No Country for Oldowan Men: Emerging Factors in Language Evolution

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Abstract

Language evolution has long been researched. I will review a number of broad, emerging research directions which arguably have the potential to contribute to our understanding of language evolution. Emerging topics in genomics and neurolinguistics are explored, and human-specific levels of braincase globularity – and the broader process of self-domestication within which globularity seems capable of being encapsulated – will be argued to be the central pillars of any satisfactory and interdisciplinary model of language evolution.

Keywords: Domestication syndrome, molecular clock, genetic drift, globularity, language evolution, basicranial angle, birdsong

Introduction

In recent years, a number of models have been proposed to explain the implementational basis of hierarchical phrase structures (reviewed in Aboitiz, 2017; Friederici, 2017). A range of paleoanthropological, paleoneurological and genetic data has also been consulted in an effort to map out an accurate path that language evolution likely took (Beaudet, 2017; Benítez-Burraco & Boeckx, 2015; Murphy & Benítez-Burraco, 2018a, 2018b; Zollikofer & Ponce de León, 2013). My intention here is to review some possible connections between these distinct modes of inquiry by exploring a specific set of phenotypic traits and evolutionary processes which have the potential to explain the emergence of core features of language such as syntactic complexity and unrestricted semantic combinatorics.

This review will begin by focusing on genetics ('Gene Regulation', 'Genetic Drift', 'Comparative Genomics', 'Molecular Clock', 'DNA Sequencing') and then progress to broader evolutionary themes ('Globularity', 'Tool Use') and emerging directions ('Domestication', 'The Cerebellum and Speech').

Gene Regulation

Beginning with the genetic foundation of a possible model of language evolution, we can consider what the likely *mutational profile* of its initial stages were. It has been proposed that there exist 1,241 primate-specific genes (Zhang et al., 2011), 280 of which are human-specific. 54% of these human-specific genes are upregulated in a brain area implicated in higher cognition, the prefrontal cortex. These new genes are significantly more likely to be involved in gene regulation (Diller & Cann, 2013, p. 256), although, as we will see below, exploring the genetic basis of other brain regions will also be required to account for language evolution. The mutation of some regulatory gene may have reorganised the neuronal populations in the neocortex and its concomitant computational properties (although the precise nature of these neurolinguistic properties is beyond the scope of this general review; see Friederici, 2017). Given the level of regulatory complexity identified by Chakravarti (2011) – 'compromising the activity of one gene need not cripple an entire network'; 'variation in the regulatory machinery of genes is much more frequent than that in the structure of gene products' – it is more likely

that the neurocomputational properties required for language emerged after the mutation of multiple regulatory genes acting in concert, and not a singular mutational event as often claimed in the generative and biolinguistics literature (e.g. Chomsky, 2010): 'Genes and their products almost never act alone, but in networks with other genes and proteins and in [the] context of the environment' (Chakravarti, 2011, p. 15).

Is there any indication that this general picture is reasonable? Consider how the transition from the many digits of lobe-finned tetrapods to only 5 was not the result of new genes, but rather of distinct regulations of existing genes, namely regulation of *Hoxa11* (Kherdjemil et al., 2016). A similar account may be applied to core features of language, in particular given that there exists no strong correlation between the total number of genes in a given species and the level of biological complexity it achieves (for instance, mice and humans have comparable numbers). Of relevance here is the finding that human evolution has slowed down, often called the 'hominoid slowdown': '[R]ates of occurrence of de novo mutations decreased as enhanced DNA repair mechanisms and larger generation times evolved' (Goodman, 1985, p. 10). Hominoids appear to have reached a certain mesa of complexity, with only slight tuning yielding novel benefits.

In summary, a slight regulatory change could have produced an alteration in the human computational system yielding the capacity for constructing hierarchical phrase structures.

A separate question now concerns when this took place. Putting aside precise dates, and assuming that anatomically modern humans emerged around 300-150kya (kya: thousand years ago), it appears that the vast majority of complex forms of symbolic representation did not emerge until 100-60kya (Hurford, 2011). We will present a more detailed timeline below after considering a broader range of topics, but for now we can note that this time also correlates with the emergence of new migration patterns (Mellars, 2006), leading to the possibility that properties of the environment acted as release factors for language. Encountering new forms of social organisation and environments may have served to prompt the basic combinatorics of mammalian cognition and encourage novel forms of conceptual combination. Bolender (2007) has suggested along these lines that an increased human population, leading to a greater complexity of inter-group communication, acted as a trigger for the use of syntactic word movement, hitherto dormant. If this is correct, then investigating syntactic phenomena from a purely computational perspective, not considering the influence of the development and emergence of the phenotype, would be missing a crucial part of any psychological or cognitive account.

Genetic Drift

We can now turn to a related topic, which has become just as controversial in the language evolution literature. One of the most general distinctions in this literature is between theories that assume language emerged suddenly, and theories that assume it emerged gradually. What does the archaeological record have to say about this? Unfortunately, since the African middle Pleistocene hominin record is sparse, it is currently not possible to determine whether fossils like Omo Kibish 1 mark the earliest forms of the constellation of human features or whether older types exist. Another major question concerns whether human features emerged through natural selection or through random *genetic drift*. This occurs when the proportion of a gene variant in a population changes due to external events ('chance'). Coyne (2009, p. 14) notes that 'genetic drift may play some evolutionary role in small populations and probably accounts for some nonadaptive features of DNA'. Examining cranial measurements, Weaver et al. (2008) show that the differences between Neanderthals and anatomically modern humans could have emerged under drift over a period of around 400,000 years. Moreover, Weaver and

101 Stringer (2015) show that these cranial differences emerged in a highly unconstrained way
102 thanks to cultural buffering, relative to morphological divergences documented between crania
103 of subspecies of *Pan troglodytes*.
104   While it is well known that only ~4% of the human genome differs at the nucleotide level
105 from the chimpanzee genome (Varki & Altheide, 2005), the way that these genes are expressed
106 is far from uniform. For instance, there is up to an 8% difference in splicing rates in the cortex
107 between humans and chimpanzees (Calarco et al., 2007), with NDE1 (a gene involved in
108 cortical neurogenesis) recently being shown to exhibit human-specific splicing patterns.
109 Splicing consequently seems to be a major mechanism of brain evolution and cognitive
110 development (Mosca et al., 2017).
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Comparative Genomics

115 Comparative genomics yields other fruitful insights into the likely origins of language. Gronau
116 et al. (2011) analysed the whole-genome variation diversity patterns of six people from
117 contemporary sub-populations: European, Yoruban, Han Chinese, Korean, Bantu, and San
118 African. The final group (speakers of Khoisan) were discovered to have likely split from the
119 rest of the human population around 157-108kya, and since they possess the ability to acquire
120 language this indicates a likely timeline. Behar et al. (2008) report that mitochondrial DNA
121 (mtDNA, transmitted through maternal inheritance) in the Khoisan peoples diverged from
122 mtDNA in the human gene pool as early as 160kya years ago, remaining separate until around
123 40kya. The genetic isolation of the San people matches with the isolation of a core part of their
124 language use. All Khoisan groups use clicks; Moisik and Dediu (2017) use a biomechanical
125 model to show that a reduced alveolar ridge aids the production of clicks, and that this has been
126 selected for amongst Khoisan groups. Clicks are complex obstruents externalised via a double
127 closure in the oral cavity. Huybregts (2017) notes the intriguing possibility which follows from
128 these findings. The common human population shared by the San and the rest of contemporary
129 human societies must have had language but may not have solved the problem of
130 externalisation, i.e. they may have exhibited the ability to recursively construct hierarchical
131 representations, but not the ability to map this capacity to the sensorimotor system for
132 externalisation via speech, gesture, and so forth. The San population and the non-San
133 populations therefore solved the problem in different ways, indicating a clear timeline: the
134 computational system of language evolved before it was linked to externalisation.
135   Nielsen et al. (2017) also discuss how 'genetic markers with uniparental inheritance and
136 linguistic studies suggest that click-language-speaking hunter-gatherer populations may
137 originally have been more widespread and were replaced in areas other than southern Africa
138 or, alternatively, that they may have originated in eastern Africa and then migrated to southern
139 Africa in the past 50 kyr'. Furthermore, 'other hunter-gatherer populations that speak languages
140 that use clicks, including the Hadza people and the Sandawe people, currently reside in
141 Tanzania in eastern Africa, although they display limited genomic affinity with the San people
142 of southern African'.
143   Lastly, despite the question of modern human origins in Africa remaining unsettled, a
144 multiregional origin in which modern (domesticated) features evolved in a fragmented way in
145 multiple areas connected by gene flow is a strong possibility. There is evidence, for instance,
146 for the admixture of modern humans with archaic populations in Africa (Hammer et al., 2011).
147 Statistical analyses of whole-genome sequencing data from geographically diverse hunter-
148 gatherer populations also presents evidence of archaic human lineages that underwent
149 introgression (i.e. exchanging genetic material via interbreeding) and diverged from modern
150 human lineages anywhere between 1.3mya and 35kya, and so the extent of archaic admixture

151   remains a point of controversy: 'Perhaps of greatest interest is genomic data from under-
152   sampled regions of the world, which may help to refine evolutionary theories, including the
153   question of whether there are further, as-yet uncharacterized, lineages of archaic humans'
154   (Nielsen et al., 2017, p. 308).
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157   **Molecular Clock**
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159   Another topic which I would like to argue is relevant for language evolution research is the
160   *molecular clock*, in particular given that many core hypotheses about the origin of recursive
161   hierarchical phrase structure concern sudden and chance mutations. In recent research, the
162   speed of the molecular clock has been calculated in terms of the number of mutational
163   differences in matching segments of DNA between humans and primates based on the fossil
164   record. Because it has typically been assumed that the speed was high, the 'Out of Africa'
165   migration was thought to have occurred around 70kya (e.g. Gibbons, 2012). More recently,
166   however, a new method of obtaining mutation rates has emerged which calculates the rate of
167   the full genome of present-day humans through counting the number of new mutations in the
168   nuclear DNA of a newborn compared to its parents. Scally and Durbin (2012) cite the value at
169   0.5×10^{-9} bp^{-1}year^{-1}, which is around half of the previous fossil-calibrated rate (Ike-uchi, 2016).
170   As such, the molecular clock is much slower than previously believed. Adjusting for
171   these new calculations, the migration from Africa is likely to have occurred around 130kya
172   (Ike-uchi, 2016) (as the fossil record also suggests).
173   A possible scenario for language evolution in line with these findings is that the
174   mutation(s) required for language occurred in an individual between 200-130kya in East
175   Africa. This then spread through the community, and around 130kya years ago a group
176   (composed of around ~450 individuals, according to estimates in Fagundes et al., 2007)
177   migrated north across Arabia, passing the Bab al-Mandab Straits and progressing to Oman and
178   the surrounding regions, eventually arriving in southern China and Indo-China. A separate
179   group, much later (100-50kya) also left North Africa through a different route (the Nile Valley)
180   and reached Eurasia. Of course, the hypothesis that a small number of mutations in a relatively
181   short time window led to language is naturally compatible with whatever theory one adopts
182   concerning the speed (fast or slow) of the molecular clock. But the notion of a slow clock
183   nevertheless makes the standard generative picture of a *sudden, slight mutation* somewhat less
184   appealing, and rather points to the validity of a series of mutations. None of these discrete
185   changes would have likely been sufficient to bring about the morphological and neurological
186   characteristics of the anatomically modern human brain, but when spread throughout a
187   community for extended periods they may have conspired to do so.
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190   **DNA Sequencing**
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192   Having covered some broad topics in genomics, what can be said about the emerging theme of
193   technological advances with potential to inform models of language evolution? Developments
194   in DNA sequencing recently resulted in sequence data covering much of the Neanderthal
195   genome (Green et al., 2010). Shortly thereafter, a list of 87 genes with protein-coding
196   differences between humans and Neanderthals was released (Prüfer et al., 2014). This allows
197   hypotheses to be drawn up concerning the existence of certain language-relevant cognitive
198   components in Neanderthals. The most famous (and notorious) candidate for a 'language gene'
199   is *FOXP2*. This codes for a transcription factor (a protein able to bind DNA and modify the
200   expression of other genes) connected to a large network of genes that can be up- or down-

201 regulated (Vernes et al., 2007). In modern humans the gene exists in a species-specific allele,
202 coding a protein differing from that of chimpanzees (Enard et al., 2002). *FOXP2* currently
203 seems to have no variation that might have distinguished Neanderthals/Denisovans from
204 humans. But as DeSalle and Tattersall (2017) note, this is an extremely weak basis from which
205 to claim that Neanderthals/Denisovans had language. Prüfer et al. (2014) drew up a list of
206 candidates for the Neanderthal genome and, as DeSalle and Tattersall (2017, p. 5) comment,
207 these authors 'do not appear to have made any strong connections between language and any
208 of the genes they determined as important in the differentiation of the Neanderthal/Denisovan
209 genomes'. Of all the candidate genes for language summated via extensive review by DeSalle
210 and Tattersall (2017), only one has a serious and promising connection to the Prüfer et al.
211 (2014) database: CNTNAP2. This plays an important role in nervous system development and
212 covers 1.5% of chromosome 7, although it currently remains unclear how it could causally
213 relate to language evolution (see Mountford & Newbury, 2018 for further discussion). A
214 regulatory region of FOXP2 was recently identified exclusively in modern humans at a binding
215 site of the transcription factor POU3F2 (Maricic et al., 2013). This documented POU3F2
216 change that enhanced FOXP2 expression in the human brain was also not part of the gene flow
217 from humans into Neanderthals that occurred in the Levant or Southern Arabia 125-100kya
218 (Kuhlwilm et al., 2016). Since this likely resulted in improved speech, it is not unreasonable to
219 associate linguistic externalisation with this POU3F2 haplotype at FOXP2, suggesting that
220 externalisation was a late development occurring after the initial computational system had
221 emerged. This research suggests that 'differences in gene regulation and expression may be
222 involved in cognitive function, and that species differences are due to far more than just two
223 variants in a single gene' (Mountford & Newbury, 2018, p. 55).
224   Building on these developments, Murphy and Benítez-Burraco (2018b) argue that since
225 we cannot track the neuronal activity of the brain from extinct hominins, it is reasonable to use
226 our current understanding of the language 'oscillogenome' (that is, the set of genes responsible
227 for basic aspects of oscillatory brain activity relevant for language; see Murphy & Benítez-
228 Burraco, 2018a) to infer some properties of the Neanderthal oscillatory profile. Several
229 candidates for the language oscillogenome show differences in their methylation patterns
230 between Neanderthals and humans, and Murphy and Benítez-Burraco (2018b) claim that
231 differences in their expression levels could be informative of differences in cognitive functions
232 important for language (e.g. working memory).
233   Exploring a broad topic such as the genetics of language will require a number of linking
234 hypotheses between genes, neural anatomy and cognitive processes. Without such linking
235 hypotheses, it becomes extremely difficult to draw any substantial conclusions about the
236 genetic foundations of language. For instance, the gene *SRGAP2* has often been invoked in
237 discussions of language since it has been shown to be involved in cortical growth (Hillert,
238 2015). The occurrence of certain hominins correlates with copies of the genes, but also with
239 the appearance of different artefacts, and so it is difficult to even generate any inferences let
240 alone adjudicate between different hypotheses.
241   More broadly, Fisher (2013) makes the crucial point that genes do not specify
242 behavioural outputs, and do not even code for specific cognitive 'modules'. Rather, gene
243 products (usually proteins) interact with one another in complex networks to construct neural
244 circuitry through modulating neuronal proliferation and migration, neurite outgrowth, axon
245 pathfinding, synaptic strength, and so forth. Most genes, in particular regulatory genes, play
246 multiple roles within an organism ('pleiotropy'). In short, genes do not code for 'language' or
247 'speech', and an individual gene is rarely expressed in only one part of the central nervous
248 system, with *FOXP2*, for instance, being expressed in the cortex, basal ganglia, thalamus and
249 cerebellum (Lai et al., 2003).
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252 **Globularity**
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254 Pushing our timeline back even further now, the human lineage began around 6 million years
255 ago, when our common ancestor with chimpanzees split into separate lineages. Likely the
256 closest we have to a last common ancestor was *Ardipithecus*, who lived in trees but was capable
257 of bipedalism. Standing at 4 feet tall, their brains are estimated to have been at around 500
258 cubic centimetres. The oldest fossils ascribed to the genus *Homo* (emerging around 2.5mya)
259 are from Kenya, Ethiopia, Tanzania and South Africa, and include cranial and postcranial
260 specimens. These are classified as *Homo erectus*. While there is some controversy about the
261 earliest suggestive evidence of *Homo* in species such as *Homo habilis*, *Homo naledi* and *Homo*
262 *erectus* (a fragmentary upper jaw with a partial dentition from Ethiopia, dated at 2.33mya),
263 these cranial and postcranial specimens are the earliest fossils we can ascribe with confidence.
264 Skulls of subsequent members of *Homo* exhibit an increasingly high and globular
265 morphology, forming the marked parietal bone eminences of anatomically modern humans.
266 With respect to the development of the posterior inferior frontal gyrus, the general trend
267 throughout hominin evolution appears to be a reduction in size on the left relative to the right,
268 while the region more broadly projects more laterally and antero-posteriorly on the right side.
269 Consequently, left Broca's area appears more globular (Balzeau et al., 2014). Recent re-
270 evaluations of the fossil record have revealed a more complex picture of frontal lobe evolution
271 than is typically assumed, such that the inferior frontal gyrus and Broca's cap have indeed
272 assumed a more globular shape (in line with the rest of the forebrain more generally), i.e. they
273 have assumed a rounder shape as opposed to a flatter projection across the cortex (Beaudet,
274 2017).
275 Building on these concerns of globularity, a recent review of 20 *Homo sapiens* endocasts
276 from different time periods employing computed tomographic scans and geometric
277 morphometric analyses was conducted by Neubauer et al. (2018). Endocasts approximate outer
278 brain morphology very closely due to the fact that the brain, meninges and cranial bones
279 interact during development. The authors showed that while modern human brain size was
280 assumed as early as 300kya (hominin fossils from Jebel Irhoud, Morocco), it was not until 130-
281 35kya that our modern, globularised brain shape emerged (that is to say, the Jebel Irhoud fossils
282 were not globular). Crucially, Neubauer et al. (2018) note that this process 'paralleled the
283 emergence of behavioral modernity as seen from the archeological record'. They add that 'the
284 "human revolution" just marks the point in time when gradual changes reach full modern
285 behavior and morphology and does not represent a rapid evolutionary event related to only one
286 important genetic change' (see also Murphy, 2018 for a proposal that this process of
287 globularisation granted 'travelling' neural oscillations the ability to migrate across new areas
288 of the cortex and subcortex).
289 This suggests that while the capacity for constructing hierarchically organised linguistic
290 structures (or phrase structure building) was available before the final stages of globularisation,
291 these documented changes in brain shape (and their concomitant neural re-wiring) likely
292 allowed this computational system to gradually interface with other previously encapsulated
293 cognitive systems, due to this re-shaping reducing the number of 'spatial inequalities' (Salami
294 et al. 2003) in the brain, and hence the number of possible cross-regional connections. The
295 phrase structure capacity may have emerged first, but also may not have achieved its full,
296 modern reach until globularisation occurred. This suggests that language-music, language-
297 mathematics and language-morality interfaces (assuming a common computational link
298 between these capacities, à la Hauser & Watumull, 2017) emerged at different evolutionary
299 timepoints and that it may be possible to plot a timeline for the emergence of these interfaces.
300 For instance, we can date musical instruments to around 35kya (such as bone and ivory flutes;

Conard et al., 2009). In terms of their neuroanatomy, mathematical knowledge and language appear to involve distinct cortical networks (Amalric & Dehaene, 2019).

Additionally, no CT data of the Herto skull (160kya) is available, and so it is possible that modern human-like globularisation was found as early as 160kya, possibly before. If this is the case, then a more saltationist model of language evolution may be accurate such that language interfaced with other cognitive systems rapidly. Regardless, what can be said with certainty is that modern humans exhibit a more acute basicranial angle than other Great Apes, achieving a much more extreme level of globularity.

Turning to the related theme of neurolinguistics, neuronal networks have been shown to obey Rent's rule (a 'third factor' in language evolution), a rule from computing logic, exhibiting hierarchical modularity that optimises a trade-off between physical cost and topological complexity, such that these networks are cost-efficiently wired. Rent's rule states that the following relationship exists between several chip parameters.

$$T = AK^P$$

Where T is the number of terminals, K the number of blocks within the chip, A the average number of terminals for one block and P the Rent exponent. As Sengupta et al. (2013) summarise: 'A modular design balances the savings in metabolic costs, while preserving computational capacities'. A more globular braincase hosting a 'folded' brain (which, through gyrification, permits a large surface area to fit inside a smaller skull), in conjunction with Rent's rule, maximises computational efficiency and large-scale circuit integration. The implications for cognitive evolution may be substantial.

Although these empirical discoveries are novel, the general themes supporting them remain classical. Ever since Broca (1861) and Dax (1863), human brain asymmetries have been documented, often being used to help differentiate between different species. However, the oft-discussed process of lateralisation is 'probably shared by all hominins' (Balzeau et al., 2014, p. 126), and so some other neural changes may have likely been responsible for language evolution. Consider Australopithecines, who comprise the human clade along with the extant genus *Homo*. These are assumed to lack the diverse behavioural and biological features exhibited by *Homo*, though the fossil record is far from complete. The oldest stone tools have been dated to around 2.6 million years ago, close to the likely appearance of the first *Homo*. This had led some to speculate whether the larger brains associated with early *Homo* specimens were required for the conceptualisation involved in using this type of tool (see Mann, 2011). Indeed, throughout the evolution of *Homo* brain size has almost tripled in volume. The earliest *Homo* had a braincase volume of 510-775cc, whereas modern *Homo sapiens* exhibit braincases with volumes ranging from 1200cc to over 1500cc. Influences of changing climate, environmental demands, and social competition are thought to be the major influences driving brain size change (Bailey & Geary, 2009). Although the trend toward brain size increase has been well documented in hominin evolution (Sousa & Wood, 2007), there are some important exceptions such as *Homo floresiensis* (Kubo et al., 2013) and the size reduction in *Homo sapiens* since the Upper Paleolithic (Balzeau et al., 2014), a period lasting from 40-12kya.

Tool Use

Another domain with implications for language evolution, and one which has long been seen as relevant not just to linguistics but cognitive science more generally, is tool use. Archaeologists studying the Paleolithic period have discovered the types of technology created by *Homo*. One such technology is composed of three types of basic stone tools: hammers,

351 cores, and flakes. These are termed Oldowan tools, or Mode 1. These tools display substantial
352 spatio-temporal uniformity with few modifications for more than 1 million years. Hominins
353 used Mode 1 tools to kill and butcher medium- and large-sized mammals. Stone tools were
354 also used to access bone marrow, and the surfaces of certain tools suggest that roots might also
355 have been pounded (Wrangham, 2009). Upon the emergence of *Homo erectus*, Acheulean tools
356 (Mode 2) emerged, which were effectively enhanced versions of Mode 1 tools with the addition
357 of a 'biface'; namely, the margins of the tools were trimmed to either produce symmetrically
358 sharp sides (as in the Acheulean hand axe) or a modified side meeting an unmodified side (as
359 in cleavers). Acheulean tools were used to slice open animal skins, carve meat and break bones.
360 Two examples of cutting tools typical of early Acheulean sites are pointed hand axes and picks,
361 involving intentional shaping. Moreover, the intentional procurement of raw materials and the
362 development of a multicomponent quarrying process was required to produce these tools. Mode
363 1 tools had no existence outside their conditions of use, but Mode 2 acquired a somewhat more
364 abstract function. *Homo erectus* carried them around, using them for distinct purposes and to
365 achieve different goals, participating in the cultural life of the species. In this sense they
366 acquired a symbolic, memetic existence, and they also naturally helped *Homo erectus* consume
367 the necessary amounts of meat needed to fuel its enlarged brain.
368   Indeed, it has often been suggested that because remains of one-million-year old
369 campfires have been discovered and are thought to have been constructed by *Homo erectus*,
370 the invention of cooking might have provided a new range of nutrients feeding brain growth in
371 *Homo* (Aboitiz 2017, p. 452). DeCasien et al. (2017) provide novel statistical techniques to
372 demonstrate that primate brain size is predicted by diet, not by degree of sociality, suggesting
373 that studies of language evolution could benefit from a shift of attention towards ecological
374 factors. The enlarged brain, in turn, seems to have been capable of coordinating spatial
375 representations with shape recognition, necessary requirements for a biface; a process
376 demanding an enlarged working memory for *Homo erectus* relative to earlier *Homo* (Gibson,
377 1993). After these advances in mentally manipulating three-dimensional Euclidean space, it is
378 not at all clear whether substantial advances in spatial cognition were made until the present,
379 or whether the spatial reasoning skills of modern humans are closely comparable to those of
380 *Homo erectus*. One of the less controversial topics in human evolution involves the usefulness
381 of dietary changes in providing the necessary nutrients and energy for sustaining hominin brain
382 enlargement in early *Homo*. The modern human adult brain uses 20% of the body's metabolic
383 energy, whereas new-borns use around 60% (Aiello et al., 2001), with growing brains needing
384 a substantial range of foods (captured via sophisticated hunting tools) with high nutrient
385 density. It is possible that these dietary (and, hence, social) changes had a selectional impact
386 on certain aspects of speech or babbling (DeCasien et al., 2017).
387   Turning to Neanderthals, this species has always suffered from something of an image
388 problem: In the early 20th century, the discovery of a Neanderthal skeleton from La Chapelle-
389 aux-Saints in France exposed deformities which were at the time thought to be indicative of
390 their cognitive and cultural degeneracy, yet it is now known that these were simply a reflection
391 of the old age of the particular individual. The Neanderthals in Eurasia were a population whose
392 lineage split from that of *Homo sapiens* around 500kya, and who disappear from archaeological
393 history around 30kya. They exhibited use of Mode 3 tools, namely Mode 2 tools with 'flake
394 technology', producing intricate grooves along the sides of objects (surpassed only by Mode
395 4, or Solutrean tools; thin, sharp blades used by modern *Homo sapiens*). They also introduced
396 hafting of stone points onto spears, and lived in small communities, enjoying little to no contact
397 with other Neanderthal groups outside local territory. Neanderthal remains have been found
398 across Europe, and consequently play a major role in discussions of human evolution given
399 that both species appear to have trekked out of Africa. Relative to modern humans,
400 Neanderthals possessed a low, flat braincase, sloping foreheads and large brow ridges. Their

401 brains were slightly larger than those of humans. Their chests were barrel-like, indicating 'a
402 body morphology adapted to the cold conditions of ice age Europe' (Mann 2011, p. 279).
403 Different Neanderthal groups exhibited distinctive features: 'Fossil finds in northern Israel,
404 such as those from the Tabun and Amud caves and the skeleton lacking a skull from the Kebara
405 cave … possess features similar to other Israeli specimens, the Qafzeh and Skhul samples,
406 which have been termed early modern humans' (Mann 2011, p. 280).
407   Neanderthals also appear to have been capable of pyrotechnology. Early Neanderthals
408 from the late Middle Pleistocene site of Poggetti Vecchi, Italy, seem able to have appropriately
409 selected timber to create 'digging sticks' (Aranguren et al., 2018; see also Hoffeckerl, 2018 for
410 a review of Neanderthal technology). Kibblewhite et al. (2015) even propose a predictive
411 framework for the preservation of materials (including bones, teeth, metals and organic
412 materials) in soil across the European Union based on the chemical properties of discovered
413 materials and the soil they were found in, allowing them to predict the most likely 'hot spots'
414 for future discoveries relevant for cultural/cognitive research.
415   Moving forward to the time of modern *Homo sapiens*, the stone tools found at the Nubian
416 Complex in the Dhofar region of Oman have been dated at 106kya (Rose et al., 2011),
417 providing evidence for the existence of a northeast African Middle Stone Age technocomplex
418 exhibiting the Levallois technique of stone knapping, a complex method involving the
419 extraction of a small plane from a larger surface. Humans may well have been responsible for
420 this, and if so they likely left Africa as early as 110kya.
421   However, Armitage et al. (2011) document how Levallois assemblages from Jebel Faya
422 in the United Arab Emirates share close affinities with late Middle Stone Age assemblages
423 from North East Africa. The authors date these Jebel Faya assemblages to 125kya, pushing the
424 migration out of Africa even further back to around 130kya. In addition, the Lunadong hominin
425 fossils discovered at Luna Cave in Guangxi, southern China, include one left upper second
426 molar (M2) and one right lower second molar (m2). Bae et al. (2014) note that M2 is
427 exclusively assigned to modern humans, while m2 is also likely to be. The teeth are dated
428 between 127-70kya, in turn suggesting an early migration from Africa and Arabia. Bae et al.
429 (2017) review recent results from hominin paleontology, geochronology and genetics,
430 concluding that there must have been multiple dispersals from Africa into Eurasia, rather than
431 a single exodus.
432   In summary, we can say with some confidence that the apparently human-unique
433 capacity for language-specific syntax emerged within the last 200kya, and we can say this
434 thanks to the development of sophisticated tools, cultural artefacts, complex trading
435 relationships, and paintings. Indeed Miyagawa et al. (2018) draw a connection between cave
436 paintings and 'archeoacoustics', noting that cave art is typically connected to the acoustic
437 properties of the chambers they are located in. Being sensitive to the echoes generated in these
438 chambers, Miyagawa et al. speculate that cave paintings may have been a form of cross-
439 modality information transfer through which acoustic signals are transformed into visual
440 representations. Although we will likely never know whether these complex cave paintings
441 demanded the existence of language to produce, they are nevertheless part of a wider movement
442 in cultural flourishing which are indicative of substantial cognitive advances.
443   Given the hunter-gatherer culture in which this capacity emerged, what can we say of the
444 'first words' (or units of semantic communication) which would have been externalised?
445 Naturally we can only speculate, but it seems reasonable to assume that these words took the
446 form of mimetic gestures or even sounds imitating whatever the shared object of attention was
447 (likely food/carcasses or tools). As Studdert-Kennedy and Terrace (2017, p. 121) speculate,
448 '[t]he vocal modality would have come to prevail, leaving hands and eyes free to go about their
449 more important functions'. Before processes such as grammaticalization took control of
450 complex morphology, initial vocalisations would have been simple linearizations relying on

451 pragmatic procedures to derive the full meaning of expressions (Murphy, 2016b). Yet Cataldo
452 et al. (2018) conducted the first assessment comparing the efficiency of speech (unaided by
453 gesture) with gesture and also gesture-plus-speech as tool-making transmission aids. They
454 demonstrated that subjects instructed by speech alone underperformed in stone tool-making
455 compared to subjects instructed through either gesture alone or gesture-plus-speech. They
456 conclude that 'gesture was likely to be selected over speech as a teaching aid in the earliest
457 hominin tool-makers', and that 'speech could not have replaced gesturing as a tool-making
458 teaching aid in later hominins, possibly explaining the functional retention of gesturing in the
459 full language of modern humans'. They also suggest that speech may therefore have emerged
460 for reasons unrelated to tool-making; it may have been a response to increased trade and more
461 complex intra-group interactions bolstered by population increases.
462 In 1949, one of the most influential palaeontologists of the twentieth century, G.G.
463 Simpson (1949, 291-292), wrote:
464
465 Man arose as a result of the operation of organic evolution and his being and
466 activities are also materialistic, but the human species has properties unique to itself
467 among all form of life, superadded to the properties unique to life among all forms
468 of matter and of action. Man's intellectual, social, and spiritual natures are
469 altogether exceptional among animals in degree, but they arose by organic
470 evolution.
471
472 It is common in the field for researchers to claim that because language is such a complex
473 system – 'altogether exceptional' (Corballis 2017) – its evolutionary roots must extend very
474 far back. As DeSalle and Tattersall (2017, p. 6) review, the first anatomical *Homo* exhibited
475 'little if any of the zeal for change and innovation, and none of the ability to reconceptualise
476 the world, that so richly characterize their modern language-endowed descendants'. But these
477 debates presuppose a clear understanding of what *language evolution* is, as distinct from the
478 evolution of closely related capacities. When it comes to the relevance of the fossil record to
479 questions of *speech evolution*, Wood and Bauernfeind (2011, p. 271) conclude their data review
480 by claiming that 'the fossil evidence for archaic hominins contains little, or no, reliable
481 evidence about the speech capabilities of these taxa'. But, going beyond fossils, what about the
482 evolution of language and communication, distinct from speech? Assuming, as is commonly
483 done, some form of relationship between symbolic communication and linguistic competence,
484 there are a number of higher cognitive capacities that we share with our close relatives
485 according to existing paleoanthropological accounts. Consider the Makapansgat manuport, a
486 small stone (2×3 inches) found amongst Acheulean tools in South Africa in 1925 and
487 putatively collected by *Australopithecus africanus* around 3mya (other Acheulean tools are
488 dated somewhat later). It seems to closely resemble a human face, suggesting that
489 Australopithecus could grasp connections between arbitrary symbolic forms and abstract
490 meanings; otherwise known as iconicity. Since this semantic property appears so deeply rooted
491 in hominin evolution, this might explain its prevalence amongst early religionists (see also
492 Peterson, 1999, 2018).
493 Examining the neural basis of primitive tool technology, Hecht et al. (2015) compared
494 brain responses while learning either the basic Oldowan technique or the more complex
495 Acheulean technique. The latter exhibited increased activation in the right inferior frontal gyrus
496 and bilaterally in other regions, suggesting an increase in the requirement for cognitive control.
497 Toolmaking typically involves the dominant hand making repetitive, rhythmic motions while
498 the subordinate hand holds the object and occasionally rotates it (Uomini & Meyer, 2013).
499 According to Uomini and Meyer (2013), hemispheric dominance arose due to the separation
500 of competing neural processing strategies, one implicated in complex sequential behaviours

like hand motions, and the other involved in coarse motor routines. Coordinating two different processes simultaneously (low-frequency and high-frequency motor commands) in what can arguably be described as a hierarchically organised form of behaviour (though of limited hierarchy; Stout & Chaminade, 2012) may well led to the selection for certain neural subroutines which the language system recruited when structuring the processing of units of different hierarchical complexity, i.e. when processing multiple syllables into a single word, and ultimately processing multiple words into a single phrase. Indeed, Morgan et al. (2015) discovered that students learned to make stone tools faster under verbal instruction, pointing to a potential co-evolution between toolmaking and speech (although it should be stressed that simply because verbal instruction enhances performance on a certain task, it does not follow that verbal abilities and this given task co-evolved). Note that this hypothesis does not lead to any causal explanation for language evolution (e.g. it does not commit one to the assumption that language evolved directly from toolmaking), it simply proposes that when the language faculty did emerge it was embedded within a sophisticated computational network.

Another related example comes from the Erfoud manuport, dated at around 300,000 years old and discovered in eastern Morocco. Seemingly collected by *Homo erectus*, the manuport is a cuttle fish bone shaped like a phallus (Everett, 2017). What is the possible relationship of these findings to language evolution? Conceiving of language as a recursive combinatorial system involving the construction of hierarchically organised syntactic objects, generative linguists such as Chomsky (2010) or Hornstein (2009) would likely not be too impressed with a penis-shaped cuttle fish bone. Yet clearly the capacity to bind bodily concepts either to concrete instantiations or more abstract symbolic representations in the form of manuports involves some form of impressive semantic mapping of the kind subsequently exploited by the language system in anatomically modern humans. Moreover, the development of the 300-400,000-year-old Schöningen spears point towards a sophisticated culture amongst *Homo heidelbergensis*, since not only do they act as tools but they also have symbolic cultural meaning, such that the spear can denote the act of hunting in abstraction, i.e. in the absence of any particular hunt. And unlike many other tools used throughout the animal kingdom, Everett (2017, p. 143) notes that these spears display aspects of Peircean signs in that 'only certain parts of the tools are meaningfully connected to their tasks, e.g. the edge of the tool'. This greater degree of abstraction seemingly came about shortly before the time that language would have emerged among anatomically modern humans (200-300kya), and so the generous and rapidly developing cognitive toolbox of *Homo heidelbergensis* (a variant of *Homo erectus*, or even identical according to some researchers) may well have been passed down to modern humans. *Homo heidelbergensis* additionally had a great number of nerves linking the brain and tongue than its predecessors, suggesting that it possessed the ability to refine and control vocalizations.

With this toolbox at the ready, the bow and arrow was used by humans as early as 71kya (McBrearty, 2012), a weapon which goes considerably beyond the complexity of the spear, likely involving a degree of sophisticated communication in order for it to be taught and implemented in a coordinated, strategic fashion. Likewise, most researchers concur that the capacity for complex symbolic thought (i.e. combining distinct symbolic representations in novel, 'imaginative' ways, of the kind found in polysemy; Falkum & Vicente, 2015; Murphy, Forthcoming; Pustejovsky, 1995, 2008) was needed to construct bodily ornaments such as beads and decorative objects (Vanhaeren et al., 2006; Texier, 2010); both of which appeared around 100-60kya.

The capacity for complex orthography, and potentially also the ability to associate symbolic meaning with indentations, can also be found as far back as 540kya in the form of zigzag marks on a shell made by a member of *Homo erectus* and found in Java. Interestingly, a sea voyage was likely made by the creator (from mainland Asia to Java), who might have

551 represented the sea through these patterns. The intentional act of creating marks to represent
552 abstract icons also provided an important pre-linguistic trait for anatomically modern humans,
553 who presumably would have been able to externalise their new Language of Thought after the
554 emergence of human-specific syntax in precisely the same way as *Homo erectus*, with the
555 exception of using such markings to represent more complex, composite representations, as
556 opposed to simple concepts like SEA or FACE. Likewise, *Homo erectus* crafted a wide number
557 of tools (including choppers and pounders). These could not have feasibly been created
558 systematically from any random motor sequence, but require planning and imagination, as well
559 as the ability to communicate to others the methods of production. The expanded cognitive
560 power required for mastering these procedures, which soon became a necessary part of survival
561 (in particular in the event of tribal warfare), may well have led to an important role for natural
562 selection: namely, selection for expanded fronto-parietal circuits to satisfy the growing demand
563 for cognitive control networks. Thus, we find the world's oldest piece of art, the 250kya Venus
564 of Berekhat Ram, a rock carved in a female shape with evidence of intentional red ochre
565 colouring for decoration, an object crafted with precision and imagination.
566 These ideas – of syntax ultimately being couched within pre-existing semantic properties
567 – are quite distinct from the hypothesis proposed by Everett (2017). His claim is that 'with
568 symbols + concatenation, there is language' (2017, p. 160). While a certain amount of
569 compositionality might be derived from a semantic system relying on this architecture,
570 hierarchically organised phrases plus long-distance dependencies cannot emerge from this.
571 Combining representations of any format into syntactically hierarchical phrases is not a job for
572 symbolism and concatenation alone (Murphy, 2015, 2016a). Likewise, the engraved ochre and
573 bones found in Blombos Cave are suggestive of symbolic manipulations, yet as Botha (2011,
574 p. 307) notes any links to syntactic language are highly questionable since 'beads, ochres, and
575 engraved bones cannot stand as evidence for modern cognition, including language, unless it
576 is specified what cognitive abilities these artefacts require'. Indeed, although the use of
577 pigments pre-dates Blombos Cave and even implicates Neanderthals, these were non-symbolic
578 and displayed little variation (Neanderthal pigments were generally black, for instance).
579 Finally, one of the core characteristics of the tools of early *Homo sapiens* is that they
580 were crafted for durability just as much as immediate usefulness. This suggests a familiarity
581 not only with symbolic behaviour, but with long-range planning. These planning and
582 strategizing capabilities are neurologically and computationally separate from purely linguistic
583 processes, suggesting that modern cognition demanded certain developments in executive
584 reasoning skills as well as the evolution of language.
585 The general picture that emerges here is the following: The Oldowan tools dated around
586 3mya are suggestive of dexterity, motor control and intentional modifications of inanimate
587 objects; the Acheulean tools dated slightly later (perhaps around 2mya) are suggested of
588 hierarchical cognition and/or complex motor planning, along with complex emotions. The
589 axes, cleaver and spears of *Homo heidelbergensis* dated around 400kya are suggestive of visual
590 imagination, emotional control, symbolism, and possibly a sense of self. The Levallois method
591 is generally dated around 300kya, and is suggestive of advanced hierarchical cognition, tuition,
592 and an unusual degree of patience. Lastly, the technology of modern *Homo sapiens* dated
593 around 200kya is suggestive of an improved memory, creativity, and an awareness of past and
594 future.
595
596
597 **Domestication**
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599 Closely tied to the theme of language evolution is the broader, and closely related (indeed,
600 arguably identical) theme of *human evolution*. If we define *Homo sapiens* based on derived

601 skeletal features, then the fossil record would place human origins somewhere in the African
602 late middle Pleistocene. The relevant fossil data includes Omo Kibish 1 and the Levantine
603 material from Skhul and Qafzek. Some of the oldest morphologically modern humans have
604 been found at the Omo Kibish sites, and date to ~195kya (McDougall et al., 2005). Yet the
605 genetic data indicates that both anatomically modern humans and *Homo neanderthalensis*
606 shared a common ancestor in the middle Pleistocene (400-700kya), a date some 200kya earlier
607 than the fossil-determined date.
608   Stringer (2016) notes that findings of this kind suggest that the morphology of *sapiens*
609 exhibited no linear progression, and 'there was chronological overlap between different
610 "archaic" and "modern" morphs' (2016, p. 1). Extant humans exhibit a number of shared traits,
611 including a high neurocranium, a small face retracted under the frontal bone, small
612 discontinuous supraorbital tori, and a narrow trunk and pelvis (Stringer, 2016). Anatomically
613 speaking, it is possible to detect humans in the fossil record through focusing on these and
614 broader features like cranial globularity and basicranial flexion (Arsuaga et al., 2015).
615 Particularly relevant for language is a certain feature of the cranial vault: The parietal region is
616 highly distinctive in humans, being expanded in certain areas (Bruner, 2010). Modulating and
617 strengthening the connections of this expanded parietal region with other regions, such as
618 anterior temporal regions and subcortical structures like the thalamus, may have contributed to
619 novel cross-modular communication.
620   In this connection, it is increasingly becoming clear that the topic of *domestication* has a
621 clear potential to inform our understanding of human brain evolution. The notion that
622 anatomically modern humans are a fundamentally domesticated species has a long and rich
623 history, dating back to Darwin (1871) and Boas (1938), with the latter commenting that '[m]an
624 is not a wild form, but must be compared to the domesticated animals. He is a self-domesticated
625 being' (Boas, 1938, p. 76). Concerning the general processes of self-domestication, Boas added
626 that '[i]t is likely that changes of mental character go hand in hand with them' (1938, p. 140),
627 and it is only very recently that researchers have been able to propose concrete hypotheses
628 which expand on these speculations.
629   Domesticated species (including dogs, cats, foxes, pigs and sheep) are usually defined
630 based on their shared phenotypic traits, referred to collectively as the 'domestication syndrome'
631 (Zeder, 2012) and which include depigmentation, reduced ears, shorter muzzles, smaller teeth,
632 smaller cranial capacities, and a reduction of sexual dimorphism (feminisation). Many of these
633 features are exhibited by anatomically modern humans, and in fact distinguish humans from
634 Neanderthals (Theofanopoulou et al., 2017), and they may also reflect a generalised deficit in
635 the neural crest, an embryonic structure responsible for pigmentation and the cranial skeleton,
636 amongst other things (Wilkins et al., 2014). Domesticated animals used to be regarded as
637 entirely separate species but are now thought of as sub-species of their wild progenitors. Le
638 Douarin (1980) discovered that transplanting neural crest cells from chicks to quails resulted
639 in the chimeric hatchlings producing intermediate chick/quail vocalisations, suggesting that the
640 process of self-domestication, involving the neural crest, contributed in some fashion to the
641 emergence of vocal learning. Interestingly, Theofanopoulou et al. (2017, p. 4) document how
642 interspecific domestication events suggest that 'the selective pressure for our self-
643 domestication need not have been qualitatively different from those experienced by other
644 species'. For instance, the silver fox (*Vulpes vulpes*) was intentionally domesticated through a
645 project initiated by Belyaev (1979) based on a single criterion: tameness towards humans. After
646 only twenty years of selection for tameness, a range of features typically associated with
647 domestication emerged, suggesting a strong, causal link between the above noted phenotypic
648 characteristics of domesticants.
649   It is therefore likely that selection for tameness, prosocial behaviour or related traits
650 associated with the syndrome brought about human self-domestication after the split from our

last common ancestor. Self-domestication can potentially explain – 'for free' – a number of human-specific traits, with the possible exception of the descended larynx, an explanation for which remains in relative obscurity. Speaking to this hypothesis, recent work suggests that humans, unlike monkeys, are adept at turning competitive situations into cooperative ones (Marquez, 2017). Tomasello et al. (2005, p. 685), discussing 'shared intentionality', note that 'it is almost unimaginable that two chimpanzees might spontaneously do something as simple as carry something together or help each other make a tool'. More generally, as Theofanopoulou et al. (2017, p. 12) note: 'It is also not unreasonable to suspect that byproducts of the domestication process, such as enhanced sensory-motor perceptual and learning pathways, may provide a foundation for more complex communicative abilities, including vocal learning abilities'.

Recent work has emphasised the potential for studies of dog vocal social perception to enhance our understanding of how linguistic and non-linguistic signals are represented in the mammalian brain in particular given that dogs have lived in anthropogenic environments for at least 16-32kya (Andics & Miklósi, 2018). This perspective goes somewhat beyond the standard focus on great apes, giving the study of vocal social perception a broader mammalian basis. It has been argued in the literature that dog domestication enabled this species to survive in small human groups (Serpell, 1995), fast becoming man's 'best friend', with this process selecting for dogs with the genetic potential to develop human-compatible behaviours. Dog brains also appear to have dedicated voice areas, preferring conspecific vocalisations over other sounds (Andics et al., 2014). These areas are located in anterior temporal regions, including the bilateral temporal poles. One possible interpretation of these findings, as Andics and Miklósi (2018, p. 60) note, is that 'conspecific preference in dogs and humans relies on homologous brain structures, implying that voice areas have been there in the last common ancestor of the two species, but convergent evolution provides an alternative interpretation that voice areas developed independently in the ancestors of dogs and humans, after their lineages split'.

The importance of examining the brain in order to properly distinguish humans from Neanderthals is highlighted in recent work in paleoneurology. Mounier et al. (2016) document how endocranial features are more informative than features of the calvarium (supporting research efforts geared towards domestication) and how human endocranial anatomy dramatically changed during the end of the Middle Pleistocene. Cultural development seems to have appeared alongside domesticated features like a smaller braincase, with a reorganisation of the cranium altering many neural features.

Wrangham (2009) maintains that the cultural developments of anatomically modern humans are the result of self-domestication via inhibiting aggression and related traits. His line of research points to comparable developments within certain ape societies. For example, while chimpanzees display a range of cooperative traits their culture is typically plagued by aggression and violence (Hare et al., 2012). Bonobos (pygmy chimpanzees), in contrast, display a juvenile appearance (in line with domestication models) and live in far more peaceful societies (though, it should be noted, not as peaceful as stereotypes would suggest due to clear carnivorous tendencies). Like humans, bonobo societies are much larger than those of chimpanzees, with the rapidly increasing size of early human tribes likely playing a role in their domestication. As Aboitiz (2017, p. 452) summarises: 'As we domesticated other species, we adapted ourselves to the process of domestication, forming an evolutionary circle that maintained our genetic evolution and drags other species with it'. This cyclic process of self-domestication involved adapting to the needs of human groups while also domesticating a range of plants and animals in ways dynamically responding to such needs, with the newly-domesticated plants and animals in turn influencing the social structure of human societies (see also Murphy, 2019).

701   Turning to a related field of study, Okanoya (2012, 2013) reports that comparisons of the
702 songs of wild finches (white-rumped munia) and domesticated finches (Bengalese finch)
703 suggest that the latter produced songs of greater complexity, differing in acoustical morphology
704 and the order of elements. Lansverk et al. (2018) replicate and expand on these results and also
705 explore their genetic underpinnings. The sound density was also found to be 14dB higher in
706 Bengalese finches than in white-rumped munias during recordings from identical settings. The
707 most recent research in this direction has even suggested that domesticated birds have smaller
708 brains but a larger cortex, in particular the forebrain (Olcowicz et al., 2016). As such,
709 domestication seems broadly responsible for increases in syntactic complexity, with the
710 complex syntax of Bengalese finch songs developing from simple neurological changes
711 (Katahira et al., 2013).
712   In summary, it appears from recent evidence that self-domestication helped lay the
713 ground work for enhancing in modern humans some of the communicative, semantic and
714 syntactic capacities of our ape ancestors.
715
716
717 **The Cerebellum and Speech**
718
719 Although left-frontal and parietal regions enjoy the most attention in discussions of language
720 evolution, I would like to briefly address the potential importance of the *cerebellum*, which is
721 increasingly being implicated in language processing. Of course, there are many other regions
722 in the brain for which the same type of evidence presented below could be used in support of
723 the idea that they are important for language, but the cerebellum more tightly fits into the
724 present theme of brain shape modification.
725   The human cerebral cortex is approximately 3 millimetres in depth, while the cerebellum
726 is considerably larger and contains 60 out of the brain's 86 billion neurons. Yet its role in higher
727 cognition remains somewhat unclear. Pursuing the above line of inquiry, Ogihara et al. (2018)
728 conducted a three-dimensional geometric morphometric analysis of reconstructed Neanderthal
729 and early human endocasts. Their results indicated that ecto- and endocranial shapes are
730 quantitatively different between the two species. The cranium of early humans displayed
731 relative enlargement of the cerebellar region and a notable parietal expansion. This is perhaps
732 the strongest evidence that the neuroanatomical organisation of the two species was
733 significantly distinct. Following directly on from this documented cerebellum expansion,
734 Tanabe et al. (2018) note that while the cerebellum has typically been seen as being involved
735 largely in fine motor control, an emerging consensus is that this region is also involved in
736 certain cognitive functions, including language. It exhibits a unique gross anatomy and
737 microstructure, and the cerebellar cortex contains circuitry functioning as a learning system
738 able to construct and store internal models of the world. Tanabe et al. (2018) show that the
739 greater volume of the cerebellar cortex, the greater number of internal models it is able to
740 construct and store. It seems likely that the cerebellum is therefore implicated in forms of long-
741 term memory, with some of the complex representations it stores being constructed initially by
742 the language system. In this sense, it may act as a post-linguistic long-term storage site,
743 functionally distinct from parts of Broca's area (e.g. BA 44v, following standard sub-
744 parcellation) which seem to act as a short-term memory 'buffer' site for phrase structures.
745 Finally, cerebellar dysfunctions in humans lead to distinct speech motor deficits referred to as
746 ataxic dysarthia (Ackermann, 2008; see also Murphy & Benítez-Burraco, 2017). The
747 cerebellum is assumed to be involved in the control of coarticulation effects given its
748 involvement in sequencing syllables into fast, rhythmically structured larger utterances.
749 Nozaradan et al. (2017) also provide EEG evidence that the cerebellum and basal ganglia are

750 involved in the neural representations of rhythmic sequences, in particular those demanding
751 the encoding of precise sub-second events (see also Obleser et al., 2017).
752   More recently, Smaers et al. (2018) investigated the lateral cerebellum (a structure unique
753 to mammals) across a range of species and mapped its evolutionary diversification, finding that
754 relative volumetric changes of the lateral cerebellar hemispheres are correlated with measures
755 of domain-general cognition in primates. These are furthermore characterised by a combination
756 of parallel and convergent shifts towards similar levels of expansion in distantly related
757 mammalian lineages. This suggests that increased behavioural complexity (for our purposes,
758 of the kind found in the emergence of language) from a range of directions may be traced back
759 to a common selection on a shared neural system, the cerebellum. This implies that this brain
760 region aided certain other forms of higher cognition in a range of mammals, while in humans
761 it seems to have aided rhythmicity and memory load, directly exploited by the language system.
762   Deepening these connections, Pidoux et al. (2018) show that the cerebellum provides a
763 strong input to the song-related basal ganglia nucleus in zebra finches. Cerebellar signals are
764 transmitted to the basal ganglia via a disynaptic connection through the thalamus, before being
765 conveyed to their cortical target and to the premotor nucleus controlling song production. These
766 authors also showed that cerebellar lesions impair juvenile song learning.
767   As such, paleoneurological evidence bearing on the morphology of the cerebellum will
768 likely inform our understanding of when certain language-related capacities emerged.
769
770

Future Directions

772

773 The unanswered questions emerging from this discussion cut across a range of domains: Which
774 features of (self-)domestication have had an impact on the language architecture? How does
775 the speed of the molecular clock impact either saltationist or adaptationist hypotheses
776 concerning the emergence of language? What are the potential ways domestication can
777 influence the externalisation component of a given species? Which factors (e.g. nutrition,
778 climate) had the potential to impact features of human cognition relevant to language
779 comprehension during the course of modern human evolution? To what extent could future
780 studies of archaic hominin admixture provide insights into the evolution of language? What
781 specific brain regions were impacted by globularisation, and how did this process impact
782 language (and language-related) processes? How might globularisation have impacted higher
783 cognition in other species?
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