

Stasis and change in Paleolithic times. A brief assessment of the Lower and Middle Paleolithic evolutionary dynamics

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Abstract: Based on dual-inheritance and macro-evolutionary models, the paper focuses on the conformist dimension of cultural transmission and on the growth limits inherent in foragers' eco-cultural niche building. The apparent lack of innovation noticed in the Lower and Middle Paleolithic is briefly explored. The crucial role of demographical networks in the spread and persistence of innovation is also emphasized.

Several lines of evidence suggest an early, Middle Pleistocene age for the emergence of typically human cooperative arrangements and cultural inheritance systems. A mosaic pattern of innovations is also recorded during the Middle and particularly Late Pleistocene. Their repeated failure in spreading and lasting is attributed to the dominant opportunist forager strategy and ultimately to the small size and vulnerability of local demographic networks.

Rezumat: Pornind de la modelele propuse de teoria „dublei mo teniri” și de cea a macro-evoluției, articolul tratează apariția și absența inovațiilor în paleoliticul inferior și mijlociu, punând accent pe dimensiunea conformistă a transmiterii culturale și pe limitele de dezvoltare inerente construcțiilor și elor eco-culturale de către populațiile de vânători-culegători.

Mai multe tipuri de dovezi sugerează apariția timpurie, încă din Pleistocenul mijlociu, a sistemelor tipice umane de cooperare și transmitere a informației culturale. Totodată, în Pleistocenul mijlociu și, în particular, în Pleistocenul final se înregistrează un mozaic de inovații. Eșecul repetat al acestor inovații de a se răspândi și rezista în timp este pus pe seama strategiilor dominante oportuniste ale vânătorilor-culegătorilor și, în ultimă instanță, pe seama dimensiunii reduse și vulnerabilității rețelelor demografice locale.

Keywords: macro-evolution, cognition, demography, Lower Paleolithic, Middle Paleolithic.

Cuvinte cheie: macro-evoluție, cogniție, demografie, paleolitic inferior, paleolitic mijlociu.

◆ Introduction

Cultural evolution is generally acknowledged as largely autonomous and certainly, as much faster than biological evolution. Indeed, in comparison to the slow rhythms of geology and to the deep history of organic forms, the evolution of human species entails a short chapter, essentially reduced to the last 2.5 million years. Yet, the amount of accumulated cultural information is spectacular: a present-day *Homo sapiens* hosts a volume of extra-somatic data rivaling his genome in size (P.J. Richerson, R. Boyd 2001, p. 199). Conventionally, this impressive outcome is due to our species' unique cerebral architecture, which, among others, facilitated the fast transmission of adaptive information through the use of symbols and, in particular of language (M. Donald 1991).

It is no less true that, despite its rapidity, cultural evolution displays many episodes of slow, almost imperceptible change. The Paleolithic period offers the most obvious examples. Although undoubtedly inaccurate, Eurocentric, and relying mainly on the limited behavioral yardstick provided by lithic technology, the inner chronological landmarks are speaking for themselves: the Lower Paleolithic extends between 2.5 million and 200 ka BP, while the 'shorter' life of the Middle Paleolithic covers the following interval to ca. 40 ka BP. Taking these huge numbers at face value, many scholars tend to see these epochs as long intervals of stasis or at least adaptive redundancy, in which the cumulative character of cultural evolution is anything but obvious (cf. S. Kuhn, E. Hovers 2006). Negative innate differences i.e. lack of cognitive fluidity (S. Mithen 1996), discursive consciousness (C. Gamble 1999) or articulated language (R.G. Klein 2009) are often identified as the main causes for the low rates of cultural innovation and accumulation recorded during the Lower and Middle Paleolithic. As a consequence, the shifting pace of cultural evolution associated to the Upper Paleolithic in Western Eurasia is sometimes attributed to a reorganization of the executive functions of the pre-frontal cortex (S. Mithen 1996; W. Noble, I. Davidson 1996; F.L. Coolidge, T. Wynn 2001; R.G. Klein 2009).

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The purpose of this paper is to show that, paraphrasing the famous reply of Laplace to Napoleon, the last hypothesis 'is not necessary', starting at least with the Middle Pleistocene. On the one hand, based on the tenets of dual-inheritance and macro-evolutionary theories, I will suggest that the rationales of cultural stasis are inherent to the very nature of human cultural evolution and *Homo sapiens sapiens* makes no exception. These inner growth limits are particularly powerful in the case of a forager lifestyle and must have been forcefully augmented by the Pleistocene environmental settings and demographical patterns. On the other hand, on archaeological grounds, I will attempt to show that at least some of the allegedly missing key cognitive components were already present, starting with *Homo heidelbergensis* and all the more in the case of archaic *Homo sapiens* like Neanderthals. Innovative behaviors are also recorded from the Middle Pleistocene on. Finally, I will try to look for an alternative explanation for the slow evolutionary rhythm of the Lower and Middle Paleolithic, rather focused on the demographical networks carrying the human creativity than on biological essentialism.

◆ Gene and culture co-evolution

The dialogue between social sciences and biology has never been particularly harmonious (D. Nettle 2009). As a consequence, although focused on a lengthy period of crucial biological and cultural evolutionary changes, the Paleolithic research still relies on often incommensurable theoretical models, inspired either by primate ethology and behavioral ecology, or by hunter-gatherers ethnography (for a review, see R.L. Bettinger 1991). Notwithstanding this traditional segregation, the last decades witnessed an increasing number of contributions focused on the common features of both forms of evolution and on the complex feedback relations connecting them. One of the main outcomes of these convergent approaches bringing together environment, genes and culture, is the development of several related and increasingly coherent bodies of theory inspired by the neo-Darwinian synthesis, such as cultural evolutionism (W.H. Durham 1990), double-inheritance theory (for comprehensive outlines see P.J. Richerson, R. Boyd 2005; R. Boyd, P.J. Richerson 2005) and macro-evolutionary theory (see contributions in A.M. Prentiss et alii 2009)¹.

The central tenet of all these approaches is that culture, as extra-somatic information acquired from others, acts like a system of descent with modification and that Darwinian 'population thinking' can be fruitfully applied to cultural evolution. However, contrary to more orthodox Darwinian approaches like sociobiology, for which cultural evolution is equated to epigenetic/phenotypic development, this theoretical family grants culture and group level selection a key place in guiding human evolution. Many peculiar features of human social behavior, such as the high-level of non-kin cooperation, undifferentiated altruism, behavioral conformism, strong emotional affiliation to larger (e.g. ethnic) groups or simply deleterious cultural practices are explainable as outcomes of complex co-evolutionary games involving bias transmission, various forms of reciprocity, kin or group-selection, or moralistic punishment (see P.J. Richerson, R. Boyd 2005; R. Boyd, P.J. Richerson 2005).

Another important position commonly held by dual-inheritance and macro-evolution theorists is that, similarly to animal niche construction (F.J. Odling-Smee et alii 2003), culture creates novel environments, which in turn lead to new pressures for natural and social selection on both genes and behavior. These eco-cultural niches, generally seen as complex packages unifying environment, technology and social structures (I. Kuijt, A.M. Prentiss 2009; W.E. Banks et alii 2006), may be considered to express local optima of adaptive equilibrium in a rugged fitness landscape with multiple potential peaks². Once a population reaches a particular fitness peak, climbing another, albeit higher, becomes difficult, as this transition necessarily involves a temporary reduction in fitness. However, severe environmental or demographic stress may serve to dislodge a population from its current fitness peak, allowing it to escalate a higher one, if accessible. Moreover, if historical hazard brings different adaptive strategies in close proximity they may compete, with the most successful eventually increasing on the expense of the other. Both ways of descending into fitness "valleys" are therefore leaving room for the directional, cumulative growth praised in most traditional social-evolutionary scenarios (R.L. Bettinger 2009).

Specific biases in transmission mechanisms (e.g. imitation) allow human to acquire fastly new behavioral rules, without exhaustively examining the immense amount of available social and

¹ For brevity reasons, some other important theoretical members of the Darwinian family, such as cultural selectionism (R.L. Lyman, M.J. O'Brien 1998) or human behavioral ecology (E.A. Smith, B. Winterhalder 1992) will not be analyzed here.

² For an evaluation of Sewall Wright's "fitness landscape" concept in cultural evolution, see R.L. Bettinger 2009.

environmental information. While granting culture its peculiar, cumulative character, the reliance on learning entails important trade-offs, with conformism as a most typical outcome (J. Henrich, R. Boyd 1998). To put it otherwise, living into a cultural niche, while advantageous in many respects, may also mean getting trapped into it.

Various interfering with the co-evolutionary processes, demography plays a vital role in cultural evolution and thus provides a key candidate in explaining any major episode of cultural accretion or, for that matter, stasis. As a rule, cultural sophistication moves faster and further in larger than in smaller populations. The latter are always vulnerable to information loss and cultural "impoverishment" (i.e. the Tasmanian effect – J. Henrich 2004). Hysteresis loops further reinforce the pattern: preexisting larger populations have a strong tendency to remain large in times of crisis and have also better chances of escalating a higher adaptive peak, while small initial populations are more vulnerable to further demographic decrease and information loss (P.J. Richerson et alii 2009).

◆ Cultural stasis and the "sapient paradox"

Although there is little doubt that the gene and culture co-evolution started much earlier and carried huge consequences for the path subsequently followed by human evolution, the best evidence for this process comes from Late Pleistocene and Holocene times, for which improved environmental, genetic, and archaeological data are available. However, even in these cases involving strictly the modern human anatomy long episodes of stasis appear quite common in cultural evolution.

Colin Renfrew's "sapient paradox" (2001) provides a case at point: although the modern anatomy emerged somewhere in sub-Saharan Africa about 200 ka ago (I. McDougall et alii 2005), little cultural innovation is actually recorded before 50 ka BP. With the exception of several episodes of apparent sophistication (S. McBrearty, A.S. Brooks 2000), which punctuate the otherwise quite homogeneous record of African Middle Stone Age (MSA), no particularly cumulative effects are visible before the advent of the Upper Paleolithic around 40 ka BP, when the use of Mode 4 technology, together with portable and parietal art, spread across Western Eurasia. Thus, for thousands of millennia, *Homo sapiens sapiens* in both Africa and Middle East apparently behave similarly to his Neanderthal counterparts in Europe.

Even after the successful colonization of Western Eurasia by *Homo sapiens sapiens*, which undoubtedly brought important changes in mobility and subsistence patterns, technology and symbol use (P. Mellars 2005), the pace of change is still slow, at least in comparison to the Holocene cultural explosion. Pan-European technocomplexes such as the Aurignacian or the Gravettian, acknowledged as such precisely on the grounds of their quite homogenous material culture, lasted about ten millennia each. In various parts of the Old World (e.g. Australia, South Asia), the Late Pleistocene lifestyle and the related technology (including Mode 3 lithic technology) survived to recent historical times. Furthermore, recurring episodes of stasis and accelerated change are documented archeologically in various parts of the Holocene New or Old World (J.C. Chatters 2009; I. Kuijt, A.M. Prentiss 2009).

Thus, contrary to the narratives stressing a gradual increase in social complexity, the big picture of cultural evolution appears much more complicated, with long periods of stasis and adaptive equilibrium punctuated by episodes of fast, cumulative change. Highly dependent on unstable environmental settings, hunter-gatherers seem particularly susceptible in experiencing such a syncopated evolutionary pattern.

◆ Hunter-gatherers in the fitness landscapes

Although still a highly debated socio-type (S.B. Kusimba 2005; K.E. Sassaman 2004), hunter-gatherers, including the Paleolithic ones, are paradigmatically approached from an environmental perspective (R.L. Bettinger 1991), which generally allows only for simple, usually two-folded typologies. The most popular dichotomies separate foragers from collectors (L.R. Binford 1980), travelers from processors (R.L. Bettinger 2001), and immediate-return from delayed-return societies (J. Woodburn 1982). All these typological attempts found a systemic correlation between ecological settings and hunter-gatherers' subsistence, mobility, technology, demography and social arrangements.

As a large number of ethnographical case studies show, hunter-gatherers habitually respond to short and medium term environmental challenges through changes in location, mobility, seasonal

scheduling or group fusion/fission. Their choices are obviously channeled by preexisting environmental and technological knowledge and by their basic social structures; as a rule, socio-technical systems (B. Pfaffenberger 1992), for which hunter-gatherers actually provide textbook samples, are very resilient to piecemeal changes (J.C. Chatters 2009). In fact, the acknowledged socio-economic typological categories appear more or less conterminous to the adaptive strategies, or, in more elaborate terms, Resource Management Strategies (I. Kuijt, A.M. Prentiss 2009) gravitating around local adaptive peaks. Even in the context of the powerful presence of complex neighboring societies, the imbricated nature of these strategies makes the hunter-gatherer lifestyle very resilient to change (A. Barnard 2007). In order to explain their reluctance to innovation, some scholars even proposed a hunter-gatherers' "syndrome" (G. Lenski 2002): while subsistence base, mobility and technology inhibit the scope of material accumulation and social competition, the absence of the latter further dampens any important change in subsistence or technology. The egalitarian ethos characterizing most of these societies provides a strong mechanism discouraging innovation. Hereditary ranking, one of the most important outcomes and stimulus of complexity, is a rare occurrence among hunter-gatherers. More important for the current arguments, the middle-range (or "transegalitarian") societies are rare, precisely because, when initiated, social stratification makes fast progresses, leading rapidly towards the complex end of forager typologies (D. Owens, B. Hayden 1997; A.M. Prentiss et alii 2007). As a low demography is crucial for the elaborated collective control needed to sustain this peculiar circularity in social reproduction (K. Kosse 1994), any notable population growth, either as a local population growth or through extended contacts between groups (S. Shennan 2001), threatens it and gives way to novel adaptive responses.

Contrary to the short timespan available for ethnographers, Late Pleistocene and Holocene archaeology benefits from a better perspective on the *longue durée* in hunter-gatherer adaptation. Ethnographically, the more complex hunter-gatherer adaptations are associated to particularly productive environments (K.M. Ames 1995) and an elaborated technology (R. Torrence 2001), allowing for subsistence intensification (S.L. Kuhn, M.C. Stiner 2001). What archaeology in turn reveals is a more complicated picture, with "simple" and more "complex" strategies often succeeding each other (R.L. Bettinger 2001, 2009; S.B. Kusimba 2005; K.E. Sassaman 2004; I. Kuijt, A.M. Prentiss 2009). While small micro-evolutionary changes were frequent, any important alteration of basic adaptive strategies proved much more difficult and required dramatic shifts in hunter-gatherers natural or social landscape (R.L. Bettinger 2001; J.C. Chatters 2009). Prolonged times of environmental instability seem particularly prone in triggering niche cracking, which may be followed by adaptive innovations in isolated sub-populations (I. Kuijt, A.M. Prentiss 2009) or simply by important cultural loss (A.M. Prentiss, M. Lenert 2009).

Summing up, perhaps opportunistic in economic terms, the hunter-gatherer groups, like most human societies, are less flexible in the social realm and resilient to purposeful change. In fact, as Holocene archaeology suggests, many revolutionary leaps in hunter-gatherers' evolution, including the adoption of domesticates, were actually motivated by the desire to maintain the previous social and economic arrangements - G. Barker 2006. Their inner growth limits are not, however, explicable on cognitive capabilities. Although the demographic, environmental or social variables might have worked differently in Pleistocene contexts³, it seem nevertheless reasonable to take any important resemblance in subsistence, technological or settlement patterns as documenting at least comparable structural constraints and opportunities.

◆ Meat, fire and children: solving coordination problems

Despite the recently widespread adherence to the neo-Darwinian research program, very few attempts have been made to link the co-evolutionary models with archaeological and paleoanthropological data provided by extinct hominids. Although in theory perfectly suited for macro-evolutionary modeling, the Pleistocene selective environments are considerably harder to reconstruct⁴ - and evaluating ancient minds seems by far the most challenging task. Reconstructing past cognition,

³ Environmental productivity, demographic encapsulation or technological innovations granted Holocene hunter-gatherers cultural responses which were neither needed, nor possible in the Pleistocene social and natural landscapes (R.L. Bettinger 2001).

⁴ Most existing attempts are still focused on the Late Pleistocene (e.g. W.E. Banks et alii 2006).

and particularly the pre- or non-sapient minds, is a delicate endeavor, on both epistemological⁵ and practical grounds. Restricted to analogical reasoning and bound to the preserved remains of past material culture, archaeology has only a poor access to individual rationality; what archaeology actually evaluates is a socially and culturally biased average, that is, the “collective” intelligence. Unfortunately, and sociologists know it for a long time, there is often a huge gap between individual possibilities of acting rationally and their actual behavioral choices in social contexts (J. Elster 2007). The focus here will be on the data proving the generic cognitive capabilities of the Pleistocene hominids grouped into the *Homo heidelbergensis*/*neanderthalensis* clade (I. Tattersall, J.H. Schwartz 2007). The reasons for selecting this Eurasian sample are pragmatic, as they provide a richer archaeological record.

There are serious grounds to infer that these big-brained hominids (G.P. Rightmire 2004) have had already solved complex adaptive issues, in both technological and social realms. The most important accomplishments refer to the cooperative arrangements involved in big game hunting, fire use and child rearing. While active scavenging probably represented the main means for meat acquisition in earlier periods (J.P. Brantingham 1998; P.S. Ungar et alii 2006), successful big game hunting is solidly documented from the Middle Pleistocene on (P. Vila, M. Lenoir 2009). The 400 ka old Schöningen spears (H. Thieme 1997) provide irrefutable direct evidence. Neanderthals’ extensive reliance on herbivore hunting is widely acknowledged (for an overview, see M. Patou-Mathis 2000). Similarly, although on occasion contested (K. Schick, N. Toth 2001), fire control (and presumably cooked food) represents another early behavioral acquisition of the genus *Homo*, possibly predating the Middle Pleistocene (N. Alpers-Afil, N. Goren-Inbar 2006). Furthermore, the fragile newborns and the “modern” life history suggested by the anatomy of both *H. heidelbergensis* and Neanderthals makes a strong case for an early existence of some form of collective breeding.

Obviously, all these innovations must have had a long and complex social-evolutionary history and their first recording in the Middle Pleistocene may be simply a preservation artifact. The main point, however, is the existence of an extensive resource and risk pooling already in the Lower Paleolithic. As B. Dubreuil recently suggested (2010), solving these public good games required by default the existence of an inhibitory control on behavior. As sticking to cooperative arrangements in the face of competing motivations is an executive function of the pre-frontal cortex, no further changes of this area need to be associated to the emergence of *Homo sapiens sapiens*. However, as the same author suggested, a higher association of the areas in the temporo-parietal cortex, presumably responsible for superior perspective taking and a high-level theory of mind, was still needed. This missing neural reorganization seems to explain, for Dubreuil at least, the absence of symbolism, art or cumulative culture in the case of *Homo heidelbergensis*. Notwithstanding, following his very argument⁶, proving archaeologically the existence of these features in the Neanderthal case, for instance, would make the changes in the temporo-parietal cortex redundant. Increasing archaeological evidence suggests that this was precisely the case.

◆ Early living in the cultural niche

An increasing amount of evidence, such as the Acheulean “Venuses” from Berekhat Ram (Israel) and Tan-Tan (Morocco) (F. d’Errico, A. Nowell 2000; R. Bednarik 2003), or the pervasive use of ochre in both domestic (M. Soressi, F. d’Errico 2007) and funerary contexts (P. Pettitt 2002) during the European Middle Paleolithic, supports an early emergence of symbolism. Complex lithic and organic technologies, including hafting (A.F. Pawlik, J.P. Thissen 2011), much like logistical hunting (M. Patou-Mathis 2000), long-distance transport of lithic raw material and elaborated settlement structures⁷ are occasionally documented long before the Upper Paleolithic. The gradual colonization of higher, colder and highly seasonal environments by Neanderthals (T. Hopkinson 2007) implicitly points to other skills, such as tailored clothing. All these behavioral features, way remote from the aptitudes of any other primate, point to effective social networks and typically cultural transmission mechanisms, such as imitation, conformism, active social learning and teaching. To put it otherwise,

⁵ Our own sapient cognitive framework, which by definition uses abstract concepts (E.J. Lowe 1998) renders difficult, if not virtually impossible a proper understanding of animal intelligence, for instance.

⁶ “When a behavioral pattern is shared within one clade, it is more parsimonious to assume that it is produced by the same proximate mechanisms” (B. Dubreuil 2010, p. 61).

⁷ Ranging from mammoth bone shelters in open air locales, such as Ripiceni-Izvor site (Al. P. unescu 1993) to “curated” cave settlements (J. Speth 2006).

although only few traces of inherently complex adaptations are preserved, living in the typically human “cultural niche”⁸ (R. Boyd et alii 2011) was already accomplished. Additional evidence in the form of long-lasting traditions in stone knapping further strengthens the case for this, essentially “modern”, extra-somatic inheritance system.

The Acheulean handaxes appear in the archaeological record about 1.5 Ma ago and occur sporadically in many assemblages in Africa and Eurasia until 200 ka BP, thus transcending several taxonomic clusters of the Homo genus, including the archaic Homo sapiens sapiens (K. Schick, N. Toth 2001). For some authoritative voices in dual-inheritance theory, the morphological similarities between the Acheulean handaxes argue against a purely cultural transmission, which would have automatically led to important divergences (P.J. Richerson, R. Boyd 2005, p. 142). However, although the actual diversity of Lower Paleolithic industries is certainly underestimated (K. Schick, N. Toth 2001), in the lack of an extra-somatic learning mechanism like imitation, the handaxes’ longevity would have not been possible at all (S. Shennan 2001).

The gradual expansion of Mode 3 flake technology in both Africa and Eurasia proves another long-lasting trend, again cutting across acknowledged paleoanthropological subdivisions. Furthermore, there is now compelling evidence for the existence of some clear directional trends in the Mousterian (M. Langley et alii 2008). Stable technological traditions, or rather “social memory units” (J. Richter 2000; see papers in S.L. Kuhn, E. Hovers 2006), are documented in many areas in Europe and Middle East. If not a simple preservation artifact, their increased visibility in the second half of the Last Glacial clearly points to cumulative developments unconnected to any anatomical changes whatsoever. With the important exception of Chatelperronian⁹ (J. Zilhão 2006), these patterns of change were not leaning towards the Upper Paleolithic style technological adaptation (i.e. blade production, bone industry), which makes perfect sense from a fitness landscape perspective (S.L. Kuhn 2006).

In sum, although the Lower and Middle Paleolithic do indeed appear as intervals of relative cultural stasis at least in what the generation of entirely novel forms of behavior is concerned (S.L. Kuhn, E. Hovers 2006), multiple lines of evidence indicates human learning abilities virtually indistinguishable from their modern counterparts. The issue to be addressed is therefore why innovations, clearly taking place at certain times and places, failed in disseminating into a wider social realm before the second half of the Last Glacial.

◆ A niche for few: the Lower and Middle Paleolithic adaptation

Although grounded on different theoretical perspectives, several approaches concur in granting demography a powerful explanatory role in Pleistocene cultural evolution (S. Shennan 2001; P.J. Richerson et alii 2009; L.S. Premo, S.L. Kuhn 2010; T. Hopkinson 2011). From my point of view, they provide a much needed help for a better understanding of the Lower and Middle Paleolithic evolutionary dynamics.

As already suggested, there is a strong correlation between the population size and the promotion, spread and persistence of innovation. Most Pleistocene demographic estimations put forward remarkably small numbers, suggesting both low local density¹⁰ and an overall population growth rate close to zero. As J.L. Boone (2002) convincingly demonstrated, the explanation for the low rate stands in a long-term averaging across periods of relatively rapid local population growth interrupted by infrequent but massive crashes, caused either by local resource depletion or by dramatic environmental changes. Larger inter-birth intervals, higher physical stress and fertility levels below the extant foragers’ average were also inferred for extinct hominids like Neanderthals (E. Trinkaus 1995). Models derived from metapopulation ecology (T. Hopkinson 2011), much like the genetic bottlenecks recorded (M.M. Lahr, R.A. Foley 1998) concur in reinforcing the image of a saw-like demographic graph, punctuated by possibly rapid growth and dramatic extinctions of local populations. Moreover, even the documented Middle Paleolithic patterns of change are far from sustaining a continuous, gradual accumulation of innovating behaviors, but rather fast cumulative

⁸ If a culturally mediated migration was indeed involved in maintaining the low level of genetic diversity recorded for the Middle and Upper Pleistocene humans (S.L. Premo, J.J. Hublin 2009), it would point to an early emergence of symbolic principles of social inclusion/exclusion.

⁹ If indeed a Neanderthal work, the Chatelperronian dilutes irrevocably the case of cognitive differences between archaic humans and Homo sapiens sapiens.

¹⁰ The actual size of Paleolithic local groups is uncertain, but numbers close to the ethnographical forager average of 50 individuals are usually acknowledged (C. Gamble 1999).

"sprints", often followed by cultural loss. This mosaic evolutionary pattern seems therefore connected to the size and dynamics of local populations than to the evolution of global metapopulation (T. Hopkinson 2011).

On a large, biogeographical scale, the huge niche expansion initiated from Eastern and Southern Africa by Lower and Middle Pleistocene hominids was certainly connected to the ability of selecting suited habitats, that is, patchy, tropical grasslands (for an overview, see C. Finlayson 2004). The first persistent colonization of open and cold Eurasian is actually recorded very late, after the advent of Upper Paleolithic some 40 ka ago. The expansion of the *Homo erectus* ecumene suggests repeated fissions in previously unoccupied spaces, once the local environmental carrying capacity was reached. Involving carnivore competition, temporary shortages, colonization of unfamiliar landscapes, etc., this ability to "surf the ecological tide" was in no way unproblematic and certainly encouraged a strong selection for increasingly cooperative arrangements. However, simply sticking to familiar ecological niches, that is, less variable environmental settings might have entailed important consequences, such as low local populations and their propensity for conformism (J. Henrich, R. Boyd 1998; R. Boyd et alii 2011). This outcome is particularly likely if populations packed in adjacent areas maintained as expected a moderate level of inter-group mobility, but practiced a preponderantly vertical transmission of adaptive information (S. Shennan 2001). On a theoretical level, innovations are expected to preferentially occur in marginal populations, in which conformist pressure is lower (A.M. Prentiss et alii 2009). However, if the isolation of local populations was avoided, or if these occasionally isolated populations had only a short life¹¹ (T. Hopkinson 2011), the incorporation of new behaviors into the larger metapopulation could have repeatedly fail in spreading and being adopted. That would have led to a slow pace of innovation, acting as a gradual drift at the higher, metapopulation level. This seems to have been the case for a great part of the Lower and Middle Pleistocene. The crystallization of similar socio-technical packages (i.e. adaptive convergence) or mechanical constraints (i.e. technical convergence) might have also contributed to the largely homogenous aspect of Mode 1 and Mode 2 technologies. Furthermore, the Lower Paleolithic lithic hardware is mainly composed from expedient or highly symmetrical tools (e.g. handaxes), with a quite limited room left for morphological variation. Their overall simplicity also suggests a rather low investment in the technological aids to adaptation, which further questions the solidity of lithic-based assessments of Lower and Middle Paleolithic cognition and cultural evolution in general (M. Anghelinu, L. Niț 2008).

The late Middle and early Upper Pleistocene adaptation, when a shift towards a top predator niche followed by a relative extension of the social life is recorded (R.A. Foley, C. Gamble 2009), suggests a more intricate scenario. The details of the successful switch to herbivore hunting are unclear. Yet, once adopted and confronted to increasingly varying environments, the new adaptive strategy (which definitely involved diverse local tactics, indirectly expressed in the ethological diversity of hunted species - M. Patou-Mathis 2000), though higher in the fitness landscape, maintained nevertheless potentially high extinction rates for local groups. There are serious reasons to consider this forager adaptation as stable, effective, but nevertheless risky. Limited to habitats displaying mixed biota (C. Finlayson 2004) and focused on prime-adults herbivore hunting¹² with restricted technological means¹³, the MSA/Mousterian almost by default implied residentially mobile, small local groups, quite vulnerable to swift environmental changes, local demographic crashes and information loss (L.S. Premo, S.L. Kuhn 2010). Given the constant relocation to more productive patches or refugia as a common reaction to climate degradation, the lack of correlation between environmental settings and Mousterian technological responses in both space and time (S.L. Kuhn, M.C. Stiner 2001; J.P. Boquet-Apel, A. Tuffreau 2009) appear less surprising.

From the Acheulean emergence to the MSA precocious developments and to the more complex Upper Paleolithic adaptations, possibly including the sexual division of labor and intensive use of low-ranked resources (S.L. Kuhn, M.C. Stiner 2006), Africa appears as a cradle of innovation. In the

¹¹. Obviously, colonizing unfamiliar landscapes, coupled with environmental events certainly provided countless opportunities not only for the extinction of local populations, but also for isolating larger metapopulations. These occurrences are highly visible in the taxonomical diversity of *Homo erectus*, but less accurately captured in the archaeological record.

¹² A similar pattern seems to have characterized the MSA prey choice (cf. S. Shennan 2001).

¹³ Except for the increased flexibility allowed by hafting and flake/blade production and the production of lithic points of various shape (Levallois, foliate), the MSA/Mousterian preserved technologies show no spectacular progresses in comparison to the late Middle Pleistocene.

same time, the size and stability of African hominid populations is clearly supported both by the current genetic diversity and by repeated wave of emigrants leaving the continent during the Pleistocene (M.M. Lahr, R.A. Foley 1998).

Similar arguments can be advanced for western Eurasia. At least some directional trends in the Eurasian Mousterian appear connected to local demographic increases (for the Middle East Mousterian, see L. Meignen et alii 2006). Both micro-evolutionary purposeful changes and simple drift could explain these gradual changes. The main point, however, is that although sharing a similar adaptive strategy, the MSA/Mousterian fitness landscape did not necessarily stand in peaks of equal heights; multistable population densities and hysteresis loops may actually explain the palimpsest of Mode 3 and 4 technologies recorded during the Late Glacial (P.J. Richerson et alii 2009). Anywhere favorable environmental circumstances allowed for denser demographic networks, cultural innovations not only occurred, but also lasted.

The high visibility taken by this process during the transition to the Upper Paleolithic, although magnified by paradigmatic biases (G.A. Clark 2009), is the outcome of a very particular complex of circumstances, in which modern human anatomy played no particular role. The successful colonization of the challenging, but seasonally highly productive steppe landscapes was possible through the adjustment of a likely alloigenous adaptive strategy (C. Finlayson 2004; S.L. Kuhn, M.C. Stiner 2006) to local resources. This allowed the thinner and taller newcomers to climb quite fast a higher fitness peak in comparison to the ones occupied by Neanderthals and their African ancestor alike for hundreds of millennia. The new eco-cultural niche was already doing better in demographic matters by the time it reached Europe, and only a minor advantage would have sufficed to replace quite fast the previous strategy (E. Zubrow 1989). The advantage included a larger proportion of adult survival (R. Caspari, S.H. Lee 2004), but also the extension of social life through extensive symbol use (C. Gamble 1999; R.A. Foley, C. Gamble 2009). Both features are crucial for a successful transmission of adaptive information. Knitting together distant groups and taking advantage of the vast ungulate reservoir of the mammoth steppe, the Upper Paleolithic essentially opened a new eco-cultural niche characterized by wide communication networks. However, even this successful strategy was eventually overwhelmed by the Last Glacial Maximum and replaced through further adaptive shifts (C. Gamble et alii 2004).

◆ Conclusions

The issue of cultural stasis is certainly connected to the very complexity of human extra-somatic adaptation, whose emergence required the biologically expensive (L.C. Aiello, P. Wheeler 1995) ability for imitation. Complex, highly integrated socio-technical systems are better documented from the Upper Paleolithic on, but the cultural logic and rules governing both stasis and innovation are certainly much older. The cognitive “hardware” needed for symbolic thinking, long term cooperation and culturally-biased information inheritance most likely predates the Middle Pleistocene. In fact, it seems more profitably to focus the search for their emergence to the Lower Pleistocene and *Homo erectus* than on the heidelbergensis/Neanderthal clade.

The total lack of synchronicity between the African emergence of modern anatomy and the elaborate Eurasian Upper Paleolithic cultural repertory and the repeated episodes of stasis documented by Holocene archaeology leave little room for biologically based explanations. The African MSA, much like the European Middle Paleolithic record, is replete with examples of innovative practices which afterwards disappear with no long-lasting cumulative effects.

It was argued here that the redundant aspect of Lower and Middle Paleolithic adaptation, when contrasted to the more “creative” Upper Paleolithic, was not a matter of individual ability to innovate, but rather of finding a way for passing the innovation to larger groups. Although naturally variable in the local tactics, the opportunist forager strategy dominating these intervals both motivated and allowed only for limited innovation. Even when discovered, many novelties were subsequently lost. These failures were not simply caused by catastrophic environmental changes: previous demographic states and the limits inherent in human transmission mechanisms constantly interfered. Elaborating on their complex interplay, thus far better captured in theoretical models than in archaeological applications, opens a promising avenue for further researches on Pleistocene cultural evolution.

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