Spatial abilities, cognition and the pattern of Neanderthal and modern human dispersals

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A B S T R A C T
Neanderthals and anatomically modern humans (AMHs) are very closely related, although their skeletal morphology is distinct enough for them to be classified as separate species. Their physical differences, including the architecture of the skull and post-cranial skeletal proportions, do not explain the extinction of the Neanderthals as a species, however. The post-cranial morphology of the Neanderthals, which is generally believed to reflect an active lifestyle under cold conditions, falls within the range of modern human variation. Their cranial capacities are essentially identical and skull morphology does not convey any obvious adaptive advantage to either species. The existence of other, less easily discernible biological traits that might have contributed to the extinction of the Neanderthals — such as differences in reproductive rates or developmental histories — cannot be ruled out, but are not supported by current data. Behaviourally (culturally) based explanations for the process of replacement of Neanderthal populations by AMHs center on archaeological evidence for more complex patterns of social organisation, associated with the use of symbols and the development of new technologies. This paper explores the link between social complexity, spatial distribution and cognition during the Late Pleistocene, suggesting a mechanism whereby cognitive differences between hominin species may have arisen.

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1. Introduction

Modern human dispersal into Eurasia and the subsequent extinction of Neanderthals during the Late Pleistocene are two of the most fascinating and enduring problems in prehistory. Various explanations have been suggested over the years, mostly centered on attempts to identify an adaptive advantage for modern humans, whether biological or cultural, that would link the two processes. Paleontological and archaeological data, including the spatial distribution of archaeological sites, evidence for the production of material culture and subsistence strategies all come into play in attempts to resolve this puzzle. This paper focuses on the development of spatially extensive social networks and heightened mobility, associated with the adoption of a modern hunting-gathering way of life, as a factor stimulating the development of spatial abilities in modern humans that may have resulted in the emergence of differences in spatial cognition.

2. Biological explanations

Skeletal indicators of an adaptation to cold climates (Howell, 1952; Trinkaus, 1981; Trinkaus et al., 1999) were originally considered significant insofar as they corroborated the hypothesis that Neanderthals evolved from a geographically isolated, Western European hominin population during the course of the Late Pleistocene. The brachial and crural indices of Neanderthals are considered an adaptation to cold temperatures following Allen’s rule (Howell, 1952) — in contradistinction to the more “tropical” body proportions of AMHs — and their capacious nasal cavities are also thought to represent an adaptation to the cold, although in both cases the observed traits fall within modern human variation (Trinkaus, 1981). Their post-cranial morphology does not explain the disappearance of Neanderthals at the end of the last Glacial — a time when a physical adaptation to cold conditions should have been advantageous, however.

Another biological explanation for adaptive differences between AMHs and Neanderthals is genetic. The role of genetic difference in this debate is difficult to assess, however. The FOXP2 gene, which makes human speech possible, was once thought to differentiate between AMHs and Neanderthals (Klein, 2000; Enard et al., 2002), but is now known to exist in the Neanderthal genome (Krause et al., 2007a; Trinkaus, 2007).

Cognitive differences between AMHs and Neanderthals have also been invoked, despite the difficulties involved in constructing bridging arguments between cognition and the archaeological record (Wynn, 2003). The distribution of archaeological sites and the organisation of their settlement systems led Binford (1989) to suggest that AMHs were able to plan logistically, whereas Neanderthals lacked...
tactical depth, moving from site to site as required, pursuing an opportunistic strategy of resource procurement. Archaeozoological evidence suggests that Neanderthals were not limited to opportunistic resource procurement strategies, however. On the contrary, Neanderthals were clearly capable of targeting gregarious prey species, anticipating their movements and making efficient use of the landscape to hunt them—a strategy that requires planning depth (Farizy and David, 1989; Farizy et al., 1994; David & Enloe 1993; Gaudzinski, 1996; Gaudzinski & Roebroeks 2000; Burke, 2000; Patou-Mathis and Chabai, 2003). Based on the faunal evidence, therefore, there is little reason to suggest that Neanderthals lacked an innate (cognitive) inability to plan ahead and think tactically.

3. Archaeological explanations

Attempts to identify a culturally based adaptive advantage for AMHs in the archaeological record are reviewed in full elsewhere (Bar-Yosef, 2002) and are only briefly summarized here. Most of the technological advantages once thought to distinguish the Upper Palaeolithic (UP) are now known to have appeared earlier in the archaeological record. The production of blades, for example, is now recognized as a feature of both AMH and Neanderthal lithic industries at different times during the MP/MSA (Bar-Yosef and Kuhn, 1999; Meignen, 1994). The invention of hafting, thought to signal the relative sophistication of UP tool making abilities, is now recognized in both the MP and the MSA (Boeda et al., 1996; Kay, 1998; Hardy et al., 2001; Lombard, 2005; Wadley, 2005; Wadley et al., 2009) and a developed bone tool industry is incontrovertibly part of the MSA (e.g. Henshilwood et al., 2002; d’Errico and Henshilwood, 2007; Backwell et al., 2008). If relative technological sophistication is an indicator of cognitive abilities, therefore, there is not much to distinguish between AMHs and Neanderthals—at least during the timeframe of interest.

In terms of subsistence strategies, Neanderthals scavenged or hunted large game when and where appropriate (Speth and Trchová, 2001) and exploited small game and shellfish (Stiner, 1994, 2001; Barton et al., 1999; Stringer et al., 2008) as well as plants and nuts (Barton et al., 1999; Albert et al., 2000). Examples of specialised hunting, once thought to distinguish UP subsistence strategies, have been demonstrated in a number of Middle Palaeolithic contexts (David and Enloe, 1993; Gaudzinski, 1996; Grayson and Delpech, 2002; Costamagno et al., 2006). The distinction between AMHs and Neanderthals is once again lost as it appears that both species shared a range of subsistence strategies and exploited a wide range of resources, adjusting to local conditions (Bar-Yosef, 2004). Neither the paleontological nor the archaeological records, therefore, yield convincing evidence for the existence of a clear adaptive advantage that would explain the successful dispersal of AMHs and the eventual extinction of the Neanderthals.

4. Spatial patterning

Spatial patterning, on the other hand, hints at significant differences between Neanderthals and AMHs. The spatial distribution of a species provides information about its ecological requirements, environmental limitations and adaptive flexibility; the core range reflects the environment within which a species initially evolved through a process of adaptation, while the effective range reflects both innate adaptive flexibility and the outcome of interactions with other species (prey and competitors). Lamentably, the total extent of hominin ranges during the Late Pleistocene cannot be assessed, because ancient coastlines, now submerged, cannot be surveyed without considerable effort (e.g., Bailey et al., 2008). In addition, the reliability of Late Pleistocene time series for the critical time period between ca. 32 and 35 ka $^{14}$C is questionable, despite recent advances in radiocarbon calibration (Weninger and Joris, 2008). These and other confounding factors make reconstructing the demographic patterns of humans (AMHs) and Neanderthals a bit of a black art. Nevertheless, it is clear that the initial ranges of these species differed and that spatial separation was maintained for a relatively long time.

Western Europe is considered to be the “classic” (or “core”) Neanderthal range based on the distribution and relative age of known archaeological sites (Bocquet-Appel and Demars, 2000) and the distribution of dated skeletal remains (Serangeli and Bolus, 2008). The total geographic range of Neanderthals is known to extend as far south as the Levant, and as far east as the Altipl (Krause et al., 2007b). Neanderthals, therefore, were capable of living in a variety of environments under different climatic conditions—whether they thrived in all of them is questionable, however, and the implications of this observation will be discussed below.

On a regional scale, Neanderthals are generally considered to have moved frequently within relatively small territories, intensively using local resources (Mellars, 1996), although they were capable of exercising variable degrees of mobility according to the structure of the environment (Davies, 2007). The observation that raw material transfer distances in Europe during the MP are regionally variable and correlate broadly with landscape variability supports this suggestion (Féblot-Augustins, 1993). Nevertheless, Neanderthals generally appear to have mapped onto relatively smaller territories than AMHs, e.g. (Meignen and Brugal, 2001; Adler et al., 2006; Conard et al., 2006).

On a continental scale, MP sites are relatively under-represented in the archaeological record of the East European Plain (Vishnýosov and Nehorošev, 2004) where they are distributed almost exclusively in the south (Hoffecker, 1999; Pavlov et al., 2004). In contrast, not only is the Upper Palaeolithic record of the East European Plain relatively richer, it also suggests a pattern of rapid colonization (Dolukhanov, 1999). Accepting that Neanderthals were morphologically adapted to cold conditions, capable of existing in a range of distinct landscapes, technologically advanced and able to prey upon large-bodied, gregarious herbivores, then the northern plains of Europe should not have represented an insurmountable geographical challenge. The fact that AMHs were apparently better equipped for life in the Eastern European plains than Neanderthals indicates that other aspects of their adaptation have to be considered.

One explanation for the observed spatial patterns is the new pattern of social organisation that emerged during the MSA (Gamble, 1991; McBrearty and Brooks, 2000; Henshilwood et al., 2002; Wadley et al., 2009). The development of a “modern” way of life is indicated by the presence of tools for the communication of social identity and the expression and maintenance of personal relationships in absentia and over long distances (Gamble, 1998). The archaeological and ethnographic records suggest that social identities are constructed and maintained through the production of material culture accompanied by stylistic variation (Weissner, 1984) and symbolic expression. Early manifestations of symbolic expression through the production of material culture are documented for the MSA by McBrearty and Brooks (2000) and others (d’Errico et al., 2005; Bouzouggar et al., 2007; d’Errico and Henshilwood, 2007) as well as for the MP of the Levant (Hovers et al., 2003; Bar-Yosef Mayer et al., 2009) associated with AMHs. Symbolic behavior is not absent in Neanderthal contexts (Langley et al., 2008; Zilhão et al., 2010) but is a rare occurrence before the arrival of UP industries in Europe. The more “modern” aspects of the material culture of Homo sapiens identified by McBrearty and Brooks (2000), interpreted as signs of a gradual process of cultural intensification, are not uniformly present during the MSA which leads the authors to suggest a stepwise, sometimes intermittent process; this process may be linked to population pressure in regional
populations (Henshilwood and Marean, 2003). The fact that relatively “late” Neanderthal cultures, such as the Chatelperronian, hint at the emergence of similar cultural developments in Western Europe could be seen as validating this hypothesis, since the contraction of Neanderthal populations into their core ranges towards the end of MIS 3 (Bocquet-Appel and Demars, 2000; Serangeli and Bolus, 2008) could have resulted in population pressure through demographic packing. This implies the existence of similar adaptations to social and demographic pressures, and social cognition, in both species but different timing for the triggering of the process (earlier for AMHs, later — possibly too late — for Neanderthals).

The cultural manifestations identified in the MSA (and the Levant) therefore, are harbingers of a modern pattern of social organisation that would fully emerge during the Upper Palaeolithic, enabling the emergence of socially integrated regional groups (Conkey, 1980, 1984; Gamble, 2000). Another result of this development is that local groups could counter resource stress by redistributing members within a wider regional population (Weissner, 1982; Cashdan, 1985). Information (crucial to fine-tuning movements to coincide with resource availability) would also have flowed more efficiently as individuals moved between groups (Whallon, 2006). The flow of information and people on a regional scale would have maintained equilibrium between resource availability and local group size within the population, facilitating adaptation to challenging environments.

The relative success of AMH dispersals, particularly in difficult environments such as the Northern Plains of Eurasia (Hoffecker and Cleghorn, 2000), may therefore be explained. While AMHs would develop and maintain spatially extensive, well-integrated social networks during the course of the MSA, culminating in wide-spread dispersals, Neanderthals, by and large, retained a more local pattern of social interaction.

5. Spatial abilities and spatial cognition

The development of a modern hunting and gathering way of life could have conferred an adaptive advantage on dispersing AMH populations for the reasons explained above. It may also have fostered the development of cognitive differences between AMHs and Neanderthals. The challenge of maintaining complex, spatially extensive social networks, implying heightened mobility and spatial awareness, requires the deployment of specific cognitive skills related to wayfinding, stimulating the development of spatial abilities that could eventually lead to changes in spatial cognition.

Golledge (1999:47) defines wayfinding as: “purposeful movement to a specific destination that is distal and thus cannot be perceived by the traveller”. Two distinct wayfinding strategies are used by humans. The first strategy (an “allocentric” or “survey strategy”) uses Euclidian metrics (direction and distance estimates) and an “enduring […] object—object or environment—object association” (also known as a “cognitive map” or “cognitive representation” (Golledge, 1999, 2003; Kitchin, 1994)). The second strategy is an “egocentric” or “landmark strategy” that relies on landmark recognition (or “transient action-oriented egocentric self-object associations” (Burgess, 2006)). The process of linking the two representations (aka “spatial updating”) ensures that humans can recognise their current position and translate it onto the enduring representation. The internal representations (cognitive maps) are built up from direct experience of the world through a process of path integration (Golledge, 1999; Loomis et al., 1999) and landmark recognition (Foo et al., 2005), implying the motivated and deliberate encoding of environmental information (Golledge, 2003:30).

Allocentric and egocentric wayfinding strategies make use of distinct spatial skills and correlate with the development of different spatial abilities in humans (Shelton and Gabrieli, 2004). For example, the link between preference for a “survey” strategy and good mental rotation skills is thought to result from differential stimulation of the hippocampus (part of the brain implicated in spatial cognition and in the performance of mental rotation) during allocentric encoding (Burgess et al., 2006; Parslow et al., 2004). This is supported by the observation that people who have a high dependence on their wayfinding skills and habitually use maps develop relatively enlarged posterior hippocampi (Maguire et al., 2000). Preferential use of a particular wayfinding strategy, therefore, leads to the development of, or alternatively reinforces existing differences in spatial ability and may result in concomitant changes to the brain.

Ranging patterns (mobility) are linked to sex-based preferences for one or the other wayfinding strategy in some species of mammal and correlate with differences in spatial abilities (Gaulin and Fitzgerald, 1989). In humans, experimental psychologists have noted differences between the sexes in the performance of tests designed to measure spatial abilities that could reflect preferences in the selection of a wayfinding strategy. For example, men typically out-perform women in tests of spatial perception and mental rotation (Montello et al., 1999; Voyer et al., 1995), whilst women are better than men at memorizing spatial configurations (Barnfield, 1999; Toitenham et al., 2003; Levy et al., 2005). These differences are thought to correlate with use of survey strategies in men and landmark-based strategies in women.

Evolutionary psychologists suggest that differential spatial abilities of men and women reflect differences in spatial cognition that evolved through time as a result of the adoption of a gendered division of labour in hunting and gathering societies and with it, gendered patterns of mobility (Eals and Silverman, 1994; Silverman et al., 2000, 2007; Ecuery-Dab and Robert, 2004). Men are generally considered to range further than women in hunting and gathering populations, and since allocentric representations of space work best when distances are great (Burgess, 2006) proponents of the “Hunter—gatherer theory of spatial sex differences” (HGT) suggest that hunters develop a preference for a “survey based” or “allocentric” strategy. This preference would explain a male advantage in mental rotation tests. Conversely, the smaller-scale mobility assumed to be correlated with foraging activities is proposed as the context within which spatial memory is selected for in women, explaining the female advantage in object-location memory tests (Ecuery-Dab and Robert, 2007).

The HGT, therefore, suggests that differences between the spatial abilities of men and women reflect sex-based differences in spatial cognition that evolved as a result of the adoption of gendered activity patterns. It is debatable whether observed differences in spatial abilities in men and women reflect sex-based differences in spatial cognition, or whether they are the result of a gender-based training effect promoting the differential development of spatial abilities. Feng et al. (2007) show that individuals can be trained to perform equally well in mental rotation tests, irrespective of their sex. Similarly, a recent study of orienteering suggests that trained participants of both sexes perform navigation tasks with the same efficiency (Burke et al., nd). The existence of a training effect is supported by evidence that length of exposure to complex wayfinding tasks requiring the use of an allocentric perspective is positively correlated with physical changes to the brain (Maguire et al., 2003). In other words, the plasticity of the human brain allows significant differences in spatial abilities (and neuroanatomical changes) to develop when a subject is provided with training opportunities. Regardless of whether or not sex-based differences in spatial abilities exist as a result of training or innate, cognitive differences, there is clear evidence for a link between their development and habitual patterns of activity in humans.
The link between patterns of mobility and the development of spatial abilities allows for the suggestion that when AMHs developed the ability to maintain extensively spatial social networks and adopted a more mobile lifestyle (i.e., during the course of the MSA) they created conditions under which specific spatial abilities were selected for, thus placing new demands upon the neural substrate (Maguire et al., 2003; Hartley et al., 2007). Furthermore, exploratory travel, such as would have occurred during the initial phases of dispersal, makes very different demands upon the brain than travelling a known route (Hartley et al., 2003). The effort required to maintain relatedness over greater distances and the skills deployed during exploratory travel together would have promoted the use of allocentric wayfinding strategies, which work best in situations where distances are great and more locations have to be remembered (Burgess, 2006). Put another way, modern human dispersals were facilitated by the development of a more generalised, transferable system for learning a landscape, rather than a reliance on detailed local knowledge (Kelly, 2003). Dispersing populations of AMHs would have been drawing upon different cognitive resources than Neanderthals, therefore, given the spatial patterning in the archaeological record discussed above; eventually, this could have resulted in physical changes to the brain (Maguire et al., 2003). This process would have cycled through generations, reinforcing itself over time and widening the cognitive gap between AMHs and Neanderthals. The pace of change would have been similar to that proposed in the accretion model of the development of fully modern culture during the MSA proposed by several authors (e.g., McBrearty and Brooks, 2000; Clark, 2002).

What is proposed here, therefore, is a cultural mechanism for the emergence of differences in spatial abilities, possibly accompanied by structural changes to the brain, which would have enabled the emergence of differences in spatial cognition between AMHs and Neanderthals. It is possible to make predictions about the archaeological record on the basis of this hypothesis. The development of a “modern” hunting and gathering adaptation including spatially extensive social networks and more mobility will be correlated with the adoption of allocentric wayfinding strategies which enable rapid movement and exploratory travel over greater distances and in turn, will have facilitated rapid population dispersal. Information about novel landscapes will have been more efficiently relayed through spatially extensive social networks and would also have facilitated dispersal. These developments would have made AMHs better able to colonise vast, relatively undifferentiated spaces which present a challenge to wayfinding strategies requiring detailed local knowledge and landmarks being less “legible”, sensu Collardey (1999). The pace of hominin dispersals is difficult to measure given the relative paucity of sites attributable to the early UP, their spatial distribution and the error associated with dating methods. Nevertheless, looking at the distribution of archaeological sites in the East European plain suggests that AMHs were the first to really penetrate the plains (Hoffecker, 2002; Pavlov et al., 2004) and that colonization was probably a relatively rapid event (Dolukhanov, 1999). In contrast, the Neanderthals thrived on the fringes of the plains in more topographically complex regions, better-suited to landmark-based wayfinding strategies, such as the Crimean Peninsula (Burke, 2006). The pattern of site distribution in the East European Plain suggests that the prediction made above is supported by the archaeological record.

It is also possible to predict that along with an ability to maintain connectedness over greater distances, humans developed a more efficient means of communicating information about the landscape. One of the most efficient ways of communicating about the landscape is via schematic representations, i.e., maps. Mapping abilities are a universal aspect of modern human spatial cognition (Blaut et al., 2003). It is hard to say when schematic representations of the landscape first developed but the archaeological record suggest that the first such representations of the landscape appear during the Upper Palaeolithic. The existence of symbolic expressions interpretable as attempts to schematize the landscape all date to the UP (Kozlowski, 1992; Svoboda, 2007; Utrilla et al., 2009). The existence of landscape representations, therefore, could signal the culmination of the process of evolution of modern human spatial cognition during the Upper Palaeolithic.

6. Conclusion

It is likely that the extinction of the Neanderthals was a complex process involving climatological, biological, cognitive and social factors. Here, we have concentrated on the link between spatial abilities and changes in social organisation and consequently, mobility, that emerged during the MSA. The development of tools for the symbolic expression of social identity, which in turn allowed humans to create large social networks and maintain relatedness over great distances, is linked to the emergence of heightened mobility just prior to the appearance of Upper Palaeolithic cultures in the archaeological record. These factors combine to create a context for the differential development of enhanced spatial abilities in AMHs. In contrast, the less spatially extensive social systems of the Neanderthals did not make the same demands upon their cognitive systems. Enhanced spatial abilities in AMHs set the scene for the evolution of differences in spatial cognition between AMHs and Neanderthals. The emergence of a preference for allocentric wayfinding strategies which accompanied this process would explain evidence for rapid human dispersals across new landscapes, including the northern plains of Eurasia. Differences in spatial cognition leading to the successful colonization of new regions could have played a role in the relative evolutionary success of AMHs at the expense of the Neanderthals.

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References


Wedley, L., 2005. Putting ochre to the test: replication studies of adhesives that may have been used for hafting tools in the Middle Stone Age. Journal of Human Evolution 49 (5), 587–601.


