

1 A dual larynx motor networks hypothesis

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Abstract

22

23 Humans are vocal modulators par excellence. This ability is supported in part by the dual representation of the
24 laryngeal muscles in the motor cortex. Movement, however, is not the product of motor cortex alone but of a
25 broader motor network. This network consists of brain regions which contain somatotopic maps that parallel
26 the organisation in motor cortex. We therefore present a novel hypothesis that the dual laryngeal
27 representation is repeated throughout the broader motor network. In support of the hypothesis we review
28 existing literature which demonstrates the existence of network-wide somatotopy, and present initial evidence
29 for the hypothesis' plausibility. Understanding how this uniquely human phenotype in motor cortex interacts
30 with broader brain networks is an important step toward understanding how humans evolved the ability to
31 speak. We further suggest that this system may provide a means to study how individual components of the
32 nervous system evolved within the context of neuronal networks.

33 Humans are vocal modulators par excellence. This is usually characterised as the capacity for Vocal Production
34 Learning (VPL), which is the ability to learn to produce novel vocalisations [1]. Few species of mammals, such as
35 cetaceans and bats [2,3], have displayed strong VPL abilities, and none of these species has a close phylogenetic
36 relationship to humans. Monkeys are particularly weak vocal learners [4]. Non-human apes appear to have
37 intermediate VPL, being able to learn certain kinds of limited vocal behaviour from humans [5,6], though there
38 is little evidence of this behaviour in the wild [7]. The human VPL capacity is attributable in part to specialised
39 adaptations in motor cortex that grant voluntary control over the voice. However, complex behavioural abilities
40 such as VPL are not the product of the motor cortex alone but are an emergent property of their interaction
41 with a broader motor network.

42 Human motor cortex is composed of a band of specialized grey matter along the precentral gyrus and the
43 anterior bank of the precentral sulcus, which is the main source of motor output from the central nervous
44 system. Penfield's seminal neurosurgical studies [8] described the conspicuous somatotopy of the human
45 primary motor cortex (M1), in which the muscles of the foot are represented at one end of the somatotopic map
46 and the muscles of the head represented at the other end [9–11]. Similar somatotopic maps have been
47 described throughout the network of brain areas that control movement, including the cerebellum,
48 supplementary motor area (SMA), basal ganglia (BG), and the middle cingulate cortex (MCC) [12–15].

49 Penfield's original mapping was uncertain of the somatotopic location of the laryngeal muscles, which control
50 the sound source of the voice. More recent neurosurgical [16,17], molecular genetic [18], and brain imaging
51 studies [19–24] provide compelling evidence that the laryngeal muscles are unusual in being controlled by two
52 distinct loci within the human motor cortex. While other effectors such as the digits of the hand may also have
53 multiple representations in motor cortex, these tend to be contiguous and may represent either subdivision at
54 a finer scale (i.e., muscles of flexion vs. extension) or correlated movements with nearby muscles that exert a
55 common influence over shared joints [25–28]. In contrast, the dual laryngeal representations are non-
56 contiguous, being located at opposing ends of the orofacial motor zone - which is a marked deviation from the
57 single larynx area observed in other primates [29,30]. The two representations have therefore been referred to
58 as dorsal and ventral laryngeal motor cortex (dLMC, vLMC). This adaptation has clear implications for the
59 evolution of speech since the neural control of the larynx supports one of the requirements of spoken language
60 [31,32], namely a high degree of control over the voice source beyond the capabilities of other primates [4,33].

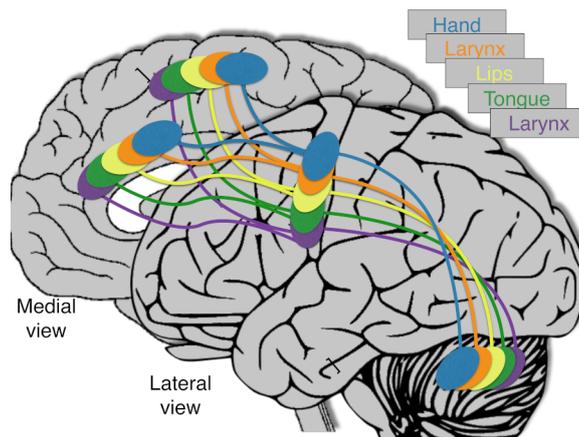
61 Despite extensive searches spanning new world monkeys (primarily *Macaca mulatta*), old world monkeys
62 (primarily *Saimiri sciureus*), and all extant genera of great apes including Chimpanzees (*Pan troglodytes*),
63 Orangutans (*Pongo* sp.), and Gorillas (*Gorilla* sp.) [29,34,35], humans appear to be the sole primate with the
64 neural trait of dual larynx representation, and much has been written about the possible implications of this
65 phenotype for the evolution of speech [36–41]. Here, we outline a novel hypothesis that this human phenotype
66 is not restricted to the motor cortex but extends throughout a network of somatotopically-arranged brain areas
67 that comprise the motor system, including the cerebellum, SMA, BG, and MCC and the axonal projections
68 between these regions.

69 **Hypothesis: Dual larynx motor networks**

70 We hypothesize that each motor region contains two representations of the laryngeal muscles within their
71 respective somatotopic maps: one between the hand and the orofacial muscles, and a second at the end of the
72 orofacial representation (see Figure 1). This hypothesis is supported by the observations that i) somatotopic
73 maps throughout the motor network follow a similar ordering of representations from foot to face and ii) nodes
74 in the motor network project to one another homotopically, suggesting that motor regions beyond motor cortex
75 must have target zones that receive the projections from the dLMC and vLMC. Somatotopic maps in different
76 regions vary in orientation. For instance, somatotopy proceeds dorso-ventrally in the motor cortex but antero-
77 posteriorly along the medial wall. Therefore, it may not be constructive to use the labels dorsal and ventral
78 larynx areas for somatotopic maps beyond motor cortex. We have therefore adopted the convention of referring

79 to larynx somatotopic regions in the MCC, SMA, cerebellum, and BG as dLMC-related or vLMC-related to denote
80 their respective positions within the somatotopically arranged motor network.

81 An alternative hypothesis is that only the dLMC benefits from the gain in function concomitant with support
82 from the broader motor system. Only dLMC is composed of primary motor cortex, while vLMC is likely to be
83 located in a qualitatively different cytoarchitectonic motor region (see a more detailed discussion below).
84 Moreover, dLMC is a novel phenotype in humans and robustly observed in human functional brain imaging
85 studies, which points towards a prominent role in brain architecture. Therefore, if only one larynx representation
86 is observed in the network of somatotopic maps, then we predict that it will be the dLMC-related locus in a
87 position between the hand and the articular muscles. If this turns out to be the case, it will regardless be
88 important to understand the evolution of the dLMC in the context of a broader motor network.



89

90

91 **Figure 1:** Depiction of the dual laryngeal motor network hypothesis. The middle cingulate cortex,
92 supplementary motor area, and cerebellum are depicted with simplified somatotopic maps for conceptual
93 convenience. The broader motor somatotopy follows the organisation of motor cortex, but with
94 idiosyncratic orientations following a different axis in each brain region (basal ganglia not shown for
95 simplicity). The hypothesised dLMC-related and vLMC-related networks are shown in orange and purple,
96 respectively.

97

98 ***A human-specific phenotype in motor cortex***

99 Compared to other primates, lower motor neurons in the human spinal cord and brainstem receive a far greater
100 proportion of their inputs from neocortex. These connections contribute to the dexterity and behavioural
101 flexibility of our species [42–44]. Included in this abundance of cortical efferents is a direct projection to motor
102 neurons in the nucleus ambiguus [36–40], which is a brainstem motor nucleus that controls the muscles of the
103 larynx. Such a direct cortico-bulbar connection is lacking in monkeys [45], extant but sparse in non-human apes
104 [35], and further elaborated in humans [46,47]. An analogous phenotype distinguishes birds who are strong
105 vocal learners such as songbirds (*order Passeriformes*), humming birds (*order Apodiformes*), and parrots (*order*
106 *Psittaciformes*) from weaker vocal learners [48,49]. Thus, it appears that multiple phylogenetic lineages with
107 strong VPL abilities have converged on similar neurophenotypes with direct efferent projection from upstream
108 motor areas to voice-motor nuclei [50,51].

109 Evidence for the presence of this direct connection between the neocortex and the nucleus ambiguus in humans
110 has come from natural experiments due to cerebrovascular events [46,47], in which large cortical lesions caused
111 the axons of upper motor neurons to degenerate. Tracing the course of these damaged axons against the more

112 intact surrounding white matter allowed the authors to demonstrate the existence of the direct cortico-bulbar
113 pathway. However, these lesions all resulted from cerebrovascular accidents of the middle cerebral artery (MCA)
114 that can result in widespread damage across the speech relevant portions of motor cortex (hence the prevalence
115 of speech-motor and swallowing disorders following MCA infarcts; [52,53]). Thus, lesion studies provide limited
116 information about the cortical source of the direct pathway.

117 Researchers using functional neuroimaging to investigate speech motor control initially presumed that the
118 larynx was represented at the ventral-most extent of primary motor cortex [54], in the location that would be
119 expected from the larynx's position within the throat and proximity to the homologous region in non-human
120 primates [29,55,56]. However, later studies demonstrated that the human brain in fact has two separate
121 representations of the larynx, at either end of the orofacial somatotopic map of the precentral gyrus [19–23].
122 Though the dual larynx representations have not been consistently labelled as such in earlier brain imaging
123 research, it was nonetheless consistently present near the predicted location [54].

124 The dLMC is located in canonical primary motor cortex in Brodmann Area (BA) 4, which is cytoarchitecturally
125 defined as the region containing a high abundance of giant pyramidal neurons in cortical layer V - these
126 pyramidal neurons are the source of the descending motor pathways of the cortico-spinal and cortico-bulbar
127 tracts [57–59].

128 In contrast, the human vLMC is localized to the most ventral segment of the central sulcus or the lateral segment
129 of the anterior subcentral sulcus [17,18,60]. The localisation of the vLMC may be particularly variable due to a
130 high degree of individual variation in the morphology of nearby sulci [60], which may explain why the vLMC
131 escaped notice by many early functional magnetic resonance imaging (fMRI) studies. Unlike its dorsal
132 counterpart, quantitative neuroimaging has also suggested that the vLMC is not located in primary motor cortex
133 [60]. Although no study has both localized the vLMC and performed a cytoarchitectural analysis of the underlying
134 tissue, the location of the vLMC corresponds to BA 43 in the Brodmann atlas. While Brodmann believed that this
135 region most strongly resembled somatosensory cortex based on its cellular composition [57], Vogt believed that
136 it more strongly resembled motor cortex based on the degree of myelination of cortical layer V, which is an
137 indicator of the large myelinated axons that form the efferent motor pathways that carry motor commands to
138 the peripheral nervous system [58,59]. In contrast to the evidence from humans, the larynx representation in
139 non-human primates has been identified in premotor cortex [45], but no separate representation in primary
140 motor cortex has been described. This observation is in line with the theory that primary and premotor cortex
141 contain one single somatotopic map spanning cytoarchitectural zones [61].

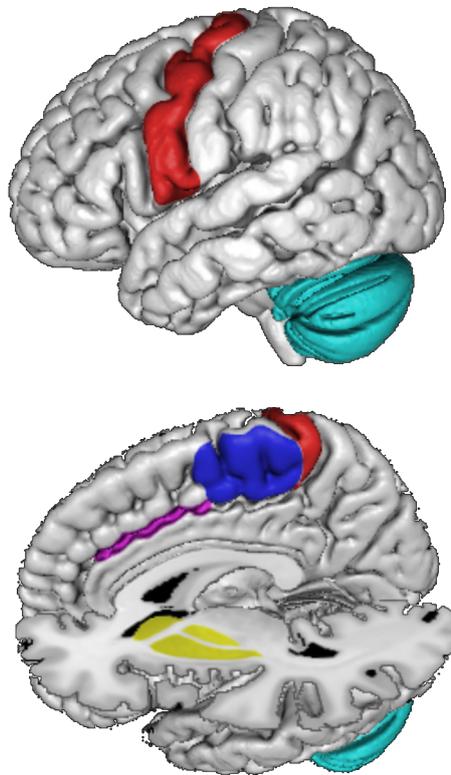
142 Whether the dLMC and vLMC make separate functional contributions to voice motor control, and what those
143 might be, remains an active area of research. Identifying behaviours that activate one of these regions over the
144 other is challenging, given that the dLMC may be easier to detect than the vLMC. However, electrical stimulation
145 studies in humans have observed that stimulation of the dLMC elicits a vowel-like vocalisation, while stimulation
146 of the vLMC elicits grunting [8,16,62]. The dLMC is bounded posteriorly by a putative larynx sensory cortex on
147 the posterior central gyrus. This Larynx Sensory Cortex (LSC) is larger and activates more strongly in professional
148 Opera singers than non-singers, suggesting that these individuals make greater use of proprioceptive feedback
149 to guide highly skilled motor control [63,64].

150 It is not clear whether the vLMC is bounded posteriorly by a sensory zone, analogous to the dLMC. However, the
151 vLMC may itself have some sensory function not matched by its dorsal counterpart. While the vLMC has
152 primarily been localized as a correlate of vocal motor behaviour [17,20–23], activation of this region has also
153 been observed in response to sensory stimulation of the larynx by applying an external puff of air [65].
154 Somewhat paradoxically, anaesthetising the larynx does not reduce vLMC activation [19]. A recent cortical
155 parcellation based on multi-modal brain imaging confirms that this region is distinct from both primary motor
156 and primary somatosensory cortex and suggests a combination of sensorimotor functions [66]. Further research
157 on the relationship between the vLMC and the broader motor system may shed further light on its function.

158 ***The motor system and its somatotopic maps***

159 Motor cortex is the main source of output from the motor system. However, motor control is not the product
 160 of M1 alone, but requires a broader motor network that supports complex voluntary movements. This network
 161 includes brain regions such as the basal ganglia, supplementary motor area (SMA), cingulate cortex, and the
 162 cerebellum (See Figure 2). In this section we review the existing evidence that each of these brain regions
 163 contains its own somatotopic map akin to motor cortex. Intriguingly, the somatotopic maps in the brains of
 164 individuals born without one hand undergo a neuroplastic remapping that may occur in parallel across multiple
 165 brain regions within this network [67], which may suggest that somatotopic maps across the motor network are
 166 driven by common developmental mechanisms.

167



168 **Figure 2:** Major components of the motor network. A) Lateral surface view of MNI152 atlas brain, b)
 169 medial surface view with digital transections at $x=0$ and $z=0$ showing the motor cortex (red), middle
 170 cingulate cortex, (Pink), basal ganglia (yellow), supplementary motor area (blue), and cerebellum (cyan).

171

172 ***Motor Cortex***

173 The somatotopic map in primary motor cortex (BA 4) is well characterized and is sometimes referred to as a
 174 homunculus in the brain after its reflection of the physical body. The muscles of the foot are located at one end
 175 of the somatotopic map and the muscles of the head located at the other [9–11]. For conceptual convenience,
 176 zones within these somatotopic maps are often referred to by simplistic labels based on the effectors with which
 177 they are most strongly associated (e.g., $M1_{hand}$ for the predominantly hand controlling zone). However, at a finer
 178 spatial scale these zones are composed of tessellated fields and individual effectors can be controlled by
 179 discontinuous but clustered representations [68]. These representations have been described as either encoding

180 the states of muscles [69,70], the spatial properties of movement vectors [71,72], or ethologically meaningful
181 combinations of effectors that pattern whole movements [61,73]. These levels of encoding are not mutually
182 exclusive [74].

183 Distinct functional contributions of the dLMC and vLMC remain elusive [75,76]. However, electrical stimulation
184 of these regions in the human brain elicit vowel sounds and grunting, respectively [8,16,62]. These separate
185 behaviours produced by the same ensemble of muscles is suggestive of distinct ethological functions of the
186 dLMC and vLMC, though further evidence is required. It is hoped that an understanding of the connections of
187 these two regions with the broader motor system will begin to elucidate their respective functions.

188 *Cortico-cerebellar loops*

189 The cerebellum maintains a broad pattern of connections throughout the brain and has some part in a wide
190 range of central nervous system function [77,78]. Among these functions the cerebellum plays a critical role in
191 making online adjustments that fine-tune movements. The cerebellum receives an efferent copy of motor
192 commands from M1 and compares expected proprioceptive feedback with observed proprioceptive feedback
193 [79–82]. The difference between intended and observed movements produces an error signal that is returned
194 to M1 to implement online corrections to ongoing movements.

195 The cerebellum contains at least two separate somatotopic maps [83]. The anterior lobe of the cerebellum
196 contains a somatotopic map with the foot located antero-dorsally and the head postero-ventrally, while the
197 posterior lobe has a somatotopic map with the face represented postero-dorsally and the foot antero-ventrally
198 [84–88]. More recent evidence suggests that the anterior lobe may contain an additional somatotopic map along
199 lateral-to-medial axis [89], though further replication is required.

200 *Cortico-striatal loops*

201 The supplementary motor area and basal ganglia form part of the cortico-striatal loop which is involved in motor
202 learning [90,91]. The motoric processing loop of the basal ganglia forms a circuit through its various component
203 nuclei including the putamen (a part of the striatum for which this circuit is named), globus pallidus, subthalamic
204 nucleus, and substantia nigra, which sends outputs via the thalamus back to the cortex [92]. This circuit receives
205 dopaminergic inputs from reward centres to mediate reinforcement learning [93,94].

206 The SMA and a region anterior to it called the pre-SMA both contain a distinct set of motor representations,
207 with a clear somatotopy at least in SMA (Picard and Strick 1996). This somatotopic map spans from the legs
208 posteriorly to the orofacial muscles anteriorly [13,95–98]. The putamen receives inputs from both M1 and the
209 SMA and these inputs retain the somatotopic organization of their sources [15]. Inputs from M1 and the SMA
210 innervate distinct portions of the putamen and it has therefore been suggested that the putamen may contain
211 two parallel somatotopic maps [99]. Somatotopy may also be retained throughout the entire cortico-striatal
212 loop [100], including the globus pallidus [101,102] and thalamus [103] though on a spatial scale that is
213 inaccessible to current non-invasive brain imaging methodologies.

214 *Cingulate cortex*

215 The cingulate cortex is nested in the medial surface of the brain following the curvature of the corpus callosum.
216 This brain region combines cognitive, affective, and motoric functions for the motivation and initiation of goal-
217 directed behaviours [104–107]. It is divided grossly into the anterior, middle, and posterior cingulate cortex
218 (ACC, MCC and PCC, respectively). The MCC has approximate boundaries anteriorly at the genu of the corpus
219 callosum and posteriorly at the marginal sulcus [108–110]. This macro-anatomically defined region itself
220 comprises multiple cytoarchitecturally defined subregions. Of these, area 24c is in the cingulate sulcus, which
221 contains a series of three cingulate motor areas [12,111]. These cingulate motor areas are all involved in action
222 selection, with increasingly more complex movement patterns involving the more anterior divisions [112–114].

223 The middle cingulate sulcus contains three distinct motor regions [12,111] each of which contains a somatotopic
 224 map with the feet represented posteriorly and the orofacial muscles anteriorly [12,114–118]. Somatotopic
 225 mapping in the cingulate cortex may be further complicated by the high degree of anatomical variability of this
 226 region, since in a subset of human brains the motor regions of the cingulate sulcus are divided across separate
 227 cingulate and paracingulate sulci [12,119–121].

228 *White matter somatotopy*

229 The descending motor pathways which form the corticobulbar and corticospinal outputs from the motor system
 230 maintain a clear somatotopic map that is observable in white matter [122–125]. This somatotopy facilitates the
 231 mapping of upper motor neurons in primary motor cortex onto their corresponding lower motor neurons in the
 232 brainstem and spinal cord. Likewise, the somatotopic maps of M1 in either hemisphere project preferentially to
 233 homotopic sites in the opposite hemisphere, retaining ordered somatotopy in the white matter of the corpus
 234 callosum [126,127]. At least some of the individual brain regions that make up the motor network also display
 235 preferential functional connectivity between somatotopically analogous regions [87,128], maintaining
 236 somatotopy in the white matter pathways that connect them [115,129].

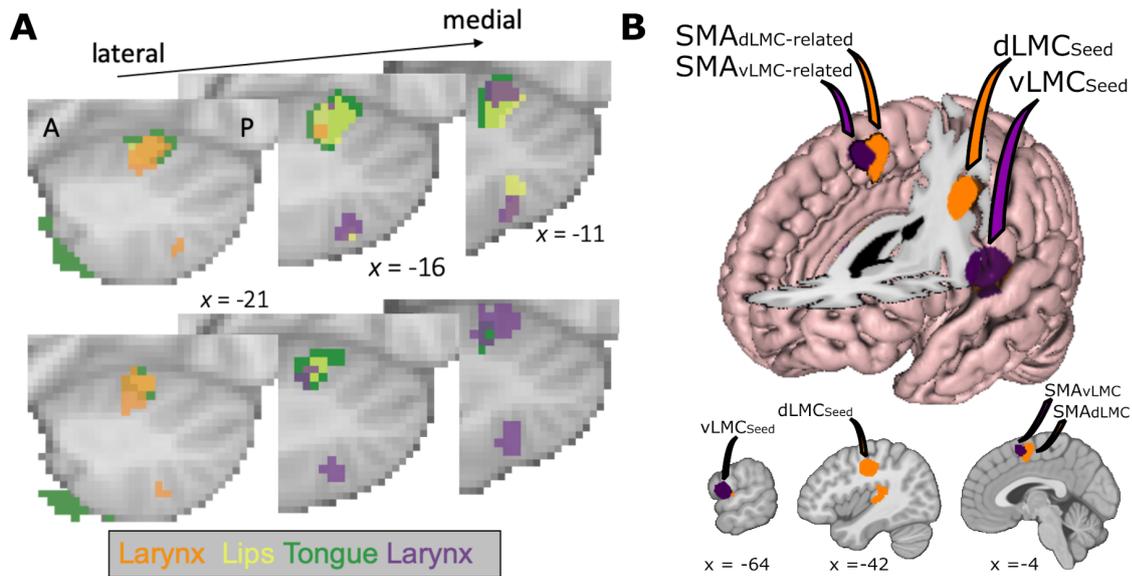
237 ***Initial evidence for dual laryngeal representations in the cerebellum and SMA***

238 *Cerebellum*

239 We re-analysed an existing fMRI dataset to test whether two distinct representations of the laryngeal muscles
 240 can be observed in the cerebellum (see [21] for details on data acquisition). The study was approved by the
 241 Central University Research Ethics Committee at the University of Oxford (CUREC, R55787/RE001) in accordance
 242 with the regulatory standards of the Code of Ethics of the World Medical Association (Declaration of Helsinki).
 243 Twenty participants performed speech movements to localize lips, tongue, and laryngeal activity during
 244 vocalization. Participants produced non-linguistic utterances overtly, articulating silently, using an isolated
 245 vowel, or as covert speech. The LMC was then localized using a factorial model comparing overt speech and
 246 vowel production with silent articulation and covert speech. See [21] for a detailed description of the functional
 247 paradigm and analysis.”

248 In addition to conventional group-level statistical activation maps, we derived overlap maps of individually
 249 thresholded and binarized volumetric maps (see Figure 3A for details of analysis). A larynx-lip-tongue-larynx
 250 pattern can be observed along a lateral/anterior-to-medial/posterior axis. The coordinates of these regions are
 251 consistent with lobule VI of the posterior cerebellar lobe [130]. Two distinct activations for the larynx can be
 252 observed at the group level (Figure 3A, top) as well as in individual participants (Figure 3A, bottom). Activations
 253 for the lips and the tongue fall in between the two larynx activations as they do in motor cortex, though at the
 254 present resolution these activations are largely overlapping. The dLMC-related activation is observed antero-
 255 laterally to the articulators while the vLMC-related activation is observed postero-medially. All activations are in
 256 close proximity and within the same anatomical lobule.

257 Our results are most consistent with one continuous somatotopic map in lobule VI of the cerebellum that
 258 contains two distinct laryngeal representations. We note also that additional activations are present at a lower
 259 threshold in the remaining lobules, which may reflect additional somatotopic maps [84–88].



260

261

262 **Figure 3:** Initial evidence for laryngeal motor network somatotopy. A) Cerebellar task activations during
 263 movement of the lips, the tongue and during larynx activity. Shown are sagittal slices of the left
 264 hemisphere (A-P: anterior-posterior). Larynx activity is shown in orange and purple to indicate dLMC- and
 265 vLMC-related activation, though we note that these are correlated activations derived from the same
 266 contrast. Top: Binarized group-level task activations (voxel-wise threshold $z > 4$, $n = 20$). Bottom: Binarized
 267 overlap maps (individual maps: voxel-wise threshold of $z > 3.1$, overlap map: thresholded at $n > 10$
 268 participants). B) Results of ALE meta-analysis from the two LMC seed regions displayed on the MNI152
 269 atlas brain. Top: The surface brain is digitally transected sagittally at $x=0$, axially at $z=10$, and coronally
 270 with an oblique slice following the precentral gyrus. Bottom: Sagittal slices transecting the two see regions
 271 and the SMA. The dLMC-related supplementary motor area (orange) is posterior to the vLMC-related
 272 supplementary motor area (purple) in line with the expected somatotopy of this region.

273

274 *Supplementary motor area*

275 We conducted a meta-analysis of brain imaging studies that activated the dLMC and vLMC to identify brain
 276 regions that are co-activated with each larynx area. We searched the BrainMap database [131] for fMRI studies
 277 that reported activation within a 5 mm radius sphere of the dLMC ($x=-41$; $y=-16$; $z=38$) or the vLMC ($x=-66$; $y=-$
 278 4 ; $z=14$). This search was performed blind to the tasks being performed by the participants and was concerned
 279 only with activation within the seed regions [132]. Coordinate tables in Montreal Neurological Institute (MNI)
 280 space were retrieved from the database on 04/04/2020 (see S1 and S2). This searched yielded 512 foci of
 281 activation across 29 participant groups for the dLMC, and 294 foci across 19 participant groups for the vLMC.
 282 Each set of activation coordinates was analysed using Activation Likelihood Estimation [133–135] using
 283 GingerAle software (v3.0.2) with a cluster-level family wise error rate of $p < 0.01$ computed with 5000
 284 permutations. Results were visualized using Mango (v4.1, Research Imaging Institute, UTHSCSA).

285 The dLMC-related ALE yielded a network of motor and auditory related brain regions including the contralateral
 286 dLMC, the superior temporal gyrus (STG), putamen, cerebellum, and the SMA (see Figure 3B and Table 1). The
 287 vLMC-related ALE yielded a much more restricted network, as expected from the smaller pool of studies in that

288 analysis, including the contralateral vLMC, the insula, and the SMA. Both ALEs revealed co-activation with the
 289 SMA, but at spatially distinct sites. The dLMC-related SMA was posterior to the vLMC-related SMA. This pattern
 290 is consistent with the expected somatotopy of this region and with the previously observed network somatotopy
 291 between the SMA and motor cortex [128,129].

292

dLMC					
Brain Region	Hemisphere	x	y	z	ALE Value
dLMC [seed]	Left	-42	-16	38	0.125
dLMC	Right	46	-12	38	0.045
SMA	Left	-4	0	56	0.041
Putamen	Right	26	0	4	0.032
Cerebellum	Left	-12	-62	-20	0.032
STG	Left	-60	-14	10	0.027
vLMC					
Brain Region	Hemisphere	x	y	z	ALE Value
vLMC [seed]	Left	-64	-4	14	0.098
vLMC	Right	66	-4	22	0.024
SMA	Left	-2	8	58	0.025
Right Insula	Right	42	-6	8	0.024

293

294 **Table 1:** Coordinates of peak likelihoods from ALE meta-analysis for seed regions in the dLMC (upper) and
 295 vLMC (lower). Brain regions are listed along with their x, y, z coordinates in MNI stereotaxic space and
 296 their Activation Likelihood Estimation scores which provide a relative measure of confidence.

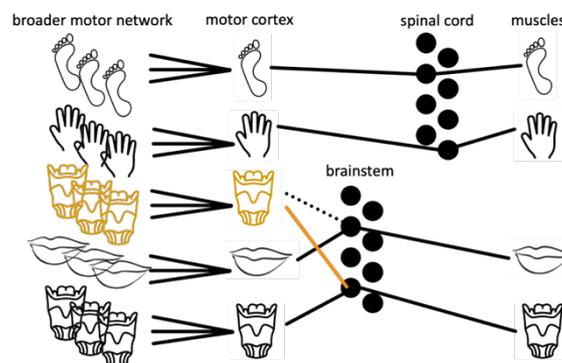
297 *Mechanisms of brain network evolution*

298 We have hypothesized that the human brain has evolved not only a dual representation of the laryngeal muscles
 299 in motor cortex, but a dual laryngeal motor network to support it. However, this broader characterization of the
 300 phenotype raises important questions about how natural selection may act simultaneously on an entire network
 301 of brain regions whose functions are strongly interdependent. Among these questions is how the emergence of
 302 a novel pathway overcomes strong allometric constraints, for example that dictate the relative volume of grey
 303 matter to white [136,137], or how individual neural adaptations can be accommodated within the highly
 304 conserved organisation of neocortex [138,139].

305 There is some debate about the extent to which evolution is able to influence individual brain regions to form
 306 an evolutionary mosaic [140,141] as compared to concerted change over the entire brain [142,143]. While brain
 307 area size is highly predictable from overall brain size taken at a broad taxonomical scale (e.g., across mammals),
 308 individual brain regions violate this trend when examined at a finer taxonomic scale (e.g., across primates),
 309 which is a likely driver of inter-species behavioural differences [42,144].

310 Pairs of functionally related brain structures have correlated sizes across species even after controlling for brain
 311 size, indicating that brain networks may evolve together and at least partially independently of other brain
 312 structures [140]. Furthermore, natural selection may be capable of acting on individual brain regions and their
 313 corresponding networks due to genetic mechanisms that provide independent regulation of brain region sizes
 314 [141]. The primate cortical sheet has not expanded uniformly as brain size increased, with the occipital lobe
 315 expanding least and the frontal and temporal lobes expanding most, but this pattern is conserved and species
 316 differences appear to be the product of brain size [145].

317 A remarkably analogous instance of network-wide brain evolution is found in the song system of parrots. Strong
 318 vocal learning abilities have evolved independently in three lineages of birds, and of these parrots are among
 319 the most prodigious vocal learners [50,146]. The avian song system is composed of a series of nuclei, some of
 320 which are analogous to structures in the human vocal-motor system including the putamen, motor cortex, and
 321 nucleus ambiguus [18,147], and are regulated by specialised patterns of gene expression [148,149]. The parrot
 322 brain is unusual in containing two parallel song systems [150]. Nuclei in the parrot song system are composed
 323 of a core that is analogous with the song system of other avian vocal learners, and a surrounding shell that forms
 324 a rudimentary second song system. The core and shell song systems form parallel networks, however only the
 325 core sends direct projections to the brainstem motor nucleus that controls the syrinx (i.e., the analogue to
 326 mammalian nucleus ambiguus). Chakraborty & Jarvis (2015) proposed that such a phenotype could arise by
 327 mutations that cause the entire network to duplicate as an ensemble, in line with a previous proposal that the
 328 avian song system itself may have evolved as a specialization from a pre-existing limb and body motor network
 329 [152].



330

331 **Figure 4:** Conceptual depiction of parallel effector-specific circuits feeding from the broader motor
 332 network to upper motor neurons in motor cortex and onto lower motor neurons in the brainstem and
 333 spinal cord (black circles). We propose that evolutionary changes that add novel downstream targets
 334 (orange line) to the efferent motor pathway change the function of the corresponding portion of motor
 335 cortex as well as the broader motor networks to which it is connected. The example above depicts a novel
 336 projection from a patch of motor cortex to brainstem, which in turn alters the function of the motor
 337 network in which it is embedded in to support voice motor control. The dotted line indicates that this
 338 patch was previously recruited by a different effector.

339 We suggest that only a relatively minor change to an existing portion of mammalian motor cortex may have
 340 been sufficient to evolve a novel laryngeal motor network in humans. We propose that the emergence of novel
 341 efferent pathways to the nucleus ambiguus de facto alters the functional significance not only of these cortical
 342 neurons in the motor cortex but also the broader network in which they are embedded (see Figure 4). Given
 343 that somatotopic motor networks are defined by the effectors that they control (e.g., M1-hand is that part of
 344 motor cortex which projects to hand lower motor neurons in the spinal cord, SMA-hand is that part of the SMA
 345 that projects to M1-hand, etc.) modifications to the descending efferent pathways of motor cortex alter the
 346 function of corresponding sites throughout motor network. Hence, we propose that the evolution of novel
 347 projections from one or both of the LMCs was sufficient for the emergence of vocal motor networks, thereby
 348 acquiring novel functions. Such a mechanism would leverage existing long-range connections in the brain,
 349 thereby preserving existing allometric relationships between the grey and white matter volumes and
 350 overcoming hard barriers for morphological changes.

351 One mechanism that has been proposed to drive the development of novel laryngeal motor specialisations in
 352 humans is the evolution of novel patterns of gene expression in the dLMC and vLMC relative to surrounding
 353 cortex [18]. This specialisation includes genes of the slit and plexin family, that encode axon guidance molecules

354 and neuronal growth cone receptors, respectively [153,154]. These genes are likely candidates for a molecular
355 genetic mechanism that may drive the direct projection to nucleus ambiguus in humans. Alternatively, such a
356 specialisation may simply arise as a consequence of the increased proportional size of neocortex. Larger brain
357 regions send more axonal projections and compete more effectively for limited dendritic space [155,156]. For
358 example, among mammals, proportionally larger neocortical size is correlated with deeper penetration of the
359 spinal cord by corticospinal axons, which in turn mediates improved manual dexterity [42,43]. Hence, the
360 increased proportional size of human neocortex alone may have been a driving factor in evolving novel vocal
361 motor networks in humans. As cortical expansion increased the total number of corticobulbar axons, they may
362 have invaded novel territory in the nucleus ambiguus, potentially at the expense of other inputs that mediate
363 unlearned vocalisations, such as the periaqueductal grey [157,158].

364 We note that the human brain has undergone numerous other large scale structural changes relative to non-
365 human primates [159–164]. The emergence of vocal motor networks is itself not sufficient for the
366 communicative behaviours of humans. Rather, it is part of an ensemble of neural adaptations that support the
367 vocal, auditory, semantic, syntactic, and pragmatic faculties which are needed for speech and language, and
368 which may have separate evolutionary histories [31,32,165]. However, we do suggest that the small-scale
369 modification of the corticobulbar outputs of motor cortex may have had large-scale functional implications for
370 the motor network.

371 **Summary**

372 We have proposed a novel hypothesis that the dual representation of the laryngeal muscles found in the motor
373 cortex is repeated throughout the motor network. Somatotopic organization is a feature that is found across
374 the network of brain regions that control voluntary movement. Each of these brain regions contains
375 representations of muscle groups following a predictable order based on the plan of the body. These motor
376 regions project preferentially to somatotopically homologous regions (e.g., M1-hand to SMA-hand) to form an
377 extended somatotopic network. Initial evidence suggests that the cerebellum and SMA may also contain dual
378 representations of the larynx, thereby contributing the functions of the cortico-cerebellar and cortico-striatal
379 loops to voice motor control. These findings require further replication and should be extended to other motor
380 regions such as cingulate cortex and the basal ganglia. This hypothesis raises important questions about how
381 adaptations at the level of motor cortex may impact the broader network in which it is embedded. We have also
382 discussed brain evolution in search of a parsimonious mechanism for the emergence of this complex phenotype
383 in the human brain.

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