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Research

Evolution, revolution or saltation scenario for the emergence of modern cultures?

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Crucial questions in the debate on the origin of quintessential human behaviours are whether modern cognition and associated innovations are unique to our species and whether they emerged abruptly, gradually or as the result of a discontinuous process. Three scenarios have been proposed to account for the origin of cultural modernity. The first argues that modern cognition is unique to our species and the consequence of a genetic mutation that took place approximately 50 ka in Africa among already evolved anatomically modern humans. The second posits that cultural modernity emerged gradually in Africa starting at least 200 ka in concert with the origin of our species on that continent. The third states that innovations indicative of modern cognition are not restricted to our species and appear and disappear in Africa and Eurasia between 200 and 40 ka before becoming fully consolidated. We evaluate these scenarios in the light of new evidence from Africa, Asia and Europe and explore the mechanisms that may have led to modern cultures. Such reflections will demonstrate the need for further inquiry into the relationship between climate and demographic/cultural change in order to better understand the mechanisms of cultural transmission at work in Neanderthals and early *Homo sapiens* populations.

Keywords: symbolism; Neanderthals; anatomically modern humans; modernity; Middle Stone Age; Mousterian

1. INTRODUCTION

It is too easy to argue that since we are the only hominin species left on the planet we must be unique and special in some respect. This proposition does not tell us what were the paths that our ancestors took to become so distinctive and to what extent we share partially, or entirely, this supposed uniqueness with our present or past relatives.

The question of the origin of the attributes that define us as humans is the subject of a lively debate among scholars from disciplines such as primatology, archaeology, palaeoanthropology, genetics, evolutionary psychology and linguistics. Ongoing gradual integration of results from these disciplines enables researchers to ask the old questions about who we are and from where do we come on new bases, and hopefully providing more informed answers. Once firmly separating us from the remainder of present and past hominids, genetic and behavioural boundaries are becoming less and less well defined. Depending on the exact comparison made, chimpanzees share about 95–98% of our genes [1], and have the capacity to develop cultural variants—for example in gathering or processing food—which are largely independent of environmental opportunities and genetic differences between groups [1]. We now know that symbolic thinking—the capacity to attribute specific meaning to conventional signs—is not peculiar to us and that we share that capacity with a growing number of primate and non-primate species [1]. The recent finding that significant interbreeding occurred between Neanderthals and modern populations [2] refutes the long-standing model that proposes all living humans trace their ancestry exclusively back to a small African population that expanded and completely replaced archaic human species, without any interbreeding. These discoveries raise again, but in a more cogent way, the question of what factors drove cultural evolution in our lineage, how these factors interacted, and what was the timing of the emergence of quintessential human features such as modern cognition, language, imagination, art, religious beliefs and so forth. A number of different explanations have been proposed to account for the origin of cultures comparable to ours. Some authors consider that a genetic mutation in the functioning of the brain is the most probable prime mover and have argued that such a mutation, leading to a sudden diffusion of modern traits, must have occurred approximately 50 000 years ago (50 ka) among African anatomically modern humans (AMH) [3]. Others situate this neurological switch between 60 and 80 ka and associate it with cultural innovations recorded at this time in southern

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Africa [4]. These views have been strongly challenged by authors supporting the scenario of a gradual emergence of modern cultural traits in Africa as a consequence of the selection processes that have led to the emergence of our species in that continent [5,6]. Other authors share the view of the three previous models that modern cultural traits may have arisen among AMH populations in Africa, but consider that population size rather than a speciation more plausibly accounts for the spread, episodic disappearance, and re-emergence of innovations in Africa [7–9]. Finally, partisans of what could be called the 'cultural' model argue that the cognitive prerequisites of modern human behaviour were already largely in place among the ancestors of Neanderthals and modern humans and cite social and demographic factors, arguably triggered by climate change, to explain the asynchronous emergence, disappearance and re-emergence of modern cultural traits among both African 'modern' and Eurasian 'archaic' populations [10–15]. In such a scenario, 'modernity' and its corollary 'cumulative culture' is the end product of a saltational cultural evolution within human populations that were to a large extent, and irrespectively of their taxonomic affiliation, cognitively modern. The main driving force in this last scenario is long-term climatic and environmental variability and its effect on population dynamics.

How can we test these scenarios? Many behavioural features considered as keys to crossing the Rubicon towards cultural modernity, such as altruism, enhanced memory, complex language and increased social learning leading to cumulative cultures [8], leave little direct archaeological traces behind them, and we are forced to infer their emergence in ancient human populations from the occurrence of elements of material culture that may signal their acquisition. Thus, evaluating the pertinence of the above models depends on the cultural traits we label as 'modern', the chance that they leave a durable and unambiguous trace in the archaeological record, and reliable dating. It also hinges on the abilities of the various schools of thought to convincingly link a favoured mechanism (genetic mutation, speciation, demography, climate, etc.) to a predicted outcome (stochastic event, gradual emergence, punctuated equilibrium, saltational evolution, etc.), and to demonstrate that the favoured mechanism was at work during the entire time span that led to the emergence of cultures comparable to ours. Ideally, we would also expect the preferred mechanism(s) to account for the cultural variability observed among historically known human societies, and the societies of our extant and extinct closest relatives.

The criteria used to identify modern cultures in the archaeological record—or degrees of cultural modernity in the case of gradual scenarios—vary according to the authors [3,5,11,13,14], and are far from unanimously accepted. Exploitation of coastal environments; greater complexity of food gathering procedures, such as the use of nets, traps, fishing gear; complex use of fire for cooking, food conservation; ecosystem management; producing and hafting stone tools; invention of specialized tool-kits to adapt to extreme environments; higher population densities approaching those of modern hunter–gatherers; complex tools, the styles of which may change rapidly through time and space; structures such as huts that are organized for different activities; long-distance transport of valued materials; formal artefacts shaped from bone, ivory, antler, shell; musical traditions; sea crossing and navigation technology; personal ornamentation in the form of body painting and personal ornaments; art, including abstract and figurative representations; evidence for ceremonies or rituals; complex treatment of the dead: the more the 'checklist' of modern traits has expanded in the last decade, the more it appears that preferences in the selection made were largely dictated by the conscious or unconscious intention of favouring one scenario over another. Additionally, many historically known modern human societies were either lacking a consistent number of these features or, while displaying them, would have left little evidence of them behind for recognition by future archaeologists. However, some consensus exists on the fundamental role played by symbolically mediated behaviours in the creation of modern cultures [16]. This innovation, which demonstrated the ability of sharing, storing and transmitting coded information within and across groups, has played a crucial role in creating and maintaining technical and social conventions, beliefs and identities that characterize all known human societies. Chimpanzees clearly have the capacity to develop and transmit cultural traditions [1], but they have never been observed creating systems of symbols in the wild, embodying them in their material culture or displaying them on their bodies. In this paper, we will evaluate the scenarios proposed to account for the origin of modern cultures in the light of the earliest archaeological evidence for crucial cultural innovations, including symbolically mediated behaviours, in Africa, Asia and Europe. Such reflections demonstrate the need for further inquiry into the relationship between climate and demographic/cultural change, in order to better understand the mechanisms of cultural transmission at work within Neanderthal and early *Homo sapiens* populations.

2. ARCHAEOLOGICAL EVIDENCE FOR THE ORIGIN OF MODERN CULTURES

(a) *Subsistence strategy and technology*

Recent discoveries have dramatically changed our knowledge concerning the chronology of the emergence of modern traits, and the fossil human populations with which they were associated. For most of the last century, the astonishing evidence of the complexity of Cro-Magnon behaviour in Europe convinced a large part of the scientific community that modern features had a punctuational origin, coinciding with the beginning of the Upper Palaeolithic in Europe, approximately 40 ka. This perception was to a large extent determined by a lack of information on Africa and Asia, and a reductive view of Neanderthal cultural achievements. Research conducted in southern Africa has challenged the idea [3] that the reduction in prey size, in high ranking prey abundance, and shift to fast moving creatures such as birds or

hares, recorded at Later Stone Age (LSA) sites, results from the lack of suitable technology and cognition in preceding Middle Stone Age (MSA) populations. Data now show that MSA people were competent hunters with a focus on large ungulate prey, but who also opportunistically exploited smaller ungulates, tortoises and small mammals, probably using traps and snares [17]. Fishing and shellfish exploitation are attested at coastal sites [6] but were, apparently, strictly controlled by changes in coastline configuration determined by sea-level fluctuations [18]. Demographic pulses are now seen as a best-fit explanation to account for changes in hunting strategies between the MSA and the LSA but also within each of these periods [17,19]. It has also become clear, as more data have become available, that there are both time related and geographical variations among MSA faunal assemblages, suggesting that subsistence strategies were both complex and adaptable [17]. Technology during the Middle Stone Age shows a pattern of innovation followed by disappearance. Blade technology and formal stone tools in the form of backed pieces—tools modified by retouch on a side—are signalled at sites such as Twin Rivers and Kalambo Falls, Zambia, dated at approximately 300 ka [20], but absent at many others. Uncertain instances of small blade production come from a Pinnacle Point cave dated at approximately 160 ka [6]. Although changes in lithic technology are recognized between the MSA I (approx. 110–115 ka) and the MSA II (approx. 94–85 ka) at Klasies [21], no formal stone tools nor a dedicated knapping technology to produce them are recorded before the Still Bay. Characterized by foliate bifacial points used as spear tips (figure 1*a*), this technocomplex apparently spans only 1–3 ka, and disappears near the transition between the end of the last interglacial (*sensu lato*) and the downturn to Marine Isotope Stage (MIS) 4 (approx. 70 ka). After a possible gap corresponding to the peak of this isotopic stage, interpreted as a phase of depopulation or low population density [22], lithic technology became characterized by the production of small blades retouched into segments [23], and other backed pieces (figure 1*b*), called Howiesons Poort (HP), spanning between approximately 65 ka and 59 ka. This gives way, during the following post-Howiesons Poort, to unifacial points on flakes (figure 1*c*), similar to the Mousterian points made by Neanderthals in Europe [23,24], and subsequently to unstandardized microlithic tools produced by the bipolar technique during the early LSA. A precocious emergence of technical innovation is also observed in north Africa, where new dating situates the earliest occurrences of the distinctive pedunculate point forms typical of the Aterian at 145 ka [25].

Evidence for a controlled use of fire to increase the quality and efficiency of stone tool manufacturing processes has been reported from Pinnacle Point, Mossel Bay, approximately 72 ka [26]. Laborious heat treatment to produce compound glues combining plant gum and ochre is attested in the Howiesons Poort layers of Sibudu Cave [27]. Location of such adhesives on small HP backed pieces indicates the latter were used as barbed spear [23] or arrow points [28]. One of the major discoveries of MSA archaeology in the last decades has been the identification of a varied and relatively complex bone technology, previously seen by many authors as an innovation directly stemming from the spread of AMH across Europe at the beginning of the Upper Palaeolithic. Large harpoons made from substantial mammals limb bones (figure 1*d*), found at Katanda, central Africa, may possibly go back to approximately 90 ka [29]. Fully shaped bone tools (projectile points, awls and spatulas) are found at southern African Still Bay and HP sites such as Blombos and Sibudu [30,31]. The careful deliberate polishing of the approximately 75 ka Blombos bone projectile points (figure 1*e*) has no apparent functional reason and, rather, seems a technique used to give a distinctive appearance and/or an "added value" to this category of artefacts. This may imply that symbolic meaning was attributed to bone tools. Reduction in size between the Still Bay and HP projectile points (figure 1*f*) has been tentatively interpreted as a shift from the use of hand-delivered bone spear heads to bow and bone arrow technology, possibly with the use of poison [28]. This hypothesis is now reinforced by the morphometric and microscopic analysis of HP segments [28]. However, it is unclear why, if they represented an advantageous innovation, bone tools occur only at a few MSA sites and are absent or rare after the HP. It is equally unclear why no evidence for the use of bows and arrows is found among modern human populations during their expansion in Asia and Europe.

New discoveries and reappraisal of key Mousterian sequences in Europe and the Near East identify trends in Neanderthal subsistence strategies and technology that parallel in many respects the pattern of innovation followed by disappearance described for Africa. Very few scholars would argue now, as was routine in the early 1980s and 1990s, that contrary to Upper Palaeolithic Cro-Magnons, Neanderthal subsistence strategies were based on scavenging large mammal carcasses, constrained to favourable biotopes, that these populations had limited planning capacities, and were only able to develop expedient technologies involving a low degree of conceptualization. Now we know from prey hunted that Neanderthals were effective, flexible hunters, at a number of sites they were able to live in cold inhospitable environments, and at times they also exploited a broad range of terrestrial and marine resources [32–35]. Ongoing research on the technological variability of the Mousterian in Europe identifies variations in time and space in lithic technology and tool types interpreted as discrete cultural adaptations, comparable to those observed in contemporary African populations. As with Africa, in Europe we observe the punctuated emergence and disappearance of blade technology (figure 1*g*) and more 'formal' stone tools (figure 1*h*) since 200 ka, with an apparent acceleration in the turnover of types of *débitage* and tools after the last interglacial [36]. This culminated in a clear regionalization of cultural features during the millennia that immediately preceded the recognized arrival of modern humans in Europe. Research conducted in the Levant reveals that at sites with diagnostic Neanderthal and modern human

Figure 1. Archaeological material cited in the text: (*a*) Still Bay bifacial point from Blombos Cave, Cape Province, South Africa, (*b*) Howiesons Poort segment from South Africa, (*c*) Post-Howiesons Poort point from Sibudu Cave, (*d*) bone harpoons from Katanda, Democratic Republic of Congo, (*e*) bone projectile points from Blombos Cave, (*f*) possible bone projectile point from Sibudu Cave, (*g*) flint blades from the Mousterian site of Etouville, Normandy, France, (*h*) Mousterian stone tools from Haldenstein-Höle (left) and Königsaue (right) (*i*) birch bark pitches from Königsaue, Germany, (*j*) Châtelperronian bone awls from Grotte du Renne, France, (*k*) Uluzzian bone awl from Castelcivita Cave, Italy, (*l–o*) pigmental material from Blombos Cave (*l*), Skhul, Israel (*m,n*), Pech de l'Azé, Dordogne, France (*o*), (*p–s*) marine shell beads from Blombos (*p*), Oued Djebbana, Algeria (left) and Skhul, Israel (right) (*q*), Grotte de Pigeons, Taforalt, Morocco (*r*), Rhafas (left) and Ifri N'Ammar (right) (*s*), (*t*) Glycimeris shell with a natural perforation and traces of red pigment from Qafzeh, (*u*) ostrich egg shell beads from Mumba rock shelter, Tanzania, (*v*) Glycimeris shell with a natural perforation from Cueva de Los Aviones, Spain, (*w*) Pecten bearing residues of red pigment on its external white aspect from Cueva Anton, Spain, (*x*) Châtelperronian personal ornaments from Grotte du Renne (from the left perforated fox canine, grooved bovid incisor, perforated rein deer phalange, grooved Rynconella fossil bivalve) and Quinçay (perforated red deer canine), (*y*) engraved haematite slab from the Still Bay layers of Blombos Cave and (*z*) fragments of engraved ostrich egg shell from the Howiesons Poort layers of Diepkloof, Cape Region, South Africa. Credit for images: (*a,d–f,j,k–s,v,w,y*), photos F. d'Errico; (*b,x*), courtesy of M. Vanhaeren; (*c*), courtesy of P. Villa; (*g*), modified from [79]; (*h*, left), courtesy of H. Jensen, Department of Early Prehistory and Quaternary Ecology, University of Tübingen; (*h*, right) and (*i*), courtesy of J. Liptak, LDA Sachsen-Anhalt; (*t*), reproduced with permission from [69]; (*u*), courtesy of M. Malina, University of Tübingen; (*z*), reproduced with permission from [73].

remains, the two populations hunted the same species, produced their tool kits by applying Levallois flaking and manufactured a comparable range of tool types [37]. Differences between the Middle and Upper Palaeolithic of Europe in lithic raw material procurement strategies [38] have been interpreted as evidence for more reduced Neanderthal geographical ranges and social networks. However, such distances are extremely variable within the Mousterian, for example reaching figures comparable with those recorded in the Upper Palaeolithic in eastern Europe [39]. On the other hand, very local procurement strategies are recorded at many MSA sites in South Africa, including HP sites [23,24].

Recent research has shown that Neanderthal hunting weapons were comparable to those used by broadly contemporaneous Middle Stone Age populations in southern Africa. Wooden spears over 2 m long, made of spruce and pine, have been discovered at Schöningen in Germany, dating from approximately 300 to 400 ka. These were probably used as thrusting spears but might also have been javelins, as suggested by their forward centre of gravity [40]. This has been contested [41] on the basis of the upper limb morphology associated with projectile-throwing Upper Palaeolithic humans (but absent in Neanderthals), on the too-close range of hand-thrown spears to hunt large animals and the fact that the Schöningen spears are too

heavy to be thrown. However, it has been shown contra [41] that the Romans and Greeks used long and quite heavy javelins in war, and for hunting wild animals, and that over-arm throwing was not necessarily an habitual activity until the late Upper Palaeolithic [42]. Moreover, a large literature now supports the view that the hunting equipment of Neanderthals was not limited to simple wooden spears. Tip morphology, evidence of hafting and the presence of diagnostic impact scars indicate that at a number of sites from Europe and the Levant, going back at least to early MIS 6 (approx. 186 ka), Levallois and retouched Mousterian points were used as weapon armatures [42].

As far as hafting and the production of composite tools are concerned, the level of technical development of Neanderthals seems comparable to that recently identified at HP sites from South Africa. At the Italian site of Campitello, dated to MIS 6, Neanderthals heated birch bark in a reductive environment to temperatures of *ca* 350° in order to obtain pitch for hafting flint flakes, found associated with elephant bone [43]. A similar treatment is attested at the Middle Palaeolithic site of Königsaue in Germany, dated to approximately 48 ka, where two fragments of birch-bark pitch (figure 1*i*) still show the imprint of the bifacial tool once adhering to them [44]. Heat treatment of lithic raw material to facilitate knapping is so far unrecognized among Neanderthals, Upper Palaeolithic modern humans before the Solutrian (approx. 22 ka), and most African and non-African modern humans contemporaneous with or posterior to the Pinnacle Point instances of this technique. An alternative 'ecological' explanation to the 'cognitive' one, favoured by Brown *et al*. [26], might better account for this pattern: heat treatment may be an innovation that occurs in situations in which ecological constraints exert pressure for the creation of specialized stone tool kits made of highly anisotropous raw material, thereby creating something that does not occur naturally in the environment.

The most common use of bone during the Eurasian Lower and Middle Palaeolithic is that of long-bone shaft fragments to retouch lithic tools [45]. Knapped handaxes and scrapers were also occasionally produced at Acheulian and Mousterian sites. Bone industries showing a level of technological complexity equivalent to that normally associated with Upper Palaeolithic cultures are only found in 'transitional' technocomplexes such as the Châtelperronian in France (figure 1*j*) and the Uluzzian in Italy (figure 1*k*). The former technocomplex is now firmly attributed to Neanderthals [46] while such an attribution is still tentative for the latter due to the scarcity and undiagnostic character of the human remains associated with those layers. The interpretation of the Châtelperronian bone tools and, as we will see later, personal ornaments, in particular those from the Grotte du Renne, Arcy-sur-Cure, is controversial [10]. Their presence in Châtelperronian layers has been interpreted as the result of independent Neanderthal innovation, as reflecting trade or scavenging from abandoned contemporary Aurignacian sites, as intrusion from overlying Aurignacian layers or, more recently, to the fact that the Châtelperronian makers of those tools may have well been modern humans [47]. A number of factors, linked to the stratigraphic distribution of the bone tools, personal ornaments, human remains and diagnostic Châtelperronian tools, as well as to the presence of by-products of bone tool manufacture, indicate that Châtelperronian Neanderthals were the makers and the users of the bone tools [10,48]. This conclusion is further supported by similar finds from the Châtelperronian site of Quinçay, Vienne region, where contamination from later AMH occupation can be excluded, as none exists. The conclusion that Châtelperronian bone tools were made by Neanderthals does not resolve the contentious problem of whether this technology was independently invented prior to the arrival of AMH in western Europe or if it was in some way adopted or re-elaborated as a result of contact with the latter [10,49]. To address this question, we need a consensual stratigraphic, chronological and palaeoclimatic framework for the early Upper Palaeolithic technocomplexes [50] and a refined knowledge of the material culture associated with them.

Archaeozoological, technological and microscopic analyses of Châtelperronian and Uluzzian bone tools [48,51] demonstrate that they are not expedient tools used in single instances to fulfil immediate needs, but rather are the result of planned chains of complex technological actions, shared by groups belonging to the same cultural tradition. This is demonstrated by the consistency that we have identified in the choice of the species and bone type, technique of manufacture, overall tool morphology and resharpening techniques. Such know-how does not appear qualitatively different from that recorded at more recent Upper Palaeolithic sites. This indicates that even if it was demonstrated that the use of bone tools or personal ornaments by Neanderthals was the result of cultural contact with moderns, this would in fact reinforce rather than dismiss the modern character of their cognition, as it would show their ability, as observed in many historical instances among modern human populations, to incorporate external stimuli and reshape those influences in order to make them an integral part of their own culture.

(b) *Symbolic mediated behaviour*

What is the earliest evidence for symbolic behaviour in the archaeological record? Although inhumation and treatment of the dead are generally regarded as quintessential features of modern humanity, carrying of infant corpses—in one case for 68 days—and attention paid to corpses of adults has been reported from a number of primates in the wild [52]. We ignore the meaning of these practices and whether they are to some extent symbolic in nature, but they suggest that chimpanzees may have a greater awareness of death and dying than previously thought. A second problem when searching for early funerary practises is, of course, their variable archaeological visibility: burials will leave more traces than exposure in the open. A rapid survey of the evidence reveals that this reason can account for the patchiness of the archaeological record, and that both Neanderthals and modern humans probably engaged very early in a variety of funerary practices. The claim for a polish

suggestive of curation of a skull at the approximately 160 ka old site of Herto in Ethiopia has not, so far, been supported by further data [53]. At present, the approximately 115 ka cave occupation of Skhul in Israel has the oldest known symbolic burial, an early modern male interred clasping the lower jaw of a massive wild boar [54]. The 100 ka occupation of Qafzeh Cave near Nazareth also has a number of modern human burials, one of which was a child whose body was covered by deer antlers [55]. However, we hardly pick up this practise again in modern humans for more than 40 ka. Only three MSA burials are known, that of the Border Cave, with a possible age of 70 ka, and those of Nazlet Khater [56], and Taramsa, Egypt [57] dated, respectively, to 40 ka and 68 ka. In Europe the oldest burials are Gravettian and date to approximately 30 ka. The bodily traces of earlier moderns in Europe, the Aurignacians, are mainly in the form of pierced human teeth [58] suggesting that they preferred to carry traces of their enemies or their ancestors with them rather than burying them. Around 40 ka two individuals were interred separately at Mungo [59] in south eastern Australia—a woman was cremated at high temperature and another adult (sex uncertain) was buried stretched out and with a covering of haematite pigment (perhaps originally on the skin, or perhaps on some covering material such as a hide or bark). Neanderthal burials in the Levant are as old or might be even older than those of moderns, if one accepts the most ancient date for the Tabun C1 burial [60]. Neanderthal burials in Europe are numerous but concentrated in a few areas, suggesting that Neanderthals, as modern humans in Africa, may have engaged in funerary practices leaving no traces in the archaeological record. Although in a number of cases this information is difficult to verify now, grave goods consisting of stone tools, bone retouchers, engraved bone and a rock slab engraved with cupules were reported at Neanderthal burials such as La Ferrassie, La Chapelle-aux-Saint, Le Moustier in France, Amud and Dederiyeh in the Middle East [61]. The oldest known human bone used as a tool is a fragment of Neanderthal skull from La Quina in the Charentes region of France [62].

Although systematic exploitation of pigmental material is generally interpreted as the archaeological expression of symbolic behaviour, this view remains controversial. Supporters of the symbolic interpretation stress deliberate choice for intense red hues, preference for pigment from far away sources, deliberate heating to change pigment colour, presence on just one side of an object, coloration of shell beads, and the inferred light colour of Neanderthal skin appropriate to receive black painting [63–65]. Supporters of the functional interpretation often do not deny that pigment may have also been used for symbolic purposes, but they stress the difficulty of firmly demonstrating such an interpretation. They rely on the attested ethnographic use of pigmental material to propose alternative functions such as skin protection from sun or insects, as medicine, for tanning hides, or as a binding agent to facilitate hafting [27]. The debate between the two sides has probably become unnecessarily polarized. Ethnographically, the symbolic/functional divide would be an alien concept to most contemporary hunter–gatherer societies, who do not perceive such distinctions between material, actions and causality. Symbol use and its material expressions are ultimately functional in the sense of creating or marking individual and group identities and as such, have potential adaptive value by enhancing group cohesiveness. In other words, a systematic and purely functional use of pigments is difficult to conceive. Red pigmental material, attested in Africa at archaeological sites dated to approximately 160 ka [6] and possibly at sites dated to approximately 280 ka [5] becomes a common feature of approximately 100 ka (figure 1*l*) and younger MSA sites [5,63]. In the Middle East the oldest evidence for systematic use of pigments dates back to approximately 100 ka (figure 1*m*,*n*) and comes from Qafzeh [66] and Skhul [65]. Clear evidence of heating, probably to change the colour of the pigmental material, is attested at these two sites [65]. Pigments, mostly black but also red, have been used by Neanderthals in Europe (figure 1*o*,*w*) since approximately 300 ka [64], but their use became systematic only after approximately 60 ka [64]. The last-known Neanderthals in France made intensive use of both black and red pigments. A case in point is the 18 kg of red and black pigments, often bearing traces of use, found in the Châtelperronian layers of the Grotte du Renne, Arcy-sur-Cure [50], the largest quantity of pigmental material found so far at a Palaeolithic site.

Convincing evidence for the use of personal ornaments, consisting of perforated marine shells belonging to a single species at each site, is found from caves in south Africa, north Africa and the Middle East dated to between 120 and 70 ka [67]. At Blombos Cave, 49 deliberately perforated *Nassarius kraussianus* shell beads (figure 1*p*) with clear evidence of use-wear, some bearing traces of ochre come from approximately 75 ka old levels. The perforated *Conus* shell from Border Cave, associated with the burial of a young individual may be as old as 76 ka according to the recent chronological attribution of this burial [68]. Perforated *Nassarius gibbosulus* shells were recovered at the Aterian site of Oued Djebbana, Algeria (figure 1*q*), and Skhul from approximately 100 ka levels that include 10 *Homo sapiens* burials. Perforated shells of the same species (figure 1*r*,*s*) showing traces of intentional modifications, possible deliberate heating to change the colour of the bead, use-wear and traces of red ochre were recovered from approximately 80–70 ka levels at Grotte des Pigeons, Rhafas, Ifri n'Ammar and Contrebandiers in Morocco [67]. Other marine shells interpreted as beads (figure 1*t*) come from the approximately 90 ka Mousterian levels at Qafzeh Cave in Israel [69]. They consist of 10 naturally perforated *Glycymeris insubrica* shells. The only Neanderthal site that has yielded possible evidence for the use of shell beads by Neanderthals is the Cueva de los Aviones in southern Spain [12]. The Mousterian layers of this site, dated to approximately 45–50 ka BP, contained a marine shell assemblage including three valves of *Acanthocardia* and *Glycymeris*, bearing natural perforations (figure 1*v*). One of the latter

contained a residue of red pigment identified as haematite. Beads seemingly disappeared in Africa and the Levant between approximately 70 ka and approximately 40 ka [67], and reappeared almost everywhere in Africa and Eurasia after this time span; approximately 40 ka old beads from Europe are associated with both Neanderthals and AMH [64]. They differ from their approximately 120–70 ka antecedents in that they take the form of hundreds of discrete types, identifying regional patterns [58]. As with formal bone tools (see above), the minimalistic consensual interpretation of personal ornament use by Neanderthals (figure 1*x*) is that they were fully able to incorporate new categories of symbolic items in their own culture. At approximately 40 ka, beads in Africa were made on ostrich egg shells (figure 1*u*), and only later are diverse ranges of raw material introduced for bead manufacture. In southeast Asia, the oldest documented ornament is a perforated tiger shark tooth found in New Ireland, New Guinea at a site dated between 39.5 and 28 ka [70]. The earliest evidence for bead use in Australia comes from the site of Mandu Mandu, Cape Range of Western Australia, where 22 *Conus* sp. shell beads were recovered in a layer radiocarbon dated to *ca* 32 ka [71].

The earliest secure abstract designs, engraved on bone and ochre, are found in South Africa and are dated to ca 100 ka [72]. Examples are the complex geometric patterns on ochre (figure 1*y*) from approximately 100 to 70 ka levels at Blombos Cave and from MSA layers at Klein Kliphuis in the Western Cape, and approximately 73 ka old notched and engraved bone from Blombos and Klasies [30]. Abstract designs on artefacts seem to disappear in southern Africa between approximately 70 ka and 55 ka, after which they reappear at Diepkloof shelter (figure 1*z*) in the form of engraved ostrich eggshells [73]. Evidence from the Middle East includes an engraved cortex dated at approximately 50 ka from the Mousterian site of Quneitra that could be associated with *H. sapiens* or Neanderthals, and an engraved lithic core from approximately 90 ka levels at Qafzeh. A number of objects bearing putative engravings have also been reported from Lower and Middle Palaeolithic sites in Europe. Some of these 'engravings' resulted from natural phenomena and carcass processing. Others were deliberate engravings [64], but still need detailed publication. Figurative representations consisting of painted, engraved and carved animals, are so far only well dated to much later, at approximately 31 ka in Africa, at Apollo 11 shelter [74], Namibia, and at approximately 35 ka in Europe, for example at Chauvet, Fumane and in southern Germany [75]. The oldest known carved musical instruments, consisting of flutes made of bird bone and mammoth ivory decorated with notches, are found in Europe and also date back to approximately 35 ka [76]. No convincing musical instruments are associated with Neanderthals, so far [77].

3. DISCUSSION AND CONCLUSION

Our review of the evidence contradicts the idea that the emergence of crucial technological innovations and symbolic material culture was the result of a sudden change in human cognition occurring in Europe or Africa approximately 40–50 ka, or just in Africa approximately 60–80 ka. Possible differences in subsistence strategies and technology between anatomically modern and late archaic humans, as well as their variations in time and space, do not prove the case for an inherent incapacity of the latter to reach the degree of fitness that we observe in their penecontemporaneous modern counterparts. Although comparisons between cultural adaptations in very different and changing environmental settings are obviously difficult to draw, it is clear that in some instances European Neanderthals developed knapping techniques and tool types that were more 'advanced' than those of some African Middle Stone Age groups, that the opposite also occurred, and that in other situations, such as in the Levant, technology was virtually identical. Instances of symbolically mediated behaviours comparable to those observed in historically known human populations are recorded by at least 100 ka, probably before, in Africa, by approximately 120–100 ka in the Middle East and probably by at least 60 ka in Europe. This contradicts the assumption that the crucial innovations that have made us as we are can only have come from, or have been assimilated from an anatomically modern humanity, and counters the simplest versions of the Out of Africa model for the origin of modern cultures that directly link the origin of these innovations to events taking place in Africa at about 200 ka, or between 40 and 80 ka. Evidence also shows that no uninterrupted accretion of innovations or exponential growth, as predicted by this model, is observed in Africa (or in Europe). During the period between approximately 160 ka and 20 ka complex technologies, adaptation to hostile environments, engravings, pigments, personal ornaments, formal bone tools and burial practices apparently appear, disappear and reappear in different forms, suggesting major discontinuities in cultural transmission. The discontinuous nature in time and space of this process, and the commonalities found in both hemispheres, indicate that local conditions must have played a role in the emergence, diffusion and the eventual disappearance or continuity of crucial innovations in different regions. These local conditions must have been closely linked to the size and organization of cultural systems and ecological settings in which these populations evolved, and sometimes probably disappeared.

A string of recent papers [8,9] following the seminal work of Cavalli-Sforza, Feldman and Boyd and Richerson have explored the role of demography in the emergence and loss of cultural innovations through modelling.

Powell *et al.* [9] reach the conclusion that the number and size of subpopulations and the degree of interaction between them are key factors in the emergence, maintenance, spread and loss of innovations. They speculate that population size in Africa could have reached a critical threshold about 100 000 years ago, when population density and enhanced contact between groups could have allowed the rate of accumulation of innovations to significantly overtake their loss. Thus, cultural change in the Middle Stone

Age greatly accelerated and the increased store of learning was beneficial to the survival of individuals and their groups. In turn this would have started a feedback mechanism, leading to a further increase in population density and contacts and so on. Their results are significant because they provide a sound explanation for the emergence and loss of innovations without invoking speciation as a prime mover. However, one may argue, particularly after the publication of the preliminary results of the Neanderthal Genome Project, that the model they develop could equally be applied to explain the emergence and loss of similar innovations among Neanderthals and the asynchronous emergence of innovations in other regions of the planet. Behavioural differences between Neanderthals and modern humans, as well as between different subpopulations belonging to these human types, may largely depend, following the logic of Powell *et al.*'s own conclusions, on group size and cultural exchange rate rather than on in-built differences in cognition. Also, the predictions of Powell *et al.* rather leave open the question of what stimulated demographic growth in the first place. For example, they evoke the climatic deterioration of MIS 4 as a possible factor leading to population decline and the loss of cultural innovation that we observe in north and south Africa after approximately 70 ka, but no clear mechanism is proposed to explain how this deterioration might have produced a similar demographic demise in areas of the planet where this climatic deterioration certainly had very different impacts. This suggests to us that in order to make further progress in this field, we need a research strategy that allows us to model and quantify the link between environment and a particular past cultural adaptation, predict the response of that adaptation to climatic change and verify whether the rise and spread of innovations result in an expansion or contraction of the eco-cultural niche of a given population. Assumptions about cognition based on taxonomic affiliation should play no *a priori* role, and the key tools would then be archaeology, palaeoenvironmental studies, climate modelling and methods to integrate results from these disciplines. At present this appears to us to be the best way to reconstruct the timing and mode of emergence of key innovations in material culture in Europe and southern Africa, to identify whether and how climatic changes have influenced the distribution of Neanderthal and modern human populations and behavioural patterns in these two regions, and to understand the mechanisms that have governed cultural transmission and social learning during this crucial time span for the evolution of human cultures. The predominance of Africa in the story of modern human origins was probably primarily because of its larger geographical and human population size, which gave greater opportunities for morphological and behavioural variations, and for innovations to both develop and be conserved, rather than the result of a special evolutionary pathway. Exactly as with our present genetic diversity, 'modernity' was not a package that had a unique African origin in one time, place and population, but was a composite whose elements appeared at different times and places, including some outside the African continent, either shared or developed in parallel. These were then gradually assembled through a variety of paths and processes to assume the form that we recognize as behavioural modernity today. However, the Neanderthal Genome Project adds another level of complexity to the issues that we have attempted to unravel in this paper in that it has identified a number of genes that appear to be unique to the modern humans sampled, and some of these appear to have as yet unresolved cognitive and physiological functions. The likelihood that modern humans both within and outside of Africa have small but different suites of 'archaic' genes acquired through introgression [78] and that archaic populations might in return have received varying 'modern' components, may shed further light on the complex issue of the emergence of 'behavioural modernity'. Increases in archaeological resolution—most of the evidence presented here was unknown a decade ago—and new insights into our genetic history may aid in unravelling the mechanisms that have driven our ancestors' genetic-cultural coevolution.

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