Why *not* the Neandertals?

Milford H. Wolpoff, Bruce Mannheim, Alan Mann, John Hawks, Rachel Caspari, Karen R. Rosenberg, David W. Frayer, George W. Gill and Geoffrey Clark

Abstract

Some workers have suggested that a hypothetical genetic mutation in an African population less than 100,000 years ago led to a cascade of neurological changes in the human brain that culminated in the appearance of modern language. Language then triggered the socioeconomic and cognitive changes we associate with behavioral modernity and Africans, armed with behavioral modernity, then spread out from that continent, out-competing, displacing, extirpating, outbreeding or, most generally, replacing the Neandertals and other archaic humans throughout the middle latitudes of the Old World. The Neandertals of Europe are the best-known, best-represented and longest studied test case for this theory. In this paper we present evidence from skeletal anatomy, mitochondrial DNA, morphology and genetics of speech and the archaeology of the Middle-Upper Paleolithic transition in Europe that directly contradicts all of the elements in this replacement scenario. The processes leading to modernity involved the entire human species, and were based on the ethnogenic principle of communication and reticulation among populations.

Keywords

Modern human origins; Neandertals; language; cognitive evolution.

Introduction

His large head, with the thick frontal bones, must have been very good for butting a brother Neandertal, but it was no use against the stone wall of advancing civilization, and like the Tasmanian and Bushman, the Red Indian and Australian of nowadays, he fades out of the picture and his place is taken by a cleverer people.

(Quennell and Quennell 1945: 66–7)

Paleoanthropology is well known for being a contentious and argumentative field, and important findings or commentaries are often followed by expressions of differences of opinion. Our colleague Richard Klein (2003) recently published such a commentary, called 'Whither the Neanderthals?' It is a well-organized, up to date, logical presentation of the replacement position, and we believe it can act as an effective baseline for our own discussion of this position, and more generally of the place of Neandertals in human evolution. Reading it, we feel compelled to ask the question in his title slightly differently with: 'Why *not* the Neandertals?'

Klein believes that 'the longest continuous debate in paleoanthropology is nearing resolution', and we agree. However his assertion that 'modern humans replaced the Neandertals with little or no gene exchange' is the easy solution to a complex issue and is counter to the emerging evidence. As we outline here, there are ample, compelling reasons to propose a different resolution. In this paper we show that both old and new evidence from paleontology, paleogenetics and archaeology all point to continuity between European Mousterian and Upper Paleolithic populations.

The four areas of evidence that Klein (2003) cites in his commentary directly contradict the replacement scenario he proposes. Specifically, the evidence of skeletal anatomy, mitochondrial DNA, morphology and genetics of speech, and archaeological evidence of behavior all suggest that Neandertals are indeed among the ancestors of some modern human populations. This does not mean that the modern humans are Neandertals, or that the Neandertals are the only ancestors of any group of modern humans. The existence of differences between Neandertals and modern humans is repeatedly advanced as evidence for the impossibility of Neandertal ancestry in modern populations (most recently by Harvati et al. (2004) and references therein, but there are many others). This is a straw man. While we certainly recognize a number of such differences, they are fully consistent with an evolving lineage: ancestors are never identical to their descendants. Do modern Europeans have a single unique African ancestry, or are European Neandertals among their ancestors? We show here that *the hypothesis that Neandertals are a significant part of the ancestry of Europeans* is well supported, and we explain why we believe it has not been disproved.

To be clear, 'significant' in this context means that Neandertal are among the ancestors of later Europeans, not that Neandertals are the unique or only ancestors of later Europeans. 'Among' and 'significant' do *not* mean a single Neandertal ancestor mixed with many others, or, as one author put it (Pearson 2000: 589), 'enough gene flow to be considered a flood' but rather that Neandertals provided enough of a genetic contribution for their traits to be readily identifiable in later Europeans, and some even found in Europeans today. Of course Neandertals are biologically and culturally extinct, just as all human populations removed from us by 1500 or more generations are extinct today, but extinct in an ethnogenic sense (Moore 1994) and not extinct without issue (Brace 1962).

If any hypothesis has been disproved, it is the argument that Neandertals had little or nothing to do with subsequent European evolution. We review below the evidence for Neandertal replacement as it is reflected in recent publications.

Why Neandertals are not European ancestors

Skeletal anatomy

The debate about a Neandertal ancestry for *later* Europeans has recently been informed by issues raised in a description of an *earlier* African, from the Ethiopian site of Herto (see Plate 1). White et al. assert that 'many morphological features shared by the Herto crania with AMHS [anatomically modern *Homo sapiens*], to the exclusion of the penecontemporaneous Neandertals, provide additional fossil data excluding Neandertals from a significant contribution to the ancestry of modern humans' (2003: 745). But this argument, amounting to the oft-repeated claim that the modern type coexisted with Neandertals, can make sense only from a typological perspective. An evolutionary perspective recognizes that polytypic species may evolve over time, so that the test of a Neandertal ancestry for later Europeans is the pattern of ancestor–descendant relations within Europe. African populations 100,000 years removed from the latest Neandertals could be ancestral to Neandertals, Upper Paleolithic Europeans, both or neither, but they cannot inform the issue of whether the Neandertals are among the ancestors of the Later Europeans. If morphology is the marker for determining ancestry of 'anatomically modern' European *Homo sapiens*, these and other researchers continue to look at the wrong end of the time perspective and in the wrong geographic region. Stringer et al. recognized this in assembling a long list of traits in their 'identification of derived characters that are actually unique only to the Neandertals (autapomorphies)... provide[ing] important evidence for excluding them from the ancestry of modern humans' (1984: 54). They list nineteen characters (1984: 55) for the cranial and postcranial skeleton and similar lists of such evidence are reiterated in Stringer and Gamble (1993: 76–7), Conroy (1997: 421), Klein (1999: 272–82) and numerous other scientific and popular sources essentially repeating these. These lists of characters did not first emerge as Neandertal distinguishing features in 1984, but stretch back 120 years to 1864 in William King's 'The reputed fossil man of the Neanderthal'. King (1864) contended that features of the face and braincase of the Feldhofer Cave individual linked it more closely to 'the Chimpanzee, as to doubt the propriety of generically placing it with Man'.

By now, twenty years later, most of these features are no longer recognized as unique to Neandertals. Many are not even what Stringer et al. call 'common' in Neandertals, if common means reaching frequencies above 50 per cent of the known specimens. This observation is fully compatible with the evidence that the Neandertal habitation of Europe was not a period of reduced gene flow and that Neandertal features did not become more common, or accrete over time there because of genetic isolation[1] (Hawks and Wolpoff 2001a). Neandertal features are not uniformly spread across the Neandertal range, with sharp boundaries with other contemporary populations. Instead, they vary clinally, reducing in frequency to the south east and east. In the Levant, it has been seriously questioned whether the specimens should be called 'Neandertal' at all because they share few diagnostic features with the Europeans (Arensburg and Belfer-Cohen 1998; Wolpoff 1999). To the east, specimens such as Teshik-Tash lack many of the European midfacial features distinguishing western Neandertals (see below), and instead have character states similar to those found in eastern Asia today (observations by Gill).
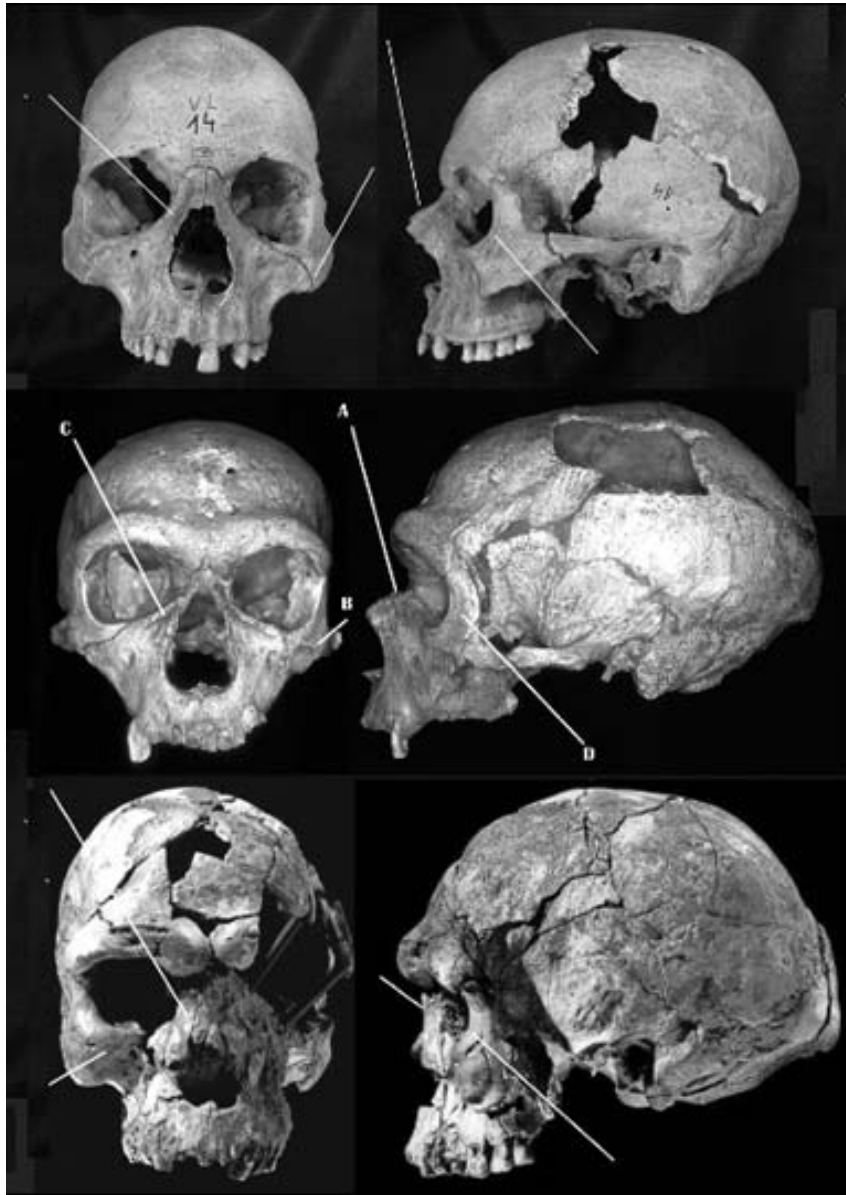
Plate 1 Some distinctive Neandertal features remain common in Europe today.[1] Here we show four features of the midface in La Chapelle (center), with similar anatomy in the modern specimen above, a Copper Age male from a eighth- to tenth-century Croatian site – Lijeva Bara (Vukovar, Croatia) – shown above, and contrasting anatomy in the Herto Ethiopian below (from White et al. 2003) that is supposed to be a modern human dated earlier than the Neandertal. Crania are shown to the same approximate size. The European regional characteristics marked are: A, the high nasal angle defined by the slope of the lofty nasal bridge as it rises up between the orbits and incorporates the frontal processes of the maxillae as well as the nasal bones themselves (not preserved in La Chapelle, the view shows the nasal process of the maxilla); B, the course of the zygomaxillary suture (enhanced) that turns inward at its most inferior aspect; C, the maxillary expansion at the lateral nasal borders, resulting in a 'pinching' of the region so that these borders are laterally oriented; D, the lateral orientation of the zygomatic bone.

The supposedly unique Neandertal features, such as the retromolar space (Franciscus and Trinkaus 1995), posterior placement of the mandibular mental foramen (Trinkaus 1993), taurodontism (Weidenreich 1943), the lateral (in contrast to superior) frontal sinus conformation (Szilvássy et al. 1987), mastoid tubercle (Frayer 1992), suprainiac fossa (Caspari 1991), lambdoidal flattening (Wolpoff 1989), H-O mandibular foramen (Gorjanovic-Kramberger 1906; Smith 1978), dorsal axillary border configuration of the scapula (Churchill 1996), all show considerable variation within the Neandertals and a continuous distribution from Mousterian to early Upper Paleolithic populations.

We are aware of the Bräuer and Broeg (1998) paper, cited by Klein (2003) in support of his argument, which contests some of these observations. These authors dispute the evidence for regional continuity between Neandertals and subsequent Upper Paleolithic populations in Central Europe. However, the definition of regional continuity they employed is incorrect. They equate regional continuity with gradualism, and wrote 'during the long period of coexistence, mixing and gene flow between Neandertals and the dispersing modern populations might have occurred to varying degrees in different regions. . .such gene flow could have mimicked some degree of continuity' (1998: 106). This does not support Klein's argument because the process they describe is actually multi-regional evolution, which is not 'mimicked' by gene flow but is based on it (Wolfpoff and Caspari 1997; Wolpoff et al. 2000). In other words, this kind of reticulating process would demonstrate a Neandertal ancestry for later Europeans, and therefore could not disprove it as Bräuer and Broeg believed. It seems as though the only evidence they would accept as showing continuity would be a demonstration that the post-Neandertal populations of the region were actually Neandertal populations

But of course they were not, although the earliest post-Neandertal Europeans retain the highest frequencies of Neandertal features (Duarte et al. 1999; Frayer et al. 2005; Wolpoff et al. 2005) We recognize it is not reasonable to calculate frequencies for the very small samples of the earliest known post-Neandertal Europeans, but we find it significant that numerous features common or ubiquitous in Neandertals are even preserved in this small sample. For instance, Largo Velho shows enough mixture of features for some to describe it as a hybrid (Zilhão 2001), Mladeč 6 has a suprainiac fossa of elliptical form (contra Bräuer and Broeg, see Caspari 1991), extensive lambdoidal flattening and a short posterior face on its occipital. Mladeč 5 has a very Neandertal-like sagittal contour, a well-developed occipitomastoid crest, minimal mastoid projection and evidence of midfacial prognathism (insofar as the marked anterior projection of the upper face predicts this). Mladeč 8 has an exceptionally large maxillary canine and a groove along the inferior nasal margin and the remnant of a medial projection on the internal wall of the nasal aperture. In fact, the Mladeč males have sagittal dimensions and profiles that deviate far less from the Neandertals than they deviate from the Skhul/Qafzeh males (Wolpoff 1989).

Some of the comparisons leading to these conclusions are metric and others are based on non-metric evaluations. Metric features cannot be treated as non-metric ones, and the issues of character state are not easily resolved. This has not prevented decades of attempts to show that Neandertals are a different species because they are too metrically distinct from living humans, or (less often) from the human populations that follow them in Europe, to serve as credible ancestors. This can be described as the 'evolution is too slow' argument, which persists in spite of evidence that morphological evolution can proceed

quite quickly even under low magnitudes of selection, more than quickly enough to account for how Neandertals could have evolved into later Europeans (Eckhardt 1985; Frayer 1997). Compared with other primate species, the amount of difference is just not that great. Harvati and colleagues (Harvati et al. 2004) analyzed the pattern of three-dimensional variation between fifteen standard craniofacial landmarks and compared five Neandertal males with samples of other humans and a number of non-human primate species. The mean morphological differences between two *Gorilla* subspecies and two *Papio* subspecies were not significantly smaller than the difference between the male only Neandertals and modern humans,[2] in spite of the fact that the difference between the male Neandertals and modern humans is amplified by the presence of modern human females in the comparisons, and by the mean time difference between the samples.

Attempts to redefine and expand a list of large metric differences and autapomorphies continue, and Weidenreich (1943: 44) now sounds prescient when he quipped more than sixty years ago:

> It almost became a sport of a certain group of authors to search for the skeletal parts of Neandertal Man for peculiarities which could be claimed as 'specialization', thereby proving the deviating course this form has taken in evolution. There is not one single peculiarity which has not been taken by some author to represent a unilateral specialization. Yet, evidence proving the correctness of such statements is lacking in all of the cases.

Even the most recent attempts to discern new Neandertal autapomorphies are regularly beset with fundamental problems, so that the distinctive nasal features proposed by Schwartz and Tattersall (1996) have been shown to be either inaccurately described (Franciscus 1999) or not unique to Neandertals (Wolpoff and Frayer 2004). Klein (2003) discusses the 'singular configuration of the bony labyrinth of the inner ear', citing the Châtelperronian-associated temporal bone from Grotte du Renne at Arcy-sur-Cure (Hublin et al. 1996) as an example. However, he overlooks a more recent study showing that the bony labyrinth of the Le Moustier Neandertal cranium was modern in form (Ponce de León and Zollikofer 1999). The same is true of the characteristics Rak (1998, Rak et al. 2003) recently proposed as autapomorphies for the Neandertal mandible, which are, in fact, neither monomorphic nor unique to them (Jabbour et al. 2002; Wolpoff and Frayer 2004).

Some of the variation in these features turns out to be temporal. There are trends within Neandertal populations which show the emergence of more 'modern' features (such as higher foreheads and the development of chins) and metric dimensions (such as the reduction of facial prognathism and brow-ridge dimensions) over time (Ahern et al. 2003; Frayer 1997; Wolpoff 1989), which demonstrate these populations were never static or one dimensional in any of their so-called autapomorphies, but moving to a more 'modern' configuration, as might be expected were these populations connected to the rest of humanity by genetic and cultural exchanges.

Most important for the position we take here are the numerous common Neandertal features now known to persist into the early Upper Paleolithic (Frayer 1992) at high enough frequencies that a hypothesis of 50 per cent Neandertal ancestry for these

European populations cannot be rejected (Wolpoff et al. 2001). Early Upper Paleolithic samples preserve evidence of mixture between Neandertals and populations entering Europe during the interstadials (Frayer 1986; Frayer et al. 2005; Wolpoff 1999), and the significant number of Neandertal traits extending into these later populations (Frayer 1992; Wolpoff et al. 2001) cannot be explained without gene flow between Neandertal and the subsequent populations of Europe – an observation based not on one or two individuals but on the details of many individuals from the European early Upper Paleolithic. In fact, if there is a clear break in the majority of these 'Neandertal autapomorphies', it is between the Aurignacian and the Magdalenian/Mesolithic – populations for which no one seriously doubts an ancestor–descendant relationship – and any significant number of genes remaining did not survive the population replacement and extinction at the onset of the Neolithic (Chikhi et al. 1998, 2002). But, using the logic of the Neandertal 'rejectionists', the Aurignacian/Gravettian populations of Europe would have no ancestral relationship to the Magdalenian and Mesolithic people, in fact no known ancestors at all since all previous groups are different from them. And, the Skhul/Qafzeh specimens are not the way out of this conundrum, since they differ in substantial ways from the fossil Europeans, whether at 30 kyrs or 10 kyrs.

Where are these Neandertal features today? The answer is that some have disappeared while others remain in Europe, and some of these are commonly used in forensic applications for determining ancestral affinities (Frayer 1992, 1997; Gill and Rhine 1990; Lampl et al. 1991; Szilvássy et al. 1987). Most never consider these later traits as evidence of a Neandertal heritage, but they appear in European Neandertals at higher frequencies than other groups contemporary with them and parsimony explains them as Neandertal features. Included in these are the four indicated in Plate 1: (1) the high nasal angle involving the slope of the lofty nasal bridge, as it rises up between the orbits, incorporating the frontal processes of the maxillae as well as the nasal bones themselves; (2) the course of the zygomaxillary suture (turning inward at its inferior aspect); (3) the maxillary expansion at the lateral nasal borders; and (4) the lateral zygomatic orientation (marked respectively as A, B, C and D on the plate). These features, and others like them, are not present in Neandertal contemporaries, such as those from Qafzeh in Western Asia or the Herto Ethiopian (shown in Plate 1). While we would never consider them to be 'autapomorphic' for Europeans, they are indisputably more common in fossil and contemporary Europeans than other groups, thereby linking these populations through time and making it very unlikely that the source populations of recent and modern Europeans are uniquely from Africa.

Klein (2003) does accept the evidence for the mixture of Middle and Upper Paleolithic artifact types, and observes that 'if Upper Paleolithic technology allowed more effective use of natural resources and larger human populations, it is puzzling that Neanderthals failed to adopt it more widely. If they had done so, then their unique skeletal traits and genes would be more obvious in succeeding populations.' We shall never know how often Neandertals acquired early Upper Paleolithic technology, or for that matter whether Neandertals invented it independently (d'Errico et al. 1998), because the vast majority of the earliest Upper Paleolithic sites lack diagnostic skeletal material, but, as detailed above, we *do* know that Klein is quite incorrect in asserting that Neandertal skeletal traits are not evident in succeeding European populations – they are evident enough to be significant in their frequency of occurrence,

Mitochondrial DNA

There is significant disagreement in how ancient mtDNA studies can be used to address Neandertal ancestry. The most commonly cited interpretation is that 'mitochondrial DNA extracted from Neandertal bones…indicate that the last shared ancestor of Neandertals and living humans lived 500,000 to 600,000 years ago' (Klein 2003: 1525). But this interpretation omits important details. Even a complete and ancient mtDNA separation could not support the contention that Neandertal and modern populations had a last shared ancestor at this ancient time (Nordborg 1998), since genetic differences must always substantially antedate any population divergence. In the case of Neandertal mtDNA, it remains quite possible that no divergence between populations occurred at all (Serre et al. 2004). The data are simply uninformative on this point.

Moreover, more recent analyses have weakened the case for Neandertal extinction by questioning both the pattern of mtDNA relationships and the date of mtDNA divergence. The recovered Neandertal mtDNA sequences are not more similar to Europeans than to other humans (Krings et al. 1997). But such a similarity is not a necessary prediction of a partial Neandertal ancestry (Relethford 2001). Gutierréz et al. (2002) showed that considering the hypervariable I (HVI) and II sequences together gives a different result than the initial studies that incorporated only HVI. The fuller dataset shows that ten African sequences form an outgroup to 367 Africans and non-Africans and two Neandertals, who thereby are not on a different branch from later humans. In other words, the topology of the mtDNA tree cannot justify a strong separation of Neandertals from living humans. These authors also point to the possibility that Neandertal sequences have been degraded, most notable in the comparison between the most ancient Neandertal sequence, which is most divergent from humans, and the most recent (Mezmaiskaya), which is closest to humans (Caldararo and Gabow 2000, Gutierréz et al., 2002). This contradicts a separate lineage interpretation which requires that the divergence increases with time and is strongest in the most recent specimens. This discrepancy might also be explained by the possibility that Mezmaiskaya is not a Neandertal (Hawks and Wolpoff 2001b), which would provide strong evidence of the survival of their mtDNA into later humans.

But these considerations may well be irrelevant, because all fail to consider that a very likely explanation for the level of diversity of this single genetic locus (Spuhler 1988) is selection (Elson et al. 2004; Gillespie 2001). Selection explains why the observed mtDNA sequence variation in recent humans is lower than that in Late Pleistocene humans, as well as accounting for the long-recognized evidence that mtDNA variation is non-neutral (Merriwether et al. 1991; Nachman et al. 1996). The fixation of an advantageous mtDNA variant during the Late Pleistocene may well have been within a single human species including both Neandertals and other ancestors (Elson et al. 2004). Such an evolutionary change may have involved any of the functions of the mtDNA sequence, because selection on any small part of it is the same as selection on the whole (Gillespie 2001; Kim and Stephan, 2000; Nachman et al., 1998). This hypothesis leads to the prediction that all earlier mtDNA variants will be equally related to the many current mtDNA lineages, descendants of the most recent selected variant, a prediction that remains uncontested (Serre et al. 2004). Thus, it is not evident that any information can be gained about Neandertals from this locus, other than that they existed before the currently advantageous variant had spread to Europe.

Genetics and the morphology of speech

If modern humans replaced the Neandertals in Europe without mixture, what advantage might have allowed this? Over and over again the answer to this has been human language (Klein 2003; Krantz 1980, 1994; Lieberman and Crelin 1971; Milo and Quiatt 1993), an increasingly accepted explanation that, curiously, has yet to accrue a single strand of testable, scientific support.[3] The evidence indicating a late origin for language is by far the most equivocal. Long ago it was suggested that the vowel space of modern humans provides fixed quantal points through which individuals can co-ordinate vocal representation. The first reconstruction of the Neandertal vocal tract showed it to have a significantly different vowel space from modern humans (Lieberman and Crelin 1971). However, more recent reconstructions (Heim 1989) and simulations (Boë et al. 2002) show that, contrary to the earlier assumptions, the vowel space of Neandertals is quite similar to that, of modern humans. Moreover, cineradiographic images of a variety of mammals show that during vocalizations, the larynx is retracted deep into the pharynx (Fitch 2002), making the human condition not necessarily a unique development for language.

Discovery of a mutation on the FOXP2 gene (Enard et al. 2002) is important for both the suggested date range it is thought to provide for the origin of language (Klein 2003), and for its functional implications. The selective fixation of the present human allele, which likely occurred within the past 200,000 years (Enard et al. 2002), would imply that any Neandertal population connected by gene flow would have shared the allele as well, a possibility supported by the human-like vowel space now reconstructed for Neandertals (Boë et al. 2002) and the persistence of Neandertal features in later Europeans (Frayer 1992). The appearance of a human-like vowel space is improbable were it not associated with other requisites for human language, and therefore with human language itself, since it is a change that jeopardizes an individual's survival because it increases the likelihood of choking to death. The implication of persisting Neandertal features is even more direct; it must reflect a history of gene flow and population mixture.

While the pathology of the FOXP2 gene is known, its normal function is not, in either humans or chimpanzees. Enard et al. suggest that FOXP2 controls fine facial musculature,[4] which would indeed be involved in speech. Yet the evidence from research on FOXP2 impairment is equivocal as to whether the accompanying linguistic disorder is primarily cognitive or articulatory. Gopnik and colleagues argue for the former (Gopnik and Crago 1991; Ullman and Gopnik 1999). Thus, the relevance of their findings to Klein's argument is less clear than he would have us believe[5] because Enard and colleagues (2002), whom he cites, assume an articulatory function. While at first glance it sounds plausible to say that the spread of the modern human FOXP2 gene marks the emergence of 'more proficient spoken language,' as Enard and colleagues claim, there is no known measure of the proficiency of a first language (or other primary signaling system). Further, in the absence of knowledge of what the gene does, there can be no understanding of the core deficit that might be related to other alleles.

In fact, it turns out that FOXP2 is one of a number of genes, including several involved in the development of hearing, that have been identified as differing between humans and chimpanzees and evolving at a rate fast enough to imply the action of positive selection in the human lineage (Clark et al. 2003). The demonstration of positive selection is important

in this discussion because genes under selection cannot be used to address chronology; their variation reflects the history and intensity of the selective forces acting on them, and not the length of time since they first appeared, which could be the case only if their evolution was neutral. For example, ASPM is a gene with a pathological allele that induces one form of congenital microcephaly in humans. A comparison of the human pattern of genetic variation compared with chimpanzees indicates that positive selection has fixed approximately fifteen adaptive mutations since the human-chimpanzee common ancestor (Evans et al. 2004). A straightforward interpretation of this pattern is that this gene has changed repeatedly on a scale of 300,000–400,000 years during human evolution. This pattern of change is by far more likely, considering fossil evidence for a gradual increase in endocranial volume (Lee and Wolpoff 2003), than the alternative hypothesis that most neurological changes occurred suddenly due to a single mutation within the past 200,000 years.

There is no single silver bullet that will pin down language chronologically through either genetics or anatomy. Even if Neandertals or other contemporary humans lacked the modern form of the FOXP2 allele entirely, or any of the other genes that have evolved uniquely in the human lineage, no evidence suggests that the mere presence of a modern allele is a *sine qua non* for modern linguistic ability. Language is a highly polygenic trait, and scores of selective sweeps must have occurred as the trait evolved during the Pleistocene. No single genetic change was *sufficient* for language, and it is a mistake to assume that the evolution of this highly complex trait was primarily saltational (Hauser et al. 2002). Rather, we must understand language in its fullest cognitive and social senses as involving a cluster of related features; among them theory of mind (Cheney and Seyfarth 1990; Povinelli et al. 2000; Povinelli 1987, 1993), perspective taking and attention (Baldwin 1995; Tomasello and Barton 1994; Bloom 2000; Bernieri and Rosenthal 1991), interactional synchrony (Couper-Kuhlen 1993; Erickson 1993; Auer *et al.* 1999) and co-ordination of interpretative contextualizations (Gumperz 1992; Silverstein 1993), some of which will be indexed physiologically in ways we have not even begun to explore.

It is very likely that language is an emergent property of human cognition (Premack 2004) rooted deeply in our evolutionary history as social primates (see, e.g., Cheyney and Seyfarth 1990; Hauser 1996; papers in Hauser and Konishi 1999). Arguments from cognitive neuroscience, psychology, non-human primate capacity, early hominid intelligence and the successful, long-term radiation of early hominids in the absence of large-scale genetic change all suggest that a 'language-like' communicative *repertoire* was present during the Middle, and probably Lower, Pleistocene. If the epigenetic and developmental predisposition for language acquisition is 'hard-wired' into hominid brains, as these studies suggest, it might even go back to the origins of *Homo* at *c*. 2 mya (Frayer and Wolpoff 1993). Although modern language is symbolic, it almost certainly evolved from non-symbolic gestural and/or representation antecedents, and then subsequently exapted (i.e. took on other functions, see Hauser et al. 2002). When this occurred is subject to debate, but it clearly was a 'process' (Caspari 2002) and not – as Klein (2003) would have it – an 'event', and the process almost certainly had nothing to do with either genetic superiority or the over-simplistic replacement scenarios so prevalent in the archaeology of modern human origins (Clark 2003). There is nothing radical in these observations. Darwin (1871) himself suggested that language was a gradually selected capability that

emerged from more primitive forms of communication evident in animals. It may well be that the only uniquely human characteristic of language is recursion (the ability to generate an infinite range of expressions from a finite set of elements), but even that might have arisen for reasons other than communication (e.g. computational system outside the domain of language, as suggested by Hauser et al. 2002).

Archaeological evidence of behavior

Using Mellars' (e.g. 1989) criteria for defining the Middle-Upper Paleolithic transition as a baseline, Klein (2000, 2003) compares a number of behavioral differences between Neandertals and Cro-Magnons, ranging from the absence of projectile weapons to a much smaller population size and lower population density in the Neandertals. Although the extent to which these criteria can be generalized has been called into question (e.g. Clark 1999), every one of these differences can be explained by the fact that the Neandertal populations were on average earlier than Cro-Magnon ones (Clark 2002; Zilhão and d'Errico 1999), for the most part substantially so. Klein (2003) provides the strongest argument in support of this point, discounting evidence for the apparent survival of late Neandertals in Russia, Croatia and Spain by 'the ever present possibility of minute, undetectable contamination with recent carbon' and by observing that 'only the alternation of Neanderthal and Cro-Magnon layers within a single site could provide unequivocal evidence for substantial chronological overlap'. However, no known European site provides such alternation.

Klein (2003) contends that Neandertals lacked the cognitive ability to compete successfully with Cro-Magnons, as evidenced by the differences between Middle and Upper Paleolithic inventories. However, pattern searches on the commonly accepted archaeological monitors of human adaptation (i.e. lithic technology, typology; raw material variation, reduction strategies, blank types and frequencies, organic technologies, ornaments, subsistence strategies, settlement patterns) have consistently shown a temporal and spatial mosaic wherever the transition interval is recorded (Clark 1997, 2002; Camps 2004; Straus 1996, 1997).

Rather than expediency tools, Châtelperronian awls appear instead as the expression of an articulated know-how transmitted from generation to generation. Their prolonged use and reuse after breakage or resharpening suggest that those tools belonged to specific individuals who spent days, if not weeks, on domestic activities planned long ahead. These awls were used to produce ten to 100,000 holes, probably in hides of different toughness. The presence of deliberate decoration on a number of these pieces suggests that, far from being an intrusive behavior, poorly assimilated and limited to a few bartered objects, symbolism permeates all aspects of Châtelperronian life (d'Errico et al. 2003: 267).

The notion that Upper Paleolithic (i.e. Châtelperronian) artifacts associated with Neandertal fossils at several sites in France and Spain can be explained only as the result of Neandertal imitation of the tool-making skills of their Cro-Magnon neighbors has been contested by several workers (e.g. Zilhão and d'Errico 1999) and is not supported by lithic analysis of the different assemblages (d'Errico et al. 1998). Others have argued that Châtelperronian tools made by Neandertals have an entirely different pattern of

manufacture and represent a distinct stone-tool tradition, not one derived from those of the Cro-Magnons (e.g. Pelegrin 1995; d'Errico et al. 2003). Still others have taken issue with the essentialism inherent in the basic analytical units (e.g. Aurignacian, Châtelperronian) used to describe variation on either side of the Middle–Upper Paleolithic transition (e.g. Clark 1999, 2002). In our view these associations are neither idiosyncratic nor accidental. They are refutations of Klein's causal hypothesis that a genetically based cognitive leap not shared by Neandertals is necessary to account for the increased sophistication implied by the conventional criteria used to define the Upper Paleolithic.

Even if, in spite of the evidence of dating and archeology, the Châtelperronian Neandertals were 'only' copying other Upper Paleolithic industries, the fact is that one does not copy what one cannot understand. We believe it unlikely that the Upper Paleolithic reflects a change in the genetic basis of cognition or intelligence. The strongest argument against a cognitive saltation is the archaeological record itself. Klein's case for Neandertal cognitive inferiority depends upon the ecological assumption that 'Upper Paleolithic technology allowed more effective use of natural resources and larger human populations', and the associated assumption that 'Neanderthals failed to adopt it...widely'. But a primarily ecological view of technological change does not imply cognitive limitations among those who fail to adopt it. The technological developments of the last century have had far more dramatic effects on population and resources than did those that supposedly define the Upper Paleolithic, yet neither gasoline engines, vaccines nor qwerty keyboards imply any genetic saltation in cognition – indeed, any cognitive evolution at all. The material culture left behind by Native Tasmanians for archaeologists to ponder is meager by comparison with that of most other living peoples. But Tasmanians were modern humans nevertheless, and had a rich social and cultural life (Diamond 1998). None of this would have been apparent to an archaeologist excavating a Tasmanian living site.

Technologies, like blades, bone tools and ornaments, found in Mousterian contexts and the association of Neandertal remains with Upper Paleolithic industries are not explained by Neandertal acculturation or by the speculation that virtually every late Neandertal find has been misdated due to radiocarbon contamination.[6] As is true of people today, among Neandertals, culture is not related to biology.

Conclusions

After more than 150 years of Europeans' 'second' encounter with Neandertals, is there any reason to exclude them from the ancestry of Europeans? We believe the answer is only if we exclude a lot of other ancestors too. Rather than the continual drumbeat of Neandertals as the 'other' and the constant exclusion of evidence and rejection of interpretations that suggest otherwise, it is time to recognize them as ancestors and begin the analyses that will help us to account for the evolutionary changes that include them within the European family, not the oddball, celibate outsider. For us Europeans, the Neandertal debate is nearing resolution and the conclusion is that they are one of us. Recognizing this is a key step in the process of understanding how and why we became different

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Alan Mann, *Department of Anthropology, Princeton University*
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Karen R. Rosenberg, *Department of Anthropology, University of Delaware*
David W. Frayer, *Department of Anthropology, University of Kansas*
George W. Gill, *Department of Anthropology, University of Wyoming*
Geoffrey Clark, *Department of Anthropology, Arizona State University*

Notes

1 The interpretation of Middle Pleistocene European isolation has been so strongly entrenched in paleoanthropological thinking since Howell's publications (beginning with Howell 1952) that even when a European Neandertal is shown to be more similar to penecontemporary Skhul specimens than to other Neandertals (Sládek et al. 2002), the obvious interpretation of gene flow is not considered.
2 Nevertheless, the authors conclude: 'we interpret the evidence presented here as supporting the view that Neanderthals represent an extinct human species' (Harvati et al. 2004: 1152).
3 Regarding his theory of a recent neurological change at the time of language origins, Klein admits that 'unfortunately, then, for the moment a biological (neural) explanation for behavioral change 50 to 40 ky ago cannot be tested independently of the archaeological evidence it is advanced to explain' (2000: 27).
4 'A predominant feature of the phenotype of affected individuals is an impairment of selection and sequencing of fine orofacial movements, an ability that is typical of humans and not present in the great apes' (Enard et al. 2002).
5 Even though Enard and colleagues (2002) cite Klein in support of their arguments.
6 Which, if true, would remove one of the pillars supporting the replacement hypothesis in Europe by revoking evidence for temporal overlap between Neandertal and 'modern' populations.

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Milford H. Wolpoff, Professor of Anthropology at the University of Michigan, is a paleoanthropologist with research and publication experience with the human and anthropoid primate fossil record throughout the world. Author of *Paleoanthropology* (1980, 1999) and numerous other books and papers from *Sahelanthropus* to the Neandertal issue, he is known as a founder of Multiregional Evolution.

Bruce Mannheim, Professor of Anthropology, University of Michigan, is a leading linguistic anthropologist with formal training in linguistics and in social anthropology. He is author of *The Language of the Inka since the European Invasion* (1991) and coeditor of *The Dialogic Emergence of Culture* (1995). Professor Mannheim is a past Guggenheim fellow, a National Endowment for the Humanities fellow, and was twice a fellow of the Institute for the Humanities at Michigan.

Alan Mann is Professor of Anthropology at Princeton University and Research Associé, Laboratoire d'Anthropologie, Université de Bordeaux 1. He has been a Fulbright Scholar in France and a Visiting Professor at the University of Cape Town, the Collège de France, and the Katholieke Universiteit in Leuven. He is co-director of the excavation at the

Middle Paleolithic site of Les Pradelles in the Charente. Professor Mann is known for his research in dental evolution and for contributions to casting and preservation.

John Hawks, Assistant Professor of Anthropology, University of Wisconsin-Madison, specializes in evolutionary genetic approaches to fossil and molecular evidence of human origins and evolution. After receiving his PhD from the University of Michigan, he completed a postdoctoral fellowship in molecular demography at the University of Utah. He is author of the upcoming textbook, *Human Evolution*.

Rachel Caspari, Research Scientist and Lecturer in Anthropology at the University of Michigan, is a paleoanthropologist interested in various perspectives on the meaning of evolutionary modernity. She is co-author of *Race and Human Evolution* (1997) where she examined the effects of the relationship between racial politics and science on our understandings of modernity. She is currently researching life history changes associated with the Middle/Upper Paleolithic transition.

Karen R. Rosenberg, Associate Professor and Chair of Anthropology, University of Delaware, is a paleoanthropologist with interests in the origin of modern humans and the evolution of human childbirth. She has studied human fossils and modern human skeletal material in Europe, Asia and Africa, has analyzed prehistoric Native American remains from Delaware, and is founding co-editor of the on-line journal *PaleoAnthropology*, journal of the Paleoanthropology Society.

David W. Frayer, Professor of Anthropology, University of Kansas, studies European fossil material from the Neandertals to the Neolithic. His research addresses the problem of variation and its role in human evolution, focusing on questions of form and function, and the interpretation of past behavior. Currently, he is involved with the compilation of a comprehensive bibliography of the Krapina Neandertal site in Croatia.

George W. Gill, Professor of Anthropology, University of Wyoming, is a skeletal biologist/bioarchaeologist with an interest in the origins and relationships of modern populations. He has excavated and studied skeletons in Mexico, eastern Polynesia and the Great Plains of North America. He is also a board-certified forensic anthropologist, has served as Chairman of the Physical Anthropology Section of the American Academy of Forensic Sciences, and has co-edited (with Stanley Rhine) *Skeletal Attribution of Race* (1990, 2004), a leading forensic handbook for the assessment of ancestry.

Geoffrey Clark, Regents' Professor in the Department of Anthropology, Arizona State University, is a paleoanthropologist with career interests that straddle paleolithic archaeology and human paleontology. Clark is the editor of *Perspectives on the Past* (1991), co-editor (with Cathy Willermet) of *Conceptual Issues in Modern Human Origins Research* (1997) and (with Mike Barton) of *Rediscovering Darwin* (1997), and founding editor (1989) of the *Archeological Papers of the American Anthropological Association* (AP3A).