doi 10.4436/jass.94022
e-pub ahead of print

JASs Invited Reviews
Journal of Anthropological Sciences
Vol. 94 (2016), pp. 1-22

The false dichotomy: a refutation of the Neandertal indistinguishability claim

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Summary – *In the debate about the demise of the Neandertal, several scholars have claimed that humanity's nearest relatives were indistinguishable archaeologically, and thus behaviorally and cognitively, from contemporaneous* Homo sapiens*. They suggest that to hold otherwise is to characterize Neandertals as inferior to* H. sapiens*, a false dichotomy that excludes the possibility that the two human types simply differed in ways visible to natural selection, including their cognition. Support of the Neandertal indistinguishability claim requires ignoring the cranial differences between the two human types, which have implications for cognition and behavior. Further, support of the claim requires minimizing asymmetries in the quantity and degree of behavioral differences as attested by the archaeological record. The present paper reviews the evidence for cognitive and archaeological differences between the two human types in support of the excluded middle position.*

Keywords – *Neandertals, Encephalization, Globularization, Cognitive Evolution.*

Introduction

The discovery of the first Neandertal fossil in 1856 initiated a seemingly endless debate concerning its status. Should Neandertals be considered a different species, as exemplified by William King's 1864 proposal for *Homo neanderthalensis,* or should they be counted as a subspecies of *Homo sapiens*? Lurking beneath this debate have been two apparently incompatible interpretations of Neandertal behavior, with one extreme painting a picture of brutish simplicity, and the other presenting Neandertals as indistinguishable from modern humans. This disagreement has hinged on the relative absence of more sophisticated archaeological artifacts and behaviors like parietal art, stylized figurines, and highly ritualized burials among Neandertal archaeological remains. Was this evidence for cognitive differences, or was the absence of these behaviors merely an artifice of deposition and discovery? It is undoubtedly the case that, especially in the late 19th and early 20th centuries, the Neandertals were considered inferior and portrayed as rather brutish cave dwellers. Today, not only has the pendulum swung in the opposite direction, it shows signs of becoming stuck at the far extreme, in which Neandertals appear just like us. This is the Neandertal indistinguishability claim. Even the demise of the Neandertals has been contentious, with various sides claiming that

it was just a simple quirk of fate ("there but for the grace of God go we"), contemporaneous *H. sapiens* were in direct competition and killed the Neandertals off in some fashion, the Neandertals' own behavior contained the seeds of their demise, or the Neandertals were simply assimilated into the *H. sapiens*' population.

Recently, Villa & Roebroeks (2014) and Zilhão (2014) have further inflamed the debate by claiming that the Neandertals were archaeologically – and thus behaviorally and cognitively – indistinguishable from contemporaneous *H. sapiens*. They represent the opposition to this position starkly: Those who support it believe Neandertals were inferior, *H. sapiens* superior, because they are afflicted by "a persistent, if subconscious influence … of Victorian-age ideas of evolution-as-progress and ancient-as-primitive" (Zilhão, 2014). It is our present contention that they are creating a false dichotomy by excluding a middle position that holds Neandertals and *H. sapiens* were simply different from each other in ways visible to natural selection. The middle position also presupposes that the differences between the two human types made neither one better or worse than the other (e.g., Langbroek, 2012; Mithen, 2014). As Mithen astutely observed, differences in the "cognitive characteristics" of Neandertals and *H. sapiens* are "entirely unrelated to making value judgments" about them (p. 8).

As Wynn & Coolidge noted in 2004:

> *"Neandertals did compete on a par with anatomically modern humans for thousands of years and may even have out-competed them for several millennia in the Levant (Arsuaga, 2001; Shea, 2003). Had [Neandertals] possessed a dramatically less powerful intelligence, this situation is unlikely to have occurred. Comparisons of Neandertal and modern behavior have tended either to overemphasize the differences (Binford, 1981) or overemphasize the similarities (d'Errico et al., 1998). A more appropriate solution is to posit a small cognitive difference that had profound long-term consequences" (Wynn & Coolidge, 2004, p. 468).*

What Wynn & Coolidge proposed then is likely true now: It is possible that a small but significant difference in cognition, like working-memory capacity or executive functions, made the difference in the respective fates of the two human species.

A corollary to the null hypothesis of the false dichotomy is the idea that Neandertal indistinguishability can *only* be rejected by "distortions of method and logic" and "double standards in the assessment of the evidence" (Zilhão, 2014). This is an ironic stance for indistinguishability proponents to assume for two reasons: First, support of Neandertal indistinguishability requires ignoring the *cognitive* implications of the cranial differences between the two human types; second, it requires minimizing asymmetries in the quantity and degree of behavioral differences as attested by the archaeological record. The present paper reviews the evidence for cognitive and archaeological differences between the two human types to support the middle position excluded by Villa & Roebroeks (2014) and Zilhão (2014): Neandertals and early or anatomically modern humans (AMH) differed cognitively in ways subject to natural selection. Such differences are, after all, what natural selection acts upon, even when they are subtle.

On the relationship between neuroanatomy and cognitive functions

Paleoanthropology has long recognized that the fossil crania of Neandertals and AMH differ in both size and shape. Cognitive science has long accepted the observations that cranial size and shape are produced by (and are thus related to) brain growth and development and that neuroanatomy and cognitive functioning are related. Do size and shape matter? The answer is *yes*: neuroanatomical differences in the size and shape of Neandertals and AMH fossil crania are important because they have implications for cognitive functioning.

Brain size matters

Neandertal brains were generally about 10% larger than those of AMH (e.g., Holloway *et al.*, 2009; Martin, 1984; but also see Rightmire, 2004; Stanyon *et al.*, 1993). If the 10% increase in size included a 10% increase in number of neurons (far from certain), then theoretically there might have been an increase in processing power. Increases in brain size in hominin evolution were often accompanied by increases in cultural complexity. This larger size could also have been disadvantageous; greater brain size would have increased Neandertal daily caloric requirements above those of AMH because brain tissue is metabolically expensive and bigger brains need more calories than smaller ones do. Greater brain size also might have made Neandertal brains slightly more subject to the evolutionary trade-offs associated with encephalization than AMH brains may have been, including susceptibility to metabolic heat and disease (Bruner, 2014; Bruner *et al.*, 2014) and reduction in interregional brain connectivity and the number of neurons (Azevedo *et al.*, 2009; Kaas, 2000). Bruner (2014) has further speculated that the Neandertal brain "may have reached some structural limits in [its] neurocranial organization" (p. 125), an interpretation based on the principles of cranial development and features of Neandertal crania (e.g., ossification patterns).

As the larger Neandertal brain was related to the larger Neandertal body, Pearce *et al.* (2013) have argued that Neandertal brains would likely have "invested more neural tissue in somatic areas involved in body maintenance and control compared with those of contemporary AMHs" (p. 5). In comparison, the smaller AMH brain size was related to its more globular shape (a consequence of parietal encephalization in AMH but not Neandertals, discussed later), giving AMH a slightly higher Encephalization Quotient (an allometric ratio of actual to predicted brain size that takes body mass into account) because of their reduction of brain and body size relative to Neandertals, while concomitantly reducing their caloric requirements (Hublin *et al.*, 2015). Further, "Neanderthal brains grew differently early in ontogeny, and probably prenatally, when compared with modern humans" (Bastir *et al.*, 2011, p. 5). The latter difference may have had implications for caloric requirements for Neandertals, especially in early childhood.

Brain shape matters too

The differences in the gross neuroanatomical shape also have important implications for cognitive functioning. The most demonstrable differences in the neuroanatomy of the two human types are found in the relative sizes of certain gross anatomical structures. AMH had relatively larger parietal lobes (Bruner, 2004; Bruner *et al.*, 2003), larger temporal lobe poles (Hublin *et al.*, 2015), wider orbitofrontal cortex (Bastir *et al.*, 2008), larger olfactory bulbs (Bastir *et al.*, 2011), larger cerebellums (Weaver, 2005; Hublin *et al.*, 2015), and relatively smaller occipital lobes than Neandertals (Pearce *et al.*, 2013).

Parietal expansion is perhaps the single characteristic that best distinguishes AMH brains from the brains of all other primates, including the Neandertals, whose brains appear to have a less derived morphology, including parietal size and shape (Bruner *et al.*, 2003). Parietal expansion in AMH gave the brain a rounder, more globularized cranial shape (Bruner, 2010; Bruner *et al.*, 2003, 2004; also see Fig. 1, right). These bulging parietals may have been linked to neural reorganization of component structures such as the precuneus, intraparietal sulcus, surpramarginal gyrus, and angular gyrus (e.g., Bruner *et al.*, 2014, 2015; Coolidge, 2014; Hublin *et al.*, 2015). By comparison, Neandertals' parietal expansion occurred laterally, yielding the diagnostic 'en bombe' shape to their crania (Bruner, 2014; also see Fig. 1, left). Relative to AMH brains, Neandertal brains were longer from front to back, wider from side to side, and flatter at the top above the parietal region.

Brain developmental trajectories matter as well

Bruner (2004, 2010) noted that Neandertals may have had different phylogenetic and ontogenetic brain trajectories than AMH. While Neandertals and AMH shared a common frontal

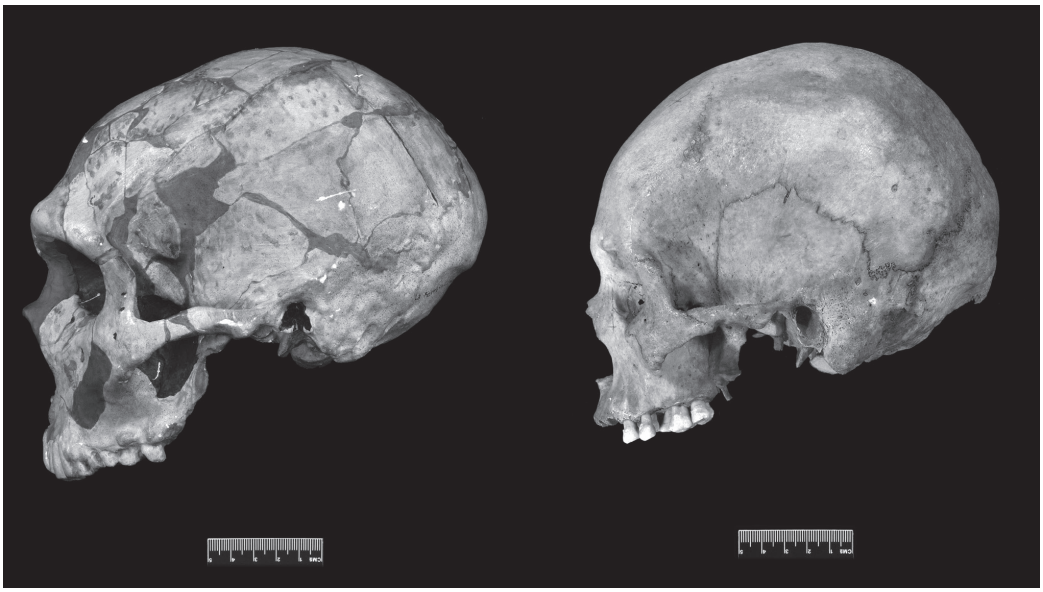

Fig. 1 –Neandertal (cast of La Ferrassie 1, left) and* H. sapiens *(modern human, right) cranial differences. Image courtesy of Chris Stringer. Reproduced with permission of Chris Stringer/Natural History Museum London. The colour version of this figure is available at the JASs website.

lobe and general cerebral expansion that differentiated both from earlier *Homo* (Ponce de León & Zollikofer, 2001), Bruner and colleagues (e.g., Bruner *et al*., 2003) found that AMH and Neandertals followed different expansion trajectories. Bastir *et al*. (2011) also concluded that there were different evolutionary trajectories between the two human types as well, particularly for olfactory systems (as will be discussed shortly) and basal and temporal poles. Pearce *et al*. (2013) have also hypothesized that the Neandertal evolutionary brain trajectory was more invested in visual and somatic systems and retained the earlier physical robustness of the likely common ancestor of both human types, *Homo heidelbergensis*. Regarding development, Gunz *et al*. (2010) have demonstrated that Neandertal brains had a different ontogenetic growth pattern than AMH, and that there was likely a different prenatal brain growth pattern as well. Sasaki *et al*. (2002) suggested that Neandertal infants had faster skeletal growth patterns, and Hublin *et al*. (2015) have suggested faster dental development pattern in Neandertals.

The impact of parietal expansion on AMH brains

Globularization of the AMH brain may have decreased inter-regional connectivity, shortening the long connections between brain regions, and consolidated intra-regional connections, increasing within-region connectivity (Rilling & Insel, 1999). Shorter, denser pathways are faster (Gibson & Petersen, 1991; Gibson, 1991) and more efficient in larger brains, which generally "reduce the proportion of connections, especially the most costly long connections" as a consequence of encephalization (Kaas, 2000, p. 17). This trade-off perhaps explains the limited interhemispheric connectivity in extant *H. sapiens*; as a percentage of total brain volume, the human corpus callosum is half or a third of that of other primates (Preuss *et al*., 2002). Globularization was perhaps also a factor in avoiding another potential consequence of encephalization, the reduction in the number of neurons (Kaas, 2000). The number of human neurons has remained isometrically proportional to the number found in other primate brains (Azevedo *et al*., 2009), despite encephalization. The evolutionary trade-offs

imply that Neandertal brains, which lacked such globularization, may have also lacked its attendant mitigation of encephalization-related issues of connectivity and neuronal numbers.

Parietal lobe functions

Research, especially within the past five years, has implicated the parietal lobe in a number of critical cognitive functions (e.g., Coolidge, 2014), including visuospatial working memory (Koenigs *et al.*, 2009), the creation of 'inner space' representations of external space (Land, 2014), the abilities to grasp and manipulate objects like tools and understand cause–effect relations in tool use (Orban & Caruana, 2014), and the sense of self, self-representation, and self-consciousness (Cavanna & Trimble, 2006; Lou *et al.*, 2004). An inner lateral portion of the parietal lobe, the intraparietal sulcus, has been implicated in quantity appreciation and number processing (see Coolidge & Overmann, 2012 for a review), and the topographical representation of number in the intraparietal sulcus may aid higher cognitive functions like abstraction (Harvey *et al.*, 2013). Recent imaging studies (fMRI) have shown that a medial and deep portion of the parietal lobes, the precuneus, may be critical to egocentric memory, the ability to create internal, stable representations of the external environment and one's place within it (Land, 2014). The precuneus has also been implicated in critical higher-order cognitive tasks, including the integration of visuospatial imagery, retrieval of episodic and autobiographical memories, and ability to take first-person perspectives in the experience of agency (Allen & Fortin, 2013; Cavanna & Trimble, 2006). Recently, Bruner & Iriki (2015) suggested that differences in brain morphology between Neandertals and AMH, particularly the upper and medial parietal lobe areas (i.e., precuneus, intraparietal sulcus), may have resulted in different ways of interfacing the environment with internal representations.

Two additional critical higher-order cognitive functions have been shown to be controlled by the parietal lobes: One is autonoetic thinking, the ability to recognize that the awareness of time is subjective, that one may travel backward and forward in it and, thus, that time may be perceived as relative (Tulving, 2002). The second critical function is prospective memory and future memory simulation (Addis *et al.*, 2007; Schacter & Addis, 2007).

Poles

Compared to Neandertals, AMH had larger frontal and temporal poles, which are the anterior ends of the frontal and temporal lobes (Bastir *et al.*, 2011; Hublin *et al.*, 2015). Greater asymmetry in the frontal and temporal poles is important because it is indicative of lateralization, the functional division of labor between the two cerebral hemispheres that informs and underlies computationally expensive processes such as language.

Orbitofrontal cortex

Hublin *et al.* (2015) have noted a wider orbitofrontal cortex in AMH than Neandertals. Modern empirical studies of extant humans have long demonstrated the importance of the prefrontal cortex (PFC) to higher level cognitive functions such as behavioral and social/emotional regulation, abstraction, theory of mind, and many others (e.g., Gazzaninga *et al.*, 2013). However, the PFC is not cellularly homogenous, as it has been shown that the dorsolateral (DL) PFC is closely interconnected to the primary sensory and motor regions, and the parietal lobes, while the orbitofrontal (OF) PFC is intimately connected to the limbic system. The arcuate fasciculus, a bundle of communication neurons, connects both the DLPFC and OFPFC to the superior posterior portion of the temporal lobes, the latter of which is the critical area for essential language functioning. The OFPFC has long received particular attention for its role in social and emotional decision-making (e.g., Bechara *et al.*, 2000). The OFPFC has also been recognized for its critical role in inhibiting responses, representing specific stimulus–outcome associations, guiding behavior by signaling emotional markers, predicting errors and assigning them to appropriate causes, and inferring value in economic determinations (Stalnaker *et al.*, 2015).

Olfactory bulbs

Bastir *et al.* (2011) have noted that cribriform plate, which connects the olfactory epithelium in the nasal cavity to the olfactory bulbs, appears to have expanded posteriorly and is larger in AMH compared to Neandertals. As the cribriform plate is highly correlated with the size of the olfactory bulbs, they surmised that the latter may also have been larger in AMH. It has long been recognized evolutionarily that forebrain expansion was driven by olfaction and the latter's critical role in approach functions related to feeding and reproduction, as well as avoidance functions such as predator detection and escape. Strous & Shoenfeld (2006) have shown that olfaction is intimately linked to the immunological system, which may be important in female's mate selection, with possible positive implications for improved immunological fitness of their progeny (also see Lübke & Pause, 2015).

Cerebellum

AMH "displayed a proportionally larger cerebellum than Neandertals" (Hublin *et al.*, 2015, p. 6), a consequence of the different evolutionary trajectories of the base of the brains of the two human types. Weaver (2005) also had earlier suggested that AMH had a larger cerebellar quotient (cerebellum volume to whole brain volume) than Neandertals. Kubo and colleagues (Kubo *et al.*, 2014) have recently confirmed that there is a high correlation ($r = .88$) between the size of posterior cranial fossa of extant skulls and cerebellar volume, a finding that should be extensible to fossil crania.

The cerebellum, which is widely interconnected with every major region of every lobe of the brain (e.g., Balsters *et al.*, 2013), has traditionally been associated with motor learning, fine motor control, and motoric action sequencing. There are highly reciprocal neural connections between the cerebellum and all of the lobes of the brain, but even more profound neural connections to the parietal and frontal lobes; this interconnectivity suggests that the cerebellum may aid in the process of creative thinking (Vandervert, 2009, 2011). Indeed, a recent imaging study (fMRI) demonstrated that the cerebellum is involved in both the control of motor sequences and higher-order decision- and rule-making for the execution of any form of information from the prefrontal cortices, regardless of the abstractness of that information (Balsters *et al.*, 2013).

Occipital lobes

Pearce *et al.* (2013) noted that Neandertal occipital lobes were larger than those of the AMH brain, a difference they speculated was related to the amount of light at different latitudes. Eye size, as measured by the orbital sockets, is related to the amount of visual cortex in living species. These authors surmised that Neandertals, being geographically distributed across more northerly latitudes, might have experienced and adapted to less light than the more equatorial AMH; the increased occipital volume would have enabled Neandertals to discern visual details under conditions of poorer light. Increased occipital volume, however, also suggests a concomitant decrease in the relative volume of the other lobes, implying attendant differences in their cognitive functionality.

Genetic evidence of cognitive differences

An additional source of evidence for evolutionarily significant cognitive differences between Neandertals and AMHs comes from a comparison of their DNA. Non-synonymous substitutions (NSS) are genetic changes that result in phenotypic change, the very thing that natural selection acts upon. To date, several NSS between Neandertals and AMH have been found in genes implicated in cognitive functions such as learning and memory, representing a difference of nearly 10% with about a third of the Neandertal data unavailable for comparison (which means that additional differences may be found when the full dataset is analyzed; see Paixão-Côrtes *et al.*, 2013). Even a single change to a single gene can profoundly affect the brain (Bakircioglu *et al.*, 2011), and many of the NSS found to date affect genes implicated in learning and memory. Further, there is evidence for a positive selection for genes relating to olfaction in AMH, well after

the lineage split between the two human types (e.g., Bastir *et al.*, 2011). Genetic data suggest that the two human types may have differed in learning, memory, and olfaction to an extent that would have been visible to selective forces, even if the differences were subtle. However, as Bruner & Iriki (2015) note, the genetic evidence suggests one of several possible mechanisms for cognitive differences; the other mechanisms and influences on intra- and inter-specific evolutionary change are environmental, enhanced metaplasticity, and epigenetic.

Paleoneurology is not yet in a position to argue from gross differences in brain size and shape to specific differences in cognitive function, and may never be in such a position. However, differences in gross brain anatomy do imply that differences in cognitive function were almost certainly in place. Neandertal and AMH brains differed from one another in significant ways. AMH brains, especially, deviated from the typical primate and hominin pattern. It is not unreasonable to hypothesize that these differences had cognitive consequences. This is not a value judgment of good vs. bad, or better vs. worse; these is no need to erect a false dichotomy. Whatever their cognitive differences might have been, both species powered successful adaptations (Roebroeks & Villa, 2011; Stewart, 2005). But today, only one survives, and it is appropriate to ask whether these cognitive differences might have played a role.

The archaeological argument

The archaeological signatures left behind by Neandertals and their contemporaries in Africa are actually very similar. On the level of basic adaptation they are indistinguishable: Both were prehistoric hunter–gatherers who relied on eclectic diets with varied mixes of local foods, employed prepared cored technologies to produce stone tools, and used composite tools and fire. Given these broad and significant similarities, it might be simplest to conclude that Neandertals' failure to prosper past about 30,000 years ago was a matter of bad luck, related perhaps to things like demographic change, resource availability, or disease. Yet the temporal coincidence of AMH expansion and Neandertal demise suggests that there may have been more to it, especially considering that all other archaic humans met a similar fate after encountering AMH. Why did AMH prevail and all others fail? It may have been a matter of social group size and demographics. This is a reasonable hypothesis with some evidentiary support in the form of site sizes and numbers (Finlayson, 2009). But there were also brain differences that should not be ignored, differences that provide a strong prima facie case for a cognitive difference. It is certainly a viable hypothesis to test, and not an anachronistic hold-over from the days of Victorian exceptionalism, as Zilhão (2014) has contended.

But how can such a hypothesis be tested using archeological evidence? As just acknowledged, the archaeological signatures of Neandertals and their contemporaries are similar. But they are not identical, as all authorities would admit. These differences could be the result of different local culture–historic developments, or they could reflect different cognitive profiles. Separating the historical differences from the cognitive differences is not an easy task. Given the difficulty of the problem, what is perhaps the most discouraging fact of the debate is the haphazard approach taken by most protagonists. The debate has played out almost entirely at the level of descriptive data, without any formal framework for comparison.

The trait list and its associated issues

The default approach used, if not favored, by almost all archaeologists interested in the problem of the Neandertal demise is the trait list, despite the fact that this approach has repeatedly been found wanting (Henshilwood & Dubreuil, 2011; Henshilwood & Marean, 2003; Mellars *et al.*, 2007; Nowell & Davidson, 2010; Nowell, 2010; Wadley, 2003). As used by most protagonists in the debate (e.g., Villa & Roebroeks, 2014), trait lists pose a number of serious problems:

1) Trait lists ignore equifinality. Multiple activities often produce the same archaeological

signature, and only by careful analysis can they be discriminated. If they cannot be effectively discriminated, the rule of parsimony must be applied (i.e., opt for the explanation with the fewest assumptions). When considering cognition, this almost invariably requires favoring the simplest form of cognition that can account for the evidence.

2) Trait lists ignore both quantification and degree. If the archaeological record yields a thousand examples of an activity for one group but only one for the other, the trait list treats them as indistinguishable. Similarly, trait lists ignore the magnitude of expression in characterizing both a stick modified for termite fishing and a computer drive as 'tools'.
3) Trait lists ignore the context of the analyses from which the items are taken, including any cautions or caveats. If the persuasive power of an activity depends on the co-occurrence of other activities, this context vanishes from a trait list.
4) The activities on the list rarely have explicit theoretical justification. Most commonly, the elements on such lists accumulate over the decades and result from archaeological history and academic inertia.
5) Trait lists, especially in the case of those purporting to document 'modern' behavior, often include items that are not equivalent epistemologically. Villa & Roebroeks' (2014) trait list, for example, included symbolism as one hypothesis and use of traps for another. The former is an inference, the latter a pattern of data.

The trait list of modernity has roots in European Palaeolithic archaeology that go back to the Victorian era mentioned by Zilhão (2014). Initially, the traits were those that distinguished the Aurignacian from the underlying Mousterian at sites such as La Ferrassie. Later, they came to be used as markers for a prehistoric invasion of Neandertal Europe by AMH. These traits were never selected with cognition in mind, but there certainly was an explicit tone of superior and inferior. This highlights the first serious problem with Villa & Roebroeks' (2014) analysis: They retained the superior–inferior piece and ignored the cognitive vacuity. In defense of Villa & Roebroeks, one could argue that they compiled their list from the work of others and that any weaknesses reflected flaws in the reasoning of the original authors; Villa & Roebroeks might simply then be seen as illustrating the folly of the approach. But their article did not appear to be intentionally ironic. Instead, Villa & Roebroeks had a very specific claim to make concerning the fate of Neandertals – that the Neandertals were so indistinguishable from AMH that they were simply absorbed into the AMH population – and thus Villa & Roebroeks embraced the trait list as a valid method with a positive conclusion.

Even if archaeologists had a valid trait list in hand, a second problem would loom: what comparison should be made? Ideally, one would compare the Neandertal and AMH archaeological records at the same point in time, in similar environmental contexts. Two circumstances obviate any chance for such a comparison. AMH and Neandertals lived in very different environments, at least until AMH moved into Europe about 40,000 years ago. AMH were tropical and sub-tropical hunter–gatherers, while Neandertals were high-latitude and temperate hunter–gatherers. This difference alone should have produced significant differences in diet, if nothing else (Binford, 2001). Second, archaeologists actually know more about Neandertals than about their contemporaries, including contemporary AMH. The African Middle Stone Age (MSA) is still poorly known when compared to the European Middle Palaeolithic. As a consequence, individual sites in Africa come to be compared to regional patterns in Europe. In such a comparison, the unusual can come to masquerade as the norm. More troubling, traits that are low in frequency at the best of times, but which are known from a few Neandertal sites, may not occur at all in the select MSA sites, biasing the comparison in favor of Neandertals.

Alternatives to the trait list

One alternative would be to compare the extensive Neandertal record to a comparably extensive record of AMH living in the same environment. The best candidate for this comparison would be the European Gravettian, which is very well known in both Western and Central Europe. But such a comparison carries a bias for AMH. Being at least 10,000 years nearer the present, preservation would be better, especially for the perishable materials that have become so important to the comparison. In other words, taphonomy alone would bias the comparison, not to mention 10,000 years of culture change. Archaeologists are left, then, with a final alternative: the only documented example of Neandertals and AMH occupying the same environment at the same time – the Aurignacian colonization of Europe. Ironically, of course, this culture contact was precisely the motivation for the original trait list comparisons of the 19th century.

However, there is a better way to compare than using trait lists: Rather than focusing on specific times and places hoping to get reliable 'flashbulb' images that provide reliable trait lists to compare, focus instead on a single behavioral/cognitive domain, devise archaeologically visible criteria for recognizing it, and examine the archaeological traces from each group for evidence of how this domain fared over time. Here this approach will be briefly applied to two domains: first, the domain most commonly invoked in comparisons of Neandertals and AMH – symbolism – followed by the domain studied by Coolidge and Wynn for the last fifteen years, working-memory capacity.

Arguably, the most contentious false dichotomy in the Neandertal debate paints Neandertals as either non-symbolic or symbolically indistinguishable from AMH. This specific debate plays out almost entirely at the level of presence or absence of particular artifact types. What is almost shocking for a scholarly disagreement of this significance is the theoretical vacuity of most of this debate. Almost never does one encounter in-depth discussions of what a symbol is, what symbolism or symbolic culture are, or how these things might be recognized archaeologically. There are exceptions, of course. Twenty-five years ago, Davidson & Noble (1989) used an informed discussion of iconicity to interpret the Palaeolithic record, and more recently Henshilwood & Dubreuil (2009, 2011) used well-defined semiotic categories to interpret the beads from Blombos Cave in South Africa – but these are the exceptions. More often than not, authors devote the majority of their discussion to placing a particular artifact in time and association, and conclude that it constitutes evidence for 'symbolic culture' without engaging the far more difficult question of just what 'symbolic culture' means.

Did Neandertals have symbolic culture? Did they even use symbols? Answering these questions must begin with a generally accepted definition of symbol as something that 'stands for' something else via an arbitrary or conventionalized link (de Saussure, 1959; Peirce, 1932, 1991). Words are symbols, and some material objects are symbols (e.g., wedding rings). Zilhão (Zilhão *et al.*, 2010) and d'Errico (d'Errico *et al.*, 2003, 2009) and others have convincingly established that Neandertals made pendants. Were these symbols? Among extant humans at least, personal ornaments are occasionally symbols, but more often they act as indexes. An index stands for something via association or direct extension (e.g., as smoke is an index of fire). When students attend university sporting multiple piercings with rings and bars and other ornamental paraphernalia, the objects are rarely symbolic, but they do mark perceived social identity. They are indexes. Thus, there are actually no grounds for concluding that Neandertal pendants were true symbols; rather, they were more likely to have been indexes of social identity. But is this not a kind of 'symbolic culture', using a more generous definition of symbolic culture as any use of material culture to send messages about identity? The answer is yes, but with this definition all examples of body marking would constitute evidence for symbolic culture, including the indirect evidence for body painting (via ground

pigment) associated with *H. heidelbergensis* in both Europe and Africa (Barham, 2002; d'Errico *et al.*, 2003).

Of course, the same critique can be – and has been – applied to AMH personal ornaments found in MSA contexts in Africa (Botha, 2008, 2010). Must it then be concluded that Neandertals and AMH are indistinguishable in this regard, as argued by Villa & Roebroeks (2014), Zilhão (2014) and others? The parallel evidence for ornaments implies something very important, but it is not that Neandertals and AMH were indistinguishable. Rather, it indicates that one component of semiotic behavior – indexical marking – can be traced back to a common source in *H. heidelbergensis*, and that it is homologous for Neandertals and AMH. However, indexical usage also appears to have developed in rather different ways in the parallel lineages. When ornament use by Aurignacian people (again, the only justifiable comparison, as was earlier discussed) is compared to that of Neandertals, a large difference in quantity is apparent: The 10,000-year Aurignacian record has yielded thousands of beads and items of personal decoration, while the entire 200,000+ years of the Neandertal record has yielded fewer than 10.

Even if the semiotic role – social marking – is held as having been the same, the actual way it developed in Aurignacian society must have been different from the way it did in Neandertal society. Aurignacian people appear to have been far more invested in social marking than Neandertals were. This difference suggests that Neandertal and AMH semiotic behavior developed along different trajectories since the time of their *H. heidelbergensis* common ancestor. They were similar but not identical. But was this difference a cognitive difference? Ironically, given the vituperative nature of the disagreement, the answer can only be "maybe." Indexical marking per se is not very challenging in a cognitive sense; it relies primarily on simple association. However, the vast difference in scale between Aurignacian index use and Neandertal index use suggests that there may have been a significant difference in social-information processing, and this points to the topic of working-memory capacity.

Coolidge and Wynn have written extensively about the role of enhanced working memory in recent human evolution (Coolidge & Wynn, 2001, 2004, 2005, 2009; Wynn & Coolidge, 2003, 2006, 2007, 2010a, 2010c, 2011), and they have also written specifically about Neandertal cognition in a separate set of publications (Wynn & Coolidge, 2004, 2010b, 2012). Their initial argument concerning working memory was developed primarily as a general evolutionary model concerning modern human cognition (that is, it was not developed to contrast Neandertals and AMH, though incorrectly characterized as such by Villa & Roebroeks, 2014). The model was based on one of the most well-developed and thoroughly researched models of cognition in the psychological literature, Baddeley's model of working memory (Baddeley, 1994, 2000; Baddeley & Hitch, 1974). This executive functions/working memory hypothesis has several features that make it a compelling hypothesis for recent cognitive evolution (Coolidge & Wynn, 2001; Wynn & Coolidge, 2010a):

1) The working-memory model is arguably the most successful and voluminously supported model of cognitive functioning developed in the last forty years.
2) The executive functions of working memory are implicated in the most sophisticated cognitive processing used by extant humans, including analogical reasoning, thought experimentation, contingency planning, levels of intentionality, and Theory of Mind.
3) Working-memory capacity varies in extant human populations.
4) Working-memory capacity and executive functions are both highly heritable, with estimates ranging from 77 to 99 percent (Coolidge *et al.*, 2000, 2004; Friedman *et al.*, 2008).
5) Working-memory capacity and executive functions are both under additive (polygenic) genetic control. Enhanced capacity could have been achieved via comparatively simple mutation, epigenetic change, or embodied resources of material culture (Overmann, 2013) in concert with neuronal recycling (Dehaene & Cohen, 2007).

The methodological challenge for Coolidge and Wynn was to identify archaeological patterns that might reflect an increase in working-memory capacity, something they termed enhanced working memory (EWM). As it turned out, no single artifact type or pattern could act as a reliable indicator for EWM (the closest to such a 'smoking gun' was the Hohlenstein-Stadel figurine), so instead, Coolidge and Wynn reviewed multiple possible lines of archaeological evidence. In the end, however, they argued that the archaeological record as it was then known was consistent with several alternative ways to understand the timing of the final enhancement of working-memory capacity, including one in which the final enhancement occurred very late indeed, after 30,000 years ago, and one in which it occurred 200,000 years ago. They did note that many of the archaeological patterns they chose to use as evidence for EWM were not apparent for Neandertals, but they also discussed at length how elusive they were for AMH. At about the same time that Coolidge and Wynn published the EWM hypothesis, they started to develop a model for Neandertal cognition that was also based on a well-developed set of theories in cognitive science (Wynn & Coolidge, 2004, 2012). This particular model allowed them to account for the many similarities between the archaeological signatures of Neandertals and AMH, and also understand the few differences.

One example of the kind of reasoning invoked in the working-memory hypothesis is the argument for use of traps. Coolidge &Wynn (Coolidge & Wynn, 2001, 2005, 2009; Wynn & Coolidge, 2003, 2010a, 2011) emphasized the role of traps in managed foraging systems, their requirement for response inhibition (a well-defined, specific component of executive control), and their temporal range of planning. Unfortunately, evidence for use of traps is elusive; direct evidence of traps dates to no earlier than 14,000 years ago (Coolidge & Wynn, 2005; Wynn & Coolidge, 2003). As a consequence, arguments for earlier trap use necessarily rely on the indirect evidence of faunal remains – the presence of large numbers of a species that can only be effectively captured using traps. Wynn & Coolidge's initial review of the archaeological evidence yielded only a single example, one from Niah Cave in Borneo (Barker *et al.*, 2007) that dated to between 42,000 and 28,000 years ago.

More recently, Wadley (2010) has made a similar argument for use of traps to capture blue duiker at Sibudu, with a much earlier date of perhaps 65,000 years ago. On its own, this indirect evidence for traps could not bear the weight of the EWM argument, so it was presented as one component among several, including use of fire to alter landscapes, which appeared about the same time at both Niah and in South Africa (Deacon, 1993). Use of managed foraging techniques implicated much longer projections of action into the future, as well as an important component of response inhibition. Both are components of executive reasoning. Coolidge and Wynn noted that these developments in managed foraging were paralleled by developments in technology, including the use of reliable weapon systems and the use of external calculating devices. Thus, the approach was not simply a number of checks off of a list, but rather an integrated model of cognitive evolution that concluded Neandertals and AMH were somewhat different.

The archaeological evidence – when interpreted as a component of an integrated model of cognitive evolution rather than through the problematic trait list technique – supports a picture of divergent lines of cognitive development for Neandertals and AMH. Working-memory capacity is something that evolved over the course of human evolution. Humans today have working memory, chimpanzees have working memory, and Neandertals had working memory. The archaeological evidence indicates that sometime after 100,000 years ago, AMH began to demonstrate behaviors that required a slightly larger working-memory capacity than anything known for Neandertals. It was not a dramatic difference, but it may have had profound, long-term consequences when people carrying Aurignacian culture colonized Europe beginning some 45,000 years ago.

The Neandertal fate: assimilation or replacement?

Proponents of the Neandertal indistinguishability claim (e.g., Villa & Roebroeks, 2014; Zilhão, 2014) have adopted it to support the idea of Neandertal assimilation, the hypothesis that the Neandertal disappearance from the archaeological record can be attributed to a wholesale incorporation and integration into the AMH population.. However, the assimilation hypothesis is challenged by the low percentage of Neandertal DNA in the human genome: only 1 to 4% of the genomes of Europeans and Asians; new evidence narrows the estimate to only 1.5–2.1% (Green *et al.*, 2006; Prüfer *et al.*, 2014). The low introgression rate, along with a skew in its directionality (i.e., from Neandertals to AMH but not the reverse), argues that interbreeding was rare, non-productive, or both (Currat & Excoffier, 2011; Currat *et al.*, 2008; Mason & Short, 2011; Neves & Serva, 2012). However, despite its low rate, introgression may have gained favorable alleles for *H. sapiens*, conferring adaptive fitness in systems interacting with new environments (Pääbo, 2015; Racimo *et al.*, 2015; Weyer & Pääbo, 2015).

While rare interbreeding seems the very opposite of assimilation, Neandertal indistinguishability proponents (Villa & Roebroeks, 2014) have adopted non-productivity in an attempt to reconcile assimilation with the low introgression rate, citing mechanisms such as Haldane's rule, a form of reproductive isolation in which hybrid offspring, usually male, are viable but infertile (Mason & Short, 2011). However, as Overmann & Coolidge (2013) observed in their analysis of possible Neandertal–AMH reproductive isolating mechanisms, hybrid sterility has been estimated as taking an average of 2.0 to 4.0 million years to develop in mammals (Fitzpatrick, 2004; Wu, 1992), a span of time that is at least double and up to eight times the length of time separating the two human types (also see discussion in Gibbons, 2014). Could hybrid sterility have developed between Neandertals and AMH in that short a time span? While it seems less likely than the other forms of reproductive isolation typical among primates, if it is ultimately borne out by genetic evidence, it would mean that Neandertals and AMH accumulated significant differences as species in a very short amount of time, differences incompatible with the idea that the two were indistinguishable. That is, the genetic distance needed to produce hybrid sterility would entail morphological, behavioral, and cognitive differences – as can be observed in the case of horses and donkeys and their (almost invariably) infertile offspring, mules and hinnies (Rong *et al.*, 1985, 1988; Vilà *et al.*, 2001; Wu, 1992) – that would preclude the possibility that Neandertals and AMH were indistinguishable.

Neandertals and AMH differed in physical form and development, as many would agree (Gunz *et al.*, 2010; Lieberman *et al.*, 2007; Smith *et al.*, 2010). Beyond their distinctive skulls, Neandertals were bigger, stockier, and had thicker bones (Ben-Itzhak *et al.*, 2005). Their teeth differed, with Neandertals retaining archaic traits for larger, shovel-shaped incisors, while AMH developed smaller, chisel-shaped ones (Bailey, 2006; Bailey & Liu, 2010; Le Cabec *et al.*, 2013). The relative size and strength of bones and teeth, as well as the analysis of things like muscle attachments to bones and dental wear patterns, point to specific behavioral differences as well, with Neandertals thought to have led more strenuous lives (Berger & Trinkaus, 1995; Bocherens, 2011; Gaudzinski-Windheuser & Roebroeks, 2011; Knüsel, 2000) and to have made greater use of their anterior teeth as 'third hands' (Bruner & Lozano, 2014; Overmann, 2015).

If Neandertals were morphologically, behaviorally, cognitively, genetically, and archaeologically different from AMH, as supported by the evidence reviewed here, they were not indistinguishable from AMH, yet one interpretation of the genetic evidence suggests that the two human types interbred enough to leave a small but significant Neandertal component in the *H. sapiens* genome. However, an alternative interpretation of the genetic evidence suggests that instead of later interbreeding, it indicates an ancient population structure (Eriksson & Manic, 2012) or

admixture occurring prior to the divergence of the two human types (Gokcumen *et al.*, 2013). If either of the alternative interpretations are ultimately borne out, it would mean that despite over 5,000 years of co-existence (Higham *et al.*, 2011, 2014; Pinhasi *et al.*, 2011), Neandertals and AMH likely did not interbreed, a finding that would further weaken the supportability of the assimilation and indistinguishability hypotheses.

Conclusion

The archaeological record is under constant scrutiny and reevaluation from new discoveries, emerging analytical techniques, and the application of inter-disciplinary insights. For example, newly discovered cave art has been attributed to Neandertals (Rodríguez-Vidal *et al.*, 2014, though not without controversy; see Davidson, 2014), site chronologies and the period of Neandertal–AMH overlap is being substantiated (Galván *et al.*, 2014; Higham *et al.*, 2014; Wood *et al.*, 2013), and paleoneurology continues to gain traction on the cognitive implications of the morphological and ontogenetic differences between Neandertal and AMH brains (Bruner, 2014). These avenues have the potential to inform and ultimately decide what really happened to the Neandertals and suggest that the archaeological approach most likely to yield an accurate account is one that embraces and integrates the work of other sciences.

The present review offered several sources of evidence as a basis for denying that Neandertals and AMH were indistinguishable. Must the alternative in the false dichotomy then be true – is the only other available viewpoint the one that considers Neandertals to be inferior to AMH? Such a view, unpalatable on its face, is not what we assert. The middle position being excluded by indistinguishability advocates (Villa & Roebroeks, 2014; Zilhão, 2014) neither lumps nor splits the two human types but readily admits the large degree of overlap and characterizes the differences as subtle but visible to natural selection. It incorporates the paleontological, genetic, and archaeological data and proposes an interpretation that attempts to account for all the available data in a nuanced and balanced fashion.

Some have compared the Neandertal–AMH difference to extant human groups who differ in material culture, and have suggested that the middle position espoused here would inevitably assign extreme differences in modern material culture to different cognitive profiles. As the literature on cross-cultural cognition demonstrates, extant human groups differ subtly in ways related to material culture (e.g., Henrich *et al.*, 2010). Yet, this hardly parallels the archaic argument, let alone affirms the false dichotomy. For one thing, such a result would be reached only if the comparison was theoretically vacuous, and based on simple checks on a list. Unlike Neandertals and AMH, which are regarded as distinct species or subspecies (Bruner, 2013; Curnoe & Thorne, 2003; Tattersall & Schwartz, 1999; Wegmann & Excoffier, 2010), extant humans are a single species with surprisingly little genetic variation, despite a misleading phenotypic variability (Ingman *et al.*, 2000). This means extant humans all have the same cognition, even if that cognition varies slightly in interaction with different material-cultural situations. Further, it is that very ability to interact with a wide range of material conditions that may truly define extant humans as a species. In competition with the Neandertals, a species with a slightly different adaptation trajectory, AMH should be predicted to have expanded its range of material-cultural variability to the extent seen across the extant human population.

The main points of the argument in favor of the excluded-middle position – small differences that were significant because they were visible to natural selection – can be summarized as follows:

1) Neurocognition: Fossil skulls and endocasts clearly indicate that Neandertal and AMH brains differed in ways that have significant implications for cognitive functioning. In addition, archaic DNA indicates that the two human types differed in genes governing neurocognitive development in key cognitive functions like learning and memory.

2) Archaeology: Comparisons based on checklists of traits for 'modern' behavior, like the one used by Villa and Roebroeks (2014), have long been identified as problematic and do not justify a finding of Neandertal indistinguishability. In comparison, models integrating archaeological with paleoneurological and genetic data suggest that Neandertals and AMH followed divergent cognitive trajectories that left subtle but detectible traces in the material record.
3) Genetic: If hybrid sterility is the correct explanation for the low rate and directionality of introgression between Neandertals and AMH, then the genetic distance entailed would preclude the two human types from being indistinguishable. If instead the archaic genome signals ancient population structure or admixture, then Neandertals did not assimilate.

Against the Neandertal indistinguishability claim, the converging evidence of multiple disciplines shows that AMH and Neandertal brains differed, their genes differed, their physiologies and behaviors differed, and their archaeological signatures differed. This evidence supports two conclusions: First, Neandertals and AMH differed cognitively; second, these cognitive differences may have played a role in the Neandertal disappearance from the archaeological record and the ultimate success of AMH. It is time, as Zilhão (2014) himself noted, to stop labeling differences as implying inferiority and superiority: This claim is not found in the extensive neuroscientific literature on archaic crania, paleoneurology, and cognitive evolution, so there is no reason to argue against it; claiming that it is being argued when it is not serves only to perpetuate the false dichotomy.

Acknowledgements

All three authors contributed equally to this work. We are grateful for the contributions of Dr. Emiliano Bruner and Dr. Giovanni Destro-Bisol, whose close and critical review of the manuscript led to its significant improvement.

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Editor, Giovanni Destro Bisol

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