

Language Abilities in Neanderthals

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Abstract

Neanderthal language abilities cannot be directly observed, but indirect evidence is available in their anatomy, archeology, and DNA. Neanderthal anatomy shows possible speech adaptations, and their archeology contains enough indicators of behavioral modernity, including symbols and ornaments, to conclude that their minds could handle symbolic communication. Neanderthal DNA, finally, indicates both that they possessed some of the language-relevant genes found in modern humans and that they could and did have children with modern humans. From the consilience of evidence from anatomy, archeology, and DNA, one can conclude that some language abilities, if not necessarily full modern syntactic language, were present in Neanderthals.

1. INTRODUCTION

Neanderthals¹ were our closest relatives before they died out around 30,000 years ago (30 Kya). They lived in social groups and engaged in cognitively nontrivial activities, so they certainly had both communicative and cognitive abilities at some level. But what was their communication like? Does it deserve to be called language? What was their cognition like? Was it anything like our “inner speech”?

These questions about Neanderthals are interesting in their own right (Johansson 2013b), but they are also interesting for the light they may shed on our own evolution. Once upon a time, our ancestors had no language, and today all people do. Clearly, at some point along our lineage there must have been an evolutionary transition from nonlanguage to language. But there is no consensus on how, when, or why this transition took place, nor on whether the transition was sudden or gradual. Our extinct relatives and ancestors may provide key evidence for that debate. Neanderthals, as our closest relatives, with humanlike capacities in many other respects (notably a brain at least as large as ours), are especially relevant here.

Some authors regard language as a defining characteristic of anatomically modern humans (AMH) only (e.g., Klein 1999, Chomsky 2010), whereas others see evidence of at least some form of protolanguage among earlier humans (e.g., Corballis 2002, Johansson 2005, Mithen 2005, Bickerton 2009, Dediu & Levinson 2013). Evidence for or against Neanderthal language would be decisive in that debate.

Whether Neanderthals had language or speech has been debated in numerous papers, ranging from Lieberman & Crelin (1971) and Schepartz (1993) to more recent efforts such as Barceló-Coblijn (2011), Johansson (2013c), and Dediu & Levinson (2013). I do not review the history of the debate; instead, I focus on recent evidence and arguments. Relevant evidence can come from a number of different disciplines outside linguistics, notably paleoanthropology, archeology, and genetics. This article is not intended as a review of either language origins in general (see, e.g., Johansson 2005, Tallerman & Gibson 2012) or Neanderthals in general (see, e.g., Conard & Richter 2011, Harvati & Harrison 2008).

2. DRAWING THE LINE BETWEEN LANGUAGE AND NONLANGUAGE

As Jackendoff (2010) put it, “Your theory of language evolution depends on your theory of language.” A nonnegligible source of disagreement and misunderstanding in the debates around language evolution can be found in different conceptions of language. To make any progress on the issue of whether Neanderthals had language, we need to be clear about what “having language” means.

The word language is used for a complex web of interrelated concepts and is not easy to define in any stringent manner. Furthermore, there is no consensus even among linguists on the definition of their object of study; multiple paradigms are in active use (Zuidema 2005). I therefore find it prudent to avoid definitions that are too theory laden; instead, I attempt to find some common denominator. I also do not prejudge the issue at hand by assuming that language by definition must be exactly like modern human language. Instead, we should ask what minimum set of components is required to call something language.

¹Ever since Neanderthals were discovered in the nineteenth century, there has been a lively debate over whether they are a separate species from us or not—*Homo neanderthalensis* or *Homo sapiens neanderthalensis*? I do not enter the naming debate here, as the name per se is irrelevant to the topic of this article; instead I refer to Neanderthals as Neanderthals and refer to the people indistinguishable from ourselves as anatomically modern humans (AMH).

There is a fair degree of consensus that modern human language contains some kind of tri-lateral mappings between forms, meanings, and structures. Different linguistic theories describe these mappings in different ways, using different terms, but contain some way of connecting a concept to a word form and plugging the result into a syntactic structure.

Syntax in some form is also a central part of modern human language and is likewise described very differently in different linguistic paradigms. Minimally, syntax entails that language has some kind of structure and is not simply a random juxtaposition of words, and that the structure carries some of the meaning of what is said.

Some authors, especially those working within the minimalist paradigm, regard syntax as a monolithic all-or-nothing affair—either you have syntax, or you don’t—and, not uncommonly, language is equated with syntax, with unbounded Merge as the defining feature of language (Chomsky 2010). Within such a view, there is no room for languages different from full modern human language. But there are proposals for a decomposable Merge even within the minimalist paradigm (e.g., Fujita 2009, Boeckx 2011), and outside the paradigm there are a number of proposals for how syntax may be built gradually, step by step (e.g., Johansson 2005, Jackendoff & Wittenberg 2014). That language is monolithic, and that its biological underpinnings are fixed and invariable in the species, is also problematic both from general evolvability considerations (Kinsella 2009) and from empirical results on genetic (Stromswold 2010) and neurological (Levinson 2012) variation among modern humans.

2.1. The Simplest Possible Language

Both Jackendoff & Wittenberg (2014) and Johansson (2005), among others, propose that the simplest possible language would have a one-word grammar in which each utterance is a single unit without meaningful substructure. In effect, this language would have basic lexical semantics but not syntax, and the trilateral mappings mentioned above would become bilateral, between form and meaning only. This minimal language is similar to the one-word stage in normal human language acquisition.

Many animals have communication systems that consist of single meaningful units, such as vervet monkey alarm calls. I would not refer to these systems as languages, even though they technically resemble the one-word language described by Jackendoff & Wittenberg (2014). I argue that what distinguishes even minimal language from animal call systems are flexibility and extensibility. New arbitrary mappings can be added to the language, easily and without limit, and each unit functions as a symbol (Deacon 1997).

For the purpose of this review, language can thus be defined as a symbolic and freely extensible communication system. This definition entails the presence of something like lexical semantics but does not require syntax in any nontrivial sense. A system that lacks extensibility (e.g., vervet monkey communication) is not language. A system that has syntax-like patterns and is extensible, but lacks mapping to meaning (e.g., birdsong), is likewise not language.

2.2. Language and Speech

Speech is the normal everyday manifestation of language among AMH, dominant to such a degree that the concepts are commonly conflated. But this presumption of equivalence is mistaken, not least in language evolution studies, in which it is ubiquitous (Botha 2009). Much of the literature purportedly about Neanderthal language is actually about (proxies for) Neanderthal speech.

Language among modern humans is clearly modality independent; our language abilities support language in spoken, signed, or whatever modality with equal facility. Thus, the presence

of language in a species does not entail the presence of speech, and conversely, the absence of language does not follow from the absence of speech.

The presence of speech does entail the presence of language, for the trivial reason that the term speech is usually reserved for the externalization of language in sound and is not used for other vocalizations. But speech differs from the vocalizations of other mammals in other respects as well; it is a combinatorial system, with an unlimited variety of utterances formed from combinations of a modest number of discrete units, emitted serially at a very rapid rate. Speech requires a vocal tract that can produce an adequate number of discrete phonemes distinctly enough and that can be controlled with sufficient speed and precision. In principle, the presence of a vocal tract with this capacity can be used to distinguish fossils of speakers from nonspeakers. Birdsong, however, requires similar vocal abilities, and the force of any inference from vocal tract to speech to language among our ancestors strongly depends on the implausibility of a singing stage in our evolution (Mithen 2005). Vocal imitation is another human ability that is absent in other apes and that requires a versatile vocal tract—imitation adaptations might be mistaken for signs of speech. Our lack of knowledge about either singing (with due respect to Mithen) or imitation abilities in Neanderthals weakens any inferences about Neanderthal speech.

It is sometimes proposed that language originated as a purely internal system, with no externalization in any modality (Jerison 1973, Chomsky 2010, Piattelli-Palmarini 2010, Berwick & Chomsky 2011, Boeckx 2013), which would in effect be a system of bilateral mappings between meaning and syntax but with no link to form. Such a scenario is implausible for several reasons (Johansson 2014) and would also fall outside my definition of language, given above. Empirically, in the case of Neanderthals or other prehistoric humans, unexternalized language might in principle be inferred from the presence of cognitive abilities requiring Merge in the clear absence of speech or other externalization abilities. But it would be empirically almost impossible to distinguish from the use of a nonspeech modality such as sign language, as proposed by, for example, Corballis (2002).

3. HOW CAN WE KNOW ANYTHING ABOUT NEANDERTHAL LANGUAGE?

Neanderthals have been extinct for a long time, and they left no direct records of their language, if they had any. Any conclusions about Neanderthal language are necessarily based on indirect evidence or proxies for language through inferences supported by bridging theories. It is highly unlikely that any single piece of evidence will be decisive. Our knowledge of Neanderthal language abilities is built more like a jigsaw puzzle, with evidence from many different fields coming together, jointly producing a picture. Consilience between multiple lines of inference will increase our confidence in the results. In this section I discuss some general methodological issues in this type of indirect evolutionary puzzling.

3.1. Parsimony

Keeping things as simple as possible is a general methodological rule in science, going back to Occam's razor. In the choice between two hypotheses that explain the data equally well, we should prefer the simpler one, the one that makes fewer assumptions and postulates fewer entities.

In an evolutionary context, parsimony takes on the more specialized meaning of preferring the simplest evolutionary history, the one involving the smallest number of evolutionary changes. If two related species have green beards, it is simpler to assume that their common ancestor also had a green beard, as that would entail green beards evolving only once. The alternative, a beardless common ancestor, means that green beards had to evolve twice, independently in each descendant

species. With multiple species and multiple features, this argument becomes more complex, but the basic principle remains the same: The evolutionary tree that minimizes total evolutionary change should be preferred.

Using parsimony, it is possible to infer the most probable features of “intermediate” species in a family tree, even in the absence of direct evidence. We know that humans and chimpanzees are descended from a common ancestor some millions of years ago. All features shared between humans and chimpanzees were likely present not only in that common ancestor but also in all other descendants of that common ancestor, notably all fossil hominins, including Neanderthals. In the absence of positive evidence to the contrary, all features shared by chimps and humans can be assumed to have been present in Neanderthals as well.

Thus, given that both humans and chimps have, for example, a tongue, we can safely assume that Neanderthals also had one, even though we have no fossils of Neanderthal tongues. All shared language-relevant features would be part of the faculty of language in the broad sense (FLB) posited by Hauser et al. (2002).

The main assumption behind inferences from parsimony is that evolutionary changes are sufficiently rare that the probability of parallel evolution or reversals is small enough to be neglected. In the case of complex features, such as most aspects of language, this is likely to be a good assumption. But in the case of many molecular and genetic traits, as well as simple quantitative traits such as the size of some bone, this assumption may not hold. Natural selection in the same direction in several lineages, such as two similar species responding the same way to a climate change, can also be problematic.

Parsimony also assumes a simple family tree, with no interbreeding between branches. As discussed in Section 5.2, below, that assumption is dubious in the case of Neanderthals and AMH, although it likely holds well enough between humans and chimps.

3.2. What Is the Appropriate Null Hypothesis?

A nontrivial methodological issue in the study of beings that are similar to us, but not quite us, is the question of what null hypothesis to use, or where the burden of proof should lie. In fields that study other humans today, such as anthropology or psychology, we assume as a matter of principle that they are people just like us, biologically if not culturally, and the burden of proof lies squarely on anybody claiming that they are not. In the archeological study of recent AMH, from the Upper Paleolithic onward, it is likewise assumed that they are basically people like us, with minds like ours.

In the study of nonhuman animals, however, the methodological principle is the opposite—the behavior should be explained at the lowest level possible, and anthropomorphism should be avoided. The burden of proof in animal studies is on the proponent of more humanlike abilities.

Which methodological principle should we apply to Neanderthals? Do we assume that they are animals until proven human, or do we assume that they are human until proven otherwise? Both alternatives are problematic, and it appears most prudent to proceed without a null hypothesis, following instead the preponderance of the evidence. A further, related problem is unconscious taxonomic bias, in which the interpretation of archeological finds and other data is colored by knowledge of which species generated the data (d’Errico et al. 2009).

3.3. What Should a Good Proxy Be Like?

A proxy for language should ideally be something that is both easily identifiable in prehistoric remains and a reliable indicator of the presence of language. A good proxy should conform to the following criteria:

1. It must be possible to determine the state of the proxy in fossil or archeological material. This criterion eliminates most soft anatomy, artifacts made of nondurable materials, and behaviors that do not leave clear archeological traces.
2. The present distribution of the proxy should match the distribution of language, so the proxy should be present in all language-using humans and should not be found among any languageless animals.
3. The connection between proxy and language should be on theoretically solid ground, with well-established bridging theories between the two (Botha 2009).
4. The connection between proxy and language should preferably be bidirectional so that the presence of the proxy entails the presence of language with an acceptable degree of certainty, and its absence likewise the absence of language.
5. Because our language ability is not necessarily a single monolithic entity, it is desirable to have separate proxies for the various subcomponents of language.

Potentially useful proxies for Neanderthal language, or aspects of language, can be found in fossil anatomy, in genetics, and in archeology. Proxies from these different areas are reviewed and evaluated in the following sections.

4. EVIDENCE FROM FOSSIL ANATOMY

Anatomical proxies for language in the abstract sense are hard to find even in living people, despite our access to all the soft tissue, and obviously much more difficult in fossils where only hard parts remain. The only conceivable locus for such proxies would be in brain anatomy, as discussed in Section 4.4, below.

Speech is more accessible because some parts of our anatomy do reflect our habitual use of speech. The vocal tract itself does not fossilize, but the surrounding bones do. Structure, muscle attachments, and nerve canals in the bones can be informative. In the hearing organs, the bones of the middle ear can provide clues about the auditory capacities of fossil species. The presence of sign language cannot be inferred from fossils, given that the required dexterity is present in many languageless primates, rendering it uninformative.

4.1. Speech Organs

As discussed in Section 2.1, the presence of speech is a fair proxy for the presence of language, barring alternative reasons for evolving adaptations for complex vocalizations. Note, however, that the absence of speech adaptations does not prove the absence of language. The absence of visible anatomical speech adaptations does not even prove the absence of speech—with a human brain in control, virtually any mammalian vocal tract could produce useful speech (Fitch 2005).

The shape of the human vocal tract, with a lowered larynx providing a two-part tube with nearly one-to-one proportions between the vertical and horizontal parts, as well as a tongue placed so that the width of the two tubes can be controlled independently, is very likely a speech adaptation because it broadens the articulatory possibilities (P. Lieberman 2007b) at nonnegligible cost (D.E. Lieberman 2008). But as Fitch & Giedd (1999) show, there is also substantial variation in vocal tract proportions in AMH, both over the lifetime of an individual and between individuals. Except possibly in young infants, this variation is not known to limit speech; we do not really know the full range of vocal tract proportions that would still provide acceptable speech performance.

A lowered larynx is not unique to humans; in some other mammals, notably big cats (Weissengruber et al. 2002), the larynx is also permanently lowered, and many can lower it

dynamically during vocalizations (Fitch 2009). A lower larynx provides a deeper voice, making an animal appear larger than it really is, which is likely to be the main reason for larynx lowering in other species, as well as for the additional lowering that occurs in human boys at puberty (Fitch & Giedd 1999). But this kind of sexual selection is an unlikely explanation for the initial larynx descent in human toddlers, both male and female—human females do find a deeper male voice more attractive (Collins 2000, Feinberg 2005), but not vice versa (Feinberg et al. 2008, Jones et al. 2008). In any case, human children start producing understandable speech long before their larynx has descended all the way, while their vocal tract is still far from the canonical one-to-one proportions and closer to the likely proportions of adult Neanderthals.

The bones that may reveal vocal tract shape in fossils are the skull base and the hyoid. However, many other factors influence the shape of the skull base, such as brain size and face size (Bastir et al. 2010), diluting its value as vocal tract proxy.

The hyoid is more interesting, as it sits directly in front of the vocal tract, with attachments to both the larynx and the tongue. Unfortunately, it is very rarely preserved in fossils, as it is the only bone in the body that is not connected with the rest of the skeleton. Nevertheless, a handful of fossil hominin hyoids are known, of which one is from a Neanderthal (Arensburg et al. 1989) and two are from *Homo heidelbergensis* (Martínez et al. 2008), possible Neanderthal ancestors that are, in any case, more closely related to Neanderthals than to AMH. All these hyoids from the Neanderthal side of the family tree are within the range of variation of AMH hyoids. Also, the microstructure of the Neanderthal hyoid is compatible with that of AMH hyoids, indicating that it was used in similar ways (D’Anastasio et al. 2013). The significance of the hyoid results is disputed. Several authors (Houghton 1993; Boë et al. 2007, 2013; Granat et al. 2007; D’Anastasio et al. 2013) conclude that Neanderthals could speak, but a few dissenting voices (P. Lieberman 2007a, 2012; Fitch 2009) argue that the Neanderthal vocal tract cannot produce all human vowels, because even with a larynx at or below the AMH position, the longer oral cavity of Neanderthals precludes a one-to-one ratio of the two parts of the vocal tract. Note, however, that a reduced vowel inventory does not by itself completely preclude the production of speech sufficient to support language in the sense of this article. From earlier hominins, we have found a hyoid from *Australopithecus afarensis*, but that is basically chimpanzee-like (Alemseged et al. 2006), and the calculations of Granat et al. (2007) do not predict that australopithecine vocal abilities were better than those of chimpanzees.

4.2. Hearing Organs

Although the hearing of many mammals, including nonhuman primates, is quite adequate to perceive human speech, human ears have a sensitivity curve that is slightly different from that of other apes. Human ears have higher sensitivity in the 2–4-kHz range, which can be connected with changes in the ossicles of the middle ear. This difference can plausibly be interpreted as a speech adaptation, as key features of some speech sounds are in this range. Fossil ossicles from both Neanderthals (Quam & Rak 2008) and half-million-year-old *Homo heidelbergensis* from Spain (Martínez et al. 2004, 2013) are within the AMH range, adding some support to the case for Neanderthal speech.

4.3. Neural Connections

Nerves do not fossilize, but the holes in bones through which nerves pass can be observed in fossils. A thicker nerve contains more neurons, presumably providing finer control and sensitivity, and of course requires a larger hole.

One such nerve hole that has been invoked in the context of prehistoric language is the hypoglossal canal, a passage for nerves controlling the tongue (Kay et al. 1998), but comparison with other primates showed that this canal is not a valid proxy for speech (DeGusta et al. 1999, Jungers et al. 2003). The canal for nerves going out to the thorax, involved in breathing control, is a more interesting case (Fitch 2009). Modern humans have wide canals here, whereas extant nonhuman primates have narrow ones. Among fossil hominins, *Homo ergaster* still had the ancestral narrow canals, but Neanderthals had the same wide canals as AMH (MacLarnon & Hewitt 1999, MacLarnon & Hewitt 2004), implying that wide canals evolved at some point between 1.5 and 0.5 million years ago (Mya). This evidence adds to the case for Neanderthal speech to the extent that enhanced breathing control is a speech adaptation, which is plausible but unproven.

4.4. Brain

The biological key to language is not really in the vocal tract and other areas discussed above; it lies in the neural circuitry in the brain. Unfortunately, we know very little about neural circuits in fossils, and even our knowledge of the relevant circuits in living humans is quite limited. What can be observed in fossils beyond general brain size and shape is simply the gross surface anatomy of the brain. Neanderthal brains are slightly larger than AMH brains on average, but well within the AMH range.

The general shape of Neanderthal brains is lower and longer than AMH brains, whereas our brains are taller (Bruner 2008). Boeckx (2012) argues that the more globular shape of the brain in AMH is key because it may enable more efficient connections between distant parts of the brain, possibly paving the way for language. This is an interesting notion, as the shape difference is real—all other hominins, including Neanderthals, preserve almost entirely the ancestral brain shape, merely enlarging it allometrically, whereas AMH brains are shorter and taller. The difference has its ontological roots in a globularization phase in AMH infancy, which is absent in Neanderthals (Gunz et al. 2012). But the proposed link from globularity to language is still purely speculative and does not at present warrant any conclusions about Neanderthal language. Bruner (2008) cautions that brain shape differences may be merely a side effect of differences in the face and skull base, rather than driven by any cognitive changes.

Frontal widening around Broca's area is shared between AMH and Neanderthals and goes back to 2 Mya (Bruner 2007). Structures with the same general anatomy as Broca's and Wernicke's areas, however, have also been found in nonhuman primates (Gannon et al. 1998, Cantalupo & Hopkins 2001), so no strong conclusions can be drawn from this observation.

Mirror neurons have been commonly invoked as a key to language origins (e.g., Arbib 2012), and Barceló-Coblijn (2011) regards both mirror neurons and von Economo neurons as relevant to the Neanderthal language issue. But both kinds of neurons are present in languageless nonhuman primates, making them totally uninformative of Neanderthal language even if we did have any evidence concerning their presence in Neanderthals—which, beyond parsimony, we do not (Johansson 2013c).

The lateralization of language processing, although not as absolute as in the traditional textbook picture (Stowe et al. 2005, Fisher & Marcus 2006, Fonseca et al. 2009), may yet provide clues. But the connection between lateralization of function and asymmetry of anatomy is far from clear-cut—ape brains are not symmetric either (Balzeau & Gilissen 2010)—and fossils are rarely undamaged and undistorted at the level needed for asymmetry studies, so the gross asymmetries of the brain reveal little about prehistoric language.

The other major human-specific lateralization, our handedness, may possibly be connected with language lateralization (Steele & Uomini 2009) because dominant-hand processing and

language processing are typically handled by the same hemisphere (Knecht et al. 2000). Other apes may be right-handed or left-handed on an individual level, but they have nothing like the human 90% population-level dominance of right-handers.² Also, there are several ways to infer handedness from fossils and archeology. The handedness of stone tool makers can be inferred from subtle asymmetries in the flaking pattern from knapping and from use-wear damage on the tools. Moreover, for people who, like Neanderthals, use their teeth as tools, the pattern of wear and scratches on the front teeth can be informative as well (Uomini 2009, Frayer et al. 2010). Neanderthals and other Middle Paleolithic people definitely had a human handedness pattern (Frayer et al. 2010), and there are some signs of right-handedness as far back as 1 Mya (Uomini 2009).

4.5. Anatomical Conclusions

The fossil anatomy of Neanderthals contains no clear indication that they had language, but also nothing that excludes it. Instead, there are various indications that some speech adaptations may have been present in Neanderthals. None of these speech signs is compelling on its own, but from their consilience we can conclude that Neanderthal speech is quite likely.

5. EVIDENCE FROM GENETICS

During the past few decades, DNA sequencing methods have advanced rapidly, to the point where the recovery of ancient DNA from well-preserved fossils has become common (as reviewed in Shapiro & Hofreiler 2014). The maximum age of fossils from which DNA can be extracted approaches a million years (Millar & Lambert 2013). The full Neanderthal genome is now available from several individuals (Green et al. 2010, Prüfer et al. 2013), as is mitochondrial DNA (mtDNA) from numerous individuals (Hodgson & Disotell 2008). Ancient DNA from two other groups of prehistoric humans has also been recovered, specifically from Denisovan fossils (Reich et al. 2010, Meyer et al. 2012, Pennisi 2013) and the Sima de los Huesos fossils (Meyer et al. 2014); the latter likely belong to *Homo heidelbergensis*, and the taxonomic status of the former is totally unknown. Somewhat surprisingly, the Sima de los Huesos mtDNA turned out to be more similar to that of the Denisovans than to that of the Neanderthals (Meyer et al. 2014), even though there was good reason to believe the Sima de los Huesos people to be Neanderthal ancestors.

Contamination with recent DNA is always a concern in the analysis of ancient DNA, especially in the case of human remains (Wall & Kim 2007, Lalueza-Fox 2009), although methods for identifying contamination are improving (Skoglund et al. 2014). DNA damage is also quite common in fossil DNA, appearing as spurious “mutations” in the reconstructed sequence. Therefore, it is imprudent to take uncorroborated ancient DNA results at face value.

5.1. The Genetics of Language

Numerous genes have some effect on language, and there is a substantial genetic component in the variation in human language abilities today (Stromswold 2001, 2010). *FOXP2* is the gene most commonly invoked as relevant to language; I discuss it further below. Others include *ROBO1*,

²Whether there is population-level handedness at all among apes is a contentious issue (Palmer 2002, Humle & Matsuzawa 2009, Hopkins et al. 2011, Llorente et al. 2011). The details have not yet been confirmed, but it is clear that any population-level effect is at best still less than two to one, nowhere near the human level.

KIAA0319, *CNTNAP2*, and *DCDC2* (Dediu & Levinson 2013), but most of the genetics of language is still not well understood.

As noted by West-Eberhard (2003), genes are commonly followers in evolution; evolutionary changes may first take place within the space of phenotypic and behavioral flexibility, and genetic adaptations to the changes come later. This sequence of events is especially likely in the context of human cultural behaviors, notably language, because the “selective advantage of a genetic change that increased language proficiency would likely be greatest in a population that was already using language” (Fisher & Ridley 2013, p. 929). The presence of genetic adaptations to language in a population thus makes it likely that language had been used for some time already.

Nevertheless, several authors have proposed (Chomsky 2010, Piattelli-Palmarini 2010, Berwick & Chomsky 2011) that the origin of language was genetically driven, triggered by a single mutation. Mutation-driven saltational hypotheses have a well-deserved poor reputation in evolutionary biology (Iordansky 2006, Kinsella 2009), and recent developments in evo-devo (evolutionary developmental biology) have not done much to change that (Gardner 2013). A single large-effect mutation might occasionally lead to something that is viable and perhaps even useful, due to robust developmental constraints and modular architecture, but for this to lead to something that is totally novel is extremely unlikely, especially in the case of something with the postulated perfection of Chomsky’s language faculty (Kinsella 2009, Johansson 2013a).

Mutations in the gene *FOXP2* are associated with specific language impairment (Lai et al. 2001). The discovery that *FOXP2* is basically identical in most mammals, with the exception of humans who have two unique changes in this gene, was widely popularized as the discovery of “the language gene.” The real story is not nearly so simple. Although *FOXP2* does appear to have some relevance for language, its effects are quite indirect; it is a regulatory gene, not one that codes for structural proteins. It is active in many parts of the organism in addition to those relevant to language and works by controlling the expression of a large number of other genes (Spiteri et al. 2007, Ayub et al. 2013). The downstream genetic networks that *FOXP2* regulates are only beginning to be explored (Konopka et al. 2012).

Relevant in this context is that the derived human-specific allele of *FOXP2* has been found both in Neanderthals (Krause et al. 2007, Green et al. 2010) and in Denisovans (Maricic et al. 2013), so these mutations predate the human–Neanderthal split by a fair margin, a dating supported also by modern genomic data (Diller & Cann 2009). To whatever extent the *FOXP2* changes affected language evolution, this observation supports Neanderthal (and Denisovan) language. One caveat is that a regulatory element for the *FOXP2* gene differs between Neanderthals and most AMH, although a minority of AMH share the Neanderthal version (Dediu & Levinson 2013, Maricic et al. 2013); if this regulatory change were crucial for language, it ought to be obvious in that minority.

Various other genes that are involved in brain development differ between AMH on one hand and Neanderthals/Denisovans on the other hand (Somel et al. 2013), although the cognitive and linguistic significance of these differences is unclear. Somel et al. (2013) suggest that the extended synaptic development period in humans is likely to be cognitively important and that AMH-specific changes in the *MEF2A* gene may have been a key adaptation. Whether *MEF2A* is relevant for language is unknown.

5.2. Interbreeding Issues

Early mtDNA results consistently indicated that Neanderthals were a separate lineage that did not interbreed with AMH (Hodgson & Disotell 2008). But the first full Neanderthal genome study (Green et al. 2010) contradicted these mtDNA results, concluding that there was nonnegligible

gene flow from Neanderthals into all non-African AMH. As long as that study was uncorroborated, the interbreeding issue remained unresolved (Johansson 2013c). Today, however, we have both several more Neanderthal genomes of better quality (Prüfer et al. 2013) and various other evidence of gene flow between AMH and several lineages of ancient humans, including Neanderthals (Mendez et al. 2013, Ovchinnikov 2013, Waddell 2013, Ding et al. 2014, Lohse & Frantz 2014). As far as this review is concerned, the interbreeding issue can be regarded as settled. Many of us carry a few percent of Neanderthal DNA (Vernot & Akey 2014).

This does not automatically mean that Neanderthals and AMH belonged to the same species—other mammalian species separated for periods comparable to the period that separated the various *Homo* species can typically interbreed, even if they only do it in zoos (Holliday 2003, Hublin 2014). But interbreeding does have some impact on the question of Neanderthal language.

The apparent gene flow from Neanderthals to AMH entails that a significant number of Neanderthals must have been reproductively successful with AMH partners and that the hybrid offspring remained and flourished with their AMH relatives. Also, because the interbreeding apparently took place after the AMH exodus from Africa, the AMH population involved must have had full modern language.

Arguably, reproductive success in a community of language users is extremely unlikely for a person lacking language. It follows that the hybrids probably had a fully functioning language faculty that developed from a mixed genome, which means that the Neanderthal side of their heritage either provided the “right” alleles of relevant genes or that a heterozygous endowment was sufficient.

Did the Neanderthal parent of a hybrid need language? The answer depends on the mating system among early AMH, about which we know very little. In a context with long-term pair bonds, which required social acceptance in the AMH community, Neanderthal language abilities would have been necessary. But in a different system, or if hybrids resulted from a chance encounter and mating (consensual or not) between a Neanderthal man and an AMH woman in the forest, language need not have been involved.

5.3. Genetic Conclusions

With our limited knowledge about language genetics and Neanderthal genetics, we can conclude only that at least some language-relevant genetic changes are shared with Neanderthals, and that possibly some are not, but what this means for Neanderthal language is unclear. If Neanderthals had a partial “linguistic genotype,” one may speculate that they also had the genetic underpinnings for at least some, but not necessarily all, components of the human language faculty. The evidence of successful interbreeding does add some modest support for Neanderthal language, even with the caveats noted above (Johansson 2013c).

6. EVIDENCE FROM ARCHEOLOGY

The evident differences between the archeological record from the European Middle Paleolithic, largely Neanderthal-made, and that from the Upper Paleolithic, largely AMH-made, are commonly invoked as evidence of major cognitive differences, including a lack of Neanderthal language (e.g., Klein 2000, Mellars 2005). But more careful scrutiny of the Neanderthal record paints a less clear-cut picture. Neanderthals do show many of the behavioral traits that indicate behavioral modernity (d’Errico et al. 2003, Zilhão 2007), even though such discoveries have been met with some resistance or even with moving goal posts and double standards (Zilhão 2012,

Hopkinson 2013).³ The once-common belief that a cognitive revolution occurred exclusively among European AMH around 40 Kya has turned out to be an illusion (McBrearty & Brooks 2000, d’Errico & Stringer 2011).

6.1. Neanderthal Symbols

The ability to use symbols has long been considered one of the characteristics, and perhaps the most important one, of modern humans, distinguishing us at an essential level from all other creatures. This position poses considerable difficulties for both theoretical and methodological reasons (Hopkinson 2013), but traces of symbolism nevertheless remain accepted as powerful archeological proxies for modern cognition and language, among both proponents and opponents of Neanderthal language (Henshilwood & Marean 2003, Mellars 2004, Bouzouggar et al. 2007, Conard 2009, Zilhão 2012, among many others).

But how can symbol use be recognized archeologically? In any strict sense, doing so is very difficult (Hopkinson 2013). As a practical matter, nonutilitarian artifacts and behaviors, especially those associated with art, culture, and symbolism among present-day people, have been invoked as proxies.

Pigments are one such proxy, under the assumption that they were used mainly for non-utilitarian decoration purposes. Neanderthals used substantial amounts of black and red pigments, and some yellow ones, both in the Châtelperronian (Dayet et al. 2014) and earlier, up to 200 Kya (d’Errico et al. 2009). For some pigment discoveries, the most straightforward interpretation is that they were used for body painting (Zilhão 2012).

There is a fair amount of evidence of intentional burial of Neanderthals (Trinkaus & Shipman 1993, Langley et al. 2008, d’Errico et al. 2009, Rendu et al. 2014), although this hypothesis is still contested (e.g., Gargett 1999). The burials may be interpreted as an understanding of mortality, an awareness of self and others, and possibly as spirituality—or simply as housecleaning. But if dead conspecifics were treated differently from dead animals, then something was going on, and at least some burials are difficult to explain as housecleaning. Zilhão (2012) describes one Neanderthal tomb containing an engraved bone and another covered by a stone slab with cup holes. It is also notable that the frequency of articulated skeletons among Neanderthal finds is much higher than among similarly cave-dwelling animals, as well as earlier hominins, which is difficult to explain without assuming that Neanderthal bodies received special postmortem treatment in some form (Zilhão 2012).

No cave paintings can be unambiguously assigned to Neanderthal artists. The dating of some paintings in Spain is just barely compatible with AMH authorship, however, but it fits more comfortably with Neanderthal residence dates (Pike et al. 2012). Also, the more famous Chauvet paintings in France have been suggested as possible Neanderthal work (Bednarik 2007). Ornaments that Neanderthals may have used include painted and/or perforated shells (Zilhão et al. 2010), a few beads (d’Errico & Stringer 2011), perforated teeth (Zilhão 2012), and feathers from raptors (Peresani et al. 2011, Morin & Laroulandie 2012).

In summary, many of the types of artifacts that are regarded as evidence of symbolism when found in AMH contexts are also found with Neanderthals, albeit at lower frequency and not always

³ “[T]he widespread application of double standards in the evaluation of the empirical evidence that underpins ongoing debates about the place of Neanderthals” (Zilhão 2012, p. 35) or “amendments to the modernity trait list, driven primarily by Middle Palaeolithic archaeology’s awkward habit of meeting its conditions. Bluntly, the rules of the game have been repeatedly changed to keep the Neanderthals out” (Hopkinson 2013, p. 222).

uncontested. Sparse as it is, the evidence for Neanderthal symbolism is solid enough that it is difficult to posit a clear dichotomy between symbolic AMH and symbol-less Neanderthals (Zilhão 2012).

Furthermore, it is not the case that all AMH cultures have produced rich, archeologically visible traces of symbolism. The Niah Cave people on Borneo, who were roughly contemporary with the people who created the Aurignacian cave art in Europe, did not (Barker et al. 2007), and the archeological record of some Australian tribes is not notably different from that of Neanderthals (Brumm & Moore 2005, Roebroeks & Verpoorte 2009), even though we know from their ethnographic record that they had a fully modern symbol-laden culture and, of course, language.

6.2. Neanderthal Technology and Subsistence

Various aspects of technology and subsistence have been invoked by different authors as proxies for either behavioral modernity in general (Henshilwood & Marean 2003, Spikins 2009) or language in particular (Coupé & Hombert 2005, Camps & Uriageraka, 2006, Ambrose 2010). Most such proxies have been found in Middle Paleolithic assemblages, made by Neanderthals.

Ambrose (2010) regards composite tools, such as hafted weapons, as a proxy for grammatical language. But evidence of hafted weapons goes back 500 Kya to the common ancestor of AMH and Neanderthals (Wilkins et al. 2012). Neanderthals apparently hafted tools using adhesives (Mazza et al. 2006, Cârciumaru et al. 2012); making adhesives in a nontrivial multistep process required sophisticated cognition (Koller et al. 2001). Evidence for other types of composite tools, such as tipped spears, has been found as well (Hardy et al. 2013).

Fire was habitually used by Neanderthals in Europe (Roebroeks & Villa 2011, Hérissou et al. 2013), and they were capable both of cooking their food (Henry et al. 2011) and of using fire as a tool (Koller et al. 2001). Brown et al. (2009) consider the latter use a proxy for modern cognition. But despite ample evidence of controlled fire use, it has been difficult to establish that Neanderthals could ignite fires, although that may be due to the use of ephemeral or expedient fire-making tools (Sorensen et al. 2014).

Seafaring is another technology that has been invoked (e.g., Coupé & Hombert 2005) as a proxy for language. Middle Paleolithic tools, most likely made by Neanderthals, have been found on Mediterranean islands that were inaccessible without boats, indicating that Neanderthals were capable of making sea crossings (Ferentinos et al. 2012), as were, indeed, earlier *Homo erectus* (Morwood et al. 1998).

Knot making is interesting because it has been proposed not simply as a proxy for language in some unspecified sense, but specifically as a proxy for core syntax. Mathematical knot theory shares formal properties with syntax; they have the same level of computational complexity (Camps & Uriageraka 2006). For largely the same reasons as Lobina (2012), I do not find the link between tying knots (as opposed to doing knot theory) and syntax totally convincing (Johansson 2013b). But there is fair evidence that Neanderthals could make strings (Hardy et al. 2013) and that they used other technologies that typically involve knots: hafting (Wilkins et al. 2012), making clothing (Wales 2012), and making beads and other perforated ornaments that make little sense without a string or thong through the hole (Zilhão 2012). So, if knots really were proxies for syntax, Neanderthals had syntax.

The organization of living spaces, with different activities taking place in different designated zones within the living area, is a different kind of technology invoked as a modernity marker. Also in this respect, there is no strong evidence that Neanderthals differed from coeval AMH (Henry et al. 2004, Shahack-Gross et al. 2014); careful excavations have revealed patterned and predictable living spaces at Neanderthal sites (Riel-Salvatore et al. 2013).

Different exploitation patterns of fauna have been invoked as indicators of cognitive modernity; different authors have considered both specialization and diversification, and there is little consensus on how exploitation patterns should be interpreted (Schepartz 1993). There is, however, no strong evidence that exploitation patterns actually differed significantly between AMH and earlier humans (Britton et al. 2011, Faith 2011, Stiner et al. 2011). Neanderthals got most of their sustenance from meat (Richards & Trinkaus 2009), but their diet also included plants (Henry et al. 2011), seafood (Cortés-Sánchez et al. 2011), and small game (Hardy et al. 2013).

Some researchers (e.g., Mellars & French 2011) argue for a substantially larger population density among Early Upper Paleolithic AMH in Europe than among the Neanderthals that they replaced, but there is no consensus on this issue (Dogandžić & McPherron 2013). If the density contrast turns out to be correct, it could be interpreted as evidence in either direction concerning Neanderthal language—either that the lower population density was a result of lower Neanderthal resource-utilizing efficiency, reflecting cognitive shortcomings including lack of language, or that the sparser cultural and symbolic record of Neanderthals was due to demographic factors alone, without any need to invoke cognitive differences (Zilhão 2007, Roebroeks & Verpoorte 2009, Cartmill 2010), because visible symbols may have been unnecessary until the population was dense enough to require group markers (Norton & Jin 2009).

6.3. Cultural Dynamism

Another possible archeological proxy for language concerns not a particular type of artifact, but instead the rate of change in the types of artifacts produced. Together, the rates of both technological progress and cultural change can be labeled cultural dynamism.

Barceló-Coblijn & Benítez-Burraco (2013) argue that a distinction can be made between static and nonstatic cultures and that complex language may be the decisive difference that makes a culture nonstatic, possibly in combination with the working-memory hypothesis of Coolidge & Wynn (2005). If Neanderthal culture were clearly static, that would argue against Neanderthal language.

Clearly, AMH culture is much more dynamic than anything found among extant apes, whose cultural dynamism is barely distinguishable from zero. Among fossil hominins, at least up to *Homo erectus*, the rate of technological progress was glacial; recognizably Acheulean tools were made for a million years or so. But after *H. erectus*, the situation became more complex. Compared with present-day Western society, any previous culture in any species was static, including Upper Paleolithic AMH. But compared with anything that went on earlier, the past few hundred thousand years saw a significant acceleration of the rate of change, both among proto-AMH and among other contemporary people, notably including Neanderthals.

Also, although most AMH are indeed more dynamic than most Neanderthals were, there is no clear-cut dichotomy between static Neanderthals and nonstatic AMH. On one hand, the Châtelperronian shows accelerated cultural change among a subset of Neanderthals (Zilhão et al. 2010, Hublin et al. 2012, Soressi et al. 2013). On the other hand, the recognizable continuity of San culture across 44,000 years (d’Errico et al. 2012) shows that not all AMH cultures are nonstatic.

7. CONCLUSIONS

The anatomical evidence indicates likely speech adaptations in Neanderthals. In Neanderthal DNA we find some, but not all, of the genes identified as relevant to language in modern humans. Neanderthal archeology displays a large fraction of all the proxies for behavioral modernity that have been proposed, including both symbolic behavior and cultural dynamism, albeit less consistently and at lower frequency than among AMH. Also, there is good evidence that Neanderthals

and AMH together produced children who grew up to be successful within a community of language-using AMH.

All this evidence indicates that Neanderthals could not have been totally without language abilities. They probably had some form of spoken language, but we really do not know whether Neanderthal language abilities were the same as AMH abilities. Possibly they had only a subset of our abilities. The archeological evidence of symbol use indicates an ability to handle symbols and connect symbols with referents. This property supports the presence of lexical semantics but is not informative of Neanderthals' syntactic abilities. There is really no good evidence one way or the other concerning Neanderthal syntax, contrary to both Dediu & Levinson (2013), who conclude that Neanderthals did have syntax, and Barceló-Coblijn & Benítez-Burraco (2013), who conclude the opposite.

7.1. Possible Future Directions

New fossil and archeological finds would of course be desirable, but their discovery is serendipitous. Nobody expected either hobbits (Brown et al. 2004) or Denisovans (Reich et al. 2010) to be found, and in the future we can surely expect other surprises. One trend in recent discoveries is that our evolutionary history is becoming more and more complex; several varieties of humans coexisted up to the fairly recent past and were connected in a web of interbreeding, rather than organized in a simple family tree. It is therefore prudent to pursue theories of language evolution that are robust against complex and changing evolutionary patterns.

A flood of genetic data is already having a major impact on the field, and this flood is still rising exponentially. Both ancient DNA from extinct people and data on genetic variation and gene expression patterns in living people are likely to make massive contributions to our understanding of both language and human evolution. The main bottleneck here is in analysis methods, finding and making sense of patterns in the data, and connecting the genetic patterns with linguistic structures and concepts. We know well enough the genetic differences between AMH and Neanderthals, but we have something akin to the granularity mismatch of Poeppel & Embick (2005), so the vast amounts of genetic data are not as illuminating as they might be. This area deserves more attention from people who understand both genetics and linguistics. One avenue of research that may become possible in the near future, given the identification of stretches of Neanderthal DNA in the genomes of living people (Vernot & Akey 2014), is to identify people carrying Neanderthal alleles of language-relevant genes and to test their language abilities or, alternatively, to determine whether Neanderthal alleles are overrepresented in language pathologies.

As the ongoing debate between P. Lieberman (2012) and Boë et al. (2013) shows, our knowledge of vocal tract anatomy, and how it affects language abilities, remains imperfect even in modern humans and could benefit from more study, especially exploration of the outer ranges of modern human anatomical variation, which may overlap with Neanderthal anatomy. In linguistic theory, it would be desirable to have further research along the lines of Jackendoff & Wittenberg (2014), looking into the decomposability and evolvability of the human language faculty from different theoretical perspectives.

7.2. Final Words

Hopkinson (2013, p. 231) concludes, "If Neanderthals . . . behaved like us and had children with us, then surely they are 'us.'" I agree. If Neanderthals are close enough to us to be our partners, then they are human, by any reasonable definition. But were they precisely like us, or were Neanderthal languages in some subtle or not-so-subtle way different from ours? As a linguist, I find the latter possibility most exciting. We could learn so much more about language if we had access to

a language faculty that is fully functional but different from the standard AMH issue. But Neanderthals are extinct, tragically enough, so we will never learn their languages.

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LITERATURE CITED

- Alemseged Z, Spoor F, Kimbel WH, Bobe R, Geraads D, et al. 2006. A juvenile early hominin skeleton from Dikika, Ethiopia. *Nature* 443:296–301
- Ambrose SH. 2010. Coevolution of composite-tool technology, constructive memory, and language. *Curr. Anthropol.* 51:S135–47
- Arbib MA. 2012. *How the Brain Got Language: The Mirror System Hypothesis*. New York: Oxford Univ. Press
- Arensburg B, Tillier AM, Vandermeersch B, Duday H, Schepartz LA, Rak Y. 1989. A Middle Palaeolithic human hyoid bone. *Nature* 338:758–60
- Ayub Q, Yngvadottir B, Chen Y, Xue Y, Hu M, et al. 2013. *FOXP2* targets show evidence of positive selection in European populations. *Am. J. Hum. Genet.* 92:696–706
- Balzeau A, Gilissen E. 2010. Endocranial shape asymmetries in *Pan paniscus*, *Pan troglodytes* and *Gorilla gorilla* assessed via skull based landmark analysis. *J. Hum. Evol.* 59:54–69
- Barceló-Coblijn L, Benítez-Burraco A. 2013. Disentangling the Neanderthal net: a comment on Johansson (2013). *Biolinguistics* 7:199–216
- Barceló-Coblijn L. 2011. A biolinguistic approach to vocalizations of *H. neanderthalensis* and the genus *Homo*. *Biolinguistics* 5:286–334
- Barker G, Barton H, Bird M, Daly P, Datan I, et al. 2007. The “human revolution” in lowland tropical Southeast Asia: the antiquity and behavior of anatomically modern humans at Niah Cave (Sarawak, Borneo). *J. Hum. Evol.* 52:243–61
- Bastir M, Rosas A, String C, Cuétara JM, Kruszynski R, et al. 2010. Effects of brain and facial size on basicranial form in human and primate evolution. *J. Hum. Evol.* 58:424–31
- Bednarik RG. 2007. Antiquity and authorship of Chauvet rock art. *Rock Art Res.* 24:1–21
- Berwick RC, Chomsky N. 2011. The biolinguistic program: the current state of its development. In *The Biolinguistic Enterprise: New Perspectives on the Evolution and Nature of the Human Language Faculty*, ed. AM Di Sciullo, C Boeckx, pp. 65–99. Oxford, UK: Oxford Univ. Press
- Bickerton D. 2009. *Adam’s Tongue*. New York: Hill & Wang
- Boë L-J, Badin P. 2013. Anatomy and control of the developing human vocal tract: a response to Lieberman. *J. Phon.* 41:379–92
- Boë L-J, Heim JL, Honda K, Maeda S, Badin P, Abry C. 2007. The vocal tract of newborn humans and Neanderthals: acoustic capabilities and consequences for the debate on the origin of language. A reply to Lieberman (2007a). *J. Phon.* 35:564–81
- Boeckx C. 2011. The nature of merge: consequences for language, mind and biology. In *Of Minds and Language: A Dialogue with Noam Chomsky in the Basque Country*, ed. M Piattelli-Palmarini, J Uriagereka, P Salaburu, pp. 44–57. Oxford, UK: Oxford Univ. Press

- Boeckx C. 2012. *Homo combinans*. Presented at 9th Int. Conf. Evol. Lang. (EVOLANG9), Kyoto, Jpn., March 13–16
- Boeckx C. 2013. Lexicon, syntax, and grammar: biolinguistic concerns. Presented at 19th Int. Congr. Linguist., Geneva, July 21–27
- Botha R, Knight C, ed. 2009. *The Cradle of Language*. Oxford, UK: Oxford Univ. Press
- Botha R. 2009. Theoretical underpinnings of inferences about language evolution: the syntax used at Blombos Cave. See Botha & Knight 2009, pp. 93–111
- Bouzouggar A, Barton N, Vanhaeren M, d'Errico F, Collcutt S, et al. 2007. 82,000-year-old shell beads from North Africa and implications for the origins of modern human behavior. *Proc. Natl. Acad. Sci. USA* 104:9964–69
- Britton K, Grimes V, Niven L, Steele TE, McPherron SP, et al. 2011. Strontium isotope evidence for migration in late Pleistocene Rangifer: implications for Neanderthal hunting strategies at the Middle Palaeolithic site of Jonzac, France. *J. Hum. Evol.* 61:176–85
- Brown KS, Marean CW, Herries AIR, Jacobs Z, Trebolo C, et al. 2009. Fire as an engineering tool of early modern humans. *Science* 325:859–62
- Brown P, Sutikna N, Morwood MJ, Soejono RP, Jatmiko E, et al. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431:1055–61
- Brumm A, Moore MW. 2005. Symbolic revolutions and the Australian archeological record. *Camb. Archaeol. J.* 15:157–75
- Bruner E. 2007. Cranial shape and size variation in human evolution: structural and functional perspectives. *Child's Nerv. Syst.* 23:1357–65
- Bruner E. 2008. Comparing endocranial form and shape differences in modern humans and Neandertals: a geometric approach. *Paleoanthropology* 2008:93–106
- Camps M, Uriagereka J. 2006. The Gordian knot of linguistic fossils. In *The Biolinguistic Turn: Issues on Language and Biology*, ed. J Rosselló, J Martín, pp. 34–65. Barcelona: Publ. Univ. Barcelona
- Cantalupo C, Hopkins WD. 2001. Asymmetric Broca's area in great apes. *Nature* 414:505
- Cârciumaru M, Ion R-M, Nițu E-C, Ștefănescu R. 2012. New evidence of adhesive as hafting material on Middle and Upper Palaeolithic artefacts from Gura Cheii-Râsnov Cave (Romania). *J. Archaeol. Sci.* 39:1942–50
- Cartmill M. 2010. The human (r)evolution(s). *Evol. Anthropol.* 19:89–91
- Chomsky N. 2010. Some simple evo devo theses: How true might they be for language? See Larson et al. 2010, pp. 45–62
- Collins SA. 2000. Men's voices and women's choices. *Anim. Behav.* 60:773–80
- Conard NJ. 2009. A female figurine from the basal Aurignacian of Hohle Fels Cave in southwestern Germany. *Nature* 459:248–52
- Conard NJ, Richter J, ed. 2011. *Neanderthal Lifeways, Subsistence and Technology: One Hundred Fifty Years of Neanderthal Study*. Dordrecht, Neth.: Springer
- Coolidge FL, Wynn T. 2005. Working memory, its executive functions, and the emergence of modern thinking. *Camb. Archaeol. J.* 15:5–26
- Corballis MC. 2002. *From Hand to Mouth: The Origins of Language*. Princeton, NJ: Princeton Univ. Press
- Cortés-Sánchez M, Morales-Muñoz A, Simón-Vallejo MD, Lozano-Francisco MC, Vera-Peláez JL, et al. 2011. Earliest known use of marine resources by Neanderthals. *PLOS ONE* 6:e24026
- Coupé C, Hombert J-M. 2005. Les premières traversées maritimes: une fenêtre sur les cultures et les langues de la préhistoire. In *Aux Origines des langues et du langage*, ed. J-M Hombert, pp. 118–61. Paris: Fayard
- D'Anastasio R, Wrie S, Tuniz C, Mancini L, Cesana DT, et al. 2013. Micro-biomechanics of the Kebara 2 hyoid and its implications for speech in Neanderthals. *PLOS ONE* 8:e82261
- d'Errico F, Backwell L, Villa P, Degano I, Lucejko JJ, et al. 2012. Early evidence of San material culture represented by organic artifacts from Border Cave, South Africa. *Proc. Natl. Acad. Sci. USA* 109:13214–19
- d'Errico F, Henshilwood C, Lawson G, Vanhaeren M, Tillier A-M, et al. 2003. Archaeological evidence for the emergence of language, symbolism, and music—an alternative multidisciplinary perspective. *J. World Prehist.* 17:1–70

- d'Errico F, Stringer CB. 2011. Evolution, revolution or saltation scenario for the emergence of modern cultures? *Philos. Trans. R. Soc. Lond. B* 366:1060–69
- d'Errico F, Vanhaeren M, Henshilwood C, Lawson G, Maureille B, et al. 2009. From the origin of language to the diversification of languages: What can archaeology and palaeoanthropology say? In *Becoming Eloquent: Advances in the Emergence of Language, Human Cognition, and Modern Cultures*, ed. F d'Errico, J-M Hombert, pp. 13–68. Amsterdam: Benjamins
- Dayet L, d'Errico F, Garcia-Moreno R. 2014. Searching for consistencies in Châtelperronian pigment use. *J. Archaeol. Sci.* 44:180–93
- Deacon TW. 1997. *The Symbolic Species*. New York: Norton
- Dediu D, Levinson SC. 2013. On the antiquity of language: the reinterpretation of Neandertal linguistic capacities and its consequences. *Front. Psychol.* 4:1–17
- DeGusta D, Gilbert H, Turner SP. 1999. Hypoglossal canal size and hominid speech. *Proc. Natl. Acad. Sci. USA* 96:1800–4
- Diller KC, Cann RL. 2009. Evidence against a genetic-based revolution in language 50,000 years ago. See Botha & Knight 2009, pp. 135–49
- Ding Q, Hu Y, Xu S, Wang J, Jin L. 2014. Neanderthal introgression at chromosome 3p21.31 was under positive natural selection in East Asians. *Mol. Biol. Evol.* 31:683–95
- Dogandžić T, McPherron SP. 2013. Demography and the demise of the Neandertals: a comment on “Tenfold population increase in Western Europe at the Neanderthal-to-modern human transition.” *J. Hum. Evol.* 64:311–13
- Faith JT. 2011. Ungulate biogeography, statistical methods, and the proficiency of Middle Stone Age hunters. *J. Hum. Evol.* 60:315–17
- Feinberg DR. 2005. Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. *Anim. Behav.* 69:561–68
- Feinberg DR, Jones BC, Little AC, Burt DM, Perrett DI. 2008. Are human faces and voices ornaments signaling common underlying cues to mate value? *Evol. Anthropol.* 17:112–18
- Ferentinos G, Gkioni M, Geraga M, Papatheodorou G. 2012. Early seafaring activity in the southern Ionian Islands, Mediterranean Sea. *J. Archaeol. Sci.* 39:2167–76
- Fisher SE, Marcus GF. 2006. The eloquent ape: genes, brains and the evolution of language. *Nat. Rev. Genet.* 7:9–20
- Fisher SE, Ridley M. 2013. Culture, genes, and the human revolution. *Science* 340:929–30
- Fitch WT, Giedd J. 1999. Morphology and development of the human vocal tract: a study using magnetic resonance imaging. *J. Acoust. Soc. Am.* 106:1511–22
- Fitch WT. 2005. The evolution of language: a comparative review. *Biol. Philos.* 20:193–230
- Fitch WT. 2009. Fossil cues to the evolution of speech. See Botha & Knight 2009, pp. 112–34
- Fonseca RP, Scherer LC, de Oliveira CR, de Mattos Pimenta Parente MA. 2009. Hemispheric specialization for communicative processing: neuroimaging data on the role of the right hemisphere. *Psychol. Neurosci.* 2:25–33
- Freyer DW, Fiore I, Lalueza-Fox C, Radović J, Bondioli L. 2010. Right handed Neandertals: Vindija and beyond. *J. Anthropol. Sci.* 88:113–27
- Fujita K. 2009. A prospect for evolutionary adequacy: merge and the evolution and development of human language. *Biolinguistics* 3:128–53
- Gannon PJ, Holloway RL, Broadfield DC, Braun AR. 1998. Asymmetry of chimpanzee planum temporale: humanlike pattern of Wernicke's brain language area homolog. *Science* 279:220–22
- Gardner A. 2013. Darwinism, not mutationism, explains the design of organisms. *Prog. Biophys. Mol. Biol.* 111:97–98
- Gargett RH. 1999. Middle Palaeolithic burial is not a dead issue: the view from Qafzeh, Saint-Cesaire, Kebara, Amud, and Dederiyeh. *J. Hum. Evol.* 37:27–90
- Granat J, Boë L-J, Badin P, Pochic D, Heim J-L, Peyre E, Benoît R. 2007. *Prediction of the ability of reconstituted vocal tracts of fossils to produce speech*. Presented at 16th Int. Congr. Phon. Sci., Saarbrücken, Ger., August 6–10. <http://www.icphs2007.de/conference/Papers/1707/1707.pdf>
- Green RE, Krause J, Briggs AW, Maricic T, Stenzel U, et al. 2010. A draft sequence of the Neandertal genome. *Science* 328:710–22

- Gunz P, Neubauer S, Golovanova L, Doronichev V, Maureille B, Hublin JJ. 2012. A uniquely human pattern of endocranial development. Insights from a new cranial reconstruction of the Neanderthal newborn from Mezmaiskaya. *J. Hum. Evol.* 62:300–13
- Hardy BL, Moncel M-H, Daujeard C, Fernandes P, Béarez P, et al. 2013. Impossible Neanderthals? Making string, throwing projectiles and catching small game during Marine Isotope Stage 4. *Quat. Sci. Rev.* 82:23–40
- Harvati K, Harrison T, ed. 2008. *Neanderthals Revisited: New Approaches and Perspectives*. Dordrecht, Neth.: Springer. Rev. ed.
- Hauser MD, Chomsky N, Fitch WT. 2002. The faculty of language: What is it, who has it, and how did it evolve? *Science* 298:1565–66
- Henry AG, Brooks AS, Piperno DR. 2011. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq, Spy I and II, Belgium). *Proc. Natl. Acad. Sci. USA* 108:486–91
- Henry DO, Hietala HJ, Rosen AM, Demidekno YE, Usik VI, Armagan TL. 2004. Human behavioral organization in the Middle Paleolithic: Were Neanderthals different? *Am. Anthropol.* 106:17–31
- Henshilwood CS, Marean CW. 2003. The origin of modern human behavior. Critique of the models and their test implications. *Curr. Anthropol.* 44:627–51
- Hérisson D, Loch J-L, Auguste P, Tuffreau A. 2013. Néandertal et le feu au Paléolithique moyen ancien. Tour d’horizon des traces de son utilisation dans le Nord de la France. *Anthropologie* 117:541–78
- Hodgson JA, Disotell TR. 2008. No evidence of a Neanderthal contribution to modern human diversity. *Genome Biol.* 9:206
- Holliday TW. 2003. Species concepts, reticulation, and human evolution. *Curr. Anthropol.* 44:653–73
- Hopkins WD, Phillips KA, Bania A, Calcutt SE, Gardner M, et al. 2011. Hand preferences for coordinated bimanual actions in 777 great apes: implications for the evolution of handedness in Hominins. *J. Hum. Evol.* 60:605–11
- Hopkinson T. 2013. “Man the symboler”: a contemporary origins myth. *Archaeol. Dialogues* 20:215–41
- Houghton P. 1993. Neandertal supralaryngeal vocal tract. *Am. J. Phys. Anthropol.* 90:139–46
- Hublin JJ, Talamo S, Julien M, David F, Connet N, et al. 2012. Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neandertal origin for the Châtelperronian. *Proc. Natl. Acad. Sci. USA* 109:18743–48
- Hublin JJ. 2014. Paleoanthropology: *Homo erectus* and the limits of a paleontological species. *Curr. Biol.* 24:R82–84
- Humle T, Matsuzawa T. 2009. Laterality in hand use across four tool-use behaviors among the wild chimpanzees of Bossou, Guinea, West Africa. *Am. J. Primatol.* 71:40–48
- Iordansky NN. 2006. The problem of the evolutionary saltations. *Zh. Obshchei Biol.* 67:256–67
- Jackendoff R. 2010. Your theory of language evolution depends on your theory of language. See Larson et al. 2010, pp. 63–72
- Jackendoff R, Wittenberg E. 2014. What can you say without syntax? A hierarchy of grammatical complexity. In *Measuring Grammatical Complexity*, ed. FJ Newmeyer, LB Preston. Oxford, UK: Oxford Univ. Press. In press
- Jerison HJ. 1973. *Evolution of the Brain and Intelligence*. New York: Academic
- Johansson S. 2005. *Origins of Language—Constraints on Hypotheses*. Amsterdam: Benjamins
- Johansson S. 2013a. Biolinguistics or psycholinguistics? Is the Third Factor helpful or harmful in explaining language? *Biolinguistics* 7:249–75
- Johansson S. 2013b. Neanderthals between Man and Beast. *Biolinguistics* 7:217–27
- Johansson S. 2013c. The talking Neanderthals: What do fossils, genetics and archeology say? *Biolinguistics* 7:35–74
- Johansson S. 2014. *Did language evolve incommunicado?* Presented at 10th Int. Conf. Evol. Lang. (EVOLANG X), Vienna, April 14–17
- Jones BC, Feinberg DR, DeBruine LM, Little AC, Vukovic J. 2008. Integrating cues of social interest and voice pitch in men’s preferences for women’s voices. *Biol. Lett.* 4:192–94
- Jungers WL, Pokempner AA, Kay RF, Cartmill M. 2003. Hypoglossal canal size in living hominoids and the evolution of human speech. *Hum. Biol.* 75:473–84

- Kay RF, Cartmill M, Balow M. 1998. The hypoglossal canal and the origin of human vocal behavior. *Proc. Natl. Acad. Sci. USA* 95:5417–19
- Kinsella AR. 2009. *Language Evolution and Syntactic Theory*. New York: Cambridge Univ. Press
- Klein RG. 1999. *The Human Career: Human Biological and Cultural Origins*. Chicago: Univ. Chicago Press
- Klein RG. 2000. Archeology and the evolution of human behavior. *Evol. Anthropol.* 9:17–36
- Knecht S, Dräger B, Deppe M, Bobe L, Lohmann H, et al. 2000. Handedness and hemispheric language dominance in healthy humans. *Brain* 123:2512–18
- Koller J, Baumer U, Mania D. 2001. High-tech in the Middle Palaeolithic: Neandertal-manufactured pitch identified. *Eur. J. Archaeol.* 4:385–97
- Konopka G, Friedrich T, Davis-Turak J, Winden K, Oldham MC, et al. 2012. Human-specific transcriptional networks in the brain. *Neuron* 75:601–17
- Krause J, Orlando L, Serre D, Viola B, Prüfer K, et al. 2007. Neanderthals in Central Asia and Siberia. *Nature* 449:902–4
- Lai CSL, Fisher SE, Hurst JA, Vargha-Khadem F, Monaco AP. 2001. A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature* 413:519–23
- Lalueza-Fox C. 2009. The Neanderthal genome project and beyond. *Contrib. Sci.* 5:169–75
- Langley MC, Clarkson C, Ulm S. 2008. Behavioral complexity in Eurasian Neanderthal populations: a chronological examination of the archaeological evidence. *Camb. Archaeol. J.* 18:289–307
- Larson RK, Déprez V, Yamakido H, ed. 2010. *The Evolution of Human Language: Biolinguistic Perspectives*. Cambridge, UK: Cambridge Univ. Press
- Levinson SC. 2012. The original sin of cognitive science. *Top. Cogn. Sci.* 4:396–403
- Lieberman DE. 2008. Speculations about the selective basis for modern human craniofacial form. *Evol. Anthropol.* 17:55–68
- Lieberman P, Crelin ES. 1971. On the speech of Neanderthal man. *Linguist. Inq.* 2:203–22
- Lieberman P. 2007a. Current views on Neanderthal speech capabilities: a reply to Boë et al. (2002). *J. Phon.* 35:552–63
- Lieberman P. 2007b. The evolution of human speech: its anatomical and neural bases. *Curr. Anthropol.* 48:39–66
- Lieberman P. 2012. Vocal tract anatomy and the neural bases of talking. *J. Phon.* 40:608–22
- Llorente M, Riba D, Palou L, Carrasco L, Mosquera M, et al. 2011. Population-level right-handedness for a coordinated bimanual task in naturalistic housed chimpanzees: replication and extension in 114 animals from Zambia and Spain. *Am. J. Primatol.* 73:281–90
- Lobina DJ. 2012. All tied in knots. *Biolinguistics* 6:70–78
- Lohse K, Frantz LAF. 2014. Neandertal admixture in Eurasia confirmed by maximum likelihood analysis of three genomes. *Genetics* 196:1241–51
- MacLarnon A, Hewitt G. 2004. Increased breathing control: another factor in the evolution of language. *Evol. Anthropol.* 13:181–97
- MacLarnon AM, Hewitt G. 1999. The evolution of human speech: the role of enhanced breathing control. *Am. J. Phys. Anthropol.* 109:341–63
- Maricic T, Günther T, Georgiev O, Gehre S, Culin M, et al. 2013. A recent evolutionary change affects a regulatory element in the human *FOXP2* gene. *Mol. Biol. Evol.* 30:844–52
- Martínez I, Arsuaga J-L, Quam R, Carretero JM, Gracia A, Rodríguez L. 2008. Human hyoid bones from the middle Pleistocene site of the Sima de los Huesos (Sierra de Atapuerca, Spain). *J. Hum. Evol.* 54:118–24
- Martínez I, Rosa M, Arsuaga J-L, Jarabo P, Quam R, et al. 2004. Auditory capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain. *Proc. Natl. Acad. Sci. USA* 101:9976–81
- Martínez I, Rosa M, Quam R, Jarabo P, Lorenzo C, et al. 2013. Communicative capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain. *Quat. Int.* 295:94–101
- Mazza PPA, Martini F, Sala B, Magi M, Perla Colombini M, et al. 2006. A new Palaeolithic discovery: tar-hafted stone tools in a European Mid-Pleistocene bone-bearing bed. *J. Archaeol. Sci.* 33:1310–18
- McBrearty S, Brooks A. 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* 39:453–563
- Mellars P, French JC. 2011. Tenfold population increase in Western Europe at the Neanderthal-to-modern human transition. *Science* 333:623–27

- Mellars P. 2004. Neanderthals and the modern human colonization of Europe. *Nature* 432:461–65
- Mellars P. 2005. The impossible coincidence: a single-species model for the origins of modern human behavior in Europe. *Evol. Anthropol.* 14:12–27
- Mendez FL, Krahn T, Schrack B, Krahn A-M, Veeramah KR, et al. 2013. An African American paternal lineage adds an extremely ancient root to the human Y chromosome phylogenetic tree. *Am. J. Hum. Genet.* 92:454–49
- Meyer M, Fu Q, Aximu-Oetri A, Glocke I, Nickel B, et al. 2014. A mitochondrial genome sequence of a hominin from Sima de los Huesos. *Nature* 505:403–6
- Meyer M, Kircher M, Gansauge M-T, Li H, Racimo F, et al. 2012. A high-coverage genome sequence from an archaic Denisovan individual. *Science* 338:222–26
- Millar CD, Lambert DM. 2013. Towards a million-year-old genome. *Nature* 499:34–35
- Mithen S. 2005. *The Singing Neanderthals*. London: Weidenfeld & Nicolson
- Morin E, Laroulandie V. 2012. Presumed symbolic use of diurnal raptors by Neanderthals. *PLOS ONE* 7:e32856
- Morwood MJ, O’Sullivan PB, Aziz F, Raza A. 1998. Fission-track ages of stone tools and fossils on the east Indonesian island of Flores. *Nature* 392:173–76
- Norton CJ, Jin JH. 2009. The evolution of modern human behavior in East Asia: current perspectives. *Evol. Anthropol.* 18:247–60
- Ovchinnikov IV. 2013. Hominin evolution and gene flow in the Pleistocene Africa. *Anthropol. Anz.* 70:221–27
- Palmer AR. 2002. Chimpanzee right-handedness reconsidered: evaluating the evidence with funnel plots. *Am. J. Phys. Anthropol.* 118:191–99
- Pennisi E. 2013. More genomes from Denisova cave show mixing of early human groups. *Science* 340:799
- Peresani M, Fiore I, Gala M, Romandini M, Tagliacozzo A. 2011. Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. *Proc. Natl. Acad. Sci. USA* 108:3888–93
- Piattelli-Palmarini M. 2010. What is language, that it may have evolved, and what is evolution, that it may apply to language. See Larson et al. 2010, pp. 148–62
- Pike AWG, Hoffmann DL, Garcia-Diez M, Pettitt PB, Alcolea J, et al. 2012. U-series dating of Paleolithic art in 11 caves in Spain. *Science* 336:1409–13
- Poeppl D, Embick D. 2005. Defining the relation between linguistics and neuroscience. In *Twenty-First Century Psycholinguistics: Four Cornerstones*, ed. A Cutler, pp. 103–18. Mahwah, NJ: Erlbaum
- Prüfer K, Racimo F, Patterson N, Jay F, Sankaraman S, et al. 2013. The complete genome sequence of a Neanderthal from the Altai mountains. *Nature* 505:43–49
- Quam R, Rak Y. 2008. Auditory ossicles from southwest Asian Mousterian sites. *J. Hum. Evol.* 54:414–33
- Reich D, Green RE, Kircher M, Krause J, Patterson N, et al. 2010. Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature* 468:1053–60
- Rendu W, Beauval C, Crevecoeur I, Bayle P, Balzeau A, et al. 2014. Evidence supporting an intentional Neandertal burial at La Chapelle-aux-Saints. *Proc. Natl. Acad. Sci. USA* 111:81–86
- Richards MP, Trinkaus E. 2009. Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proc. Natl. Acad. Sci. USA* 106:16034–39
- Riel-Salvatore J, Ludeke I, Negrino F, Holt BM. 2013. A spatial analysis of the Late Mousterian levels of Riparo Bombrini (Balzi Rossi, Italy). *Can. J. Archaeol.* 37:70–92
- Roebroeks W, Verpoorte A. 2009. A “language-free” explanation for differences between the European Middle and Upper Paleolithic record. See Botha & Knight 2009, pp. 150–66
- Roebroeks W, Villa P. 2011. On the earliest evidence for habitual use of fire in Europe. *Proc. Natl. Acad. Sci. USA* 108:5209–14
- Schepartz LA. 1993. Language and modern human origins. *Yearb. Phys. Anthropol.* 36:91–126
- Shahack-Gross R, Berna F, Karkanas P, Lemorini C, Gopher A, Barkai R. 2014. Evidence for the repeated use of a central hearth at Middle Pleistocene (300 ky ago) Qesem Cave, Israel. *J. Archaeol. Sci.* 44:12–21
- Shapiro B, Hofreiter M. 2014. A paleogenomic perspective on evolution and gene function: new insights from ancient DNA. *Science* 343:6169
- Skoglund P, Northoff BH, Shunkov MV, Derevianko AP, Pääbo S. 2014. Separating endogenous ancient DNA from modern day contamination in a Siberian Neandertal. *Proc. Natl. Acad. Sci. USA* 111:2229–34

- Somel M, Liu X, Khaitovich P. 2013. Human brain evolution: transcripts, metabolites and their regulators. *Nat. Rev. Neurosci.* 14:112–27
- Sorensen A, Roebroeks W, van Gijn A. 2014. Fire production in the deep past? The expedient strike-a-light model. *J. Archaeol. Sci.* 42:476–86
- Soressi M, McPherron SP, Lenoir M, Dogandžić T, Goldberg P, et al. 2013. Neandertals made the first specialized bone tools in Europe. *Proc. Natl. Acad. Sci. USA* 110:14186–90
- Spikins P. 2009. Autism, the integrations of “difference” and the origins of modern human behaviour. *Camb. Archaeol. J.* 19:179–201
- Spiteri E, Konopka G, Coppola G, Bomar J, Oldham M, et al. 2007. Identification of the transcriptional targets of *FOXP2*, a gene linked to speech and language, in developing human brain. *Am. J. Hum. Genet.* 81:1144–57
- Steele J, Uomini N. 2009. Can the archaeology of manual specialization tell us anything about language evolution? A survey of the state of play. *Camb. Archaeol. J.* 19:97–110
- Stiner MC, Gopher A, Barkai R. 2011. Hearth-side socioeconomics, hunting and paleoecology during the late Lower Paleolithic at Qesem Cave, Israel. *J. Hum. Evol.* 60:213–33
- Stowe LA, Haverkort M, Zwartz S. 2005. Rethinking the neurological basis of language. *Lingua* 115:997–1042
- Stromswold K. 2001. The heritability of language: a review and metaanalysis of twin, adoption, and linkage studies. *Language* 77:647–723
- Stromswold K. 2010. Genetics and the evolution of language: what genetic studies reveal about the evolution of language. See Larson et al. 2010, pp. 176–90
- Tallerman M, Gibson KR. 2012. *The Oxford Handbook of Language Evolution*. Oxford, UK: Oxford Univ. Press
- Trinkaus E, Shipman P. 1993. *The Neandertals*. London: Pimlico
- Uomini NT. 2009. The prehistory of handedness: archaeological data and comparative ethology. *J. Hum. Evol.* 57:411–19
- Vernot B, Akey JM. 2014. Resurrecting surviving Neandertal lineages from modern human genomes. *Science* 343:1017–21
- Waddell PJ. 2013. Happy New Year *Homo erectus*? More evidence for interbreeding with archaics predating the modern human/Neanderthal split. arXiv:1312.7749 [q-bio.PE]
- Wales N. 2012. Modeling Neanderthal clothing using ethnographic analogues. *J. Hum. Evol.* 63:781–95
- Wall JD, Kim SK. 2007. Inconsistencies in Neanderthal genomic DNA sequences. *PLOS Genet.* 3:e175
- Weissengruber GE, Forstenpointner G, Peters G, Kübber-Heiss A, Fitch WT. 2002. Hyoid apparatus and pharynx in the lion (*Panthera leo*), jaguar (*Panthera onca*), tiger (*Panthera tigris*), cheetah (*Acinonyx jubatus*) and domestic cat (*Felis silvestris f. catus*). *J. Anat.* 201:195–209
- West-Eberhard MJ. 2003. *Developmental Plasticity and Evolution*. Oxford, UK: Oxford Univ. Press
- Wilkins J, Schoville BJ, Brown KS, Chazan M. 2012. Evidence for early hafted hunting technology. *Science* 338:942–46
- Zilhão J, Angelucci DE, Badal-García E, d’Errico F, Daniel F, et al. 2010. Symbolic use of marine shells and mineral pigments by Iberian Neandertals. *Proc. Natl. Acad. Sci. USA* 107:1023–28
- Zilhão J. 2007. The emergence of ornaments and art: an archaeological perspective on the origins of “behavioral modernity.” *J. Archaeol. Res.* 15:1–54
- Zilhão J. 2012. Personal ornaments and symbolism among the Neanderthals. *Dev. Quat. Sci.* 16:35–49
- Zuidema WH. 2005. *The major transitions in the evolution of language*. PhD thesis, Univ. Edinburgh. 177 pp.