (periodic aggregations) in different biomes at different walking speeds.

	Group 3 Walking Time (hours)				
	For Median (Range) Radius (km)	**At Walking Speed (km/hour) of:**			
		2	**3**	**4**	**5**
Subtropical Asia	8.09 (6.80-44.29)	4.05 (3.40-22.15)	2.70 (2.27 - 14.76)	2.02 (1.70 - 11.07)	1.62 (1.36 - 8.86)
Subtropical America	22.85 (16.74 – 61.50)	11.43 (8.37-30.75)	7.62 (5.58-20.50)	5.71 (4.19-15.38)	4.57 (3.35-12.30)
Subtropical Africa	30.37 (20.48 – 61.95)	15.19 (10.24-30.98)	10.12 (6.83-20.65)	7.59 (5.12-15.49)	6.07 (4.10-12.39)
Australia	23.24 (6.40 – 116.67)	11.62 (3.20-58.34)	7.75 (2.13-38.89)	5.81 (1.60-29.17)	4.65 (1.28-23.33)
California & Northern Mexico	15.27 (8.82 – 22.52)	7.64 (4.41-11.26)	5.09 (2.94-7.51)	3.82 (2.21-5.63)	3.05 (1.76-4.50)
Desert & desert scrub	28.74 (10.97 – 63.83)	14.37 (5.49-31.92)	9.58 (3.66-21.28)	7.19 (2.74-15.96)	5.75 (2.19-12.77)
Subarctic & continental midlatitude forest	73.69 (18.85 – 142.86)	36.85 (9.43-71.43)	24.56 (6.28-47.62)	18.42 (4.71-35.72)	14.74 (3.77-28.57)
Arctic	51.48 (24.69 – 137.16)	25.74 (12.35-68.58)	17.16 (8.23-45.72)	12.87 (6.17-34.29)	10.30 (4.94-27.43)

Table A16: Walking times calculated for the radii of areas associated with hunter-gatherer ethnolinguistic Populations in different biomes at different walking speeds.

Biome	**Population Walking Time (hours)**				
	For Median (Range) Radius (km)	**At Walking Speed (km/hour) of:**			
		2	**3**	**4**	**5**
Subtropical Asia	17.66 (13.47-153.89)	8.83 (6.74 - 76.95)	5.89 (4.49 - 51.30)	4.42 (3.37 - 38.47)	3.53 (2.69 - 30.78)
Subtropical America	61.46 (9.93 – 388.96)	30.73 (4.97-194.48)	28.49 (3.21-129.65)	15.37 (2.48-97.24)	12.29 (1.99-77.79)
Subtropical Africa	61.29 (28.21 – 134.70)	30.65 (14.11-67.35)	20.43 (9.40-44.90)	15.32 (7.05-33.68)	12.26 (5.64-26.94)
Australia	53.75 (5.05 – 209.44)	26.88 (2.53-104.72)	17.92 (1.68-69.81)	13.44 (1.26-52.36)	10.75 (1.01-41.89)
California & Northern Mexico	42.99 (11.00 – 72.69)	21.50 (5.50-36.35)	14.33 (3.67-24.23)	10.75 (2.75-18.17)	8.60 (2.2-14.54)
Desert & desert scrub	43.12 (14.38 – 174.81)	21.56 (7.19-87.41)	14.37 (4.79-58.27)	10.78 (3.60-43.70)	8.62 (2.88-34.96)
Subarctic & continental midlatitude forest	145.60 (41.46 – 458.35)	72.80 (20.73-229.18)	48.53 (13.82-152.78)	36.40 (10.37-114.59)	29.12 (8.29-91.67)
Arctic	129.27 (77.15 – 343.46)	64.64 (38.58-171.73)	43.09 (25.72-114.49)	32.32 (19.29-85.87)	25.85 (15.43-68.69)

Ethnographic time allocation data

Table A17: Data on daily time allocation to subsistence and social activities for hunter-gatherers and non-hunter-gatherers, including references. For subsistence type HG=hunter-gatherer and non-HG=other traditional modes of subsistence e.g. pastoralism, small-scale agriculture.

Society	Type	References	Observation Length	Mean Subsistence Time (hours)	Mean Social Time (hours)	Definition of "Social"
Ache mean	HG	(Hill et al. 1985, Hurtado et al. 1985)	12.95	2.52	1.12	Women: Grooms others, probably also socialising during waits during foraging and when resting/sitting, but not explicitly stated as such so excluded. Also includes interaction with own and others' children, which could be classed as social. Men: Sit/rest/talk + play (plus sing & sit/rest/talk at night=0.38333 hours), NB only sing at night
Agta (female)		(Rai 1990) 9+years old: workforce of the band	13	3.6		
Batak		(Waguespack 2005)	13	3.5		
Efe men	HG	(Bailey and Peacock 1989)	12	3.93	0.77	Recreation + funerals + travel between camps (although explicitly stated that "When in camp, if a man was not making or repairing something, he was generally sitting...conversing with other members of the camp")
Gunwinggu		(Altman 1987)	9	2.68	1.42	NB 'exchange activities' (making crafts & art) are for market exchange but are included here as a proxy of manufacture of social exchange objects. Without this component social time is 0.58 hours. Social=ceremonial + gamble; leisure (includes talking) is counted as separate,
Hadza		(Hawkes, O'Connell, and Jones 1997)	13	4.92		
Hiwi		(Hurtado and Hill 1990)	13	1.79		
Interior (Australia)		(Belovsky 1987)	13	3.13		
Kade		(Waguespack 2005)	13	6.45		
Kung		(Waguespack 2005)	13	3.34		
Paliyan		(Belovsky 1987)	13	3.50		
Tasaday		(Belovsky 1987)	13	3.00		
Kapanara (New Guinea)	non-HG	Calculated from (Grossman 1984), assuming 7-day week	13	2.68	2.32	Social interaction: card-playing, beer-related (when relevant), singing-related, general social activities.
Canchinos females	non-HG	(Munroe et al. 1983)	13	6.51	0.36	Visiting
Kikuyu females	non-HG	(Munroe et al. 1983)	13	4.86	0.72	Visiting

Logoli females	non-HG	(Munroe et al. 1983)	13	3.81	0.81	Visiting
Central Africa Republic: Mean of villages Madomale & Pouyamba	non-HG	(Berio 1984)	24	3.25	2.70	Non-work (leisure, dances, visits), combined for men and women
Ivory Coast, Africa	non-HG	(Berio 1984) adults 15-59 years	13	3.42	1.15	Social
Navrongo District, northern Ghana	non-HG	(Tripp 1982)13 hour days, mean of men and women over full year (ignoring per season data)	13	4.38	1.04	Ritual + visit outside settlement
Nepal	non-HG	(Berio 1984)	16	4.00	0.23	Social activities
Upper Volta, Africa	non-HG	(McSweeney 1979)	14	4.28	1.28	Free time (social, religion, errands): 1.275hrs. If community projects and obligations were added (1.967 hours) the total would be 3.242 hours.
Maasai (Tanzania)	non-HG	Biran (1996) in (Dunbar 1998a)	13		2.80	‘Leisure’
Tenia Mayo, Mexico	non-HG	(Erasmus 1955)	13	1.60	1.12	Chatting and visiting
Machiguenga	non-HG	(Johnson 1975):	13	3.07	0.87	Visiting: mean of married males and married/unmarried females

Bibliography

Adams, A. M., S. Madhavan, and D. Simon. 2002. Women's social networks and child survival in Mali. *Social Science & Medicine* 54:165-178.

Adler, Daniel S., G. Bar-Oz, A. Belfer-Cohen, and O. Bar-Yosef. 2006. Ahead of the Game: Middle and Upper Palaeolithic Hunting Behaviors in the Southern Caucasus. *Current Anthropology* 47:89-118.

Aiello, L. C., and R. I. M. Dunbar. 1993. Neocortex size, group size, & the evolution of language. *Current Anthropology* 34:184-1983.

Aiello, L. C., and P. Wheeler. 1995. The Expensive-Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution. *Current Anthropology* 36:199.

—. 2003. "Neanderthal Thermoregulation and the Glacial Climate," in *Neanderthals and modern humans in the European landscape during the late glaciation., McDonald Institute Monographs.* Edited by T. H. van Andel and W. Davies. Cambridge: Cambridge Univeristy Press.

Aiello, L. C., and B. A. Wood. 1994. Cranial variables as predictors of hominine body mass. *American Journal of Physical Anthropology* 95:409-426.

Altman, J. C. 1987. *Hunter-gatherers today: An aboriginal economy in north Australia*: Australian Institute of Aboriginal Studies, Canberra, Australia.

Amici, F., B. Barney, V. E. Johnson, J. Call, and F. Aureli. 2012. A Modular Mind? A Test Using Individual Data from Seven Primate Species. *PLoS ONE* 7:e51918.

Andrews, T. J., S. D. Halpern, and D. Purves. 1997. Correlated Size Variations in Human Visual Cortex, Lateral Geniculate Nucleus, and Optic Tract. *Journal of Neuroscience* 17:2859-2868.

Anikovich, M. V., A. A. Sinitsyn, J. F. Hoffecker, V. T. Holliday, V. V. Popov, S. N. Lisitsyn, S. L. Forman, G. M. Levkovskaya, G. A. Pospelova, I. E. Kuz'mina, N. D. Burova, P. Goldberg, R. I. Macphail, B. Giaccio, and N. D. Praslov. 2007. Early Upper Paleolithic in Eastern Europe and Implications for the Dispersal of Modern Humans. *Science* 315:223-226.

Antón, S. C., W. R. Leonard, and M. L. Robertson. 2002. An ecomorphological model of the initial hominid dispersal from Africa. *Journal of Human Evolution* 43:773-785.

Apicella, C. L., F. W. Marlowe, J. H. Fowler, and N. A. Christakis. 2012. Social networks and cooperation in hunter-gatherers. *Nature* 481:497-501.

Arnold, C. L., L. J. Matthews, and C. L. Nunn. 2010. The 10k Trees Website: A New Online Resource for Primate Phylogeny, Version 3, Available at: http://10ktrees.fas.harvard.edu/, accessed 2011. *Evolutionary Anthropology* 19:114 - 118.

Ash, J., and G. G. Gallup. 2007. Paleoclimatic variation and brain expansion during human evolution. *Human Nature-an Interdisciplinary Biosocial Perspective* 18:109-124.

Baddeley, A. 2003. Working memory: looking back and looking forward. *Nature Reviews Neuroscience* 4:829-839.

Bailey, D., and D. Geary. 2009. Hominid Brain Evolution. *Human Nature* 20:67-79.

Bailey, R. C., and N. Peacock. 1989. *Time allocation of Efe Pygmy men and women of the Ituri Forest, Zaire. Cross Cultural studies in Time Allocation*: Human Relations Area Files, Yale University.

Bakken, T. E., J. C. Roddey, S. Djurovic, N. Akshoomoff, D. G. Amaral, C. S. Bloss, B. J. Casey, L. Chang, T. M. Ernst, J. R. Gruen, T. L. Jernigan, W. E. Kaufmann, T. Kenet, D. N. Kennedy, J. M. Kuperman, S. S. Murray, E. R. Sowell, L. M. Rimol, M. Mattingsdal, I. Melle, I. Agartz, O. A. Andreassen, N. J. Schork, and A. M. Dale. 2012. Association of common genetic variants in GPCPD1 with scaling of visual cortical surface area in humans. *Proceedings of the National Academy of Sciences* 109:3985 - 3990.

Balzeau, A., R. L. Holloway, and D. Grimaud-Hervé. 2012. Variations and asymmetries in regional brain surface in the genus Homo. *Journal of Human Evolution* 62:696-706.

Bar-Yosef Mayer, D. E., B. Vandermeersch, and O. Bar-Yosef. 2009. Shells and ochre in Middle Paleolithic Qafzeh Cave, Israel: indications for modern behavior. *Journal of Human Evolution* 56:307-314.

Baron-Cohen, S. 2009. Autism: The Empathizing–Systemizing (E-S) Theory. *Annals of the New York Academy of Sciences* 1156:68-80.

Baron-Cohen, S., H. A. Ring, S. Wheelwright, E. T. Bullmore, M. J. Brammer, A. Simmons, and S. C. R. Williams. 1999. Social intelligence in the normal and autistic brain: an fMRI study. *European Journal of Neuroscience* 11:1891-1898.

Baron-Cohen, S., S. Wheelwright, J. Hill, Y. Raste, and I. Plumb. 2001. The “Reading the Mind in the Eyes” Test Revised Version: A Study with Normal Adults, and Adults with Asperger Syndrome or High-functioning Autism. *Journal of Child Psychology & Psychiatry* 42:241-251.

Barton, C. M., G. A. Clark, and A. E. Cohen. 1994. Art as information: Explaining Upper Palaeolithic art in western Europe. *World Archaeology* 26:185-207.

Barton, R. A. 1996. Neocortex Size and Behavioural Ecology in Primates. *Proceedings of the Royal Society B: Biological Sciences* 263:173-177.

—. 1998. Visual Specialization and Brain Evolution in Primates. *Proceedings of the Royal Society B: Biological Sciences* 265:1933-1937.

—. 2001. The coordinated structure of mosaic brain evolution. *Behavioural & Brain Sciences* 24:281-282.

—. 2007. Evolutionary specialization in mammalian cortical structure. *Journal of Evolutionary Biology* 20:1504-1511.

—. 2012. Embodied cognitive evolution and the cerebellum. *Philosophical Transactions of the Royal Society B-Biological Sciences* 367:2097-2107.

Barton, R. A., and P. H. Harvey. 2000. Mosaic evolution of brain structure in mammals. *Nature* 405:1055-1058.

Barton, R. A., A. Purvis, and P. H. Harvey. 1995. Evolutionary Radiation of Visual and Olfactory Brain Systems in Primates, Bats and Insectivores. *Philosophical Transactions of the Royal Society B-Biological Sciences* 348:381-392.

Barton, R. N. E., R. M. Jacobi, D. Stapert, and M. J. Street. 2003. The Late-glacial reoccupation of the British Isles and the Creswellian. *Journal of Quaternary Science* 18:631-643.

Bastir, M., P. O'Higgins, and A. Rosas. 2007. Facial ontogeny in Neanderthals and modern humans. *Proceedings of the Royal Society B: Biological Sciences* 274:1125 - 1132.

Bastir, M., A. Rosas, P. Gunz, A. Pena-Melian, G. Manzi, K. Harvati, R. Kruszynski, C. Stringer, and J.-J. Hublin. 2011. Evolution of the base of the brain in highly encephalized human species. *Nature Communications* 2:588.

Bastir, M., A. Rosas, D. E. Lieberman, and P. O'Higgins. 2008. Middle Cranial Fossa Anatomy and the Origin of Modern Humans. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology* 291:130-140.

Beals, K. L., C. L. Smith, S. M. Dodd, J. L. Angel, E. Armstrong, B. Blumenberg, F. G. Girgis, S. Turkel, K. R. Gibson, M. Henneberg, M. Roland, I. Morimoto, R. R. Sokal, and E. Trinkaus. 1984. Brain Size, Cranial Morphology, Climate, and Time Machines. *Current Anthropology* 25:301-330.

Beaman, C. P. 2007. Modern cognition in the absence of working memory: Does the working memory account of Neandertal cognition work? *Journal of Human Evolution* 52:702-706.

Bednarik, R. G. 2009. "The Middle-Upper Palaeolithic Transition Revisited," in *Sourcebook of Palaeolithic Transitions: Methods, theories, and Interpretations*. Edited by M. Camps and P. R. Chauhan, pp. 276. New York: Spinger.

Belovsky, G. E. 1987. Hunter-gatherer foraging: A linear programming approach. *Journal of Anthropological Archaeology* 6:29-76.

Benazzi, S., K. Douka, C. Fornai, C. C. Bauer, O. Kullmer, J. Svoboda, I. Pap, F. Mallegni, P. Bayle, M. Coquerelle, S. Condemi, A. Ronchitelli, K. Harvati, and G. W. Weber. 2011. Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature* 479:525 - 528.

Berio, A.-J. 1984. The analysis of time allocation and activity patterns in nutrition and rural development planning. *Food and Nutrition Bulletin* 6:53 - 68.

Bettridge, C. 2010. Australopithecine Socioecology: Adapting Strategic Primate Models for an Extinct Species., University of Oxford.

Binford, L. R. 1980. Willow smoke and dog's tails: hunter-gatherer settlement systems and archaeological site formation. *American Antiquity* 45:4 - 20.

—. 1982. The archaeology of place. *Journal of Anthropological Archaeology* 1:5 - 31.

—. 2001. *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Sets.*: University of California Press.

Birdsell, J. B. 1958. On population-structure in generalized hunting and collecting populations. *Evolution* 12:189-205.

Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity & Distributions* 5:165-174.

Blakemore, S.-J. 2008. The social brain in adolescence. *Nat Rev Neurosci* 9:267-277.

Bookstein, F., K. Schäfer, H. Prossinger, H. Seidler, M. Fieder, C. Stringer, G. W. Weber, J.-L. Arsuaga, D. E. Slice, F. J. Rohlf, W. Recheis, A. J. Mariam, and L. F. Marcus. 1999. Comparing frontal cranial profiles in archaic and modern Homo by morphometric analysis. *Anatomical Record* 257:217-224.

boot: Bootstrap Functions [online] available at: http://cran.r-project.org/web/packages/boot/index.html (accessed 2011).

Bouzouggar, A., N. Barton, M. Vanhaeren, F. d'Errico, S. Collcutt, T. Higham, E. Hodge, S. Parfitt, E. Rhodes, J.-L. Schwenninger, C. Stringer, E. Turner, S. Ward, A. Moutmir, and A. Stambouli. 2007. 82,000-year-old shell beads from North Africa and implications for the origins of modern human behavior. *Proceedings of the National Academy of Sciences* 104:9964-9969.

Brashears, M. E. 2013. Humans use Compression Heuristics to Improve the Recall of Social Networks. *Scientific Reports* 3.

Bridge, H., S. Clare, M. Jenkinson, P. Jezzard, A. J. Parker, and P. M. Matthews. 2005. Independent anatomical and functional measures of the V1/V2 boundary in human visual cortex. *Journal of Vision* 5:93 - 102.

Bridge, H., A. Cowey, N. Raggae, and K. Watkins. 2009. Imaging studies in congenital anophthalmia reveal preservation of brain architecture in 'visual' cortex. *Brain* 132:3467 - 3480.

Bridge, H., E. A. H. von dem Hagen, G. Davies, C. Chambers, A. Gouws, M. Hoffmann, and A. B. Morland. 2012. Changes in brain morphology in albinism reflect reduced visual acuity. *Cortex*.

Brockmann, D., L. Hufnagel, and T. Geisel. 2006. The scaling laws of human travel. *Nature* 439:462-465.

Bromberg, I. Accessed 2011. "The Duration of Twilight [online], available at: http://www.sym454.org/twilight/."

Bron, A. J., R. C. Tripathi, and B. J. Tripathi. Editors. 1997. *Wolff's Anatomy of the Eye & Orbit, 8th Edition*. London: Chapman & Hall Medical.

Brown, K. S., C. W. Marean, Z. Jacobs, B. J. Schoville, S. Oestmo, E. C. Fisher, J. Bernatchez, P. Karkanas, and T. Matthews. 2012. An early and enduring advanced technology originating 71,000 years ago in South Africa. *Nature* 491:590 - 593.

Brown, P., and T. Maeda. 2004. Post-Pleistocene diachronic change in East Asian facial skeletons: the size, shape and volume of the orbits. *Anthropological Science* 112:29 - 40.

Bruner, E. 2010. Morphological Differences in the Parietal Lobes within the Human Genus: A Neurofunctional Perspective. *Current Anthropology* 51:S77-S88.

Bruner, E., and R. L. Holloway. 2010. A bivariate approach to the widening of the frontal lobes in the genus *Homo*. *Journal of Human Evolution* 58:138-146.

Bruner, E., G. Manzi, and J. L. Arsuaga. 2003. Encephalization and allometric trajectories in the genus *Homo*: Evidence from the Neandertal and modern lineages. *Proceedings of the National Academy of Sciences* 100:15335-15340.

Burke, A. 2012. Spatial abilities, cognition and the pattern of Neanderthal and modern human dispersals. *Quaternary International* 247:230-235.

Bush, E., C. & Allman, John, M. 2003. Scaling of White Matter to Gray Matter in Cerebellum and Neocortex. *Brain, Behaviour & Evolution* 61:1 - 5. .

Bush, E. C., and J. M. Allman. 2004. Three-dimensional structure and evolution of primate primary visual cortex. *Anatomical Record* 281A:1088-1094.

Canty & Associates LLC. "Weatherbase [online], available: www.weatherbase.com. Accessed November 2010."

Carpenter, J., and J. Bithell. 2000. Bootstrap confidence intervals: when, which, what? A practical guide for medical statisticians. *Statistics in Medicine* 19:1141-1164.

Cartmill, E. A., and R. W. Byrne. 2007. Orangutans Modify Their Gestural Signaling According to Their Audience's Comprehension. *Current biology : CB* 17:1345-1348.

Cashdan, E. 1983. Territoriality Among Human Foragers: Ecological Models and an Application to Four Bushman Groups. *Current Anthropology* 24:47.

Cashdan, E. A. 1985. Coping with risk: Reciprocity among the Basarwa of Northern Botswana. *Man* 20:454-474.

Cavalli-Sforza, L. L., and B. Hewlett. 1982. Exploration and mating range in African Pygmies. *Annals of Human Genetics* 46:257-270.

Cavalli-Sforza, L. L., P. Menozzi, and A. Piazza. 1994. *The History and Geography of Human Genes*. Princeton, New Jersey: Princeton University Press.

Chatwin, B. 1987 (1998). *The Songlines*. London: Vintage.

Chau, A., K. Fung, K. Pak, and M. Yap. 2004. Is eye size related to orbit size in human subjects? *Ophthalmic Physiol Opt* 24:35-40.

Chen, C.-H., E. D. Gutierrez, W. Thompson, M. S. Panizzon, T. L. Jernigan, L. T. Eyler, C. Fennema-Notestine, A. J. Jak, M. C. Neale, C. E. Franz, M. J. Lyons, M. D. Grant, B. Fischl, L. J. Seidman, M. T. Tsuang, W. S. Kremen, and A. M. Dale. 2012. Hierarchical Genetic Organization of Human Cortical Surface Area. *Science* 335:1634-1636.

Chen, W., and X. H. Zhu. 2001. Correlation of activation sizes between lateral geniculate nucleus and primary visual cortex in humans. *Magnetic Resonance in Medicine* 45:202-205.

Cohen, E. 2012. The Evolution of Tag-Based Cooperation in Humans: The Case for Accent. *Current Anthropology* 53:588-616.

Cohen, E. E. A., R. Ejsmond-Frey, N. Knight, and R. I. M. Dunbar. 2009. Rowers' high: behavioural synchrony is correlated with elevated pain thresholds. *Biology Letters*.

Cohen, J. D., W. M. Perlstein, T. S. Braver, L. E. Nystrom, D. C. Noll, J. Jonides, and E. E. Smith. 1997. Temporal dynamics of brain activation during a working memory task. *Nature* 386:604-608.

Collard, I. F., and R. A. Foley. 2002. Latitudinal patterns and environmental determinants of recent human cultural diversity: do humans follow biogeographical rules? *Evol. Ecol. Res.* 4:371-383.

Collins, C. E., D. C. Airey, N. A. Young, D. B. Leitch, and J. H. Kaas. 2010. Neuron densities vary across and within cortical areas in primates. *Proceedings of the National Academy of Sciences* 107:15927-15932.

Colson, E. 1979. The Harvey Lecture Series. In Good Years and in Bad: Food Strategies of Self-Reliant Societies. *Journal of Anthropological Research* 35:18-29.

Conard, N. J. 2003. Palaeolithic ivory sculptures from southwestern Germany and the origins of figurative art. *Nature* 426:830-832.

—. 2009. A female figurine from the basal Aurignacian of Hohle Fels Cave in southwestern Germany. *Nature* 459:248-252.

Conard, N. J., J. Richter, M. C. Fernández-Laso, M. G. C. Navarro, M. D. García-Antón, and F. Rivals. 2011. "Territorial Mobility of Neanderthal Groups: A Case Study from Level M of Abric Romaní (Capellades, Barcelona, Spain)," in *Neanderthal Lifeways, Subsistence and Technology*, vol. 19, *Vertebrate Paleobiology and Paleoanthropology*, pp. 187-202: Springer Netherlands.

Condemi, S., A. Mounier, P. Giunti, M. Lari, D. Caramelli, and L. Longo. 2013. Possible Interbreeding in Late Italian Neanderthals? New Data from the Mezzena Jaw (Monti Lessini, Verona, Italy). *PLoS ONE* 8:e59781.

Conroy, G. C., and R. J. Smith. 2007. The size of scalable brain components in the human evolutionary lineage: With a comment on the paradox of Homo floresiensis. *HOMO - Journal of Comparative Human Biology* 58:1-12.

Coolidge, F. L., and T. Wynn. 2001. Executive Functions of the Frontal Lobes and the Evolutionary Ascendancy of *Homo Sapiens*. *Cambridge Archaeological Journal* 11:255-260.

Cordain, L., J. B. Miller, S. B. Eaton, N. Mann, S. H. A. Holt, and J. D. Speth. 2000. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *The American Journal of Clinical Nutrition* 71:682-692.

Courtney, S. M., L. Petit, J. M. Maisog, L. G. Ungerleider, and J. V. Haxby. 1998. An Area Specialized for Spatial Working Memory in Human Frontal Cortex. *Science* 279:1347-1351.

Courtney, S. M., L. G. Ungerleider, K. Keil, and J. V. Haxby. 1996. Object and Spatial Visual Working Memory Activate Separate Neural Systems in Human Cortex. *Cerebral Cortex* 6:39-49.

Cummings, J. R., M. N. Muchlinski, E. C. Kirk, S. J. Rehorek, V. B. DeLeon, and T. D. Smith. 2012. Eye Size at Birth in Prosimian Primates: Life History Correlates and Growth Patterns. *PLoS ONE* 7:e36097.

Curry, O., and R. I. M. Dunbar. 2013. Sharing a Joke: The effects of a similar sense of humor on affiliation and altruism. *Evolution & Human Behaviour* 34:125 - 129.

—. in press. Do birds of a feather flock together? The relationship between similarity and altruism in social networks. *Human Nature*.

Curtis, C. E. 2006. Prefrontal and parietal contributions to spatial working memory. *Neuroscience* 139:173-180.

D'Errico, F. 2003. The invisible frontier. A multiple species model for the origin of behavioral modernity. *Evolutionary Anthropology: Issues, News, and Reviews* 12:188-202.

d'Errico, F., C. Henshilwood, M. Vanhaeren, and K. van Niekerk. 2005. Nassarius kraussianus shell beads from Blombos Cave: evidence for symbolic behaviour in the Middle Stone Age. *Journal of Human Evolution* 48:3-24.

d'Errico, F., Joao Zilhão, Michèle Julien, Dominique Baffier, and Jacques Pelegrin. 1998a. Neanderthal Acculturation in Western Europe? A Critical Review of the Evidence and Its Interpretation. *Current Anthropology* 39:S1-S44.

d'Errico, F., J. Zilhão, M. Julien, D. Baffier, and J. Pelegrin. 1998b. Neanderthal Acculturation in Western Europe? A Critical Review of the Evidence and Its Interpretation. *Current Anthropology* 39:S1-S44.

Dalén, L., L. Orlando, B. Shapiro, M. B. Durling, R. Quam, M. T. P. Gilbert, J. C. Díez Fernández-Lomana, E. Willerslev, J. L. Arsuaga, and A. Götherström. 2012. Partial genetic turnover in neandertals: continuity in the east and population replacement in the west. *Molecular Biology and Evolution*.

Davies, S. W. G. 2001. A very model of a modern human industry: new perspectives on the origins and spread of the Aurignacian in Europe. *Proceedings of the Prehistoric Society* 67:195 - 217.

Davies, W. 2012. "Chapter 8 - Climate, Creativity and Competition: Evaluating the Neanderthal 'glass ceiling.'," in *Developments in Quaternary Sciences*, vol. Volume 16. Edited by S. Elias, pp. 103-128: Elsevier.

De Miguel, C., and M. Henneberg. 2001. Variation in hominid brain size: How much is due to method? *HOMO - Journal of Comparative Human Biology* 52:3-58.

de Sousa, A. A., C. C. Sherwood, H. Mohlberg, K. Amunts, A. Schleicher, C. E. MacLeod, P. R. Hof, H. Frahm, and K. Zilles. 2010. Hominoid visual brain structure volumes and the position of the lunate sulcus. *Journal of Human Evolution* 58:281-292.

de Winter, W., and C. E. Oxnard. 2001. Evolutionary radiations and convergences in the structural organization of mammalian brains. *Nature* 409:710-714.

Deaner, R., K. Isler, J. Burkart, and C. van Schaik. 2007. Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior and Evolution* 70:115 - 124.

Deeley, Q., E. M. Daly, R. Azuma, S. Surguladze, V. Giampietro, M. J. Brammer, B. Hallahan, R. I. M. Dunbar, M. L. Phillips, and D. G. M. Murphy. 2008. Changes in male brain responses to emotional faces from adolescence to middle age. *NeuroImage* 40:389-397.

Deng, L., and J. Gwiazda. 2011. Birth Season, Photoperiod, and Infancy Refraction. *Optometry and Vision Science* 88:383-387.

Denis, D., O. Burguière, and C. Burillon. 1998. A biometric study of the eye, orbit, and face in 205 normal human fetuses. *Investigative Ophthalmology & Visual Science* 39:2232-2238.

Derenko, M., B. Malyarchuk, T. Grzybowski, G. Denisova, I. Dambueva, M. Perkova, C. Dorzhu, F. Luzina, H. K. Lee, T. Vanecek, R. Villems, and I. Zakharov. 2007. Phylogeographic Analysis of Mitochondrial DNA in Northern Asian Populations. *American Journal of Human Genetics* 81:1025-1041.

Desikan, R. S., F. Ségonne, B. Fischl, B. T. Quinn, B. C. Dickerson, D. Blacker, R. L. Buckner, A. M. Dale, R. P. Maguire, B. T. Hyman, M. S. Albert, and R. J. Killiany. 2006. An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NeuroImage* 31:968-980.

Deveci, M., S. Özürk, M. Sengezer, and Y. Pabuscu. 2000. Measurement of orbital volume by a 3-dimensional software program: An experimental study. *Journal of Oral & Maxillofacial Surgery* 58:645-648.

Dezecache, G., and R. I. M. Dunbar. 2012. Sharing the joke: the size of natural laughter groups. *Evolution & Human Behaviour* 33:775 - 779.

Dillehay, T. D. 2009. Probing deeper into first American studies. *Proceedings of the National Academy of Sciences* 106:971-978.

Dirks, R., G. J. Armelagos, C. A. Bishop, I. A. Brady, T. Brun, J. Copans, V. S. Doherty, S. Frañková, L. S. Greene, D. B. Jelliffe, E. G. P. Jelliffe, D. Kayongo-Male, C. Paque, E. L. Schusky, R. B. Thomas, and D. Turton. 1980. Social Responses During Severe Food Shortages and Famine [and Comments and Reply]. *Current Anthropology* 21:21-44.

Diwadkar, V. A., P. A. Carpenter, and M. A. Just. 2000. Collaborative Activity between Parietal and Dorso-Lateral Prefrontal Cortex in Dynamic Spatial Working Memory Revealed by fMRI. *NeuroImage* 12:85-99.

Domínguez, S., and T. Arford. 2010. It is all about who you know: Social capital and health in low-income communities. *Health Sociology Review* 19:114-129.

Donati, G., L. Santini, J. Razafindramanana, L. Boitani, and S. Borgognini-Tarli. 2013. (Un-)expected nocturnal activity in “Diurnal” Lemur catta supports cathemerality as one of the key adaptations of the lemurid radiation. *American Journal of Physical Anthropology* 150:99-106.

Dougherty, R. F., V. M. Koch, A. A. Brewer, B. Fischer, J. Modersitzki, and B. A. Wandell. 2003. Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *Journal of Vision* 3:586 - 598.

Druzhkova, A. S., O. Thalmann, V. A. Trifonov, J. A. Leonard, N. V. Vorobieva, N. D. Ovodov, A. S. Graphodatsky, and R. K. Wayne. 2013. Ancient DNA Analysis Affirms the Canid from Altai as a Primitive Dog. *PLoS ONE* 8:e57754.

Dubois, E. U. G. 1933. The seeming and the real cephalization of the Australian aborigine. *K Akad Wetensch Amsterdam Proc Sect Sci* 36:2-240.

Dumontheil, I., I. A. Apperly, and S.-J. Blakemore. 2010. Online usage of theory of mind continues to develop in late adolescence. *Developmental Science* 13:331-338.

Dunbar, R. 1998a. "Theory of mind and the evolution of language," in *Approaches to the evolution of language*. Edited by J. R. Hurford, M. Studdert-Kennedy, and C. Knight. Cambridge: Cambridge University Press.

Dunbar, R. I. M. 1991. Functional Significance of Social Grooming in Primates. *Folia Primatologica* 57:121-131.

—. 1992. Neocortex size as a constraint on group size in primates. *Journal of Human Evolution* 20:469 - 493.

—. 1993. Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences* 16:681-694.

—. 1998b. The social brain hypothesis. *Evolutionary Anthropology* 6:178 - 190.

—. 2003a. The Social Brain: Mind, Language, and Society in Evolutionary Perspective. *Annual Review of Anthropology* 32:163 - 81.

—. 2003b. "Why are apes so smart? ," in *Primate Life Histories & Socioecology*. Edited by P. M. Kappeler and M. E. Pereira: The University of Chicago Press.

—. 2008. Mind the gap: or why humans aren't just great apes. *Proceedings of the British Academy* 15:403 - 423.

—. 2009. "Why only humans have language," in *The Prehistory of Language*. Edited by R. Botha and C. Knight: Oxford University Press.

—. 2011a. "Evolutionary basis of the social brain," in *Oxford Handbook of Social Neuroscience*. Edited by J. Decety and J. T. Cacioppo. Oxford: Oxford University Press.

—. 2011b. The social brain meets neuroimaging. *Trends in Cognitive Sciences* 16:101 - 102.

—. 2012a. "On the evolution of song and dance," in *Music, Language, & Human Evolution*. Edited by N. Bannan. Oxford, UK: Oxford University Press.

—. 2012b. Social cognition on the Internet: testing constraints on social network size. *Philosophical Transactions of the Royal Society B-Biological Sciences* 367:2192-2201.

Dunbar, R. I. M., R. Baron, A. Frangou, E. Pearce, E. J. C. van Leeuwin, J. Stow, G. Partridge, I. MacDonald, V. Barra, and M. van Vugt. 2012a. Social laughter is correlated with an elevated pain threshold. *Proceedings of the Royal Society B: Biological Sciences* 279:1161 - 1167.

Dunbar, R. I. M., and J. A. J. Gowlett. in press. "Fireside chat: The impact of fire on hominin socioecology," in *The Lucy Project: Benchmark Papers*. Edited by R. I. M. Dunbar, C. Gamble, and J. Gowlett. Oxford: Oxford University Press.

Dunbar, R. I. M., K. Kaskatis, I. MacDonald, and V. Barra. 2012b. Performance of music elevates pain threshold and positive affect. *Evolutionary Psychology* 10:688-702.

Dunbar, R. I. M., and S. Shultz. 2007a. Evolution in the Social Brain. *Science* 317:1344-1347.

—. 2007b. Understanding primate brain evolution. *Philosophical Transactions of the Royal Society B-Biological Sciences* 362:649-658.

Dunbar, R. I. M., and M. Spoors. 1995. Social networks, support cliques, and kinship. *Human Nature* 6:273-290.

Duncan, C., and K. Jones. 2000. Using Multilevel Models to Model Heterogeneity: Potential and Pitfalls. *Geographical Analysis* 32:279-305.

Duncan, R. O., and G. M. Boynton. 2003. Cortical Magnification within Human Primary Visual Cortex Correlates with Acuity Thresholds. *Neuron* 38:659-671.

Dunkerley, W., M., D. De Deccker, P. Kershaw, and J. Chappell. 1998. *Quaternary Environments. 2nd Edition.*: Anold, a member of the Hodder Headline Group.

Dyson-Hudson, R., and E. A. Smith. 1978. Human Territoriality: An Ecological Reassessment. *American Anthropologist* 80:21-41.

Efron, B., and R. Tibshirani. 1986. Bootstrap Methods for Standard Errors, Confidence Intervals, and Other Measures of Statistical Accuracy. *Statistical Science* 1:54-75.

Ejima, Y., S. Takahashi, H. Yamamoto, M. Fukunaga, C. Tanaka, T. Ebisu, and M. Umeda. 2003. Interindividual and interspecies variations of the extrastriate visual cortex. *NeuroReport* 14:1579 - 1583.

Endicott, P., S. Y. W. Ho, and C. Stringer. 2010. Using genetic evidence to evaluate four palaeoanthropological hypotheses for the timing of Neanderthal and modern human origins. *Journal of Human Evolution* 59:87-95.

Erasmus, C. J. 1955. Work Patterns in a Mayo Village. *American Anthropologist* 57:322-333.

Eren, M. I., A. Greenspan, and C. G. Sampson. 2008. Are Upper Paleolithic blade cores more productive than Middle Paleolithic discoidal cores? A replication experiment. *Journal of Human Evolution* 55:952-961.

Eriksson, A., and A. Manica. 2012. Effect of ancient population structure on the degree of polymorphism shared between modern human populations and ancient hominins. *Proceedings of the National Academy of Sciences* 109:13956-13960.

Europa Technologies Google. "Googlemaps [online], available: http://maps.google.co.uk/maps?hl=en&tab=wl. Accessed July 2010.."

Evans, P. D., S. L. Gilbert, N. Mekel-Bobrov, E. J. Vallender, J. R. Anderson, L. M. Vaez-Azizi, S. A. Tishkoff, R. R. Hudson, and B. T. Lahn. 2005. Microcephalin, a Gene Regulating Brain Size, Continues to Evolve Adaptively in Humans. *Science* 309:1717-1720.

Fa, J. E., J. R. Stewart, L. Lloveras, and J. M. Vargas. 2013. Rabbits and hominin survival in Iberia. *Journal of Human Evolution* 64:233 - 241.

Farizy, C. 1994. Spatial Patterning of Middle Paleolithic Sites. *Journal of Anthropological Archaeology* 13:153-160.

Féblot-Augustins, J. 1993. Mobility Strategies in the Late Middle Palaeolithic of Central Europe and Western Europe: Elements of Stability and Variability. *Journal of Anthropological Archaeology* 12:211-265.

—. 1997. La circulation des matières premières au Paléolthique: Synthèse des données perspectives comportementales, L'Université de Liège.

—. 2009. "Revisiting European Upper Paleolithic Raw Material Transfers: The Demise of the Cultural Ecological Paradigm?," in *Lithic Materials and Paleolithic Societies*, pp. 25-46: Wiley-Blackwell.

Field, A. 2009. *Discovering Statistics Using SPSS. 3rd Edition.* London: SAGE Publciations Ltd.

Fincher, C. L., and R. Thornhill. 2008. Assortative sociality, limited dispersal, infectious disease and the genesis of the global pattern of religion diversity. *Proceedings of the Royal Society B: Biological Sciences* 275:2587-2594.

Findley, J. S. 1969. Brain Size in Bats. *Journal of Mammalogy* 50:340-344.

Finlay, B., and R. Darlington. 1995. Linked regularities in the development and evolution of mammalian brains. *Science* 268:1578-1584.

Finlay, B. L., R. B. Darlington, and N. Nicastro. 2001. Developmental structure in brain evolution. *Behavioural & Brain Sciences* 24:263-308.

Finlay, B. L., E. C. S. Franco, E. S. Yamada, J. C. Crowley, M. Parsons, J. Muniz, and L. C. L. Silveira. 2008. Number and topography of cones, rods and optic nerve axons in New and Old World primates. *Visual Neuroscience* 25:289-299.

Finlayson, C. 2004. *Neanderthals & Modern Humans: An Ecological and Evolutionary Perspective.* Cambridge: Cambidge University Press.

Finlayson, C., K. Brown, R. Blasco, J. Rosell, J. J. Negro, G. R. Bortolotti, G. Finlayson, A. Sánchez Marco, F. Giles Pacheco, J. Rodríguez Vidal, J. S. Carrión, D. A. Fa, and J. M. Rodríguez Llanes. 2012. Birds of a Feather: Neanderthal Exploitation of Raptors and Corvids. *PLoS ONE* 7:e45927.

Finlayson, C., F. Giles Pacheco, J. Rodriguez-Vidal, D. A. Fa, J. Maria Gutierrez Lopez, A. Santiago Perez, G. Finlayson, E. Allue, J. Baena Preysler, I. Caceres, J. S. Carrion, Y. Fernandez Jalvo, C. P. Gleed-Owen, F. J. Jimenez Espejo, P. Lopez, J. Antonio Lopez Saez, J. Antonio Riquelme Cantal, A. Sanchez Marco, F. Giles Guzman, K. Brown, N. Fuentes, C. A. Valarino, A. Villalpando, C. B. Stringer, F. Martinez Ruiz, and T. Sakamoto. 2006. Late survival of Neanderthals at the southernmost extreme of Europe. *Nature* 443:850-853.

Fiorenza, L., S. Benazzi, J. Tausch, O. Kullmer, and T. Bromage. 2011. Molar Macrowear Reveals Neanderthal Eco-Geographic Dietary Variation. *PLoS ONE* 6:e14769.

Fischl, B., N. Rajendran, E. Busa, J. Augustinack, O. Hinds, B. T. T. Yeo, H. Mohlberg, K. Amunts, and K. Zilles. 2008. Cortical Folding Patterns and Predicting Cytoarchitecture. *Cerebral Cortex* 18:1973-1980.

Flombaum, J. I., and L. R. Santos. 2005. Rhesus Monkeys Attribute Perceptions to Others. *Current Biology* 15:447-452.

Foley, R. A. 1993. "The influence of seasonality on hominid evolution," in *Seasonality and Human Ecology*. Edited by S. J. Ulijaszek and S. Strickland, pp. 17 - 37: Cambridge University Press.

Foley, R. A., and C. Gamble. 2009. The ecology of social transitions in human evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:3267-79.

Franco, E. C. S., B. L. Finlay, L. C. L. Silveira, E. S. Yamada, and J. C. Crowley. 2000. Conservation of Absolute Foveal Area in New World Monkeys. *Brain, Behavior and Evolution* 56:276-286.

Freckleton, R. Â P., P. Â H. Harvey, and M. Pagel. 2002. "Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence," vol. 160, pp. 712-726: The University of Chicago Press for The American Society of Naturalists.

Free, S. L., T. N. Mitchell, K. A. Williamson, A. J. Churchill, S. D. Shorvon, A. T. Moore, V. v. Heyningen, and S. M. Sisodiya. 2003. Quantitative MR image analysis in subjects with defects in the PAX6 gene. *NeuroImage* 20:2281-2290.

Fulk, G. W., L. A. Cyert, and D. A. Parker. 2002. Seasonal Variation in Myopia Progression and Ocular Elongation. *Optometry & Vision Science* 79:46-51.

Gabi, M., C. E. Collins, P. Wong, L. B. Torres, J. H. Kaas, and S. Herculano-Houzel. 2010. Cellular Scaling Rules for the Brains of an Extended Number of Primate Species. *Brain, Behavior and Evolution* 76:32-44.

Gamble, C. 1982. Interaction and Alliance in Palaeolithic Society. *Man* 17:92-107.

—. 1998. Palaeolithic society and the release from proximity: A network approach to intimate relations. *World Archaeology* 29:426 - 449.

—. 1999. *The Palaeolithic Societies of Europe*. *Cambridge World Archaeology*. Cambridge: Cambridge University Press.

—. 2010. "Technologies of separation and the evolution of social extension," in *Social Brain, Distributed Mind*. Edited by R. I. M. Dunbar, C. Gamble, and J. Gowlett, pp. 17-42. Oxford: Oxford University Press.

—. 2011. "The Social and Material Life of Neanderthals," in *Neanderthal Lifeways, Subsistence and Technology: One Hundred and Fifty Years of Neanderthal Study*, vol. 19, *Vertebrate Paleobiology and Paleoanthropology*. Edited by N. J. Conard and J. Richter, pp. 157-166. London: Springer Netherlands.

Garamszegi, L. Z., A. P. Møller, and J. Erritzøe. 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proceedings of the Royal Society B: Biological Sciences* 269:961-7.

Germonpré, M., M. Lázničková-Galetová, and M. V. Sablin. 2012. Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. *Journal of Archaeological Science* 39:184-202.

Gilmartin, B. 2004. Myopia: precedents for research in the twenty-first century. *Clinical and Experimental Ophthalmology* 32:305-324.

Goncalves, B., N. Perra, and A. Vespignani. 2011. Validation of Dunbar's number in Twitter conversations. *PLoS ONE* 6:e22656.

Gonzalez, M. C., C. A. Hidalgo, and A.-L. Barabasi. 2008. Understanding individual human mobility patterns. *Nature* 453:779-782.

Gorissen, P. Accessed July 2008, July 2010. "Google Maps Latitude, Longitude Popup [online], available: http://www.gorissen.info/Pierre/maps/googleMapLocation.php?lat=51.618017&lon=2.48291&setLatLon=Set.."

Gosden, C. 1994. *Social Being and Time*. Oxford: Blackwell.

Gravina, B., P. Mellars, and C. B. Ramsey. 2005. Radiocarbon dating of interstratified Neanderthal and early modern human occupations at the Chatelperronian type-site. *Nature* 438:51-56.

Green, R. E., J. Krause, A. W. Briggs, T. Maricic, U. Stenzel, M. Kircher, N. Patterson, H. Li, W. Zhai, M. H.-Y. Fritz, N. F. Hansen, E. Y. Durand, A.-S. Malaspinas, J. D. Jensen, T. Marques-Bonet, C. Alkan, K. Prufer, M. Meyer, H. A. Burbano, J. M. Good, R. Schultz, A. Aximu-Petri, A. Butthof, B. Hober, B. Hoffner, M. Siegemund, A. Weihmann, C. Nusbaum, E. S. Lander, C. Russ, N. Novod, J. Affourtit, M. Egholm, C. Verna, P. Rudan, D. Brajkovic, Z. Kucan, I. Gusic, V. B. Doronichev, L. V. Golovanova, C. Lalueza-Fox, M. de la Rasilla, J. Fortea, A. Rosas, R. W. Schmitz, P. L. F. Johnson, E. E. Eichler, D. Falush, E. Birney, J. C. Mullikin, M. Slatkin, R. Nielsen, J. Kelso, M. Lachmann, D. Reich, and S. Paabo. 2010. A Draft Sequence of the Neanderthal Genome. *Science* 328:710-722.

Greider, T., and L. Garkovich. 1994. Landscapes: The Social Construction of Nature and the Environment. *Rural Sociology* 59:1-24.

Gron, G., A. P. Wunderlich, M. Spitzer, R. Tomczak, and M. W. Riepe. 2000. Brain activation during human navigation:gender-different neural networks as substrate performance. *Nature Neuroscience* 3:404 - 408.

Grossman, L. S. 1984. *Peasants, subsistence ecology, and development in the highlands of Papua New Guinea*. Princeton, USA: Princeton University Press.

Grove, M. 2009. Hunter-gatherer movement patterns: Causes and constraints. *Journal of Anthropological Archaeology* 28:222 - 233.

—. 2010a. Logistical mobility reduces subsistence risk in hunting economies. *Journal of Archaeological Science* 37:1913-1921.

—. 2010b. Stone circles and the structure of Bronze Age society. *Journal of Archaeological Science* 37:2612-2621.

—. 2011. An archaeological signature of multi-level social systems: The case of the Irish Bronze Age. *Journal of Anthropological Archaeology* 30:44-61.

Grove, M., and R. I. M. Dunbar. in prep. Local objects, distant symbols: Fission-fusion social systems and the evolution of human cognition.

Grove, M., E. Pearce, and R. I. M. Dunbar. 2012. Fission-fusion and the evolution of hominin social systems. *Journal of Human Evolution* 62:191-200.

Grunstra, N. 2009 unpublished MSc dissertation. "Clothing Requirements of Upper Palaeolithic Hominins in Europe," University of Oxford.

Guemple, L. Editor. 1971. *Alliance in Eskimo Societies. Proceedings of the American Ethological Society.*: University of Washington Press.

Gunz, P., and K. Harvati. 2007. The Neanderthal “chignon”: Variation, integration and homology. *Journal of Human Evolution* 52:262-74.

Gunz, P., S. Neubauer, L. Golovanova, V. Doronichev, B. Maureille, and J.-J. Hublin. 2012. A uniquely modern human pattern of endocranial development. Insights from a new cranial reconstruction of the Neandertal newborn from Mezmaiskaya. *Journal of Human Evolution* 62:300-313.

Gunz, P., S. Neubauer, B. Maureille, and J.-J. Hublin. 2010. Brain development after birth differs between Neanderthals and modern humans. *Current Biology* 20:R921 - R922.

Haidle, M. N. 2010. Working Memory Capacity and the Evolution of Modern Cognitive Potential: Implications from Animal and Early Human Tool Use. *Current Anthropology* 51:S149-S166.

Hallos, J. 2005. “15 Minutes of Fame”: Exploring the temporal dimension of Middle Pleistocene lithic technology. *Journal of Human Evolution* 49:155-179.

Halpern, S. D., T. J. Andrews, and D. Purves. 1999. Interindividual Variation in Human Visual Performance. *Journal of Cognitive Neuroscience* 11:521-534.

Hames, R. 1990. "Sharing Among the Yanomamo: Part I the Effects of Risk.," in *Risk & Uncertainty in Tribal & Peasant Economies.* Edited by E. Cashdan, pp. 89 - 106. London.. Westview.

Hamilton, M. J., B. T. Milne, R. S. Walker, and J. H. Brown. 2007a. Nonlinear Scaling of Space Use in Human Hunter-Gatherers. *Proceedings of the National Academy of Sciences* 104:4765-4769.

Hamilton, M. J., B. T. Milne, R. S. Walker, O. Burger, and J. H. Brown. 2007b. The complex structure of hunter-gatherer social networks. *Proceedings of the Royal Society B: Biological Sciences* 274:2195-2203.

Harcourt, A. H., and J. Greenberg. 2001. Do gorilla females join males to avoid infanticide? A quantitative model. *Animal Behaviour* 62:905-915.

Hardy, B. L., and M.-H. Moncel. 2011. Neanderthal Use of Fish, Mammals, Birds, Starchy Plants and Wood 125-250,000 Years Ago. *PLoS ONE* 6:e23768.

Hardy, K., S. Buckley, M. Collins, A. Estalrrich, D. Brothwell, L. Copeland, A. García-Tabernero, S. García-Vargas, M. de la Rasilla, C. Lalueza-Fox, R. Huguet, M. Bastir, D. Santamaría, M. Madella, J. Wilson, Á. Cortés, and A. Rosas. 2012. Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. *Naturwissenschaften* 99:617-626.

Hare, B., E. Addessi, J. Call, M. Tomasello, and E. Visalberghi. 2003. Do capuchin monkeys, Cebus apella, know what conspecifics do and do not see? *Animal Behaviour* 65:131-142.

Hare, B., J. Call, B. Agnetta, and M. Tomasello. 2000. Chimpanzees know what conspecifics do and do not see. *Animal Behaviour* 59:771-785.

Hare, B., J. Call, and M. Tomasello. 2001. Do chimpanzees know what conspecifics know? *Animal Behaviour* 61:139-151.

Hawkes, K. 1990. "Why do men hunt?," in *Risk & Uncertainty in Tribal & Peasant Societies.* Edited by E. Cashdan, pp. 145 - 166. London: Westview.

Hawkes, K., J. Â F. O'Connell, and N. Â G. B. Jones. 1997. Hadza Women's Time Allocation, Offspring Provisioning, and the Evolution of Long Postmenopausal Life Spans. *Current Anthropology* 38:551-577.

Hayden, B. 2012. Neanderthal social structure? *Oxford Journal of Archaeology* 31:1-26.

Hayes, A., and L. Cai. 2007. Using heteroskedasticity-consistent standard error estimators in OLS regression: An introduction and software implementation. *Behavior Research Methods* 39:709-722.

Healy, S. D., and C. Rowe. 2007. A critique of comparative studies of brain size. *Proceedings of the Royal Society B: Biological Sciences* 274:453-464.

Heesy, C. P., J. M. Kamilar, and J. Willms. 2011. Retinogeniculostriate Pathway Components Scale with Orbit Convergence Only in Primates and Not in Other Mammals. *Brain, Behavior and Evolution* 77:105-115.

Henn, B. M., C. R. Gignoux, M. Jobin, J. M. Granka, J. M. Macpherson, J. M. Kidd, L. RodrÃ-guez-BotiguÃ©, S. Ramachandran, L. Hon, A. Brisbin, A. A. Lin, P. A. Underhill, D. Comas, K. K. Kidd, P. J. Norman, P. Parham, C. D. Bustamante, J. L. Mountain, and M. W. Feldman. 2011. Hunter-gatherer genomic diversity suggests a southern African origin for modern humans. *Proceedings of the National Academy of Sciences* 108:5154-5162.

Henneberg, M. 1998. Evolution of the human brain: Is bigger better? *Clinical and Experimental Pharmacology and Physiology* 25:745-749.

Henneberg, M., and C. de Miguel. 2004. Hominins are a single lineage: brain and body size variability does not reflect postulated taxonomic diversity of hominins. *HOMO - Journal of Comparative Human Biology* 55:21-37.

Hennigh, L. 1971. "You have to be a good lawyer to be an Eskimo.," in *Alliance in Eskimo Society, Proceedings of the American Ethnological Society. Supplement.* Edited by L. Guemple. Washington: University of Washington Press.

Henrich, J. 2004. Demography and Cultural Evolution: How Adaptive Cultural Processes Can Produce Maladaptive Losses - The Tasmanian Case. *American Antiquity* 69:197 - 214.

Henry, A. G., A. S. Brooks, and D. R. Piperno. 2011. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proceedings of the National Academy of Sciences* 108:486 - 491.

Henshilwood, C., F. d'Errico, M. Vanhaeren, K. van Niekerk, and Z. Jacobs. 2004. Middle Stone Age Shell Beads from South Africa. *Science* 304:404.

Henshilwood, C. S., F. d'Errico, K. L. van Niekerk, Y. Coquinot, Z. Jacobs, S.-E. Lauritzen, M. Menu, and R. García-Moreno. 2011. A 100,000-Year-Old Ochre-Processing Workshop at Blombos Cave, South Africa. *Science* 334:219-222.

Henshilwood, C. S., F. d'Errico, R. Yates, Z. Jacobs, C. Tribolo, G. A. T. Duller, N. Mercier, J. C. Sealy, H. Valladas, I. Watts, and A. G. Wintle. 2002. Emergence of Modern Human Behavior: Middle Stone Age Engravings from South Africa. *Science* 295:1278-1280.

Herculano-Houzel, S., C. Collins, P. Wong, and J. Kaas. 2007. Cellular scaling rules for primate brains. *Proceedings of the National Academy of Sciences* 204:3562 - 3567.

Herculano-Houzel, S., and J. H. Kaas. 2011. Gorilla and Orangutan Brains Conform to the Primate Cellular Scaling Rules: Implications for Human Evolution. *Brain, Behavior and Evolution* 77:33-44.

Herrmann, E., J. Call, M. V. Hernàndez-Lloreda, B. Hare, and M. Tomasello. 2007. Humans Have Evolved Specialized Skills of Social Cognition: The Cultural Intelligence Hypothesis. *Science* 317:1360-1366.

Hewlett, B., J. M. H. v. d. Koppel, and L. L. Cavalli-Sforza. 1982. Exploration Ranges of Aka Pygmies of the Central African Republic. *Man* 17:418-430.

Higham, T., L. Basell, R. Jacobi, R. Wood, C. B. Ramsey, and N. J. Conard. 2012. Testing models for the beginnings of the Aurignacian and the advent of figurative art and music: The radiocarbon chronology of Geißenklösterle. *Journal of Human Evolution* 62:664-676.

Higham, T., T. Compton, C. Stringer, R. Jacobi, B. Shapiro, E. Trinkaus, B. Chandler, F. Groning, C. Collins, S. Hillson, P. O'Higgins, C. FitzGerald, and M. Fagan. 2011. The earliest evidence for anatomically modern humans in northwestern Europe. *Nature* 479:521 - 524.

Hill, K., H. Kaplan, K. Hawkes, and A. Hurtado. 1985. Men's time allocation to subsistence work among the Ache of Eastern Paraguay. *Human Ecology* 13:29-47.

Hill, R., A. Bentley, and R. I. M. Dunbar. 2008. Network scaling reveals consistent fractal pattern in hierarchical mammalian societies. *Biology Letters* 4:748-751.

Hill, R., and R. Dunbar. 2003. Social network size in humans. *Human Nature* 14:53-72.

Hinds, O., J. R. Polimeni, N. Rajendran, M. Balasubramanian, K. Amunts, K. Zilles, E. L. Schwartz, B. Fischl, and C. Triantafyllou. 2009. Locating the functional and anatomical boundaries of human primary visual cortex. *NeuroImage* 46:915-922.

Hinds, O. P., N. Rajendran, J. R. Polimeni, J. C. Augustinack, G. Wiggins, L. L. Wald, H. Diana Rosas, A. Potthast, E. L. Schwartz, and B. Fischl. 2008. Accurate prediction of V1 location from cortical folds in a surface coordinate system. *NeuroImage* 39:1585-1599.

Hintschich, C., F. Zonneveld, L. Baldeschi, C. Bunce, and L. Koornneef. 2001. Bony orbital development after early enucleation in humans. *British Journal of Ophthalmology* 85:205-208.

Hoffecker, J. F. 2009. The spread of modern humans in Europe. *Proceedings of the National Academy of Sciences* 106:16040-16045.

Holliday, T. W. 1997. Postcranial evidence of cold adaptation in European Neandertals. *American Journal of Physical Anthropology* 104:245 - 258.

Holloway, R., L., Sherwood, Chet, C., Hof, Patrick R. & Rilling, James K. 2009. "Evolution of the Brain in Humans - Paleoneurology.," in *The New Encyclopedia of Neuroscience.*: Springer.

Holloway, R. L. 1981. Volumettric and Asymmetry Determinations on Recent Hominid Endocasts: Spy I and II, Djebel Ihroud I, and the Sale *Homo erectus* Specimens, With Some Notes on Neanderthal Brain Size. *American Journal of Physical Anthropology* 55:385 - 393.

—. 1983. Human brain evolution: A seach for units, models and synthesis. *Canadian Journal of Archaeology* 3:215 - 230.

—. 1985. "The Poor Brain of *Homo sapiens neanderthalensis*: See What You Please..." in *Ancestors: The Hard Evidence. Proceedings of the symposium held at the American Museum of Natural History April 6-10, 1984 to mark the opening of the exhibition "Ancestors, Four Million Years of Humanity".* Edited by E. Delson, pp. 319 - 324.: Alan R Liss.

—. 2001. Does Allometry Mask Important Brain Structure Residuals Relevant to Species-Specific Behavioral Evolution? *Behavioural & Brain Sciences* 24:286 - 287.

—. 2007. A reply and critique of the Conroy and Smith (2007) prediction of fossil primate brain component sizes. *HOMO - Journal of Comparative Human Biology* 58:229-233.

Holloway, R. L., Broadfield, Douglas C. & Yuan, Michael S. 2004. *The Human Fossil Record: Brain Endocasts: The Paleoneurological Evidence*: New York. John Wiley & Sons Publishers.

Holloway, R. L., and D. G. Post. 1982. "The Relativity of Relative Brain Measures and Hominid Mosaic Evolution," in *Primate Brain Evolution: Methods & Concepts.* Edited by E. F. Armstrong, Dean, pp. 57 - 76.: Plenum Publishing Corporation.

Holt-Lunstad, J., T. B. Smith, and J. B. Layton. 2010. Social Relationships and Mortality Risk: A Meta-analytic Review. *PLoS Medicine* 7:e1000316.

Horan, R. D., E. Bulte, and J. F. Shogren. 2005. How trade saved humanity from biological exclusion: an economic theory of Neanderthal extinction. *Journal of Economic Behaviour & Organisation* 58:1-29.

House, J. S. 2001. Social Isolation Kills, But How and Why? *Psychosomatic Medicine* 63:273-274.

Hublin, J.-J., and W. Roebroeks. 2009. Ebb and flow or regional extinctions? On the character of Neandertal occupation of northern environments. *Comptes Rendus Palevol* 8:503-509.

Hublin, J.-J., F. Spoor, M. Braun, F. Zonneveld, and S. Condemi. 1996. A late Neanderthal associated with Upper Palaeolithic artefacts. *Nature* 381:224-226.

Hublin, J.-J., S. Talamo, M. Julien, F. David, N. Connet, P. Bodu, B. Vandermeersch, and M. P. Richards. 2012. Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neandertal origin for the Châtelperronian. *Proceedings of the National Academy of Sciences* 109:18743.

Hughes, A. 1988. *Evolution and Human Kinship*. Oxford: Oxford University Press.

Hurtado, A., K. Hawkes, K. Hill, and H. Kaplan. 1985. Female subsistence strategies among Ache hunter-gatherers of Eastern Paraguay. *Human Ecology* 13:1-28.

Hurtado, A. M., and K. R. Hill. 1990. Seasonality in a Foraging Society: Variation in Diet, Work Effort, Fertility, and Sexual Division of Labor among the Hiwi of Venezuela. *Journal of Anthropological Research* 46:293-346.

Hutchinson, J. M. C., and P. M. Waser. 2007. Use, misuse and extensions of ideal gas models of animal encounter. *Biological Reviews* 82:335-359.

Iaupuni, S. M. K., K. M. Donato, T. Thompson-Colón, and M. Stainback. 2005. Counting on Kin: Social Networks, Social Support, and Child Health Status. *Social Forces* 83:1137-1164.

Ip, J. M., S. C. Huynh, D. Robaei, A. Kifley, K. A. Rose, I. G. Morgan, J. J. Wang, and P. Mitchell. 2007. Ethnic differences in refraction and ocular biometry in a population-based sample of 11-15-year-old Australian children. *Eye* 22:649-656.

Isler, K., E. C. Kirk, J. M. A. Miller, G. A. Albrecht, B. R. Gelvin, and R. D. Martin. 2008. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. *Journal of Human Evolution* 55:967-978.

Ives, A. R., and M. R. Helmus. 2011. Generalized linear mixed models for phylogenetic analyses of community structure. *Ecological Monographs* 81:511-525.

Ives, A. R., P. E. Midford, and T. Garland. 2007. Within-Species Variation and Measurement Error in Phylogenetic Comparative Methods. *Systematic Biology* 56:252-270.

Jenkinson, M., C. F. Beckmann, T. E. J. Behrens, M. W. Woolrich, and S. M. Smith. 2012. FSL. *NeuroImage* 62:782-790.

Jochim, M. A. 1983. "Palaeolithic Cave Art in Ecological Perspective.," in *Hunter-Gatherer Economy in Prehistory: A European Perspective.* Edited by G. Bailey. Cambridge: Cambridge Univeristy Press.

Joffe, T. H., and R. I. M. Dunbar. 1997. Visual and Socio-Cognitive Information Processing in Primate Brain Evolution. *Proceedings of the Royal Society B: Biological Sciences* 264:1303-1307.

Johnson, A. 1975. Time Allocation in a Machiguenga Community. *Ethnology* 14:301-310.

Johnson, G. A. 1982. "Organizational Structure and Scalar Stress," in *Theory and Explanation in Archaeology*. Edited by C. Renfrew, M. R. and, and B. A. Segraves-Whallon., pp. 389-421.: Academic Press, Inc.

Jolly, C., T. Woolley-Barker, S. Beyene, T. Disotell, and J. Phillips-Conroy. 1997. Intergeneric Hybrid Baboons. *International Journal of Primatology* 18:597-627.

Jonides, J., E. E. Smith, R. A. Koeppe, E. Awh, S. Minoshima, and M. A. Mintun. 1993. Spatial working memory in humans as revealed by PET. *Nature* 363:623-625.

Kanai, R., B. Bahrami, R. Roylance, and G. Rees. 2011. Online social network size is reflected in human brain structure. *Proceedings of the Royal Society B: Biological Sciences* 279B:1327 - 1334.

Kaplan, H., K. Hill, and A. M. Hurtado. 1990. "Risk, Foraging and Foodsharing among the Ache.," in *Risk & Uncertainty in Tribal & Peasant Economies.* Edited by E. Cashdan, pp. 107 -144. London.: Westview.

Kappelman, J. 1996. The evolution of body mass and relative brain size in fossil hominids. *Journal of Human Evolution* 30:243-276.

Kaskan, P. M., E. C. S. Franco, E. S. Yamada, L. C. de Lima Silveira, R. B. Darlington, and B. L. Finlay. 2005. Peripheral variability and central constancy in mammalian visual system evolution. *Proceedings of the Royal Society B: Biological Sciences* 272:91-100.

Katzmarzyk, P. T., and W. R. Leonard. 1998. Climatic influences on human body size and proportions: Ecological adaptations and secular trends. *American Journal of Physical Anthropology* 106:483-503.

Kay, R. F., and E. C. Kirk. 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. *American Journal of Physical Anthropology* 113:235-262.

Kelly, R. L. 1995. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways.* Washington; London: Smithsonian Institution Press.

Keverne, E. B., N. D. Martensz, and B. Tuite. 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* 14:155-161.

Kiltie, R. A. 2000. Scaling of visual acuity with body size in mammals and birds. *Functional Ecology* 14:226-234.

Kirk, E. C. 2004. Comparative morphology of the eye in primates. *The Anatomical Record Part A: Discoveries in Molecular, Cellular, and Evolutionary Biology, Special Issue: Evolution of the Special Senses in Primates* 281A:1095-1103.

—. 2006a. Effects of activity pattern on eye size and orbital aperture size in primates. *Journal of Human Evolution* 51:159-170.

—. 2006b. Eye Morphology in Cathemeral Lemurids and Other Mammals. *Folia Primatologica* 77:27-49.

Klein, R. G. 2009. *The Human Career: Human Biological and Cultural Origins. 3rd Edition.* Chicago: Chicago University Press.

Korstjens, A., I. Verhoeckx, and R. Dunbar. 2006. Time as a constraint on group size in spider monkeys. *Behavioral Ecology and Sociobiology* 60:683-694.

Kosse, K. 1990. Group size and societal complexity: Thresholds in the long-term memory. *Journal of Anthropological Archaeology* 9:275-303.

Koster, J. M., and K. B. Tankersley. 2012. Heterogeneity of hunting ability and nutritional status among domestic dogs in lowland Nicaragua. *Proceedings of the National Academy of Sciences* 109:E463-E470.

Kotler, M., I. Iancu, R. Efroni, and M. Amir. 2001. Anger, Impulsivity, Social Support, and Suicide Risk in Patients with Posttraumatic Stress Disorder. *The Journal of Nervous and Mental Disease* 189:162-167.

Koziol, L. F., D. E. Budding, and D. Chidekel. 2012. From movement to thought: Executive function, embodied cognition, and the cerebellum. *Cerebellum* 11.

Kroenke, C. H., L. D. Kubzansky, E. S. Schernhammer, M. D. Holmes, and I. Kawachi. 2006. Social Networks, Social Support, and Survival After Breast Cancer Diagnosis. *Journal of Clinical Oncology* 24:1105-1111.

Kudo, H., and R. I. M. Dunbar. 2001. Neocortex size and social network size in primates. *Animal Behaviour* 62:711-722.

Kuhn, S. L., and M. C. Stiner. 2001. "The antiquity of hunter-gatherers.," in *Hunter-Gatherers: An Interdisciplinary Perspective.* Edited by C. Panter-Brick, R. Layton, and P. Rowley-Conwy, pp. 99 - 129. Cambridge: Cambridge University Press.

—. 2006. What's a Mother to Do? The Division of Labor among Neandertals and Modern Humans in Eurasia. *Current Anthropology* 47:953-980.

—. 2007. Paleolithic Ornaments: Implications for Cognition, Demography and Identity. *Diogenes* 54:40-48.

Laeng, B., T. Brennen, Ã. k. Elden, H. Gaare Paulsen, A. Banerjee, and R. Lipton. 2007. Latitude-of-birth and season-of-birth effects on human color vision in the Arctic. *Vision Research* 47:1595-1607.

Lahr, M. M., and R. A. Foley. 1998. Towards a Theory of Modern Human Origins: Geography, Demography, and Diversity in Recent Human Evolution. *Yearbook of Physical Anthropology* 41:137-176.

Lammi, J. Last modified January 1999, accessed July 2008. "Photoperiod calculator [online], available: http://www.ou.edu/research/electron/internet/solarjav.html."

Langergraber, K. E., K. Prüfer, C. Rowney, C. Boesch, C. Crockford, K. Fawcett, E. Inoue, M. Inoue-Muruyama, J. C. Mitani, M. N. Muller, M. M. Robbins, G. Schubert, T. S. Stoinski, B. Viola, D. Watts, R. M. Wittig, R. W. Wrangham, K. Zuberbühler, S. Pääbo, and L. Vigilant. 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences* 109:15716.

Langley, M. C., C. Clarkson, and S. Ulm. 2008. Behavioural Complexity in Eurasian Neanderthal Populations: a Chronological Examination of the Archaeological Evidence. *Cambridge Archaeological Journal* 18:289-307.

—. 2011. From small holes to grand narratives: The impact of taphonomy and sample size on the modernity debate in Australia and New Guinea. *Journal of Human Evolution* 61:197-208.

Lari, M., E. Rizzi, L. Milani, G. Corti, C. Balsamo, S. Vai, G. Catalano, E. Pilli, L. Longo, S. Condemi, P. Giunti, C. HÃ¤nni, G. De Bellis, L. Orlando, G. Barbujani, and D. Caramelli. 2010. The Microcephalin Ancestral Allele in a Neanderthal Individual. *PLoS ONE* 5:e10648.

Larson, G., E. K. Karlsson, A. Perri, M. T. Webster, S. Y. W. Ho, J. Peters, P. W. Stahl, P. J. Piper, F. Lingaas, M. Fredholm, K. E. Comstock, J. F. Modiano, C. Schelling, A. I. Agoulnik, P. A. Leegwater, K. Dobney, J.-D. Vigne, C. Vilà, L. Andersson, and K. Lindblad-Toh. 2012. Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences* 109:8878-8883.

Layton, R. 1986. Political and Territorial Structures Among Hunter-Gatherers. *Man* 21:18-33.

Layton, R., and O'Hara. 2010. Human social evolution: A comparison of hunter-gatherer and chimpanzee social organisation. *Proceedings of the British Academy* 158:83 - 113.

Layton, R., S. O'Hara, and A. Bilsborough. 2012. Antiquity and social functions of multilevel social organisation among human hunter-gatherers. *International Journal of Primatology* 33:1215 - 1245.

Lee, R. B. 1972. "The Intensification of Social Life Amongst the !Kung Bushmen.," in *Population Growth: Anthropological Implications*. Edited by B. Spooner: MIT Press, Cambridge, Mass.

—. 1979. *The !Kung San: men, women and work in a foraging society*. Cambridge: Cambridge Univeristy Press.

Legendre, P. 2011 (accessed 2011). Model II Regression [online], available at: http://cran.r-project.org/web/packages/lmodel2/index.html.

Lehman, J., P. Lee, and R. I. M. Dunbar. in press. "Unravelling the function of community-level organisation," in *The Lucy Project: Benchmark Papers*. Edited by R. I. M. Dunbar, C. Gamble, and J. Gowlett. Oxford: Oxford University Press.

Lehmann, J., A. Korstjens, and R. Dunbar. 2007a. Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology* 21:613-634.

Lehmann, J., A. H. Korstjens, and R. I. M. Dunbar. 2007b. Group size, grooming and social cohesion in primates. *Animal Behaviour* 74:1617-1629.

Lent, R., F. A. C. Azevedo, C. H. Andrade-Moraes, and A. V. O. Pinto. 2012. How many neurons do you have? Some dogmas of quantitative neuroscience under revision. *European Journal of Neuroscience* 35:1-9.

Lewis, M. P. Editor. 2009. *Ethnoloue: Languages of the World, Sixteenth Edition. Online version: http://www.ethnologue.com*. Dallas, Texas: SIL International.

Lewis, P. A., R. Rezaie, R. Brown, N. Roberts, and R. I. M. Dunbar. 2011. Ventromedial prefrontal volume predicts understanding of others and social network size. *NeuroImage* 57:1624-1629.

Li, J. Z., D. M. Absher, H. Tang, A. M. Southwick, A. M. Casto, S. Ramachandran, H. M. Cann, G. S. Barsh, M. Feldman, L. L. Cavalli-Sforza, and R. M. Myers. 2008. Worldwide Human Relationships Inferred from Genome-Wide Patterns of Variation. *Science* 319:1100-1104.

Lombard, M., and M. N. Haidle. 2012. Thinking a Bow-and-arrow Set: Cognitive Implications of Middle Stone Age Bow and Stone-tipped Arrow Technology. *Cambridge Archaeological Journal* 22:237-264.

Low, B. 1990. "Human Responses to Environmental Extremeness and Uncertainty: A Cross-Cultural Perpective.," in *Risk & Uncertainty in Tribal & Peasant Economies.* Edited by E. Cashdan. Boulder, San Francisco & London.: Westview Press.

Luders, E., K. L. Narr, P. M. Thompson, and A. W. Toga. 2009. Neuroanatomical correlates of intelligence. *Intelligence* 37:156-163.

Lukatela, K., and H. A. Swadlow. 2004. "Neocortex," in *The Corsini Encyclopedia of Psychology*, 3rd edition, vol. 3. Edited by I. B. Weiner and W. E. Craighead, pp. 1070 - 2. Chichester, New York: Wiley.

Lum, J. K., and R. L. Cann. 1998. "mtDNA and language support a common origin of Micronesians and Polynesians in Island Southeast Asia," vol. 105, pp. 109-119: Wiley Subscription Services, Inc., A Wiley Company.

Lum, J. K., L. B. Jorde, and W. Schiefenhovel. 2002. "Affinities among Melanesians, Micronesians, and Polynesians: A Neutral, Biparental Genetic Perspective." *Human Biology* 74:413 - 430.

Lynch, B. M., and L. H. Robbins. 1979. Cushitic and Nilotic Prehistory: New Archaeological Evidence from North-West Kenya. *The Journal of African History* 20:319-328.

Lyon, D. C., and J. D. Connolly. 2011. The case for primate V3. *Proceedings of the Royal Society B: Biological Sciences* 279:625 - 633.

Lythgoe, J. N. 1979. *The Ecology of Vision*. Oxford: Clarendon Press.

Maca-Meyer, N., M. Arnay, J. C. Rando, C. Flores, A. M. Gonzalez, V. M. Cabrera, and J. M. Larruga. 2003. Ancient mtDNA analysis and the origin of the Guanches. *European Journal of Human Genetics* 12:155-162.

Mace, R., and M. Pagel. 1995. A Latitudinal Gradient in the Density of Human Languages in North America. *Proceedings of the Royal Society B: Biological Sciences* 261:117-121.

Machin, A. J., and R. I. M. Dunbar. 2011. The brain opiod theory of social attachment: a review of the evidence. *Behaviour*.

MacLeod, N. 2006, accessed 2011. "Regression 3, Paleo Maths 101 [online], available at: http://www.palass.org/modules.php?name=palaeo_math&page=5," Palaeontological Association.

Maddison, W. P., and D. R. Maddison. 2010. "Mesquite: a modular system for evolutionary analysis. Version 2.74 http://mesquiteproject.org."

Maguire, E. A., R. S. J. Frackowiak, and C. D. Frith. 1997. Recalling Routes around London: Activation of the Right Hippocampus in Taxi Drivers. *Journal of Neuroscience* 17:7103-7110.

Maguire, E. A., D. G. Gadian, I. S. Johnsrude, C. D. Good, J. Ashburner, R. S. J. Frackowiak, and C. D. Frith. 2000. Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences* 97:4398-4403.

Maguire, E. A., H. J. Spiers, C. D. Good, T. Hartley, R. S. J. Frackowiak, and N. Burgess. 2003. Navigation expertise and the human hippocampus: A structural brain imaging analysis. *Hippocampus* 13:250-259.

Maguire, E. A., K. Woollett, and H. J. Spiers. 2006. London taxi drivers and bus drivers: A structural MRI and neuropsychological analysis. *Hippocampus* 16:1091-1101.

Mandel, Y., I. Grotto, R. El-Yaniv, M. Belkin, E. Israeli, U. Polat, and E. Bartov. 2008. Season of Birth, Natural Light, and Myopia. *Ophthalmology* 115:686-692.

Marlowe, F. W. 2005. Hunter-gatherers and human evolution. *Evolutionary Anthropology* 14:54 - 67.

Marom, A., J. S. O. McCullagh, T. F. G. Higham, A. A. Sinitsyn, and R. E. M. Hedges. 2012. Single amino acid radiocarbon dating of Upper Paleolithic modern humans. *Proceedings of the National Academy of Sciences*.

Martín-González, J. A., A. Mateos, I. Goikoetxea, W. R. Leonard, and J. Rodríguez. 2012. Differences between Neandertal and modern human infant and child growth models. *Journal of Human Evolution* 63:140-149.

Martin, R. 1990. *Primate origins and evolution. A phylogenetic reconstruction.* London: Chapman & Hall.

Martin, R. D. 1980. Adaptation and body size in primates. *Zeitschrift für Morphologie und Anthropologie* 71:115 - 124.

—. 1982. "AllopmetricApproaches to the Evolution of the Primate Nervous System," in *Primate Brain Evolution Methods & Concepts*. Edited by E. F. Armstrong, Dean: Plenum Press.

Marwick, B. 2003. Pleistocene Exchange Networks as Evidence for the Evolution of Language. *Cambridge Archaeological Journal* 13:67-81.

Masters, M. P. 2008. Modern Variation and Evolutionary Change in the Hominin Eye Orbit, Ohio State University.

—. 2012. Relative size of the eye and orbit: An evolutionary and craniofacial constraint model for examining the etiology and disparate incidence of juvenile-onset myopia in humans. *Medical Hypotheses* 78:649-656.

Mauss, M., and H. Beuchat. 1950/1979. *Seasonal Variations of the Eskimo: A Study in Social Morphology*. London: Routledge & Kegan Paul Ltd.

McBrearty, S., and A. S. Brooks. 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *Journal of Human Evolution* 39:453-563.

McMahon, G., T. Zayats, Y.-P. Chen, A. Prashar, C. Williams, and J. A. Guggenheim. 2009. Season of Birth, Daylight Hours at Birth, and High Myopia. *Ophthalmology* 116:468-473.

McNabb, J. 2012. The importance of conveying visual information in Acheulean society. The background to the Visual Display Hypothesis. [Part of the British Academy

'Lucy to Language: Archaeology of the Social Brain' seminar series on Palaeolithic Visual Display]. *Human Origins* 1:1 - 23.

McSweeney, B. G. 1979. Collection and Analysis of Data on Rural Women's Time Use. *Studies in Family Planning* 10:379-383.

Mekel-Bobrov, N., D. Posthuma, S. L. Gilbert, P. Lind, M. F. Gosso, M. Luciano, S. E. Harris, T. C. Bates, T. J. C. Polderman, L. J. Whalley, H. Fox, J. M. Starr, P. D. Evans, G. W. Montgomery, C. Fernandes, P. Heutink, N. G. Martin, D. I. Boomsma, I. J. Deary, M. J. Wright, E. J. C. de Geus, and B. T. Lahn. 2007. The ongoing adaptive evolution of ASPM and Microcephalin is not explained by increased intelligence. *Human Moecular Genetics* 16:600 - 608.

Mellars, P. 1996. "Symbolism, language and the Neanderthal mind.," in *Modelling the Early Human Mind*. Edited by P. Mellars and K. R. Gibson: Cambridge University Press.

Mellars, P., and J. C. French. 2011. Tenfold Population Increase in Western Europe at the Neandertal to Modern Human Transition. *Science* 333:623-627.

Mercier, N., H. Valladas, J. L. Joron, J. L. Reyss, F. Leveque, and B. Vandermeersch. 1991. Thermoluminescence dating of the late Neanderthal remains from Saint-Cesaire. *Nature* 351:737-739.

Miritello, G., E. Moro, R. Lara, R. LMartinez-Lopez, J. Belchamber, S. Roberts, and R. I. M. Dunbar. 2013. Time as a limited resource: Communication Strategy in Mobile Phone Networks. *Social Networks* 35:89 - 95.

Mithen, S. J. 1996a. "Domain-specific intelligence and the Neanderthal mind," in *Modelling the Early Human Mind*, vol. McDonald Institute Monographs. Edited by P. Mellars and K. R. Gibson. Cambridge: McDonald Institute for Archaeological Research.

—. 1996b. *The prehistory of mind: A search for the origins of art, religion and science*. London: Thames and Hudson Ltd.

Moore, J. L., L. Manne, T. Brooks, N. D. Burgess, R. Davies, C. Rahbek, P. Williams, and A. Balmford. 2002. The distribution of cultural and biological diversity in Africa. *Proceedings of the Royal Society B: Biological Sciences* 269:1645-1653.

Mottaghy, F. M. 2006. Interfering with working memory in humans. *Neuroscience* 139:85-90.

Moutsiou, T. 2011. The Obsidian Evidence for the Scale of Social Life during the Palaeolithic, Royal Holloway, University of London.

Movable Type Scripts. Accessed 2010. Calculate distance, bearing and more between Latitude/Longitude points, available at: http://www.movable-type.co.uk/scripts/latlong.html.

Munroe, R. H., R. L. Munroe, C. Michelson, A. Koel, R. Bolton, and C. Bolton. 1983. Time Allocation in Four Societies. *Ethnology* 22:355-370.

Murdock, G. P. 1949. *Social Structure*. New York: Macmillan.

Mutti, D. O., and A. R. Marks. 2011. Blood Levels of Vitamin D in Teens and Young Adults with Myopia. *Optometry & Vision Science* 88:377-382 10.1097/OPX.0b013e31820b0385.

Myers, C. S. 1902. The visual acuity of the natives of Sarawak. *Journal of Physiology* 28:316 - 318.

Nash, D. J., S. Coulson, S. Staurset, J. S. Ullyott, M. Babutsi, L. Hopkinson, and M. P. Smith. 2013. Provenancing of silcrete raw materials indicates long-distance transport to Tsodilo Hills, Botswana, during the Middle Stone Age. *Journal of Human Evolution* 64:280-288.

Naval Oceanography Portal. Accessed July 2008. Sun or Moon Altitude/Azimuth Table: Locations Worldwide [online], available: http://www.usno.navy.mil/USNO/astronomical-applications/data-services/alt-az-world,.

Nelson, S. M. 1990. Diversity of the Upper Paleolithic "Venus Figurines and Archeological Mythology". *Archeological Papers of the American Anthropological Association* 2:11-22.

Nettle, D. 1996. Language Diversity in West Africa: An Ecological Approach. *Journal of Anthropological Archaeology* 15:403-438.

—. 1998. Explaining Global Patterns of Language Diversity. *Journal of Anthropological Archaeology* 17:354-374.

—. 1999. *Linguistic Diversity*. Oxford.: Oxford University Press.

Nettle, D., and R. I. M. Dunbar. 1997. Social Markers and the Evolution of Reciprocal Exchange. *Current Anthropology* 38:93-99.

Neves, A. G. M., and M. Serva. 2012. Extremely Rare Interbreeding Events Can Explain Neanderthal DNA in Living Humans. *PLoS ONE* 7:e47076.

NITRC. Accessed 2011. "1000 Functional Connectomes Project [online], accessed at: http://www.nitrc.org/projects/fcon_1000/."

Norenzayan, A., W. M. Gervais, and K. H. Trzesniewski. 2012. Mentalizing Deficits Constrain Belief in a Personal God. *PLoS ONE* 7:e36880.

O'Connell, S., and R. I. M. Dunbar. 2003. A test for comprehension of false belief in chimpanzees. *Evolution and Cognition* 9:131 - 139.

O. Soffer, J. M. Adovasio, and D. C. Hyland. 2000. The "Venus" Figurines: Textiles, Basketry, Gender, and Status in the Upper Paleolithic. *Current Anthropology* 41:511-537.

Olson, I. R., D. McCoy, E. Klobusicky, and L. A. Ross. 2013. Social cognition and the anterior temporal lobes: a review and theoretical framework. *Social Cognitive and Affective Neuroscience* 8:123-133.

Osaka City University. Accessed 2011. "Catalogue of Fossil Hominids Database, available at: http://gbs.ur-plaza.osaka-cu.ac.jp/kaseki/index.html."

Ovodov, N. D., S. J. Crockford, Y. V. Kuzmin, T. F. G. Higham, G. W. L. Hodgins, and J. van der Plicht. 2011. A 33,000-Year-Old Incipient Dog from the Altai Mountains of Siberia: Evidence of the Earliest Domestication Disrupted by the Last Glacial Maximum. *PLoS ONE* 6:e22821.

Pagel, M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* 26:331-348.

Pakkenberg, B., and H. J. G. Gundersen. 1997. Neocortical neuron number in humans: Effect of sex and age. *The Journal of Comparative Neurology* 384:312-320.

Pang, J.-F., C. Kluetsch, X.-J. Zou, A.-b. Zhang, L.-Y. Luo, H. Angleby, A. Ardalan, C. Ekström, A. Sköllermo, J. Lundeberg, S. Matsumura, T. Leitner, Y.-P. Zhang, and P. Savolainen. 2009. mtDNA Data Indicate a Single Origin for Dogs South of Yangtze River, Less Than 16,300 Years Ago, from Numerous Wolves. *Molecular Biology and Evolution* 26:2849-2864.

Parfitt, S. A., N. M. Ashton, S. G. Lewis, R. L. Abel, G. R. Coope, M. H. Field, R. Gale, P. G. Hoare, N. R. Larkin, M. D. Lewis, V. Karloukovski, B. A. Maher, S. M. Peglar, R. C. Preece, J. E. Whittaker, and C. B. Stringer. 2010. Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. *Nature* 466:229-233.

Patou-Mathis, M. 2000. Neanderthal subsistence behaviours in Europe. *International Journal of Osteoarchaeology* 10:379 - 395.

Pavlov, P., J. I. Svendsen, and S. Indrelid. 2001. Human presence in the European Arctic nearly 40,000 years ago. *Nature* 413:64-67.

Pearce, E. under review. Neanderthals and *Homo sapiens*: Cognitively different kinds of human. Proceedings of the HOBET conference.

Pearce, E., and H. Bridge. 2013. Is orbital volume associated with eyeball and visual cortex volume in humans? *Annals of Human Biology*.

Pearce, E., and L. Buck. in prep. The relationship between absolute latitude and human visual system verified in an independent dataset using different methods.

Pearce, E., and R. Dunbar. 2012. Latitudinal variation in light levels drives human visual system size. *Biology Letters* 8:90 - 93.

Pearce, E., A. Shuttleworth, M. Grove, and R. Layton. in press. "The costs of being a high latitude hominin," in *The Lucy Project: Benchmark Papers*. Edited by R. Dunbar, Gamble, C., Gowlett, J., : Oxford University Press.

Pearce, E., C. Stringer, and R. I. M. Dunbar. 2013. New insights into differences in brain organization between Neanderthals and anatomically modern humans. *Proceedings of the Royal Society B: Biological Sciences* 280.

Perez-Barberia, F., S. Shultz, and R. Dunbar. 2007. Evidence for coevolution of sociality and relative brain size in three orders of mammals. *Evolution* 61:2811 - 2821.

Pike, A. W. G., D. L. Hoffmann, M. García-Diez, P. B. Pettitt, J. Alcolea, R. De Balbín, C. González-Sainz, C. de las Heras, J. A. Lasheras, R. Montes, and J. Zilhão. 2012. U-Series Dating of Paleolithic Art in 11 Caves in Spain. *Science* 336:1409-1413.

Pinquart, M., and P. R. Duberstein. 2010. Associations of social networks with cancer mortality: A meta-analysis. *Critical Reviews in Oncology/Hematology* 75:122-137.

Plotnick, R. E. 1989. Application of Bootstrap Methods to Reduced Major Axis Line Fitting. *Systematic Zoology* 38:144-153.

Ponce de Leon, M. S., and C. P. E. Zollikofer. 2001. Neanderthal cranial ontogeny and its implications for late hominid diversity. *Nature* 412:534-538.

Potts, R. 1996. Evolution and Climate Variability. *Science* 273:922-923.

—. 1998. Environmental Hypotheses of Hominin Evolution. *Yearbook of Physical Anthropology* 41:93 - 136.

Powell, A., S. Shennan, and M. G. Thomas. 2009. Late Pleistocene Demography and the Appearance of Modern Human Behavior. *Science* 324:1298-1301.

Powell, J., P. A. Lewis, N. Roberts, and R. I. M. Dunbar. 2012. Orbitofrontal Prefrontal Cortex Volume Predicts Social Network Size: An Imaging Study of Individual Differences in Humans. *Proceedings of the Royal Society B: Biological Sciences* 279:2157 - 2162

Powell, J. L., P. A. Lewis, R. I. M. Dunbar, M. García-Fiñana, and N. Roberts. 2010. Orbital prefrontal cortex volume correlates with social cognitive competence. *Neuropsychologia* 48:3554-3562.

Powers, W. E. 1966. *Physical Geography*. New York: Meredith Publishing Company.

R-Forge. Accessed March 2011. Comparative Analyses of Phylogenetics and Evolution in R, accessed at: http://cran.r-project.org/web/packages/caper/index.html Project Admin: David Orme.

Radinsky, L. 1967. Relative Brain Size: A New Measure. *Science* 155:836-838.

—. 1982. "Some Cautionary Notes on Making Inferences About Relative Brain Size.," in *Primate Brain Evolution Methods & Concepts*. Edited by E. F. Armstrong, Dean: Plenum Press.

Rai, N. K. 1990. *Living in a lean-to: Phillippine Negrito foragers in transition*. Ann Arbor, USA: Museum of Anthropology, University of Michigan

Ravosa, M. J. 1991. Interspecific perspective on mechanical and nonmechanical models of primate circumorbital morphology. *American Journal of Physical Anthropology* 86:369-396.

Reimchen, T. E. 1987. Human color vision deficiencies and atmospheric twilight. *Social Biology* 34:1-11.

Revell, L. J. 2011 (accessed 2011). "phytools: Phylogenetic Tools for comparative biology (and other things) [online], available at: http://cran.r-project.org/web/packages/phytools/index.html."

Richards, C. 1996. Monuments as landscape: Creating the centre of the world in late Neolithic Orkney. *World Archaeology* 28:190-208.

Richards, M. P., P. B. Pettitt, E. Trinkaus, F. H. Smith, M. Paunovic, and I. Karavanic. 2000. Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. *Proceedings of the National Academy of Sciences* 97:7663-7666.

Richards, M. P., G. Taylor, T. Steele, S. P. McPherron, M. Soressi, J. Jaubert, J. Orschiedt, J. B. Mallye, W. Rendu, and J. J. Hublin. 2008. Isotopic dietary analysis of a Neanderthal and associated fauna from the site of Jonzac (Charente-Maritime), France. *Journal of Human Evolution* 55:179-185.

Riedl, K., K. Jensen, J. Call, and M. Tomasello. 2012. No third-party punishment in chimpanzees. *Proceedings of the National Academy of Sciences* 109:14824-14829.

Rightmire, G. P. 2004. Brain size and encephalization in early to mid-Pleistocene Homo. *American Journal of Physical Anthropology* 124:109-123.

Rivers, W. H. R. 1898. "Vision," in *Reports of the Cambridge Anthropological Expedition to Torres Straits*: Cambridge University Press.

Roberts, S. 2010. "Constraints on social networks," in *Social Brain, Distributed Mind*. Edited by R. Dunbar, C. Gamble, and J. Gowlett, pp. 117 - 138. Oxford: Oxford University Press.

Roberts, S. G. B., and R. I. M. Dunbar. 2011a. Communication in social networks: Effects of kinship, network size, and emotional closeness. *Personal Relationships* 18:439-452.

—. 2011b. The costs of family and friends: an 18-month longitudinal study of relationship maintenance and decay. *Evolution and Human Behavior* 32:186-197.

Roberts, S. G. B., R. I. M. Dunbar, T. V. Pollet, and T. Kuppens. 2009. Exploring variation in active network size: Constraints and ego characteristics. *Social Networks* 31:138-146.

Rockel, A. J., R. W. Hiorns, and T. P. S. Powell. 1980. The basic uniformity of the neocortex. *Brain* 103:221-244.

Rodman, P. S., and H. M. McHenry. 1980. Bioenergetics and the origin of hominid bipedalism. *American Journal of Physical Anthropology* 52:103-106.

Roebroeks, W., M. J. Sier, T. K. Nielsen, D. De Loecker, J. M. Parés, C. E. S. Arps, and H. J. Mücher. 2012. Use of red ochre by early Neandertals. *Proceedings of the National Academy of Sciences* 109:1889-1894.

Roebroeks, W., and P. Villa. 2011. On the earliest evidence for habitual use of fire in Europe. *Proceedings of the National Academy of Sciences* 108:5209 - 5214.

Rosa, M. G. P., and R. Tweedale. 2005. Brain maps, great and small: lessons from comparative studies of primate visual cortical organization. *Philosophical Transactions of the Royal Society B-Biological Sciences* 360:665-691.

Rose, K. A., I. G. Morgan, J. Ip, A. Kifley, S. Huynh, W. Smith, and P. Mitchell. 2008a. Outdoor Activity Reduces the Prevalence of Myopia in Children. *Ophthalmology* 115:1279-1285.

Rose, K. A., I. G. Morgan, W. Smith, G. Burlutsky, P. Mitchell, and S.-M. Saw. 2008b. Myopia, Lifestyle, and Schooling in Students of Chinese Ethnicity in Singapore and Sydney. *Archives of Ophthalmology* 126:527-530.

Ross, C. F., and E. C. Kirk. 2007. Evolution of eye size and shape in primates. *Journal of Human Evolution* 52:294-313.

Rosset, A. Accessed 2011. "OsiriX Imaging Software [online], available at: http://www.osirix-viewer.com/."

Ruebens, K. 2012. From Keilmesser to Bout-Coupe handaxes: Macro-regional variability in Western European Late Middle Palaeolithic bifacial tools., University of Southampton.

— -

: Macro-Regional Variability among Western European Late Middle Palaeolithic Bifacial Tools. *Bulletin de la Societe prehistorique francaise* 110:364 - 365.

Ruff, C. 2002. Variation in Human Body Size and Shape. *Annual Review of Anthropology* 31:211-232.

Ruff, C. B. 1994. Morphological adaptation to climate in modern and fossil hominids. *American Journal of Physical Anthropology* 37:65-107.

—. 2000. Body mass prediction from skeletal frame size in elite athletes. *American Journal of Physical Anthropology* 113:507-517.

Ruff, C. B., W. W. Scott, and A. Y. C. Liu. 1991. Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *American Journal of Physical Anthropology* 86:397-413.

Ruff, C. B., E. Trinkaus, and T. W. Holliday. 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387:173-176.

Rushton, J. P., P. A. Vernon, and T. A. Bons. 2007. No evidence that polymorphisms of brain regulator genes Microcephalin and ASPM are associated with general mental ability, head circumference or altruism. *Biology Letters* 3:157-160.

Sack, A. T. 2009. Parietal cortex and spatial cognition. *Behavioural Brain Research* 202:153-161.

Sallet, J., R. B. Mars, M. P. Noonan, J. L. Andersson, J. X. O'Reilly, S. Jbabdi, P. L. Croxson, M. Jenkinson, K. L. Miller, and M. F. S. Rushworth. 2011. Social Network Size Affects Neural Circuits in Macaques. *Science* 334:697-700.

Salmon, E., M. Van der Linden, F. Collette, G. Delfiore, P. Maquet, C. Degueldre, A. Luxen, and G. Franck. 1996. Regional brain activity during working memory tasks. *Brain* 119:1617-1625.

Sánchez-Quinto, F., L. R. Botigué, S. Civit, C. Arenas, M. C. Ávila-Arcos, C. D. Bustamante, D. Comas, and C. Lalueza-Fox. 2012. North African Populations Carry the Signature of Admixture with Neandertals. *PLoS ONE* 7:e47765.

Sankararaman, S., N. Patterson, H. Li, S. Pääbo, and D. Reich. 2012. The Date of Interbreeding between Neandertals and Modern Humans. *PLoS Genetics* 8:e1002947.

Sarnat, B. G. 1982. Eye and orbital size in the young and adult. Some postnatal experimental and clinical relationships. *Ophthalmologica* 185:74 - 89.

Saw, S.-M. 2003. A synopsis of the prevalence rates and environmental risk factors for myopia. *Clinical and Experimental Optometry* 86:289-294.

Scally, A., and R. Durbin. 2012. Revising the human mutation rate: implications for understanding human evolution. *Nature Reviews Genetics* 13:745-753.

Schultz, A. 1940. The Size of the Orbit and of the Eye in Primates. *American Journal of Physical Anthropology* 26:389 - 408.

Schwarzkopf, D. S., C. Song, and G. Rees. 2011. The surface area of human V1 predicts the subjective experience of object size. *Nature Neuroscience* 14:28-30.

Scotton, C. M. 1981. The Linguistic Situation and Language Policy in Eastern Africa. *Annual Review of Applied Linguistics* 2:8-20.

Seidelmann, P. K. Editor. 1992. *Explanatory Supplement to the Astronomical Almanac*: Mill Valley: University Science Books.

Shea, John J., and M. L. Sisk. 2010. Complex projectile technology and Homo sapiens dispersal into Western Eurasia. *PalaeoAnthropology*:100 - 122.

Shultz, S., and R. Dunbar. 2010a. Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proceedings of the National Academy of Sciences* 107:21582 - 21586

Shultz, S., and R. I. M. Dunbar. 2010b. Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biological Journal of the Linnean Society* 100:111-123.

—. 2010c. Species differences in executive function correlate with brain size across non-human primates. *Journal of Comparative Psychology* 124:252 - 60.

Shultz, S., E. Nelson, and R. I. M. Dunbar. 2012. Hominin cognitive evolution: identifying patterns and processes in the fossil and archaeological record. *Philosophical Transactions of the Royal Society B-Biological Sciences* 367:2130 - 40.

Shuttleworth, A. 2013. Assessing Neanderthal Behavioural Ecology. PhD Thesis., University of Liverpool.

Silk, J. B., S. C. Alberts, and J. Altmann. 2003. Social Bonds of Female Baboons Enhance Infant Survival. *Science* 302:1231-1234.

Silk, J. B., J. C. Beehner, T. J. Bergman, C. Crockford, A. L. Engh, L. R. Moscovice, R. M. Wittig, R. M. Seyfarth, and D. L. Cheney. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences* 276:3099-3104.

Simunovic, M. P., B. C. Regan, and J. D. Mollon. 2001. Is Color Vision Deficiency an Advantage under Scotopic Conditions? *Investigative Ophthalmology & Visual Science* 42:3357-3364.

Singh, K. D., N. S. Logan, and B. Gilmartin. 2006. Three-Dimensional Modeling of the Human Eye Based on Magnetic Resonance Imaging. *Investigative Ophthalmology & Visual Science* 47:2272-2279.

Slocombe, K. E., and K. Zuberbühler. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences* 104:17228-17233.

Smith, E. E., J. Jonides, and R. A. Koeppe. 1996. Dissociating Verbal and Spatial Working Memory Using PET. *Cerebral Cortex* 6:11-20.

Smith, R. J. 2002. Estimation of Body Mass in Paleontology. *Journal of Human Evolution* 43:271-287.

—. 2009. Use and Misuse of the Reduced Major Axis for Line-Fitting. *American Journal of Physical Anthropology* 140:476-486.

Smith, S. M., M. Jenkinson, M. W. Woolrich, C. F. Beckmann, T. E. J. Behrens, H. Johansen-Berg, P. R. Bannister, M. De Luca, I. Drobnjak, D. E. Flitney, R. K. Niazy, J. Saunders, J. Vickers, Y. Zhang, N. De Stefano, J. M. Brady, and P. M. Matthews. 2004. Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage* 23, Supplement 1:S208-S219.

Smith, T. M., P. Tafforeau, D. J. Reid, J. Pouech, V. Lazzari, J. P. Zermeno, D. Guatelli-Steinberg, A. J. Olejniczak, A. Hoffman, J. Radovčić, M. Makaremi, M. Toussaint, C. Stringer, and J.-J. Hublin. 2010. Dental evidence for ontogenetic differences between modern humans and Neanderthals. *Proceedings of the National Academy of Sciences* 107:20923 - 20928.

Sol, D. 2009. Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters* 5:130-133.

Sol, D., R. P. Duncan, T. M. Blackburn, P. Cassey, and L. Lefebvre. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences* 102:5460-5465.

Sol, D., N. Garcia, A. Iwaniuk, K. Davis, A. Meade, W. A. Boyle, and T. s. Szakely. 2010. Evolutionary Divergence in Brain Size between Migratory and Resident Birds. *PLoS ONE* 5:e9617.

Song, C., D. S. Schwarzkopf, R. Kanai, and G. Rees. 2011. Reciprocal Anatomical Relationship between Primary Sensory and Prefrontal Cortices in the Human Brain. *Journal of Neuroscience* 31:9472-9480.

Sorensen, M. V., and W. R. Leonard. 2001. Neandertal energetics and foraging efficiency. *Journal of Human Evolution* 40:483-495.

Sperber, D., and L. A. Hirschfeld. 2004. The cognitive foundations of cultural stability and diversity. *Trends in cognitive sciences* 8:40-46.

Spocter, M. A., and P. R. Manger. 2007. The use of cranial variables for the estimation of body mass in fossil hominins. *American Journal of Physical Anthropology* 134:92-105.

Steele, J. 1996. "Predicting hominid group sizes," in *The Archaeology of Human Ancestry: Power, Sex and Tradition*. Edited by J. Steele and S. Shennan. Abingdon, Oxfordshire: Routledge.

Stephan, H., H. Frahm, and G. Baron. 1981. New and Revised Data on Volumes of Brain Structures in Insectivores and Primates. *Folia Primatologica* 35:1 - 29.

—. 1984. Comparison of Brain Structure Volumes in Insectivora and Primates. IV. Non-cortical visual structures. *Journal fur Hirnforschung* 25:385 - 403.

Stevens, C. F. 2001. An evolutionary scaling law for the primate visual system and its basis in cortical function. *Nature* 411:193-195.

Stewart, J. R. 2004. Neanderthal–modern human competition? A comparison between the mammals associated with Middle and Upper Palaeolithic industries in Europe during OIS 3. *International Journal of Osteoarchaeology* 14:178 - 189.

Stiller, J., and R. I. M. Dunbar. 2007. Perspective-taking and memory capacity predict social network size. *Social Networks* 29:93-104.

Stiner, M., and S. Kuhn. 2006. Changes in the ‘Connectedness’ and Resilience of Paleolithic Societies in Mediterranean Ecosystems. *Human Ecology* 34:693-712.

Stiner, M. C., S. L. Kuhn, and E. Güleç. 2013. Early Upper Paleolithic shell beads at Üçağızlı Cave I (Turkey): Technology and the socioeconomic context of ornament life-histories. *Journal of Human Evolution*.

Stockman, A., and L. T. Sharpe. 2006. Into the twilight zone: the complexities of mesopic vision and luminous efficiency. *Ophthalmic Physiol Opt* 26:225-239.

Street, M., T. Terberger, and J. r. Orschiedt. 2006. A critical review of the German Paleolithic hominin record. *Journal of Human Evolution* 51:551-579.

Stringer, C. 2012. The status of Homo heidelbergensis (Schoetensack 1908). *Evolutionary Anthropology: Issues, News, and Reviews* 21:101-107.

Stringer, C. B., J. C. Finlayson, R. N. E. Barton, Y. Ferná¡ndez-Jalvo, I. Cáceres, R. C. Sabin, E. J. Rhodes, A. P. Currant, J. Rodrí-guez-Vidal, F. Giles-Pacheco, and J. A.

Riquelme-Cantal. 2008. Neanderthal exploitation of marine mammals in Gibraltar. *Proceedings of the National Academy of Sciences* 105:14319-14324.

Sutcliffe, A., R. Dunbar, J. Binder, and H. Arrow. 2011. Relationships and the social brain: Integrating psychological and evolutionary perspectives. *British Journal of Psychology* 103:149 - 168.

Svoboda, J. A. 2007. The Gravettian on the Middle Danube in Spécial table ronde (1ère partie) : Le Gravettien : entités régionales d'une paléoculture européenne, Les Eyzies 2004. *Revue D'Archaeologie Prehistorique* 19.

Testart, A. 1988. "Food storage among hunter-gatherers: More or less security in the way of life.," in *Coping with Uncertainty in Food Supply*. Edited by I. Garine and G. A. Harrison. Oxford: Oxford University Press.

Thieme, H. 1997. Lower Palaeolithic hunting spears from Germany. *Nature* 385:807-810.

Thomas, R. J., T. Székely, I. C. Cuthill, D. G. C. Harper, S. E. Newson, T. D. Frayling, and P. D. Wallis. 2002. Eye size in birds and the timing of song at dawn. *Proceedings of the Royal Society B: Biological Sciences* 269:831-7.

Thomas, R. J., T. Székely, R. F. Powell, and I. C. Cuthill. 2006. Eye size, foraging methods and the timing of foraging in shorebirds. *Functional Ecology* 20:157-65.

Tilvis, R. S., P. Routasalo, H. Karppinen, T. E. Strandberg, H. Kautiainen, and K. H. Pitkala. 2012. Social isolation, social activity and loneliness as survival indicators in old age; a nationwide survey with a 7-year follow-up. *European Geriatric Medicine* 3:18-22.

Tomasello, M., J. Call, and B. Hare. 2003. Chimpanzees understand psychological states – the question is which ones and to what extent. *Trends in Cognitive Sciences* 7:153-156.

Tomasik, E., D. Czepita, M. Zejmo, and F. Czerwinski. 2005a. Development of the human eyeball and orbit during fetal life. *Ann Acad Med Stetin* 51:37 - 40.

—. 2005b. Fetal ocular and orbital development in humans. *Durham Anthropology Journal* 12:2 - 3.

Torrence, R. 1983. "Time budgeting and hunter-gatherer technology," in *Hunter-Gatherer Economy in Prehistory: A European Perspective*. Edited by G. Bailey, pp. 11 - 22. Cambridge: Cambridge University Press.

—. 2001. "Hunter-gatherer technology: macro- and microscale approaches.," in *Hunter-gatherers: An Interdisciplinary Perspective*. Edited by C. Panter-Brick, R. Layton, and P. Rowley-Conwy, pp. 73 - 95. Cambridge: Cambridge University Press.

Trinkaus, E., and M. LeMay. 1982. Occipital bunning among later Pleistocene hominids. . *American Journal of Physical Anthropology* 57:27-35.

Tripp, R. B. 1982. Time Allocation in Northern Ghana: An Example of the Random Visit Method. *The Journal of Developing Areas* 16:391-400.

Trujillo-Ortiz, A. accessed 2011. "bootgmregress, http://www.mathworks.com/matlabcentral/fileexchange/31479-bootgmregress," vol. 2011.

Twelker, J. D., G. L. Mitchell, D. H. Messer, R. Bhakta, L. A. Jones, D. O. Mutti, S. A. Cotter, R. N. Kleinstein, R. E. Manny, K. Zadnik, and t. C. S. Group. 2009. Children's Ocular Components and Age, Gender, and Ethnicity. *Optometry & Vision Science* 86:918-935 10.1097/OPX.0b013e3181b2f903.

USA Astronomical Applications Department. Accessed 2011. "Rise, Set, and Twilight Definitions [online], available at: http://aa.usno.navy.mil/faq/docs/RST_defs.php."

van Andel, T. H., and W. D. Davies. Editors. 2003. *Neanderthals and Modern Humans in the European Landscape of the Last Glaciation - Archaeological Results of the Stage 3 Project. Simulations provided [online] at:*

ftp://ftp.essc.psu.edu/pub/emsei/pollard/Stage3/: The McDonald Institute for Archaeological Research: Cambridge. .

Van Essen, D. C., and H. A. Drury. 1997. Structural and functional analyses of human cerebral cortex using a surface-based atlas. *Journal of Neuroscience* 17:7079 - 7102.

Van Overwalle, F. 2009. Social cognition and the brain: A meta-analysis. *Human Brain Mapping* 30:829-858.

van Woerden, J. T., C. P. van Schaik, and K. Isler. 2010. Effects of Seasonality on Brain Evolution: Evidence from Strepsirrhine Primates. *American Naturalist* 176.

van Woerden, J. T., E. P. Willems, C. P. van Schaik, and K. Isler. 2011. Large brains buffer energetic effects of seasonal habitats in catarrhine primates. *Evolution* 66:191 - 199.

Vanhaeren, M., and F. d'Errico. 2006. Aurignacian ethno-linguistic geography of Europe revealed by personal ornaments. *Journal of Archaeological Science* 33:1105-1128.

Vannas, A. E., G. S. Ying, R. A. Stone, M. G. Maguire, V. Jormanainen, and T. Tervo. 2003. Myopia and natural lighting extremes: risk factors in Finnish army conscripts. *Acta Ophthalmologica Scandinavica* 81:588-595.

von dem Hagen, E. A. H., G. C. Houston, M. B. Hoffmann, G. Jeffery, and A. B. Morland. 2005. Retinal abnormalities in human albinism translate into a reduction of grey matter in the occipital cortex. *European Journal of Neuroscience* 22:2475-2480.

Waguespack, N. M. 2005. The Organization of Male and Female Labor in Foraging Societies: Implications for Early Paleoindian Archaeology. *American Anthropologist* 107:666-676.

Waitzman, A. A., J. C. Posnick, D. C. Armstrong, and G. E. Pron. 1992. Craniofacial Skeletal Measurements Based on Computed Tomography: Part II. Normal Values and Growth Trends. *The Cleft Palate-Craniofacial Journal* 29:118-128.

Wales, N. 2012. Modeling Neanderthal clothing using ethnographic analogues. *Journal of Human Evolution* 63:781-795.

Walls, G. L. 1942. *The Vertebrate Eye and its Adaptive Radiation*: Bloomfield Hills, Mich., Cranbrook Institute of Science.

Wanner, J. A. 1971. Relative brain size: A critique of a new measure. *American Journal of Physical Anthropology* 35:255-257.

Washburn, S. L., and S. B. Detwiler. 1943. An experiment bearing on the problems of physical anthropology. *American Journal of Physical Anthropology* 1:171-190.

Weaver, A. H. 2005. Reciprocal evolution of the cerebellum and neocortex in fossil humans. *Proceedings of the National Academy of Sciences* 102:3576-3580.

Weaver, T. D. 2003. The shape of the Neandertal femur is primarily the consequence of a hyperpolar body form. *Proceedings of the National Academy of Sciences* 100:6926-6929.

—. 2009. The meaning of Neandertal skeletal morphology. *Proceedings of the National Academy of Sciences* 106:16028-16033.

Weaver, T. D., C. C. Roseman, and C. B. Stringer. 2007. Were neandertal and modern human cranial differences produced by natural selection or genetic drift? *Journal of Human Evolution* 53:135-145.

Weaver, T. D., and K. Steudel-Numbers. 2005. Does Climate or Mobility Explain the Differences in Body Proportions Between Neandertals and Their Upper Paleolithic Successors? *Evolutionary Anthropology: Issues, News, and Reviews* 14:218-223.

Wetherald, R. T., and S. Manabe. 1986. An investigation of cloud cover change in response to thermal forcing. *Climatic Change* 8:5-23.

Whallon, R. 2006. Social networks and information: Non-"utilitarian" mobility among hunter-gatherers. *Journal of Anthropological Archaeology* 25:259-270.

Whitnall, S. E. 1921. *The Anatomy of the Human Orbit and Accessory Organs of Vision*: The Oxford Medical Publications, Henry Frowde and Hodder & Stoughton, London.

Wiessner, P. 1981. Measuring the impact of social ties on nutritional status among the !kung San. *Social Science Information* 20:641 - 678.

—. 1982. "Risk, reciprocity and social influences on !Kung San economics.," in *Politics & History in Band Societies*. Edited by E. Leacock and R. B. Lee, pp. 61 - 84. Cambridge, USA.: Cambridge University Press.

—. 1983. Style and Social Information in Kalahari San Projectile Points. *American Antiquity* 48:253-276.

—. 2002. Hunting, healing, and hxaro exchange: A long-term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evolution and Human Behavior* 23:407-436.

Wiessner, P., and T. Schweizer. 1998. On Network Analysis: The Potential for Understanding (and Misunderstanding) !Kung Hxaro. *Current Anthropology* 39:514-519.

Wilkins, J., B. J. Schoville, K. S. Brown, and M. Chazan. 2012. Evidence for Early Hafted Hunting Technology. *Science* 338:942-946.

Williams, B. J., and H. M. Wobst. 1974. A Model of Band Society. *Memoirs of the Society for American Archaeology*:i-138.

Williams, R., C. Cavada, and F. Reinoso-Suarez. 1993. Rapid evolution of the visual system: a cellular assay of the retina and dorsal lateral geniculate nucleus of the Spanish wildcat and the domestic cat. *Journal of Neuroscience* 13:208-228.

Wilmsen, E. N. 1973. Interaction, Spacing Behavior, and the Organization of Hunting Bands. *Journal of Anthropological Research* 29:1-31.

Winterhalder, B. 1986. Diet choice, risk, and food sharing in a stochastic environment. *Journal of Anthropological Archaeology* 5:369-392.

—. 1996. Social Foraging and the Behavioural Ecology of Intragroup Resource Transfers. *Evolutionary Anthropology* 5:46 - 57.

Wittig, R. M., C. Crockford, J. Lehmann, P. L. Whitten, R. M. Seyfarth, and D. L. Cheney. 2008. Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior* 54:170-177.

Wobst, H. M. 1974. Boundary Conditions for Paleolithic Social Systems: A Simulation Approach. *American Antiquity* 39:147-178.

—. 1976. Locational relationships in Paleolithic society. *Journal of Human Evolution* 5:49-58.

Wood, J. N., D. D. Glynn, B. C. Phillips, and M. D. Hauser. 2007. The Perception of Rational, Goal-Directed Action in Nonhuman Primates. *Science* 317:1402-1405.

Wood, R. E., C. Barroso-Ruíz, M. Caparrós, J. F. Jordá Pardo, B. Galván Santos, and T. F. G. Higham. 2013. Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. *Proceedings of the National Academy of Sciences*.

Woods, R. P., N. B. Freimer, J. A. De Young, S. C. Fears, N. L. Sicotte, S. K. Service, D. J. Valentino, A. W. Toga, and J. C. Mazziotta. 2006. Normal variants of Microcephalin and ASPM do not account for brain size variability. *Human Molecular Genetics* 15:2025-2029.

Woolrich, M. W., S. Jbabdi, B. Patenaude, M. Chappell, S. Makni, T. Behrens, C. Beckmann, M. Jenkinson, and S. M. Smith. 2009. Bayesian analysis of neuroimaging data in FSL. *NeuroImage* 45:S173-S186.

Wynn, T., and F. L. Coolidge. 2004. The expert Neandertal mind. *Journal of Human Evolution* 46:467-487.

Yang, M. A., A.-S. Malaspinas, E. Y. Durand, and M. Slatkin. 2012. Ancient Structure in Africa Unlikely to Explain Neanderthal and Non-African Genetic Similarity. *Molecular Biology and Evolution* 29:2987-2995.

Zegura, S. L., T. M. Karafet, L. A. Zhivotovsky, and M. F. Hammer. 2004. High-Resolution SNPs and Microsatellite Haplotypes Point to a Single, Recent Entry of Native American Y Chromosomes into the Americas. *Molecular Biology and Evolution* 21:164-175.

Zhong, N., K. Li, S. Lu, L. Chen, T. Yan, F. Jin, and J. Wu. 2009. Correlated Size Variations Measured in Human Visual Cortex V1/V2/V3 with Functional MRI. *Brain Informatics* 5819:36-44.

Zhou, W. X., D. Sornette, R. A. Hill, and R. I. M. Dunbar. 2005. Discrete hierarchical organization of social group sizes. *Proceedings of the Royal Society B: Biological Sciences* 272:439-444.

Zilhao, F., and F. Errico. 1999. The Chronology and Taphonomy of the Earliest Aurignacian and Its Implications for the Understanding of Neandertal Extinction. *Journal of World Prehistory* 13:1-68.

Zilhão, J., D. E. Angelucci, E. Badal-García, F. d'Errico, F. Daniel, L. Dayet, K. Douka, T. F. G. Higham, M. J. Martínez-Sánchez, R. Montes-Bernárdez, S. Murcia-Mascarós, C. Pérez-Sirvent, C. Roldán-García, M. Vanhaeren, V. Villaverde, R. Wood, and J. Zapata. 2010. Symbolic use of marine shells and mineral pigments by Iberian Neandertals. *Proceedings of the National Academy of Sciences* 107:1023 - 1028.

Zilhão, J., F. d’Errico, J.-G. Bordes, A. Lenoble, J.-P. Texier, and J.-P. Rigaud. 2006. Analysis of Aurignacian interstratification at the Châtelperronian-type site and implications for the behavioral modernity of Neandertals. *Proceedings of the National Academy of Sciences* 103:12643-12648.

Zuur, A. F., E. Pearce, and E. N. Ieno. 2012. "Review of multiple linear regression," in *A Beginner's Guide to Generalized Additive Models*. Edited by A. F. Zuur: Highland Statistics.