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Pleistocene origins of cultural and linguistic diversification: how *Homo sapiens* and Neanderthals differed

Authors

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Abstract

It is now widely assumed that Neanderthals possessed a human language-like communication system. What is yet unclear is how different this was from ours. Here we ask whether the communication system of Neanderthals shared a key feature of human languages: ergodicity. Ergodicity allows linguistic evolution to continue for purposes of social differentiation without changing the species-wide language faculty and hampering languages' universal learnability. We first review the ergodic properties of human language and propose that they are co-indicated by social group differentiation, which are present since the Middle Stone Age. We then examine the archeological record and demography of Neanderthals, which suggest that they mostly lacked the relevant indicators and demographic conditions favoring ergodicity. Finally, we conclude that our findings are also consistent with recent genetic evidence for differences related to routinization and complexity in our species. Hence, the Neanderthal communication system may have differed in fundamental ways from ours, by accumulating changes that reduced learnability by other groups and increased differentiation into subspecies.

MAIN TEXT

Introduction

Human language is largely vertically transmitted, due to the conformity of language learning in children (1, 2). Language nonetheless changes rapidly and relentlessly, driven not just by copying errors and drift but by the human predisposition to improvise or be creative. Change is typically introduced through use and when it spreads sufficiently well, it is taken up by the next generation and becomes established. This tight combination of vertical and horizontal transmission processes makes linguistic evolution distinct from most other cases of cultural evolution (3). The modifications brought about in language sometimes create new meanings (e.g. metaphors like “web” for the internet) but often they have no consequences for their utility in communicating or structuring a thought (e.g. saying ‘aren’t’ vs ‘ain’t’ does not impact the content of a message). In either case, both choices reflect powerful and highly creative signals for both belonging and differentiating social groups and identities (4–6). Such signals reflect a fundamental bias of humans, which we call here *polyphilia*. Polyphilia encompasses not only language but many other aspects of human behavior, such as ornaments, living styles, eating habits and much else. Polyphilia also underlies the accelerated differentiation when groups split, a mechanism known as schismogenesis (7–12).

We argue that polyphilia, given its ubiquity among humans, is likely to be adaptive and that one key function is to produce group markings based on the ethnicity of the individuals: the indicators of social boundaries between in-group and out-group by a variety of means (13), such that even in contemporary societies there is evidence for greater marking along ethnic boundaries (14). The key contribution of polyphilia to ethnic marking is that it produces continuously updated identity markers. The marking is janus-faced, permitting both the recognition of in-group strangers and the identification of out-group strangers. In-group strangers make reliable cooperation partners because they are part of overlapping networks of personal contacts, and therefore any defection would eventually propagate back through “gossip” to the partner’s immediate network and negatively impact his or her reputation. As a result, in pre-state, small-scale societies, people were justified in trusting strangers that shared the same set of ethnic marks. Indeed, polyphilia seems to be unique to humans among primates: despite extensive research on primate vocalization, as reviewed by (15) instances of vocal divergence between geographically close groups are extremely rare, with one study tentatively reporting it in chimpanzees (16). Instances of tool use (17) and drumming (18) in chimpanzees and foraging behavior in vervet monkeys (19) are indicative of cultural accommodation, but not of diversification aimed at establishing group identity.

Numerous traits can serve as ethnic marks, from potentially ephemeral ones like clothing, ornamentation or hair styles to more permanent ones, like scarring, tattoos, tooth filing, gestures, or indeed dialects. Ethnic marks signal the belonging to a specific group, and should not be confused with status marks, which signal social status within a particular group. Ethnic marks have high prevalence or are even universal in each social group, whereas status marks are differentiated within a group or even limited to specific individuals.

Ethnic marking is thought to be especially triggered in situations where people are in contact with both in-group strangers and out-group strangers (8, 20), creating selectivity in inter- and intra-group connectivity and giving rise to cultural identification products (4, 6, 21–23). In-group strangers emerge as a fundamental category of individuals with whom cooperation is favored in a geography of distinct but interconnected groups. Such demographic conditions are marked by expanding demes, which lead to reduced levels of contact between relatively closely related individuals that are nonetheless connected reputationally. In non-expanding small-scale societies, they are less needed, because in-group strangers are rare, and strangers are automatically out-group.

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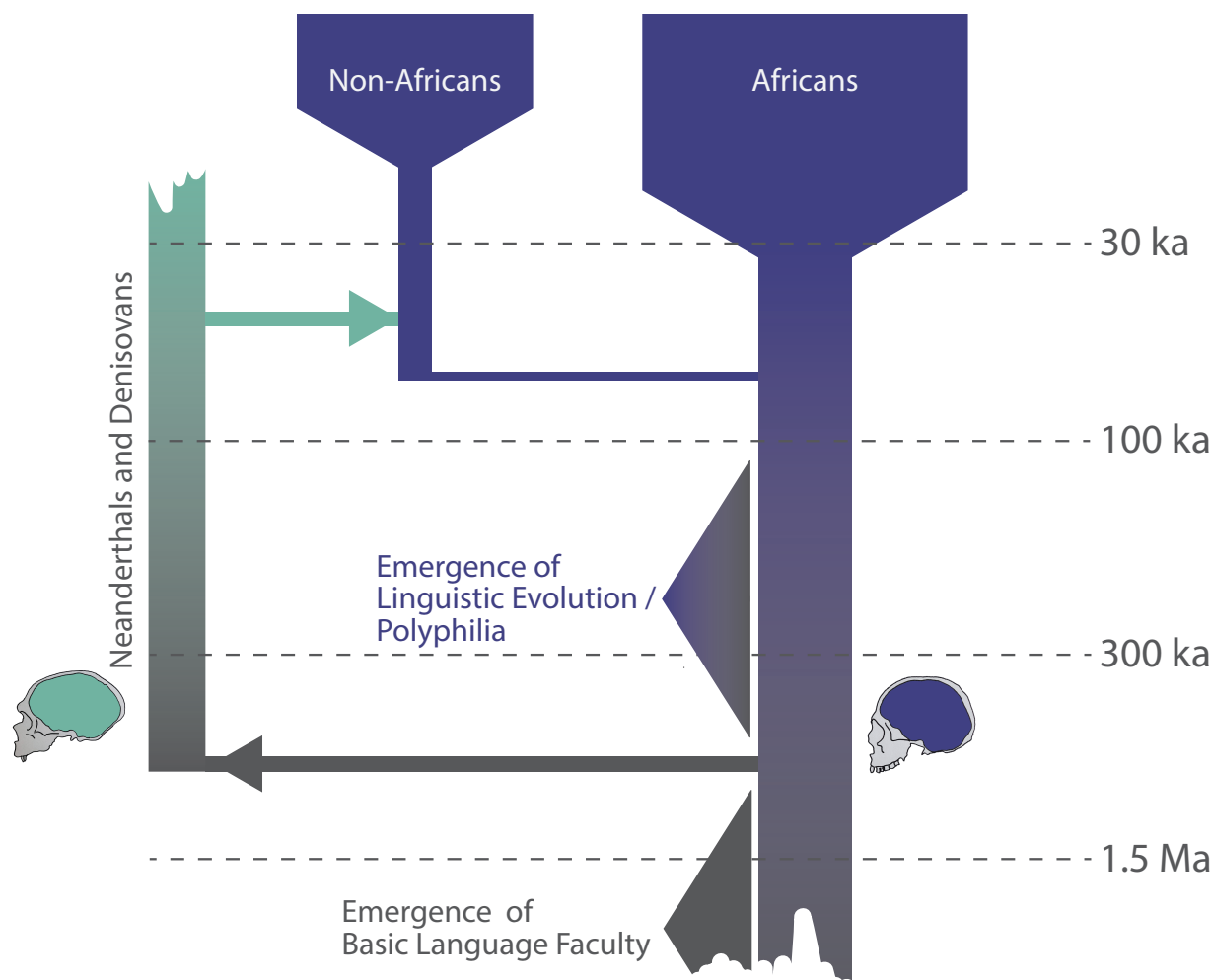
Language is a prime carrier of polyphilia. Each linguistic variety – entire languages or dialects – is sealed off from most strangers because it is difficult to acquire a second language, or even variety, accent-free after the critical period of language acquisition in childhood. This is a critical difference between language and other instances of polyphilia (such as personal ornaments). At the same time, every generation of speakers can and does launch many changes in language, and this typically keeps pace with the dynamic of the speaker’s various social alliances and identities.

This use of language for ethnic marking has a far-reaching consequence for how languages evolve (3). On the one hand, the evolutionary process must never go to fixation, where language change is no longer available as a source for ethnic marking. On the other hand, the evolutionary process cannot regularly introduce entirely novel states of the language faculty because that would either require genetic co-evolution at a pace that is unattested in long-lived animals (including humans) or it would make language acquisition exceedingly difficult for the next generation after a novel state is introduced. The scylla of fixation and the charybdis of novelty are avoided by a specific design feature in the evolution of many cultural processes, of which language is a prime example. It operates through an ergodic Markov process, i.e. a memoryless process of change between states, where the same states can be revisited in a stationary dynamic over long periods of time (24). Re-visits of this kind are sometimes observable in historical time, known as “cycles” in linguistics (25). For example, Jespersen’s cycle describes historical transitions in the form of negation, where short and long forms cyclically replace each other (English started with *ne/na* expanded to *na-wiht*, shortened to *not* and expands again to *n’t ... nothing*). Another example is the initial consonant of ‘thin’, which started out as a voiceless stop in Proto-Indo-European (*ten-*), then became a fricative *th* in Germanic (as is still the case in English *thin*), then a voiced stop in High German (*dünn*) and is now back as a voiceless stop in Swiss German (*tünn*). Because of ergodicity language change can easily lead to structures that are disfavored and difficult to process and to acquire. Examples include conjugation or gender classes (e.g. arbitrary distinctions such as the one that forces the article *il* for *problema* but *la* for *machina* in Italian) or object-initial word orders that go against universal expectations of subject-first by the processing system (26).

Other carriers of polyphilia also have ergodic properties. Styles in fashion, design or architecture recycle themes in ergodic ways (27, 28). They change radically when the state space is suddenly expanded by technical innovations (e.g. new building materials or new fabrics: (29, 30)). In striking contrast, such radical change is largely absent in language because its state space is defined by a brain and vocal apparatus that have been mostly stable in *Homo sapiens* (31). Potential exceptions are reported for genetic changes underlying pitch processing, affecting the use of tone for meaning differentiation (32, 33) and for developmental changes in tooth configurations, affecting the probability of labiodental sounds (“f”) in language (34, 35), but these features are probabilistic, and speakers still may or may not change into or away from tones and labiodentals in response to ergodicity. As a result, the faculty of language has remained largely unchanged. Without ergodicity it would be very difficult to explain the constancy of the language faculty: on one hand it causes changes, on the other, because of the demographic patterns that allow these changes to spread, it prevents genetically-based directional changes which would make learnability by genetically-different speakers impossible. To wit, a human child born anywhere in the world, if moved anywhere else, can learn (pathologies aside) the particular local language like a native speaker (even in the presence of genetic differences in pitch processing (36)). It is therefore widely assumed that the faculty of language has changed little since the period with directional changes that characterized the evolution of the language faculty ended, coinciding with the origin of *H. sapiens* (37, 38). A key prediction is that ethnic marking must have evolved concurrently with the demographic expansion and increased population density that favored between-group contacts and therefore the need to identify in-group strangers.

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It is widely assumed that Neanderthals (and potentially Denisovans) possessed an oral communication system that was speech-compatible (39–41). The aim of this paper is to explore the question of whether that communication system was also ergodic, serving polyphilia (Fig. 1). To do so, we first need to estimate when ergodicity evolved in the lineage of hominins that led to *Homo sapiens*. We will therefore look for the first archeological evidence of ethnic marking and demographic expansion in the archeological record of early modern humans (EMH). We examine: (i) the “function-free” and resource-independent modification of styles in tools, (ii) those cultural artifacts whose function is not technological but rather identity-informing, such as personal ornaments, and (iii) the demographic patterns conducive to the emergence of polyphilia, in African EMH (Fig. 2). Having established the validity of this approach, we ask whether both these archeological signals and demographic conditions are present in Neanderthals. We then discuss the implications for Neanderthal communication.



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Fig. 1. Emergence of language faculty and linguistic evolution. Simplified representation of when, in relation to the evolution of Neanderthals and *H. sapiens*, we consider the emergence of the basic language faculty (common to both species) and then the emergence of linguistic evolution, unique to our species. The population dynamics represented in the figure are modified from (123).

Contrasts in material culture

Archeological data can yield evidence for variation in styles of artifact production that do not reflect properties of raw materials. These styles are therefore widely considered markers of individual and group identity (13, 42, 43). Kuhn and Stiner (44) suggest that the late Middle

Paleolithic in Europe and the Middle Stone Age in Africa is likely the first time that interactions with “strangers” occurred on a regular basis, thus becoming a social element to manage via cultural (and linguistic) patterns of identification and differentiation that could reflect the beginnings of polyphilia. It was likely a long process, that begun in the Middle Pleistocene (ca. 400,000 years ago) (45, 46) and increased over time, culminating in the Upper Paleolithic (UP) with *H. sapiens* (47, 48).

The evidence for these claims is compelling. The archeological record of the Middle Stone Age yields evidence of local cultural taxonomic units, such as in Sibudu (~58kya, South Africa) (49), which suggest short-term behavioral variability that is independent of environmental factors but rather the consequence of social dynamics. Likewise, the European Aurignacian (43,000 – 26,000) is stylistically different from the coeval Levantine Aurignacian, both produced by *H. sapiens*, where notches constitute intentional markings (50): “Such items possibly reflect the strong ties between various Levantine Aurignacian communities by serving as a marker of “us” and “others” [...] differentiating them from the surrounding population of “strangers” [...], who did not share the social and cultural worldviews expressed through this particular cultural item” (51). In these same Levantine sites we also find tooth pendants (52).

These style variations are consistent with ethnic marking in *H. sapiens*, but come in rather late (and may reflect the poor record of EMH material culture). Nonetheless, the contrast with Neanderthals is pronounced (Fig. 2). Among them, cultural ratcheting based on the assimilation of innovations between groups, does not seem to shape technological production (53, 54). Most of the stylistic variation in tool production is plausibly attributed to geography, raw material availability and tool function (55). Overall, Neanderthal material culture production not related to utilitarian functions is extremely limited and therefore has little potential to shed light on group- or region-specific styles that could be indicative of ethnic-marking functions (Fig. 2).

While cases such as Sibudu in Africa and comparisons between the Aurignacians in Eurasia indicate styles of technological production that have some degrees of independence from functional constraints, it is mostly in ornaments that we find evidence of ethnic differentiation in EMH. Early evidence for the use of marine shells as ornaments is found in burial contexts at Qafzeh Cave in Israel, dating back to approximately 100,000 years ago (56). Similarly aged perforated marine shells have been discovered at Skhūl Cave in Israel (57) and Grotte des Pigeons in Morocco (58). Slightly more recent examples of such ornaments are found in Still Bay deposits at Blombos Cave, dating to about 75,000 years ago (59), and in Middle Stone Age contexts at Sibudu (60). Early ornaments include ostrich eggshell beads from early Later Stone Age (LSA) (50,000 to 33,000 years ago) which reveal a 3,000 km network of social connections originating in eastern Africa and spreading to southern Africa (61). It is reasonable to assume that these East African ornaments were created by EMH.

A similarly rich record associated with EMH is also found in Eurasia. Excavations at Ksar Akil in Lebanon (62) and Üçağızlı in the Hatay Province of Turkey (63, 64) have uncovered rich collections of perforated marine shells from the Initial UP period, dating to around 40,000 years ago. Similar findings have been discovered in other early UP sites around the Mediterranean, such as Riparo Mochi on Italy's Ligurian Coast (65, 66). In Europe, there is substantial evidence of a rapid increase in ornament use with the advent of the UP. Numerous early Aurignacian ornaments have been found in various regions, including the Swabian sites like Vogelherd, Geißenklösterle, and Hohle Fels (67, 68). These artifacts, in addition to incised and perforated natural objects such as teeth, include diverse ornaments made from mammoth ivory. Personal ornaments marking social identity and tracking cultural developments dating to the UP are found as far north as Siberia (69). Since approximately 40,000 years ago, ornaments are widely documented throughout most of

Eurasia and Africa. This evidence supports the hypothesis that modern cultural behaviors spread quickly between about 50,000 and 30,000 years ago in EMH (70). While ornaments are not entirely absent in Neanderthals, their presence is most likely to reveal status. There is the presence of some ornamental pendants made from raptor claws in Krapina (Croatia), which happens to also be one of the largest Neanderthal assemblages (71). Potentially, this points to within-group differentiation related to status, rather than between-group contact. Only the latter would instead determine a need for “in-group stranger recognition”. Personal ornamentation in the form of perforated marine bivalves is also present in the Iberian peninsula (72) but very limited in number. The purposeful removal of large feathers from birds that were unlikely food items has been reported (73). However, as for the raptor claws of Krapina, their limited number and geographic spread point toward status designation rather than ethnic marking. Indeed, status marking of single individuals is expected within groups, but not of entire social strata or classes, as extant nomadic hunter-gatherer societies present minimal evidence of social stratification (74). It is only when the number of individuals increases significantly within a group that one can even expect systemized differentiation that is reflective of within-group structure (as opposed to non-systemized interindividual variability), leading to what is known as sociolects in linguistics, i.e. dialects defined by social class rather than location. So, status marking leads to linguistic divergence only in response to larger group size and stratification.

Variation in ornamentation is relevant for the probability of linguistic polyphilia if it concerns social ornamentation, which is a form of ethnic marking. It is, again, within the European Aurignacian record that we find evidence of region-specific ornament production. Vanhaeren and d’Errico (75) “recorded the occurrence of 157 bead types at 98 European Aurignacian sites” and found that the observed “pattern [...] is not explained by chronological differences between sites or by differences in raw material availability, [and thus] reflects the ethnolinguistic diversity of the earliest Upper Palaeolithic populations of Europe”. Recent research integrating genetic and archeological data found that diversification in personal ornamentation does not simply follow genetic diversity and that at least nine coeval cultural groups existed in Europe between 36,000 and 24,000 years ago (76). The contrast with Neanderthals is striking: Wynn and colleagues (77) noted that “when ornament use by Aurignacian people [...] 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”. While this points to a nonlinear split in polyphilia, it does not quite yet indicate the need for ethnic identity marks. More arguments are required to extrapolate to ethnic marking and the use of language for this purpose.

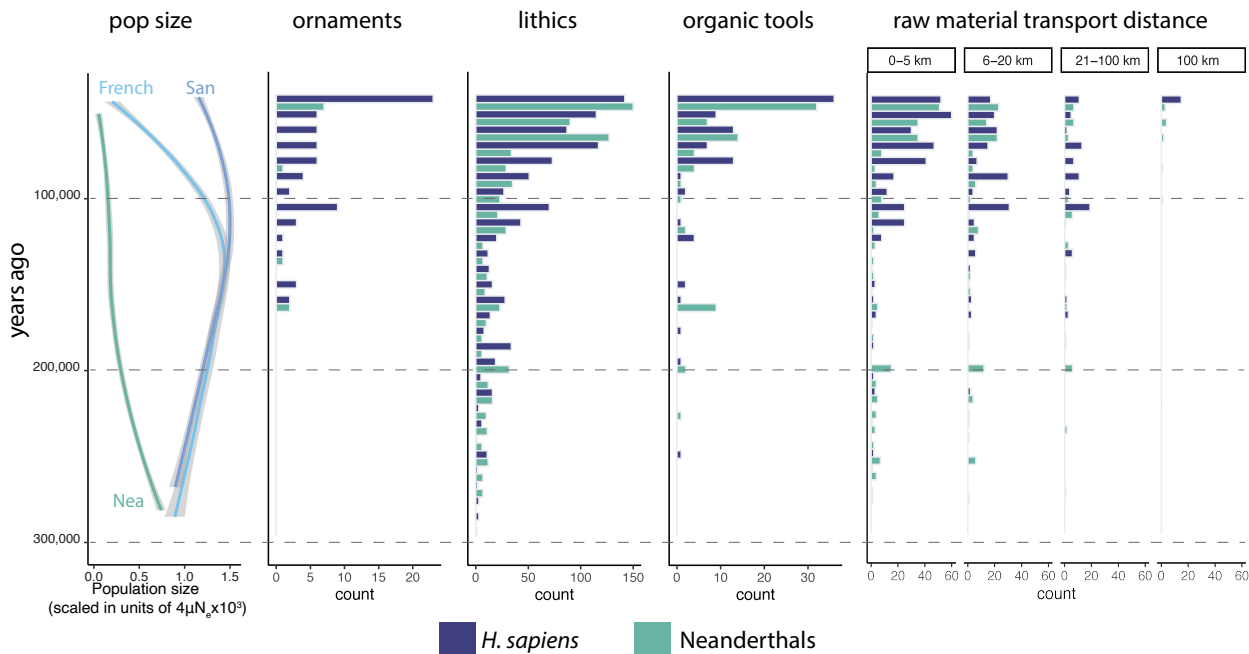
In sum, tool styles and social ornamentation emerge in Middle Stone Age EMH and continue to be found in Upper Paleolithic EMH, whereas they are almost certainly lacking in Neanderthals and Early Stone Age pre-*sapiens* African hominins (cf. (78) (Fig. 2).

Contrasts in demography

Developing ethnic identity not only requires evidence of enhanced polyphilia in EMH but also depends on demographic expansion and subsequent differentiation. During the lower Paleolithic, within an ecological context of low carrying capacity (as determined by limited technological abilities of resource exploitation), large hominin aggregations were presumably impossible, giving rise to small residential groups embedded in a larger, but sporadic, social network (79). This changed after ca 500 ka (which coincides with the genetic evidence for the origin of our lineage (80)), when residential group sizes among EHM increased, with a concurrent decrease in territory indicating a density increase (81, 82). This is the demographic situation postulated to give rise to the need to employ markers of ethnicity. However, given the evidence of

264 temporary demographic contractions (83), this situation may not apply to the full Paleolithic record
265 (84).

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267 In contrast, the high degree of inbreeding (85) points towards the combination of small size
268 of bands (86) and infrequent between-group contact and exchange (87). Further recent genetic
269 evidence indicates early (~105ka) divergence between different Neanderthal groups, with, for
270 example, one French group living for about 50ka in genetic isolation from the neighboring groups
271 (88). This picture is compatible with the inference of very low populations densities (89) in
272 Southwestern France of Châtelperronian Neanderthals compared to the partly coeval Aurignacian
273 EHM.



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275 **Fig. 2. Temporal trends in demography and artifact production in *H. sapiens* and Neanderthals.** For the temporal
276 range of 300,000 to 40,000 years ago, and for each of the two species (Neanderthals and *H. sapiens*): effective
277 population size (within *H. sapiens*, differentiated between what are currently French and San populations, as examples);
278 number of ornaments; number of lithic tools; number or organic tools; raw material transport distance, subdivided into
279 four distance categories. Population data is from (90); artifact data is from (91). Only archeological remains present in
280 the ROCEEH Out of Africa Database (ROAD) (<https://www.roceeh.uni-tuebingen.de/>) are used for the figure. To date,
281 this is the largest and most comprehensive database of archeological sites and associated assemblages. Data was
282 retrieved on February 2nd 2025.

283 284 **Contrasts in brain organization: genetic and morphological evidence**

285 Our review of the archeological and demographic data is consistent with the recent
286 discovery of incipient speciation between Neanderthals and EMH (92); with the attested evidence
287 that behavioral/communicative traits can reinforce speciation barriers (93, 94); and with genetic
288 evidence suggesting that the neurobiological differences between the two taxa (Fig. 3) might
289 underpin different oral communication faculties (95–97), as they implicate brain regions critical for
290 language.

291 Recent functional genetic research has uncovered a uniquely human variant of a splicing
292 factor (NOVA1) that is critically implicated in vocal dexterity (98). This same research suggests
293 that this variant not only is unique to humans but has also been subject to selective sweeps in our
294 lineage. Also relevant in this context is the finding that genomic loci significantly associated with
295 endocranial globularity (a key difference between us and Neanderthals) overlap with multivariate
296 genetic analyses of reading/language skills, but not with general cognition (97).

Furthermore, recent work has highlighted that some genomic regions that in humans became quickly purged of Neanderthal and Denisovan alleles (so-called “deserts of introgression”) (99), indicative of marked species divergence, significantly enrich for genes (including *FOXP2*) highly expressed in the developing cortex (100), cerebellum (95) and adult striatum (100), a set of regions necessary to ensure language fluidity and verbal executive control (101). Complementary research points to the cerebellum and basal ganglia as the two brain regions where the expression of introgressed alleles is significantly more different than expected (102), and associated with divergent brain shape (103).

Since these regions (cerebellum and striatum) are critical centers in action coordination and motor control, they are also critically involved in speech, word fluency and sentence production (104), and their structural integrity is critical to prevent language-related disorders (105). A recent metaanalysis of the neuroanatomy of developmental language disorder (DLD) (106) has identified extremely consistent anomalies only in the basal ganglia, more specifically in the anterior neostriatum. This structure was anatomically significantly different in 100% of DLD cases, with roughly half of the anomalies in the left and half in the right hemisphere. The same metaanalysis found that the other structures yielding high proportions of anomalies (above 60%) are: Broca’s region (67%), superior temporal cortex (73.9%), superior parietal cortex (68.8%) and anterior lobe of the cerebellum (74.8%). In general and not limited to language, the associative striatum is activated in initial learning, while the sensorimotor striatum is particularly active after automaticity has developed and a habit has formed (107, 108). Furthermore, in potential support of the thesis of this paper, basal ganglia have been shown to be critically involved in bilingual language control (109, 110), hence a type of language processing that requires flexibility and rapid adaptation to changing forms of language production and comprehension, maybe similar to those that are a prerequisite for polyphilia-driven change in language: a production where you deviate from the norm. While these subcortical brain regions are likely involved in enhanced automation in both speech reception and production, they are unlikely to be involved in the drive for polyphilia and creativity, more likely associated with frontal regions expansion. Whether enhanced urge for creativity precedes or follows the neural substrates to implement it remains an issue at this point. In sum, cortical regions, specifically the PFC and medial PFC are expected to be involved in allowing for increased creativity and therefore the emergence of polyphilia – and a significant difference in this region is exactly what we see when comparing Neanderthal and *H. sapiens* endocasts (103, 111); while differences in subcortical nuclei, which are also reported for these two species, may account for smoother routinization and/or automatization of the linguistic changes that emerge (Fig. 3). Finally, although subcortical structures leave no trace of their precise anatomy in the endocasts, the different brain ontogenies between the two lineages (112), reflected in distinct skull shapes, possibly partly reflect the evolution of these brain regions (103, 112), and contribute to lineage differences.

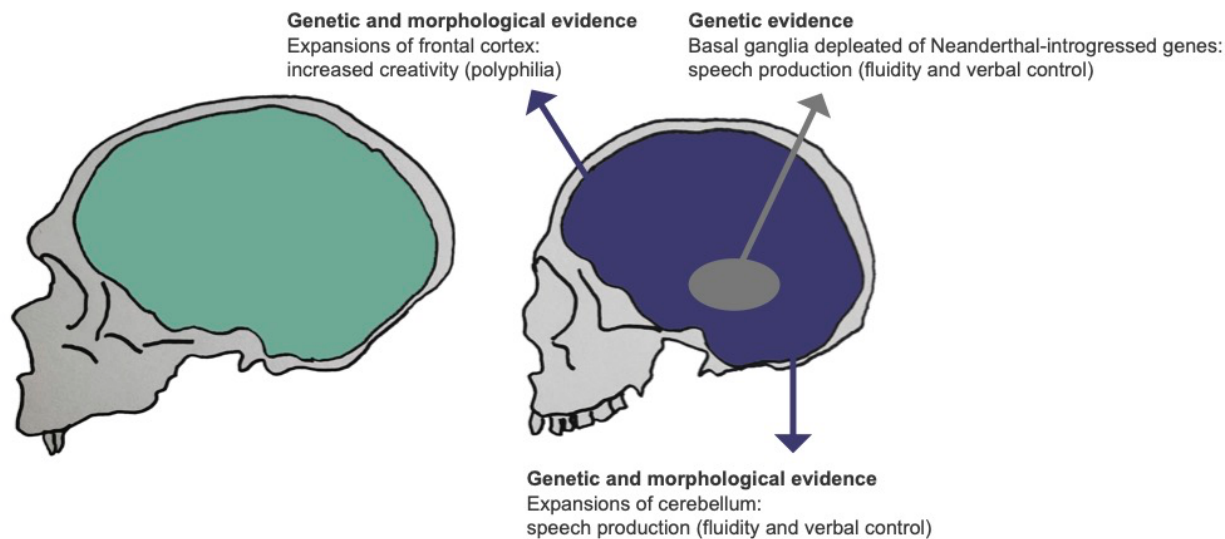


Fig. 3. Schematic representation of relevant brain differences in Neanderthals (left) and *H. sapiens* (right). Both osteological and genetic evidence point towards an expansion of the frontal cortex and cerebellum in our species. Additionally, genetic evidence indicates that regions depleted of archaic lineages are significantly enriched for genes expressed in specific brain regions, particularly in the developing cortex and adult striatum, with these regions being critical for fluid speech production.

Discussion and conclusions

There is a growing consensus that an oral communication system already resembling what became human language presumably evolved in Africa before the split that gave rise to the lineages producing EMH, Neanderthals and Denisovans (40, 113). The evidence reviewed here allows us to propose that the conditions favoring polyphilia in human language arose during the Middle Stone Age in Africa, that is after this split (Fig. 1). Indeed, many components forming the basis of modern human language likely evolved well before the emergence of our lineage (39), in the mosaic-like fashion in which complex biological adaptations relying on multiple components have been shown to evolve (114). But some properties of human language may be of more recent vintage, forcing us to consider scenarios that go beyond old dichotomies (language is very old vs language is very recent) (115). This therefore suggests that none of these three taxa initially exhibited ergodicity in their communication system. It also follows that the oral communication system of these taxa evolved directionally and independently over time and that, based on the archeological evidence reviewed above, the one of our ancestors became crystallized during the MSA (Africa) or UP (Eurasia).

Our survey of Neanderthals (and we suspect Denisovans, although the material record we have for them is currently considerably poorer) yielded virtually no evidence that their culture ever was polyphilic, making ergodic processes in their communication unlikely. First, the archeological evidence in terms of both styles of utilitarian artifacts (tools) and ornamentation does not show signs of regional differentiation that is independent of local resource availability. And second, their demography was not likely to induce either habitual between-group encounters or within-group schismogenic events. EMH, in contrast, show evidence for both, in the African MSA as well later in the Eurasian UP, suggesting that polyphilia evolved in EMH between ca 500,000 and ca 300,000 ka and that the pressure favoring it increased afterwards. Since the consensus view among paleoanthropologists is that demography was the major difference between us and our extinct cousins (116), this strongly supports our claim that the proximate conditions favoring polyphilia do not reach as far back as other ingredients of the language faculty. Future work relying on novel methods to date the emergence of (clusters of) mutations with relevant phenotypic associations (117–119) may help us sharpen this timeline, identifying mutations in our lineage that may have contributed population-wide biases that found a favorable environmental context and eventually

allowed for the group expansion and contacts that favored polyphilia. Although much work is still needed to validate the nature of these mutations, current candidates (115, 120, 121) point to domains of modification related to reduced reactive aggression and hence increased cooperative proclivities, but also a stronger tendency for exploration and creativity, driven by endogenously generated rewards. This is in line with the proposal of a more recent, ‘curiosity’-related driver of cumulative culture (122).

An important implication of these findings is that while the language faculty of *sapiens* converged on a stationary state space, the Neanderthals’ communication faculty, lacking the demographic density and frequency of contact between groups likely failed to determine the emergence of polyphilia and therefore ergodicity. Hence, Neanderthal’s communication system would have continued to change from the pre-split state, becoming increasingly different from that of EMH and therefore *sapiens*. Thus, small group sizes and large geographic distances between bands among Neanderthals (124) consistently paint a picture incompatible with either schismogenic phenomena or frequent between-group encounters. One possible consequence was that Neanderthals, who’s language faculty had evolved in an own direction, were not able to learn sufficiently well any of the languages spoken by contemporary *H. sapiens*, or far-away Neanderthal groups. Given the already massive demographic difference between the two hominin taxa when they encountered each other (125–127), the Neanderthals’ likely inability to fully speak like *sapiens* may have contributed to them being considered out-group strangers, no matter how long they stayed within a *sapiens* group. This continued “othering” may have prevented full assimilation within the colonizing groups of *H. sapiens*, and contributed to selection against hybrids, and ultimately to the Neanderthals’ demise.

The emergence of ergodicity in *H. sapiens* implies that the communicative and cognitive function of language could now for the first time change in response to ethnic marking, signaling group identity in a rich-enough demographic scenario characterized by frequent between-group encounters. It is important to stress that none of these differences are to be interpreted in terms of intrinsic cognitive superiority of EMH over Neanderthals. The key contrast we focused on here (ergodicity, and attendant polyphilia) are largely underpinned by demographic factors and social transmission opportunities that occurred in one lineage, but not in another.

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