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1 **Palaeoneurology and the emergence of language**

2 **Paléoneurologie et origine du langage**

3

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5

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15

16 **Abstract**

17 The origin of language has been much debated over the years. Recent research has centred the
18 controversies on two main ideas. Language, as defined by the Basic Property formulated by Chomsky,
19 is a characteristic unique to *H. sapiens* that developed in our species in the past 300,000 years. Other
20 scientists argue that the Basic Property is a derived characteristic shared with other hominin species,
21 such as *H. neanderthalensis* and the last common ancestor of both modern humans and Neandertals,
22 which evolved over a long period of time, perhaps as long as 2 million years. Palaeoneurology, which
23 studies the phenotype of the brain in past populations, may have left this complex topic aside because
24 of the difficulty of deducing brain morphology from endocasts (imprints of the neurocranium) and
25 inferring function from brain morphology. In this manuscript, we review the various hypotheses on the
26 evolution of language, highlighting the potential of palaeoneurology to help understand this complex
27 aspect of human evolution, and provide an updated interpretation of previously published endocranial
28 phenotypic data from fossil populations. This brings additional support to a long chronology framework
29 for the origin of language in the hominin lineage: the basic property for modern language may have
30 been in place from the last common ancestor of *H. sapiens* and *H. neanderthalensis*.

31

32 **Résumé**

33 L'origine du langage a suscité de nombreuses controverses au fil des ans. Des recherches récentes ont
34 centré les débats sur deux idées principales. Le langage, tel que défini par la propriété de base de
35 Chomsky, serait une caractéristique unique d'*H. sapiens* qui se serait développée au sein de notre
36 espèce durant les derniers 300 000 ans. D'autres scientifiques soutiennent l'idée que la propriété de
37 base serait une caractéristique dérivée partagée avec d'autres espèces d'hominines, telles qu'*H.*
38 *neanderthalensis* et le dernier ancêtre commun aux humains modernes et aux Néandertaliens, et qui
39 aurait évolué sur une longue période de temps, potentiellement sur 2 millions d'années. La
40 paléoneurologie, qui étudie le phénotype du cerveau dans les populations passées, peut avoir négligé
41 ce sujet complexe en raison des difficultés à déduire la morphologie du cerveau à partir du moulage
42 endocrânien (empreinte du neurocrâne) et à inférer la fonction à partir de la morphologie du cerveau.
43 Dans ce manuscrit, nous passons en revue les différentes hypothèses concernant l'évolution du
44 langage, nous mettons en évidence le potentiel de la paléoneurologie pour aider à comprendre cette
45 question complexe dans l'évolution humaine et nous fournissons une interprétation à jour des
46 données phénotypiques endocrâniennes précédemment publiées provenant de populations fossiles.
47 Nous apportons un soutien supplémentaire à un cadre chronologique long pour l'origine du langage
48 dans la lignée humaine : la propriété de base du langage moderne dans les populations d'hominines
49 semble avoir préexister l'apparition de la population ancestrale aux *H. sapiens* et *H. neanderthalensis*.

50

51 **Keywords:** palaeoneurology; Basic Property; *Homo neanderthalensis*; *Homo sapiens*; Middle
52 Pleistocene hominins

53 **Mots clés :** paléoneurologie, propriété de base ; *Homo neanderthalensis*; *Homo sapiens*; hominines
54 du Pléistocène moyen

55

56 In the evolution of the genus *Homo*, an area of constant debate concerns the classification of fossil
57 specimens within much discussed *Homo* taxa [1-4] and the abilities of those hominin species. One of
58 the major unresolved questions concerns the emergence and evolution of language faculties.

59

60 ***The only talking hominin***

61 There are different hypotheses regarding the evolution of language within the genus *Homo*. One of
62 the oldest hypotheses argues that language emerged at a late stage in modern humans, perhaps as
63 late as 100,000 years ago (ka) (see, [5-6]). This hypothesis was originally developed from the idea that
64 the production of differentiated vowels would have been impossible without a large pharyngeal cavity.
65 The descent of the larynx was also seen as a unique *H. sapiens* characteristic, which - *de facto* - limited
66 the emergence of modern language to our species [7]. The ideas of a descended larynx as a
67 prerequisite for producing differentiated vowels and as a unique *H. sapiens* feature have both been
68 repeatedly contested ever since [8-9]. However, this hypothesis is still strongly supported because it is
69 also rooted in the 'cultural modernity' hypothesis, which holds that modern humans acquired full
70 modern human behaviour at least 100 ka after their first appearance [10]. Advanced modern
71 behavioural traits, which include a new techno-complex (Later Stone Age, LSA in Africa and Upper
72 Palaeolithic in Europe) and symbolism, as demonstrated by the earliest prehistoric art [11], seem to
73 have been fully acquired by modern humans by 50-40 ka [12]. Before that date there is little in the
74 archaeological record linked to modern humans that shows symbolic behaviour. The earliest trace of
75 symbolic behaviour for the *H. sapiens* species can be traced back to ca 80 ka in Blombos cave (South
76 Africa) [13] and Taforalt (Morocco) [14]. The presence of this behavioural package is, in turn, often
77 used to infer the emergence of modern language.

78 More recently the 'Why Only Us' hypothesis [15] uses the 'Basic Property' of human language as a
79 landmark to infer the origin of language in hominin populations. Basic Property is described by
80 Chomsky [16] as the 'Merge' operation, which builds a "*discrete infinity of structured expressions that*
81 *are interpretable in a definite way by the conceptual-intentional system of thought and action, and by*
82 *a sensory-motor system for externalisation*" (p. 201). In other words, the Basic Property refers to the
83 way thoughts are linked with sounds and signs. For Berwick and Chomsky (15), language – as defined
84 by the Basic Property, is also restricted to *H. sapiens*, but it must have arisen within its clade earlier
85 than previously thought. The San populations split from the other modern human populations around
86 160 ka [17] and were mostly genetically isolated until 3000 years ago. Despite this genetic isolation,
87 the modern Sans possess a fully modern human language faculty. Therefore, the Basic Property for
88 modern language had to have appeared between the origin of the first modern humans, which by the
89 time of Berwick and Chomsky's publication (2017) was thought to be around 200 ka, but can now be
90 placed at around 300 ka (see, [18-20]), and the first identified split within *H. sapiens* populations at
91 around 160 ka [17].

92 The 'Why Only Us' hypothesis relies first on the scarcity of archaeological evidence of symbolic
93 behaviour within the Denisovan/Neandertal lineage to infer that the Basic Property must have
94 developed within the modern human clade only after the split between the two lineages. The new
95 date estimates for the time of the split between those lineages, 700-500 ka instead of the traditional
96 400 ka (see, [21-22]), supports this hypothesis by allowing enough time to the *H. sapiens* lineage to
97 develop genetic innovations that would ultimately lead to the acquisition of the Basic Property, and

98 hence, of a fully modern human language faculty [23]. Additionally, the genetic differences identified
99 between the Denisovan/Neandertal lineage and the modern human ones, notably in the *FOXP2*
100 genomic region [24-25] are also seen, in the 'Why Only Us' hypothesis, as evidence of the different
101 language faculties between the two clades. While Berwick and Chomsky [23] acknowledge that it is
102 unclear whether *FOXP2* plays a role in the emergence of the Basic Property, they rely on the fact that
103 some segments of the *FOXP2* transcription factor gene of an Altaic Neandertal individual appears to
104 have introgressed from modern humans [25], supporting the idea that both lineages accumulated
105 genetic differences in a key part of the genome concerning language faculties and language acquisition.

106

107 ***A long chronology for the development of modern language faculties***

108 At the other end of the spectrum, researchers argue for a much longer chronology in the development
109 of modern language faculties (i.e. Basic Property). This 'Gradual Hypothesis' is, yet again, primarily
110 based on the interpretation of hints of symbolic behaviour in the archaeological record, which in the
111 view of the supporters of a more gradual evolution of language, does not support cultural modernity.
112 A number of recent studies have indeed modified the paradigm regarding the appearance of symbolic
113 behaviour by demonstrating that hominins within the *H. neanderthalensis* lineage were capable of
114 expressing advanced modern behavioural traits as defined by Klein [12]. The most spectacular
115 discovery is the dating to ~176 ka of annular constructions of broken stalagmites which were made
116 336 metres deep into the Bruniquel Cave (Southwest France) [26]. Similarly, the debated [27-28] dating
117 of cave art in the Iberian Peninsula to ~64 ka [29] points to Neandertal authorship. This new chronology
118 establishes that before the arrival of *H. sapiens* in Europe, hominins had already developed advanced
119 symbolic behaviour. Symbolic behavioural faculties in *H. neanderthalensis* are also demonstrated by
120 funerary practices [30], although the evidence has been heavily criticised [31], and the new direct
121 dating of Neandertal hominin remains at the Grotte du Renne [32] demonstrates that the Neandertal
122 occupation was indeed contemporary with the Châtelperronian Upper Palaeolithic techno-complex
123 found at the site. Given this new archaeological evidence, it seems possible that symbolism was not
124 limited to the *H. sapiens* clade alone, and that the Neandertals and possibly the common ancestor of
125 both lineages may have been capable of similar behaviour. If these advanced behaviours are used as
126 proxies for the Basic Property for modern language, then both the Neandertals and their ancestors
127 would have had a language faculty that "*involves a cognitive architecture that maps sounds (or*
128 *gestures) into meaning through a series of combinatorial structures*" [33], p. 52). One should
129 nevertheless keep in mind that the evidence describing advanced symbolic behaviour in Neandertals
130 remains sparse and cannot compare quantitatively with later archaeological evidence associated with
131 Upper Palaeolithic humans.

132 The Gradual Hypothesis also uses the most recent genomic studies to strengthen its theoretical claim.
133 First, it stresses the fact that both lineages interbred at least three times during their isolated genomic
134 history. The mitochondrial DNA (i.e. mtDNA) retrieved from 'classic' (i.e. 130-40 ka) Neandertal
135 specimens is closer to that of modern humans than it is to the mtDNA sequenced from Denisovan and
136 Middle Pleistocene fossils from Europe that are widely considered to be early Neandertals (i.e. Sima
137 de los Huesos), indicating some gene flow between the two lineages during the mid-Middle Pleistocene
138 [34]. Neandertals and *H. sapiens* interbred when the latter first came into the Levant around 100-120
139 ka [25, 35] and the modern human fossils from Peștera cu Oase in Romania, which date back to 42-37

140 ka, probably had a recent Neandertal ancestor (i.e. 4 to 6 generations [36]). Moreover, while the
141 Neandertal and modern human clades show genetic distinctiveness, the actual number of differences
142 appears to be relatively small. Prüfer and colleagues [37] showed that only 31,389 single nucleotide
143 substitutions and 4,113 short insertions or deletions distinguished modern humans from their nearest
144 extinct relatives, among which only about three thousand of those fixed changes could have potentially
145 influenced gene expression [37]. Therefore, one could consider that with such an intricate genetic
146 history between the two lineages, it is less likely that the two would have had completely distinct
147 language faculties.

148 The final idea put forward by supporters of the Gradual Hypothesis is co-evolution of tool-knapping
149 and language faculties [38-39]. This implies that the evolution of the Basic Property for modern
150 language could have originated within the genus *Homo* with the Mode 2 technology (i.e. Acheulean)
151 whose earlier appearance in the African archaeological record is documented at 1.75 million years ago
152 [40]. This idea relies on the assumption that the transmission of skills necessary to master elaborate
153 lithic technology demands language [33]. Experimental studies have given contrasting results when
154 testing this hypothesis. In 2013 Uomini and Meyer showed that the pattern of cerebral blood flow
155 lateralization was similar when participants were asked to knap Acheulean tools and to generate cued
156 words [41]. Another study, focusing on the Oldowayan techno-complex, which appeared around 2.5
157 million years ago in the archaeological record, gives further support to Uomini and Meyer's results. It
158 shows that reliance on stone tools would have triggered selection for teaching and language. One of
159 the outcomes of this selection would have been the appearance of Acheulean, the Mode 2 technology
160 being the first techno-complex requiring more advanced faculties in both language and teaching for its
161 transmission [42]. However, Putt and colleagues [43] in a similar study suggest that selection from
162 reliance on stone tools favoured the development of the prefrontal and temporal cortices, which
163 offered a more complex toolkit to the hominins but did not play a significant role in the evolution of
164 language.

165

166 ***Towards a new paradigm?***

167 The lack of scientific consensus, which may be explained by the difficulties of evaluating traits that can
168 only be studied through proxies (anatomical or symbolic), has led to a situation where the study of
169 language evolution is often considered as out of reach for current research capacities. The first aim of
170 the Globularity hypothesis (i.e. Globularization Leads to our Brain's Language-Readiness) developed
171 by Boeckx [44], is to offer an updated framework for the study of language evolution. The globularity
172 hypothesis distinguishes between language and language-readiness, in other words, the anatomical
173 and physiological prerequisites for language acquisition and use are not sufficient and inputs from
174 cultural evolution studies are necessary to understand the complexity of grammatical systems that
175 need to be learned by children. The Globularity hypothesis aims to focus on the neurobiological
176 properties that would need to be linked to the anatomical and physiological preconditions for a
177 'language-ready brain'. This hypothesis sets out to investigate the phenotypes of both brain and
178 braincase, given their tightly correlated developmental trajectories, in order to draw inferences from
179 skull size and shape changes about the organ that generates language. For instance, Boeckx [44] links
180 the formation of a fronto-parietal-temporal loop that would provide an indirect pathway for language
181 (see, [45-46]) to the expansion of the parietal region, which could have had an impact on the

182 connection between areas of the brain believed to be part of this language loop (i.e. Broca's and
183 Wernicke's regions, see below). The expansion of the parietal region is part of the globularization
184 process within the hominin lineage [47-48] that may have played a role in the formation of a language
185 network. The Globularity hypothesis supports a rather late evolution of the Basic Property within the
186 modern human lineage, as one of its components relies on the hypothesis of self-domestication [49-
187 50] which would have led to the appearance of the modern human phenotype. This is congruent with
188 morphometric studies on encephalization trajectories within the *Homo* lineage, where *H. sapiens*
189 appears to present a different globularization trajectory, possibly triggered by the expansion of the
190 parietals [47], which may have happened late in the evolution of modern humans [51]. However, the
191 unique approach to language evolution consisting of linking the study of brain and neurocranium
192 phenotypes is important for any advances in the field.

193

194 ***Language evolution and palaeoneurology***

195 Palaeoanthropology has long been studying the phenotypes of the calvarium and the brain, through
196 the study of casts of the inner surface of the neurocranium (i.e. endocasts) of fossil specimens (e.g.
197 [52-55]). However, apart from a few exceptions (e.g. [56-58]), the implications of specific anatomical
198 features for language evolution are often overlooked. First, the object of the study in palaeoneurology,
199 the endocast, is a schematic representation of the brain's anatomy, and may not be regarded as a
200 reliable source of information. Its morphology must be considered carefully, especially when discussing
201 function. Secondly, there are few studies combining data on the morphology of the endocast and of
202 the neurocranium. To address the former, Kochiyama and colleagues [59] estimated the possible shape
203 of the actual brain of fossil Neandertals and Early *H. sapiens* in order to compare it with the brain
204 morphology of living populations. Their results confirmed that both Early and extant *H. sapiens*
205 presented a larger cerebellum than the Neandertals [60]. The cerebellum is linked to higher cognition,
206 including language [61-62], and the morphological differences identified between the two species may
207 indicate distinct language faculties. Gunz and colleagues [63] went further by deriving an index of
208 endocranial shape based on the actual morphologies of living people's brains using MRI scans. They
209 then estimated this shape index in fossil specimens and compared it with the shape of the
210 neurocranium and with gene expression data. Their results show that introgressed Neandertal alleles
211 correlate with reduced globularity of the endocranium shape in modern humans, thus demonstrating
212 the potential of their approach. Nevertheless, clarifying the correlation between morphology and
213 function will require further work, and traditional approaches in palaeoneurology should also be
214 considered as they can bring interesting insights regarding language evolution.

215 These approaches rely on the study of areas of the brain that are traditionally identified as playing a
216 part in the classic language loop: the Wernicke-Geschwind model [64-65]. This model describes how
217 different areas of the brain are involved in language comprehension and in language production [66].
218 One of the major issues regarding the Wernicke-Geschwind model lies in the fact that the definitions of
219 the regions involved in this language loop are still much debated and the usefulness of the model itself
220 is sometimes questioned. For instance, Tremblay and Dick [67] showed that scientists did not agree on
221 the actual anatomical definition of the Broca and Wernicke areas. They conducted a survey in which
222 scientists were asked to choose between seven different definitions for each area. While 73% of the
223 scientists recognised Broca's area in two similar definitions, four definitions of the Wernicke area were

224 needed to reach a similar percentage (i.e. 70%, see Fig. 1). Alternatives to this model are, however,
225 not easy to implement (see, for instance, the fronto-parietal-temporal loop discussed by Boeckx [44]),
226 while the anatomical regions referred to in the Wernicke-Geschwind model can be linked to well-
227 known areas of the brain as defined by Brodmann [68]. Broca's area generally encompasses areas 44
228 and 45, while Wernicke's area most often refers to area 39, part of areas 40 and 22. In
229 palaeoneurology, Broca's area may cover approximately the morphology of the third frontal
230 convolution (i.e. 3Fc), which encompasses areas 44 and 45 as part of area 10. Wernicke's area is more
231 difficult to define on endocasts, but part of it, the angular and supramarginal gyri, correspond to
232 Brodmann's areas 39 and 40 respectively and can be identified (see, Fig. 1 and [54, 56, 69]). The
233 development and definition of the 3Fc and of the angular and supramarginal gyri as observed in
234 palaeoneurology correspond to a certain extent to the most common definitions of the Broca and
235 Wernicke areas (see Fig 1 and [67]). Therefore, and despite the current debates on the Wernicke-
236 Geschwind model [67], those anatomical regions and their bilateral variations as observed on
237 endocasts remain the most direct source of anatomical information for palaeoanthropologists
238 discussing language evolution in fossil populations.

239

240

Figure 1

241

242 Mounier and colleagues [70] used parsimony to analyse a coded morphological database of fossil
243 hominins from the genus *Homo* which considered both ecto and endocranial morphologies. The aim
244 of the analysis was to test whether the anatomy of the endocast contributed to the phylogenetic
245 differential definition of *H. neanderthalensis* from *H. sapiens*. However, the morphological features
246 identified as responsible for the separation of the two species are mostly located on the ectocranial
247 and not on the endocranial surface. Amongst the 35 endocranial features considered in the study, 10
248 are related to either Broca (characters #14 -Definition and development of the relief of the head of
249 3Fc, #15 -Definition and development of the relief of the foot of the 3Fc, #16 -Orientation of the
250 anterior and posterior ramus of the Sylvian valley, #17 -Lateral development of the pars triangularis,
251 #18 -Sagittal development of the pars triangularis, #19 -Maximum length position between pars
252 triangularis, and #20 -Position of the base of the pars triangularis relative to the temporal pole) or
253 Wernicke areas (#22 -Definition and projection of the supra-marginal gyrus, #23 -Form of the supra-
254 marginal gyrus, #24 -Definition of the lobule of the angular gyrus). None of the endocranial characters
255 considered in the cladistic analysis were identified as a full apomorphy for the Neandertal and *H.*
256 *sapiens* clades, but four, #1 (cranial capacity), #16, #22 and #30 (position of the occipital lobes), are
257 apomorphies for both clades. Focusing on the 10 characters that describe morphologies linked to the
258 language loop, we note that some are variable within and outside taxa of the genus *Homo*, but others
259 mark the emergence of important clades. For instance, three characters describing the 3Fc, hence
260 Broca's area (i.e. #14 well-developed head of the third frontal convolution, #16 upward and frontward
261 orientation of the anterior and posterior ramus of the Sylvian valley, and #17 well-developed *pars*
262 *triangularis*), are newly emerged morphological features that separate Neandertals, modern humans
263 and their last common ancestor from *H. erectus sensu lato* and most of the Middle Pleistocene fossils
264 (Fig. 2). This is also true for Wernicke's area: both the lobule of the angular gyrus (#24) and the
265 supramarginal gyrus (#22) become strongly developed and well defined just before the split between

266 Neandertals and modern humans. A recent study [71] found that the area of the endocast where both
267 features can be observed appears slightly more spread out in *H. sapiens*. However, they did not study
268 the angular and supramarginal gyri in detail but focused instead on the shape of the parietal lobe.
269 Moreover, a well-defined and projected supramarginal gyrus constitutes a true synapomorphy for
270 both the Neandertal and modern human clades (Fig. 2). The definition and development of the relief
271 of the head of 3Fc (#14), the lateral development of the pars triangularis (#17), the maximum length
272 position between pars triangularis (#19) and the definition of the lobule of the angular gyrus (#24) are
273 not true synapomorphies in this analysis, as they undergo reversion in individual specimens within the
274 Neandertal (i.e. Gibraltar 1, Spy 1 and Saccopastore 1) and *H. sapiens* (i.e. Hofmeyr) clades. Those
275 reversions prevent morphologies that could yield information regarding the language loop from
276 appearing as derived features common to Neandertals and modern humans. However, it should be
277 noted that the study did not focus on these particular anatomical traits, and that the endocast sample
278 was not chosen for this purpose. More specimens could have been added to the study if it had focused
279 on morphologies linked to the language loop. Instead, the state of preservation of the endocasts
280 considered by Mounier and colleagues [70] is sometimes unsatisfactory, for instance the left side of
281 the calvarium of Hofmeyr and Gibraltar 1 is virtually absent, and the reported observations of
282 characters #14 (definition and development of the relief of the head of 3Fc), #17 (lateral development
283 of the pars triangularis), #19 (maximum length position between pars triangularis) and #24 (definition
284 of the lobule of the angular gyrus) are necessarily based on some degree of interpolation. Therefore,
285 these reversions should not prevent us from highlighting the underlying patterns, which show the
286 appearance, throughout the Middle Pleistocene hominin fossil record, of anatomical features related
287 to areas of the brain which have been described as playing a role in language [66]. Finally, Mounier
288 and colleagues [70] identify an additional character which is not a true synapomorphy, but which plays
289 a role in the definition of the modern human and the Neandertal clades. Character #33 defines the size
290 of the sulcus separating the cerebellar lobes, and in most Neandertals the sulcus is wider than in most
291 modern humans. It is linked to higher cognition, including language [61-62], in spite of not being part
292 of the classic language loop. This indicates a possible increase in the size of the cerebellar lobes in
293 modern humans [59-60], which could have had an impact on *H. sapiens* language faculties (see, [59,
294 72]).

295

296

Figure 2

297

298 It is interesting to note that many of the characters identified in the sequence of appearance, during
299 the Middle Pleistocene, of anatomical features related to the language loop on hominin endocasts are
300 focused on the 3Fc (i.e. #14, 16, 17 and 19). In 2014, Balzeau and colleagues [56] quantified and
301 analysed the bilateral variation in size and shape of the 3Fc within *Pan*, *Australopithecus* and *Homo*
302 specimens (including an expanded Neandertal sample, see Fig. 3): the study demonstrated that the
303 'Broca's cap' identified in hominins was due to a size reduction of the 3Fc in the left hemisphere when
304 compared to the right one. The left 3Fc is indeed shorter but presents a similar width making its shape
305 more compact, hence increasing its morphological distinctiveness. We have expanded our Neandertal
306 samples since our original study [56]. Figure 3 presents the comparison of the size of the third frontal
307 convolution and the endocranial volume, expressed respectively as their square-root and their cube-

308 root. In addition, the mean surface (in mm²) of this anatomical area in the Neandertal sample (167.7,
309 SD=32.7, N=11) is larger than the ones observed in both fossil *Homo sapiens* (133.5, SD=30.6, n=8) and
310 in the *Homo erectus* sample (110.6, SD=24.4, N=12). The small sample sizes of the groups analysed
311 make it difficult to identify statistical correlations within our data. Nevertheless, the observed global
312 variation throughout human evolution, as illustrated by these mean values and by the distribution of
313 the specimens for each sample in Figure 3, appears to show a size gradient for this anatomical area
314 between hominin species. When only the hominin sample is considered, there is a significant
315 correlation between 3Fc and the endocranial volume (RMA regression, $r=0.19$, $p=0.008$). Moreover,
316 the gradient of the degree of asymmetry as seen directly on the endocasts and partly observed through
317 morphometric data on small fossil samples [56], i.e. the distinctiveness of the morphology of the 3Fc
318 on the left hemisphere, sets Neandertals and modern humans apart from the rest of the sample. The
319 sparseness of the fossil record prevents us from performing a more detailed comparative
320 morphometric analysis of the departure from symmetry of the third frontal convolution in hominin
321 species. Nevertheless, our morphometric data showing the increase in size of this anatomical area in
322 recent hominin species concords with the repeated observation of a well-defined Broca's area in *H.*
323 *sapiens*, Neandertals and a few Middle Pleistocene fossils (i.e. *H. heidelbergensis sensu lato*) when
324 compared to other fossil hominins and *Pan* specimens [56]. Although these results should not be
325 interpreted as directly inferring speech capacities, nor as a direct characterisation of the functional
326 area related to speech, they are nevertheless based on morphological observations which constitute
327 the best available proxy for analysing Broca's cap in fossil hominins [56, 69]. Similarly, and as we
328 demonstrated above, other anatomical features of the endocast appear to be poorly delimited in
329 hominins or even absent in great apes [54-55]. In particular, the reliefs of the angular and
330 supramarginal gyri are only identifiable in Neandertals, modern humans and some Middle Pleistocene
331 fossils [54, 70]. Their definition is too faint to allow any reproducible quantification on endocasts and
332 these characters were not considered by Balzeau and colleagues [56].

333

334

Figure 3

335

336 Therefore, both analyses of the endocast morphology – through different methodological approaches
337 – identify a clear separation of modern humans and Neandertals from other hominid species, despite
338 known differences between these taxa (e.g. the relative contribution of the frontal, parieto-temporal
339 and occipital lobes [73]). In this context, the morphologies responsible for such a split in the hominid
340 clade are linked to the classic Wernicke-Geschwind model and it could be argued that they form a
341 morphological substrate of characteristics present in both Neandertals and modern humans that are
342 possibly linked to Chomsky's Basic Property for language. Indeed, the 3Fc and the angular gyrus have
343 been repeatedly associated with language processing, one controlling for muscles related to speech
344 [74] and the other having a role in the transformation of visual representations into an auditory code
345 [75]. The function of the supramarginal gyrus, and despite its position on the brain (Brodmann's area
346 40), is less clear; it has nevertheless been described as being involved with language comprehension
347 [76]. The only highlighted difference between Neandertals and modern humans concerns the
348 cerebellum which, from about 100,000 years ago, gradually became larger in *H. sapiens* [51, 59, 70,
349 72]. The cerebellum plays a role in higher cognition and possibly language, but is not part of the classic

350 language loop and it is unclear whether it influenced language faculties. Nevertheless, the
351 development of these anatomical features throughout the Middle Pleistocene and their presence in
352 both *H. sapiens* and *H. neanderthalensis* suggest that both species would have had similar language
353 faculties despite the fact that their general brain structure presents anatomical differences.

354

355 ***Origin of language – more questions than answers***

356 The literature review presented in this paper shows a complex picture of the evolution of language. It
357 remains difficult to decipher which hominin population developed the Basic Property which gave
358 hominins modern language, and when. The study of endocasts, which is often overlooked when
359 discussing the evolution of language, may nevertheless bring new insights to the debate. The
360 identification of an endocranial anatomical substrate possibly linked to language and common to *H.*
361 *neanderthalensis*, *H. sapiens* and their ancestor [56, 70] must be discussed within the wider debate
362 surrounding the origin of language. In recent years, palaeogenomics has profoundly transformed the
363 status of *H. neanderthalensis*, which now stands much closer to modern humans, given the
364 accumulating evidence regarding interbreeding between the modern and Neandertal lineages [25, 34-
365 36]. Moreover, evidence of complex behaviour (e.g. advanced modern behaviour [12]) outside of the
366 modern human clade [26, 29-30], along with experimental studies showing possible co-evolution of
367 tool-knapping and language faculties [41-42], supports the possibility of common, or at least close,
368 language faculties between both lineages.

369 However, one should keep in mind that the same evidence is sometimes used to demonstrate the
370 exact opposite: genomics data, despite interbreeding, show that the lineages were separated [23],
371 evidence of advanced modern behaviour outside of the modern clade is much discussed [31] and
372 experimental studies on tool-knapping may reach a different conclusion [43]. This is also why
373 palaeoneurology can be of importance in helping to resolve the debate surrounding the origin of
374 language, even though demonstrating the presence of the morphological traits required to develop
375 the Basic Property for modern language does not demonstrate the presence of the ability itself, as it
376 cannot be observed in the fossil record (see for instance [77]).

377 The origin of language remains a difficult topic, but new approaches [59, 63], and the study of both the
378 calvarium and endocranial morphologies, as advocated by Boeckx [44] may bring a more robust answer
379 in the near future, and palaeoneurology through the study of endocasts will certainly play a role in
380 this.

381

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401

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- 556

557 **Figure legends**

558

559 **Figure 1. (2 columns)**

560 (a to f) Most common anatomical definitions of Wernicke's area (a to d) and Broca's area (e and f) on the brain.
561 These definitions of each area have been endorsed by 70% (Wernicke, respectively 26%, 23%, 12% and 9%) and
562 73% (Broca, respectively 50% and 23%) of the respondents to the Tremblay and Dick survey [67]. (g) Anatomical
563 region of the endocrâne linked with Broca's area (green): 3Fc (third frontal convolution) and Wernicke's area (violet):
564 A. gyrus (angular gyrus) and S. gyrus (supramarginal gyrus) on the endocrâne of a modern Australian (AUS047,
565 Duckworth Collection). Despite the uncertainties regarding the definitions of both areas on the brain, the use of the
566 3Fc, angular and supramarginal gyri appears as the most reasonable proxy to observe changes related to those
567 areas in palaeoneurology. / (a à f) Définitions anatomiques les plus courantes de la zone de Wernicke (a à d) et de
568 la zone de Broca (e et f) sur le cerveau. Ces définitions de chaque zone ont été approuvées par 70% (Wernicke,
569 respectivement 26%, 23%, 12 % et 9%) et 73% (Broca, respectivement 50% et 23%) des répondants à l'enquête
570 de [67]. (g) Région anatomique de l'endocrâne liée à la zone de Broca (vert) : 3Fc (troisième circonvolution frontale)
571 et région de Wernicke (violet) : A. gyrus (gyrus angulaire) et S. gyrus (gyrus supramarginal) sur l'endocrâne d'un
572 Australien moderne (AUS047, Duckworth Collection). Malgré les incertitudes concernant les définitions des deux
573 zones du cerveau, l'utilisation de la 3Fc, des gyri angulaire et supramarginal apparaît comme le proxy le plus
574 raisonnable pour observer les changements liés à ces zones en paléoneurologie.

575

576 **Figure 2. (2 columns)**

577 Cladogram of the genus *Homo* modified from Mounier and colleagues [70] presenting the most important changes
578 along the branch of the tree (true synapomorphies $-RI=1$, and characters with $RI>0.8$) along with the appearance
579 of derived features related to the classic Wernicke-Geschwind model throughout the Middle Pleistocene and before
580 the split between the modern and Neandertal lineages (#14 and 17 respectively $RI = 0.667$ and $RI = 0.75$ due to
581 reversions). #33 is not linked to the language loop but has been linked to the evolution of language (e.g. [59]). The
582 endocrâne used to display the morphological features are, from top to bottom: Kabwe 1 (oblique view, left side),
583 Kabwe 1 (norma lateralis), Irhoud 2 (norma lateralis) and AUS 047. Character descriptions: #1, Cranial capacity;
584 #7, Number of ramifications of the middle meningeal system; #14, Definition and development of the relief of the
585 head of 3Fc; #16, Orientation of the anterior and posterior ramus of the Sylvian valley; #17, Lateral development of
586 the pars triangularis; #19, Maximum length position between pars triangularis; #20, Position of the base of the pars
587 triangularis relative to the temporal pole; #22, Definition and projection of the supra-marginal gyrus; #24, Definition
588 of the lobule of the angular gyrus; #30, Position of the occipital lobes; #33, Width of the sulcus separating the
589 cerebellar lobes; #50, Presence of a tuber parietale; #55, Form of the outline of the planum occipital in norma
590 occipitalis; # 56, Presence of a suprainiac fossa; #57, Definition of the torus occipitalis transversus; #60, Form of
591 the outline of the superior border of the temporal squama. / Cladogramme du genre *Homo* modifié de Mounier et
592 collaborateurs [70] présentant les changements les plus importants le long de la branche de l'arbre (vraies
593 synapomorphies $-RI = 1$, et caractères avec $RI > 0,8$) ainsi que l'apparition de caractéristiques dérivées liées au
594 classique Modèle de Wernicke-Geschwind tout au long du Pléistocène moyen et avant la scission entre les lignées
595 modernes et néandertaliennes (# 14 et 17 respectivement $RI = 0,667$ et $RI = 0,75$ en raison des inversions). # 33
596 n'est pas lié à la boucle linguistique mais a été lié à l'évolution du langage (e.g. [59]). L'endocrâne utilisé pour
597 afficher les caractéristiques morphologiques est de haut en bas: Kabwe 1 (vue oblique, côté gauche), Kabwe 1
598 (norma lateralis), Irhoud 2 (norma lateralis), et AUS 047. Descriptions des caractères : # 1, Capacité crânienne; #
599 7, Nombre de ramifications du système méningé moyen; # 14, Définition et développement du relief de la tête de
600 la troisième circonvolution centrale ; # 16, Orientation du ramus antérieur et postérieur de la scissure de Sylvius; #
601 17, Développement latéral de la pars triangularis; # 19, Position de la longueur maximale entre les pars triangularis;
602 # 20, Position de la base de la pars triangularis par rapport au pôle du lobe temporal ; # 22, Définition et projection
603 de la supra- gyrus marginal ; # 24, Définition du lobule du gyrus angulaire ; # 30, Position des lobes occipitaux ; #
604 33, Largeur du sulcus séparant les lobes cérébelleux ; # 50, Présence d'un tuber parietale ; # 55, Forme du contour
605 du planum occipital in norma occipitalis ; # 56, Présence d'une fosse suprainiacque ; # 57, Définition du torus
606 occipitalis transversus ; # 60, Forme du contour du bord supérieur de l'écaille de l'os temporal.

607

608 **Figure 3. (1.5 columns)**

609 Bivariate plot of the size of the third frontal convolution (square root, noted 3Fc, in mm) and of the endocranial
610 volume (cube root, noted Endo V, in mm) in *Pan paniscus* (triangles), *Pan troglodytes* (inverted triangles), *H.*
611 *sapiens* (circles), fossil *H. sapiens* (black circles), fossil hominins (black diamonds: T: Taung, 17k: KNM-WT 17000,
612 1470: KNM-ER 1470, 1813: KNM-ER 1813, 3733: KNM-ER 3733, 3883: KNM-ER 3883, 15k: KNM-WT 15000, OH
613 9, D: Dmanisi 9002, T2: Trinil 2, S2: Sangiran 2, S17: Sangiran 17, M: Mojokerto, Ng7: Ngandong 7, Ng12:
614 Ngandong 12, Sm3: Sambungmacan 3, S3: Zhoukoudian Ckn.E 1.PA.16, S12: Zhoukoudian Ckn.L 2.PA.100, LB
615 1: Liang Bua 1, SV: Skhūl V, Ar: Arago, B: Bodo, K: Kabwe 1, JB1: Jebel Irhoud 1, P: Petralona, S: Salé) and
616 Neandertals (red circle, F: Feldhofer, LC: LaChapelle-aux-Saints 1, LF1: La Ferrassie 1, Gu: Guattari, Gi: Gibraltar,
617 K3: Krapina 3, Q5:La Quina H5, Sa: Saccopastore, TC1: Tabun C1, TT: Teshik Tash, , SII: Spy 10). Modified from
618 [56]. / *Graphique bivarié de la taille de la troisième circonvolution frontale (racine carrée, noté 3Fc) et du volume*
619 *endocrânien (racine cubique, noté Endo V) chez Pan paniscus (triangles), Pan troglodytes (triangles inversés), H.*
620 *sapiens (cercles), H. sapiens fossiles (cercles noirs), hominines fossiles (diamants noirs : T : Taung, 17k : KNM-*
621 *WT 17000, 1470 : KNM-ER 1470, 1813 : KNM-ER 1813, 3733 : KNM-ER 3733, 3883 : KNM-ER 3883, 15k : KNM-*
622 *WT 15000, OH 9, D : Dmanisi 9002, T2 : Trinil 2, S2 : Sangiran 2, S17 : Sangiran 17, M : Mojokerto, Ng7 :*
623 *Ngandong 7, Ng12 : Ngandong 12, Sm3 : Sambungmacan 3, S3 : Zhoukoudian Ckn.E 1.PA.16, S12 : Zhoukoudian*
624 *Ckn.L 2.PA.100, LB 1 : Liang Bua 1, SV : Skhūl V, Ar : Arago, B : Bodo, K : Kabwe 1, JB1 : Jebel Irhoud 1, P :*
625 *Petralona, S : Salé) et Néandertaliens (cercle rouge, F : Feldhofer, LC : La Chapelle-aux-Saints 1, LF1 : La*
626 *Ferrassie 1, Gu : Guattari, Gi : Gibraltar, K3 : Krapina 3, Q5 : La Quina H5, Sa : Saccopastore, TC1 : Tabun C1,*
627 *TT : Teshik Tash, SII : Spy 10). Modifié à partir de [56].*