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## **Missing links: the functional unification of language and memory (LUM)**

*Running title:* Language and memory unification (LUM)

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# 1 **1 Introduction**

2 Language and long-term declarative memory (Tulving, 1972) are essential functions of  
3 everyday human behavior. The first scientific descriptions date back a little more than a century  
4 (e.g., Hermann Ebbinghaus 1885 for memory; Ferdinand de Saussure and his well-known  
5 "*Cours de Linguistique générale*" 1916 for language) and continue to inspire modern  
6 conceptions. Initially, linguists, psychologists, and cognitive scientists investigated language  
7 and memory, leading to the usual compartmentalization of these two functions.

8 Several deep-rooted reasons may have contributed to consider these functions as nearly  
9 antipodal. Regarding the terminology, language aims at externalization (produce, from Latin  
10 *producere*: lead forward). In contrast, memory subserves internalization (encoding: transcribing  
11 inwards). Language is traditionally assumed to involve "domain(s)-specific" processes (specific  
12 to language domains, e.g., syntax; Zaccarella & Friederici, 2015), whereas memory is regarded  
13 as a transversal function contingent on "domain(s)-general" processes (Campbell & Tyler,  
14 2018). The functional epicenters of these two functions based on lesion studies also appear  
15 separated anatomically. Language would mainly engage lateral and neocortical cerebral regions  
16 (Broca, 1865; Wernicke, 1874), and long-term memory would mainly pertain to mesial and  
17 allocortical regions (Milner, 1970; S. Squire, 1984; Figure 1).

18 Despite this first impression of cognitive and anatomical contrast, several common behavioral  
19 phenomena directly emanate from the language-memory overlap. Language skills in children  
20 condition their verbal memory (Klemfuss, 2015). Bilingual individuals bind their encoded  
21 memories to different languages (Larsen et al., 2002; Marian & Neisser, 2000). Although a  
22 variety of causes can account for verbal paraphasias (e.g., disruption of the earliest stages of  
23 lexical processing, such as the conceptual preparation stage; Levelt, 1989; Indefrey, 2012), they  
24 can also be explained by a failure of the working memory system, leading to a contamination  
25 of production by long-term declarative memory (see Schwering & MacDonald, 2020 for a

26 review). Episodic false memories and confabulations are verbally generated for the sake of  
27 discourse coherence (Conway & Loveday, 2015). Finally, dissociations between semantic and  
28 episodic memory have been reported in patients with semantic dementia (e.g., Graham et al.,  
29 2000). However, the frequent scenario of patients with lesions in "language regions" and  
30 symptoms in the memory domain or *vice versa* (e.g., Everts et al., 2010; Jaimes-Bautista et al.,  
31 2015) attests to their strong neuropsychological interconnection.

32 Nevertheless, the neuroscientific community essentially approaches these functions separately.  
33 It focuses on psychological concepts or constructs – such as verbal production, comprehension,  
34 syntax, semantic, episodic, and working memory – which are conceptually nested (see Box 1).  
35 We propose to move towards a more “naturalistic” account of neurocognitive functioning by  
36 approaching the cross-functional relationships between language and memory across their  
37 fundamental dimensions, neurocognitive operations, and implicated substrates. In contrast to  
38 conventional cognition-centered approaches built on theoretical psychological constructs, the  
39 "neuro-centric" perspective developed here stands out as an appropriate framework to address  
40 the missing links between brain and behavior (Box 2 for an overview of the basic principles  
41 that frames our considerations).

42 How do language and declarative memory interact in a unified way, ensuring our adaptive  
43 human behaviors? Owing to the emergence of the brain connectivity study and current  
44 connectomic approaches, it is now possible to highlight the neural architecture and interactive  
45 pathways underlying these wide-ranging relationships. Here, we chronologically synthesized  
46 the discovery of language and memory anatomic and functional organization (Sections 2.1 &  
47 2.2). We then outlined recent elements as a robust foundation for proposing an interactive and  
48 unified language and memory functional model (Section 2.3). We present the  
49 *Language/union/Memory* (LUM) model and link it to experimental and theoretical evidence

50 (Section 3). Finally, we illustrate LUM's application in patients and discuss prospects for the  
51 future in cognitive and clinical neuroscience (Section 4).

52

## 53 **2 Main legacies of neurocognitive observations**

### 54 **2.1. Language and memory coevolution**

55 Since the beginning of language science, linguists have distinguished two main fields of study:  
56 (i) expressive language for syntactic or articulatory aspects of language; and (ii) receptive  
57 language for language perception and comprehension. Verbal production (externalization  
58 process or "spell-out"; Bolhuis et al., 2014), the expressive language aspect closest to the  
59 physical world (de Boer, 2011; Fitch, 2010), is intimately related to embodied or "grounded"  
60 cognition (Kempe & Brooks, 2016). Several past observations have suggested that language  
61 production and the emergence of human-specific articulatory gestures may be the direct  
62 precursor of syntax (Carstairs-McCarthy, 1999; Studdert-Kennedy, 2005). At the interface  
63 between meaning and sound (Ferreira & Engelhardt, 2006), syntax allows the hierarchical  
64 combination of verbal units (e.g., combinations of words, propositions, phrases, sentences) into  
65 increasingly complex structures (Friederici et al., 2017). Thus, a complex syntax requires a  
66 robust phonological memory system adapted to flexibly organize and maintain the different  
67 verbal elements during online processing (Aboitiz et al., 2010).

68 From an evolutionary perspective, the white matter dorsal pathway composed of superior  
69 longitudinal and arcuate fascicles has been particularly extensive in humans compared to non-  
70 human primates (Goucha et al., 2017; Rilling, 2014). The dorsal circuitry's evolution allowed  
71 for the direct control of the vocalization system and made phonological processing more  
72 efficient (Aboitiz, 2012). By interconnecting the so-called "Broca and Wernicke's areas", the  
73 arcuate fascicle structures the dialogues between abstract structural building (inferior frontal

74 gyrus) and lexical entries or lexically-based argument structures (posterior temporal cortex),  
75 promoting the integration of syntactic and semantic information (Goucha et al., 2017). The  
76 recruitment and the expansion of such dorsal fascicles could have generated the crucial turning  
77 point for exploiting a complex syntactic system and an advanced verbal working memory  
78 processing, essential for language acquisition. Humans have extended working memory  
79 capacity (Reuland, 2017), including notably inner speech, favoring repetition, and access to  
80 consciousness to verbal information (Carruthers, 2013). Thus, working memory can serve as a  
81 fundamental unifying function between language production and declarative memory by  
82 facilitating conscious introspection. It allows flexible and vivid access to the content of  
83 representations in long-term memory (see Brown-Schmidt & Duff, 2016; Schwering &  
84 MacDonald, 2020) for an in-depth and up-to-date report on verbal working memory).

85 The emergence of syntax and an adapted working memory system could have led to "open the  
86 door" to a broader and richer semantic system. Combined with sophisticated assembling  
87 capacities, our semantic system might be the root of the conceptual and propositional  
88 organization of complex thought and verbal comprehension (i.e., a receptive system well-  
89 sharpened for labeling Boeckx & Benítez-Burraco, 2014; Hinzen, 2013). For instance, while  
90 monkeys can learn to visually categorize images after intensive training (Fabre-Thorpe, 2003),  
91 young children are indeed able to learn efficiently new concepts and corresponding words faster  
92 (Bloom, 2000; Waxman, 2004). This is consistent with the fact that the ventral pathway  
93 involved in lexical and semantic processing is less developed in non-human primates (e.g., the  
94 inferior longitudinal fascicle joins occipital rather than temporal regions in monkeys; Catani &  
95 Dawson, 2017).

96 As with the semantic processing, mental time travel, and episodic memory, often referred to as  
97 declarative or "declarable" memory (Squire, 2004; Tulving, 1972; Box 1), have co-evolved with  
98 language to convey our mental journeys and imaginations (Corballis, 2019). At some point, the

99 system inevitably adapted itself to integrate speech into long-term memory, leading to  
100 developing an integrative, unified, and adaptive declarative system in humans. These  
101 coevolution mechanisms between expressive-receptive language and memory systems appear  
102 to be a critical element of the foundation of human *sensus communis* (Schaeffer, 1990, for a  
103 historical and philosophical description of the theory of knowledge).

## 104 **2.2. Contemporary neurofunctional conceptions**

### 105 **2.2.1. Language**

106 Beyond the classic and localizationist, Broca-Wernicke's model and the arcuate fascicle, a vast  
107 interconnected network extending outside of the left hemisphere supports the multiple  
108 exchanges of information necessary for the production and understanding of language (Figure  
109 1 for the putative role of brain regions and fascicles in language processing). This advanced  
110 language representation has challenged the modular and serial views and demonstrated that  
111 semantic, phonological, and syntactic processing pertains to parallel large-scale cortico-  
112 subcortical sub-networks. These specialized systems would be dynamically interconnected  
113 (Duffau et al., 2014), allowing rich and flexible language skills.

114 Recent neurocognitive models of language involve a dual-stream (Duffau et al., 2014; Friederici  
115 et al., 2017; Hickok & Poeppel, 2007; Price, 2012). Temporo-parieto-frontal regions interact  
116 along the dorsal pathway through superior longitudinal and arcuate white matter fascicles. As  
117 mentioned above, the dorsal stream participates in the conversion of phonological structures  
118 into phonetic, articulatory, syntactic, and motor representations and involves verbal working  
119 memory. In contrast, occipito-temporo-frontal regions are inter-connected through the uncinata,  
120 extreme capsule, inferior longitudinal, and inferior fronto-occipital fascicles along the ventral  
121 stream. The ventral stream is mainly involved in the conversion of phonological units into their  
122 meaning. Dorsoventral transverse connections have recently been examined further because of  
123 their probable involvement in linking the ventral to the dorsal streams (Bullock et al., 2019).

124 The most prominent of them – the middle longitudinal fascicle – is notably highlighted for its  
125 double involvement in phonology and semantic processing [e.g., Luo et al., (2020) for evidence  
126 in primary progressive aphasia; Hula et al., (2020), in post-stroke aphasia]. The two main  
127 streams underlying both production and comprehension are functionally interconnected and  
128 tightly coupled (Hickok & Poeppel, 2007; Silbert et al., 2014) by bundles (or portions of fibers)  
129 of the human white-matter backbone (Herbet & Duffau, 2020) for an extensive hodological  
130 model. Figure 1 below provides a comprehensive view of the brain regions and fascicles  
131 described in the contemporary language models and their assumed roles.

### 132 **2.2.2. Declarative memory**

133 The observations of brain-injured amnesic patients allowed for the exploration of declarative  
134 episodic memory cerebral substrates, with a prominent initial focus on the mesial temporal lobe  
135 and the hippocampus (Squire, 1984; Gaffan, 1997 for a critical review). The extensive study of  
136 the very well-known Henry Gustav Molaison patient (widely referred to as "H.M." (Scoville &  
137 Milner, 1957) has demonstrated the association between mesial temporal lobe lesions and  
138 declarative episodic memory deficits (Corkin, 2013; Squire, 2009). More recently, the H.M.  
139 case has been revisited according to hodological principles (Fytche & Catani, 2005).  
140 Disconnection analyses revealed damage to various bundles (uncinate, fornix, anterior  
141 commissure, and cingulum) and the disconnection of areas not directly affected by the surgery  
142 (Thiebaut de Schotten et al., 2015). In line with this observation, a broader functional network  
143 involving subcortical but also lateral temporal, (pre)frontal, cingulate, and parietal cortices is  
144 known to be involved in declarative memory (Figure 1 for details; see also Danker & Anderson,  
145 2010; Moscovitch et al., 2006; Sheldon et al., 2016).

146 The most recent models adopt a "macroscale" neurocognitive view of long-term memory and  
147 propose a dual-stream architecture (Duvernoy et al., 2013; Ranganath & Ritchey, 2012). These  
148 models place the medial temporal cortices within a large-scale network (hippocampo-cortical



149 systems) composed of a posterior-medial (PM) and an anterior-temporal (AT) system (PMAT  
150 model; Ranganath & Ritchey, 2012). The posterior medial system includes the retrosplenial  
151 cortex involved in the spatial representation of events (Epstein, 2008), posterior cingulate,  
152 precuneus, and angular gyrus recruited for the contextual information (Baldassano et al., 2017;  
153 Richter et al., 2016; Sreekumar et al., 2018). The cingulum white matter tract mainly connects  
154 the posterior medial system. The anterior system includes the perirhinal cortex, the amygdala,  
155 and the anterior ventro-temporal and lateral orbitofrontal cortices. The perirhinal cortex  
156 supports emotional associations induced by the item (Ritchey et al., 2015). The amygdala binds  
157 item features with emotion (Yonelinas & Ritchey, 2015). The anterior ventro-temporal and  
158 lateral orbitofrontal cortices are engaged in object representation and assess items' affective  
159 significance and memory decision-making (Libby et al., 2014). The uncinate, the inferior  
160 longitudinal fascicle, and the fornix link this anterior system and therefore constitute the  
161 conceptual and emotional scaffolding. The role of the hippocampus, located at the crossroad of  
162 these paths, would be to bind multimodal contents – including verbal cues (Barry & Maguire,  
163 2019; Moscovitch et al., 2016) – both during encoding and retrieval (de Vanssay-Maigne et al.,  
164 2011; Diana et al., 2007), allowing for unified memories. Although examined mainly in  
165 isolation, the substrates and processing pathways highlighted in contemporary language and  
166 declarative memory models suggest an inevitable intertwining (Figure 1) that we aim to  
167 describe and formalize in the following sections.

168

169 -----Insert Figure 1 here-----

170

## 171 **2.3. Beyond the independence of language and memory**

### 172 **2.3.1. *Overlap of fundamental dimensions***

173 Language and declarative memory overlap. They can be considered part of a larger and  
174 interactive system, but their interaction to support unified behavior remains undetermined. The  
175 "common ground" introduced by Clark and Marshall (Clark & Marshall, 1981) as a basis of  
176 interpersonal interaction *via* language is a tangible cognitive example for explaining the unified  
177 view of language and declarative memory. Individuals communicate by relying on the shared  
178 set of beliefs, ideas, and knowledge while also making assumptions about the interlocutors'  
179 perspectives. These elements constitute the "common ground", a concept close to mentalization  
180 (Premack & Woodruff, 1978). According to the resonance-based theory of common ground,  
181 Horton (Horton, 2007) proposed that working memory information, such as current discourse,  
182 resonates with long-term memory information (such as the partner's identity, traits and  
183 attributes, past events or similar discourse) in a fast and automatic fashion (Brown-Schmidt &  
184 Duff, 2016), to ensure a relevant and contextually appropriate conversation.

185 What may be the neurocognitive foundation of common ground? First, the discrete cognitive  
186 constructs conventionally ascribed to language and declarative memory are interconnected and  
187 exhibit some entanglement (Box 1). Second, the functional brain representations associated  
188 with each of these constructs reveal a complex of three major fundamental components that  
189 may capture the language-memory continuum (Figure 2A). Finally, the arrangement of  
190 cognitive constructs within these latent canonical components further provides insight into the  
191 dimensions' composition, specificities, and characteristics (Figure 2B) and thus offers both a  
192 global and composite view (Figure 2C) of the common ground.

193 From a neurocognitive point of view, the first latent dimension – which we propose to call  
194 "**Receiver-Transmitter**" (RT System) – mainly encompasses aspects related to speech  
195 perception, phonology, articulation, and syntax. In addition, and even if to a lesser extent,  
196 working memory and comprehension saturate this dimension. This suggests that RT comprises  
197 processes related to the externalization of verbalizable outputs, implying "spell-out" and

198 sensory inputs influencing all cognitive processes and the outputs. **RT** may involve perceptuo-  
199 motor information processing operations (Giraud & Poeppel, 2012; Poeppel & Assaneo, 2020,  
200 for an example of computational principles associated with speech perception) –  
201 *selection/detection, segmentation, concatenation/linearization, conjunctive binding*. To  
202 simplify and caricatured, **RT** could proceed at the computational level as an active **in and out**  
203 cognitive "Receiver-Transmitter" **system**.

204 The second dimension is represented primarily by verbal working memory and comprehension.  
205 This component is also more broadly related to articulation, phonology, syntax, associative  
206 memory, and lexical access/retrieval. Thus, it could refer to the controlled assembly of  
207 elementary operations allowing to transform a verbal input actively into an elaborated and  
208 appropriate verbal output (i.e., the accurate mapping between meaning and sounds or,  
209 conversely, between sounds and meaning; between word and signification or between  
210 sentences/discourse and meaning, depending on the level of processing). Concretely,  
211 *incremental binding, monitoring, evaluation, or (error-)prediction* operations can be engaged  
212 as active inference algorithms (i.e., predicting future states according to the trajectory defined  
213 by a given policy; Parr & Friston, 2017). Because this dimension is related to how elements or  
214 a mixture of elements are manipulated and assembled for a specific purpose, we labeled it  
215 "**Controller-Manager**" (**CM System**). **CM** would engage operations common to language  
216 production and comprehension (Figure 2B), consistent with neuroimaging studies  
217 demonstrating a neat overlap between natural language production and comprehension's  
218 functional maps (e.g., Silbert et al., 2014).

219 The third dimension covers neurocognitive aspects related to language comprehension,  
220 associative memory, lexical access/retrieval, verbal semantic, episodic, and working memories.  
221 In a simplistic way, it can be described as a "**Transformer-Associative**" computational  
222 component (**TA System**) as it includes computations to build and maintain mental, conceptual,

223 and multimodal representations. The operations underlying **TA** encompass, for instance,  
224 *abstraction/dimensionality reduction, multimodal/relational binding, pattern*  
225 *separation/completion, and replay* (Cowell et al., 2019).

226 To summarize the findings and postulates, there is a substantial overlap between the language-  
227 memory cognitive constructs and their brain representations, revealing an underlying  
228 continuum of three main latent dimensions (Figure 2). The detected dimensions (**RT-CM-TA**)  
229 may share some features with those of previously described models in the context of functional  
230 language modeling (Berwick et al., 2013 for the "basic design of language" model; or Hagoort,  
231 2013, 2014, 2017 for the MUC model, in particular). However, the modeling we provide  
232 emphasizes no component that can be described by a (single) cognitive function or subfunction  
233 (e.g., memory, syntax, or executive functions). The nature of the canonical detected dimensions  
234 imposes instead a new ontology based on overlaps. Some constructs, such as the working  
235 memory outlined above, are positioned at the intersection of the tripartite **RT-CM-TA** complex,  
236 which could confirm their central place in the common ground and, by extension, in the  
237 language-memory unification process. Nevertheless, it is necessary to go beyond this cognitive  
238 framework to identify the specific and biologically plausible building blocks in concern. If so  
239 far, we have referred, in the Marr's spirit (Marr, 1982), the putative (1) computational goals  
240 and (2) algorithmic operations involved in such interactive components; the (3) neural  
241 implementation or neurobiological relevance of these dimensions as well as their interactions  
242 will be discussed in the following sections.

243

244 -----Insert Figure 2 here-----

245

246

247                    **2.3.2. Shared substrate**

248 Verbal communication requires a multitude of intra-language aspects (e.g., knowledge about  
249 sounds, grammar, word meaning, and general world knowledge; Hogan et al., 2014) and extra-  
250 language aspects (e.g., attention monitoring and making inferences in addition to long term  
251 memory retrieval; Kintsch & Kintsch, 2005), allowing for the flexible organization of  
252 multimodal information into a single meaningful representation. This highly interactive  
253 cognitive structure requires an adequate and specialized anatomo-functional brain substrate.

254 Few studies have explored the common substrates of language and long-term declarative  
255 memory, especially episodic memory (Duff & Brown-Schmidt, 2012). The examination of the  
256 meta-analytic functional maps for terms related to language and memory (provided by  
257 Neurosynth and based on hundreds of fMRI studies; Yarkoni et al., 2011) yields a first  
258 approximation of the relationships between these two functions and their associated constructs  
259 (Figure 3). In agreement with the prior literature, the functional meta-analysis emphasizes the  
260 concept of working memory at the intersection of language-memory functions (Figure 3B).  
261 Common brain regions and fascicles have been previously associated with executive processes  
262 (Acheson et al., 2010) and mostly correspond to the cerebral representation of working memory  
263 (Eriksson et al., 2015). However, neocortical temporal and hippocampal regions and ventral  
264 and mesial fascicles classically described for their involvement in episodic and semantic  
265 memory (Figure 1) are also considered "shared areas". This is in line with some recent proposals  
266 that include mesial regions at the interface between language and memory (e.g., Brown-  
267 Schmidt & Duff, 2016; Covington & Duff, 2016) and indicate that the interactions are complex  
268 and not limited to the verbal working memory component alone (Figure 3).

269

270                    -----Insert Figure 3 here-----

271 These common territories express a certain degree of functional cooperation or joint neural  
272 integration. Nevertheless, despite its great interest, the conceptualization of interdependencies  
273 between different cognitive "domains" is not yet fully established in the current literature. Since  
274 connectivity analysis explicitly "bridges localizationist and distributed theories of brain  
275 function" (Medaglia & Bassett, 2018), we formalize here their interplay through the lens of  
276 networks to propose new conceptions. This perspective expands Hagoort's proposal of  
277 "networks of interest" (NOIs; Hagoort, 2014) beyond language and the perisylvian network.

278

### 279 *2.3.3. Synergistic networks interactions*

280 Modern accounts of the functional connectome organization at various space-time scales have  
281 described hierarchical networks, such as the Default Mode Network (DMN; Mazoyer et al.,  
282 2001; Raichle et al., 2001), whose activity is strongly coupled to the resting state. These  
283 networks are composed of several key regions that confirm the "multifocal" conception of brain  
284 functioning proposed by Mesulam in the early 1990s and which "gives rise to brain-behavior  
285 relationships that are both localized and distributed" (Mesulam, 1990). The regions involved in  
286 these networks are essential for certain types of cognitive state or processing (e.g., in visual  
287 perception or executive control; Rosazza & Minati, 2011), thus making it possible to attribute  
288 a "cognitive" dimension to functional networks.

289 Intrinsic functional networks follow an ordered sequence of attributes (i.e., properties such as  
290 the degree or the nature of functional integration of the representations). The cortical  
291 organization extends along a functional continuum that spans from unimodal sensorimotor  
292 areas to transmodal associative regions of the DMN, passing by attention and executive areas  
293 (Margulies et al., 2016; G1 in Figure 4B). Unimodal networks are more modular and  
294 segregated. More specifically, the organization of the connectivity of sensorimotor, visual, and

295 auditory networks follows topographic representations across adjacent cortices, favoring  
296 hierarchical serial processing of information (in terms of complexity). Conversely, the  
297 connectivity profiles of transmodal executive-associative networks, such as the DMN, the  
298 fronto-parietal control network (FPN), or even the ventral salience and dorsal attentional  
299 networks (SAL and DAN, respectively; Yeo et al., 2011) consist in "long-range" networks  
300 linking spatially distant regions (and not close neighbors). Overall, modern conceptions  
301 described the general neurocognitive functioning as hybrid architecture. Such architecture will  
302 combine modularity and interconnectivity and balance between integration/segregation of  
303 networks, facilitating an efficient transfer of information (Achard & Bullmore, 2007). The  
304 dynamical synchronization between networks (or multi-network state or meta-systems (Cocchi  
305 et al., 2013) supports a "hierarchical encapsulation" involving nested networks within networks  
306 (Hilgetag & Goulas, 2020). These complex configurations of inter-networks coupling may be  
307 at the origin of interactions between cognitive functions (Herbet & Duffau, 2020). Therefore,  
308 the re-evaluation of language and declarative memory under this prism brings new grounds for  
309 a less fragmented view of the functioning and addresses how the multiple facets are  
310 synergistically embedded in an adaptive, harmonious, and unified process.

311

### 312 **3 Towards a unified view of language and memory**

#### 313 **3.1. LUM formalism and main principles**

314 To account for the dynamic exchanges, we conceive language and memory on a continuum  
315 composed of the three fundamental dimensions (RT-CM-TA; Figure 2C) in interactions (Figure  
316 4A). The proposed interactive neurocognitive new framework "LUM" (for  
317 *Language/union/Memory*) adopts a neuro-centric and connectivity-based vision to reconcile the  
318 language-memory relations' cognitive manifestations within a biologically plausible structure.

319 We argue that language and memory relationships cannot be described by a unique stationary  
320 network but mainly through a network's interactions' triplet (Figure 4A). Specifically, the SAL,  
321 FPN, and DMN networks appear to be primarily engaged in the **RT**, **CM**, and **TA** latent  
322 dimensions that we propose, respectively. This proposal relies on direct evidence from the  
323 observation of the functional connectome (Figure 4B) and the literature's experimental findings  
324 (e.g., Braga et al., 2020; Wang et al., 2019 for recent research). LUM engages large dynamic  
325 configurations and reconfigurations of online/offline transient states. This framework argues  
326 that these networks' global and regional functional dynamics are crucial to describe language-  
327 memory behaviors. At the global level, the dialogues between the networks form a "ballet of  
328 networks", underpinning the inter-function relationships (Hagoort, 2014). Key regions (hubs)  
329 may have a functional architecture that actively sustains and coordinates networks at a local  
330 level. The synergy of these global and local dynamics orchestrates and supports language-  
331 memory operations. Box 2 summarizes the principles that govern the LUM framework.

332

333 -----Insert Figure 4 here-----

334

335

### 336 **3.2. LUM dimensions and functional modules**

337 While there is a continuum between these SAL-FPN-DMN associative networks, they all carry  
338 their functional characteristics. Their anatomical topology is independent, with abrupt spatial  
339 transitions between the connectivity patterns (Yeo et al., 2011), aligning with the LUM latent  
340 dimensions formalized (at least partially) distinct modules.

341



### 342           3.2.1. *SAL, the cognitive "Receiver-Transmitter"*

343   Accompanied by information from the sensory-motor network (SMN, including mainly motor  
344   and auditory-perceptive networks), the ventral attentional network [also called salience network  
345   (SAL)] presents the functional properties to support the *Receiver-Transmitter* dimension (**RT**  
346   **System**). SAL is triggered by the salience of external stimuli and the detection of relevant  
347   external targets, thus managing the attention's top-down and "exogenous" reorientation  
348   (Matthen, 2005). Linked to sensory awareness, SAL filters the environment, allowing the rapid  
349   and active-controlled integration of exteroceptive information, and providing relevant  
350   information in working memory (Parr & Friston, 2017). Therefore, the SAL network has  
351   optimal intrinsic properties for supporting the cognitive reception-transmission dimension of  
352   auditory and verbal information (e.g., for active listening or controlled externalization).

### 353           3.2.2. *FPN, the "Controller-Manager"*

354   The *Controller-Manager* dimension (**CM System**)'s primary function is the organization,  
355   development, and maintenance of verbal representations. It would be underpinned by a top-  
356   down controlled network (sometimes called Multiple Demand Network: MDN or Central  
357   Executive Network: CEN; Doucet et al., 2019). More precisely, the fronto-parietal control  
358   network (FPN), especially lateralized in the left hemisphere, could be involved in a privileged  
359   way. FPN is observed in verbal and autobiographical planning (Benedek et al., 2016) or  
360   semantic control (Xu et al., 2017). In general, this network supports cognition and goal-oriented  
361   behaviors and is linked to verbal working memory and fluid intelligence (Assem et al., 2020).  
362   Thus, the fronto-parietal network properties could facilitate managing the various executive  
363   operations required for verbalization and declarative memory.

### 364           3.2.3. *DMN, the "Transformer-Associative"*

365 Processes related to the *Transformer-Associative* dimension (**TA System**) mainly involve the  
366 highly integrative default network (DMN). Indeed, the DMN has previously been associated  
367 with internal and offline attention (Buckner et al., 2008), allowing the elaboration of self-  
368 generated, introspective thinking built on memory content (Andrews-Hanna et al., 2014;  
369 Konishi et al., 2015). The DMN would also be engaged in mental imagery and, therefore,  
370 episodic memories. It would allow temporal, spatial, and content distortion, offering the  
371 possibility to imagine never-experienced situations and produce complex thoughts (Binder &  
372 Desai, 2011; Boyer, 2008). It could thus underlie the "mental time travel" involved in episodic  
373 memory (Humphreys & Lambon Ralph, 2015; Lau et al., 2013; Raichle, 2015; Wang et al.,  
374 2020), especially when coupled to the limbic system (Jeong et al., 2015; McCormick et al.,  
375 2014). Several studies have shown its involvement in semantic declarative memory's various  
376 cognitive tasks, facilitating the resonance between environmental characteristics and those  
377 derived from similar prior knowledge and states (Binder & Desai, 2011; Constantinescu et al.,  
378 2016). As a multimodal experiential system (Xu et al., 2017), the highly integrative  
379 characteristics of DMN appear indispensable to support the internalization dimension of  
380 elaborated representations (**TA System**). The DMN activity would be "prosocial" and has  
381 probably adapted to the evolution of language. In humans, the DMN collects and facilitates  
382 auditory information integrations (Simony et al., 2016) and promotes social content (Dohmatob  
383 et al., 2020; Krienen et al., 2010).

384

### 385 **3.3. LUM interactions: global and local dynamics**

#### 386 *3.3.1. Non-stationary global dynamics of networks*

387 We can assume that a "networks ballet", happening through SAL-FPN-DMN transitions and  
388 dynamical synchronizations (Figure 4), can actively and synergistically support the LUM  
389 cognitive states and the "common ground" mentioned in section 2.3.1. Some research on

390 language or semantic memory highlights a synergy of different network components (multi-  
391 network states; Braga et al., 2020; Gordon et al., 2020; Hagoort, 2019; Ji et al., 2019; X. Wang  
392 et al., 2020). Networks maintain complex mutual relationships with each other, controlling  
393 other networks' functions, others acting in interaction (Buckner et al., 2013). Recently, Cocuzza  
394 et al. (Cocuzza et al., 2020) have proposed that cognitive task control can be performed  
395 dynamically by high-level controlled networks but differently. SAL would play the role of  
396 "flexible switcher" and the FPN would be a "flexible coordinator". More precisely, FPN  
397 actively coordinates other regions' activities to obtain information relevant to the goal to be  
398 achieved. It thus allows cooperation between networks initially considered as antagonistic (e.g.,  
399 DMN-SAL or DMN-DAN synchronization; Spreng et al., 2013; Wang et al., 2020). Unlike  
400 FPN, SAL dissolves transiently (intra-network decoupling) to lend processing resources to  
401 other networks pertinent to the objectives. This transition is described as a dynamic "switch",  
402 allowing to initiate the transition from an interoceptive state (DMN) to a goal-oriented state  
403 (FPN and FPN-DMN coupling, involved in phasic vigilance; Cocchi et al., 2013). Within the  
404 LUM framework, FPN and SAL's interaction can control processing towards the most critical  
405 external cues in a conversation. In interaction with the DMN, FPN can actively extract relevant  
406 internal information from previous experience and knowledge.

### 407 **3.3.2. Local dynamics of integrative hubs**

408 By attempting to locate the language within the organization of intrinsic networks, DiNicola et  
409 al. (2020) showed that language-associated regions exhibit a similar pattern of juxtapositions  
410 of several networks. These cortical sites, located at the crossroads of the leading networks, thus  
411 present essential properties to act as "connector hubs" that are core regions able to integrate  
412 information from the different networks locally (see also Braga et al., 2013 for a description of  
413 the local multi-networks echo phenomenon). Among these convergence areas, the inferior  
414 frontal gyrus (IFG complex) follows a SAL-FPN-DMN gradient during the transition from *pars*

415 *opercularis* to *pars orbitalis* (Figure 4C). The IFG complex could functionally and gradually  
416 integrate phonological, syntactic, and semantic representations.

417 The associative role of the IFG is concordant with its previously reported role in the  
418 construction of conceptual and syntactical hierarchies (Goucha et al., 2017). More than the  
419 region *per se*, the connections to and from the IFG confer this role of assembling linguistic  
420 representations. These observations fit with the MUC model proposed by Hagoort (Hagoort,  
421 2016), describing a tripartite "Memory-Unification-Control" hierarchy within the IFG,  
422 maintained by structural connections with other areas of functional convergence such as the  
423 temporoparietal junction (TPJ) or the posterior part of the mean temporal gyrus (pMTG).  
424 Indeed, anatomically, these connector hubs receive the projection of crucial structural pathways  
425 (e.g., the arcuate and branches II-III of the superior longitudinal fascicle; Figure 4C) and thus  
426 constitute essential convergence zones for inter-network integration. Similar local gradients  
427 exist in the insula, the supramarginal and angular gyrus, the posterior upper/mid temporal gyrus,  
428 the supplementary motor area, the dorsolateral prefrontal cortex, the cerebellum, and the basal  
429 ganglia. These local integrators could serve as interfaces to interconnect the different LUM  
430 dimensions by manipulating external information and internal mental representations. Their  
431 role could be particularly crucial when the demand for inter-network connection is reinforced,  
432 e.g., during online activity.

433 Finally, the role of "peripheral hubs" that strengthen intra-network connections is also central  
434 (for instance, Dohmatob et al., 2020) to clarify the offline functional specialization of the main  
435 hubs belonging to the DMN). One of these peripheral hubs is the hippocampus linking  
436 information from the anterior-posterior DMN regions at rest (Barnett et al., 2020). Due to its  
437 intrinsic properties and connectivity (see the next section for more details), the hippocampus  
438 would have an active role in relational binding (i.e., binding multimodal information; Jonin et  
439 al., 2019) using high-fidelity information coming from the other DMN regions.

## 440 **4 Relevance and future directions**

### 441 **4.1. Functional specialization**

442

443 The LUM interactive model provides benchmarks to apprehend interactions between functions,  
444 specifically language and declarative memory. The formalization of these broader (and  
445 interactive) configurations shows that the cognitive-centric nomenclature classically used to  
446 account for these behaviors (Box 1) is not adequate. Cognitive processes and psychological  
447 constructs are traditionally identified from observable and salient behaviors and are hybrid  
448 concepts with blurred definable (Cowell et al., 2019; Figure 2A), which limit our understanding  
449 of brain-behavior relationships (Anderson, 2011). It would now be advisable to provide a new  
450 vocabulary to circumscribed cerebral mechanisms rather than looking for cerebral mechanisms  
451 behind psychological constructs (see Buzsáki, 2020, for an opinion review on the topic).

452 Neurocognitive operations or neurooperations describing latent neuro-mechanisms (as opposed  
453 to constructs resulting from observable processes) may be good candidates. Operations indeed  
454 reflect the brain's *modus operandi* or how the brain manipulates information to generate mental  
455 representations and behaviors (i.e., neuro-computational manipulations). They thus enable to  
456 approach brain-behavior relationships with a neuro-centric and a connectivity-based vision,  
457 which is necessary for the study of interactions not directly observable by essence. It would  
458 explain functional specialization from a different perspective than the one used so far. Given  
459 that a specific brain region is often involved in a large variety of behaviors (functional  
460 polyhedron; Genon et al., 2018), it becomes difficult to infer the functional specialization  
461 without an understanding of the core neuro-computational function(s).

462 In linguistics and for example, the latent operation "Merge" has been proposed to account for  
463 the combinatorial mechanism that brings elements together to form an unordered set of higher-  
464 order items and would thus be the crucial operation behind what we called syntax (Chomsky,

465 1995; Goucha et al., 2017, for a neurocognitive description). "Labeling," by operating  
466 classification of verbal information into an ordered set of elements here enables the creation of  
467 categories considered as a critical characteristic of human communication (Boeckx & Benítez-  
468 Burraco, 2014) and is proposed as a neuro-relevant operation (Benítez-Burraco & Murphy,  
469 2019; Murphy, 2015a, 2015b, for a model of brain dynamics as well as an algorithmic  
470 description). In the memory field, neurocognitive operations such as pattern separation, pattern  
471 completion, and replay are key neuro-mechanisms of encoding, retrieval, and active  
472 maintenance, respectively (Cowell et al., 2019; Pidgeon & Morcom, 2016; Yassa & Stark,  
473 2011). Memory is an integral part of each cortical zone's functioning (see Hasson et al., 2015  
474 and their hierarchical conceptualization of memory). For example, a conjunctive binding, by  
475 the co-occurrence of perceptive attributes (Jonin et al., 2019), involved in visual recognition  
476 also requires pattern completion operations. The property of relational binding, leading to  
477 multimodal and unified representation, emerges only collectively because of interactions  
478 between different brain circuits.

479 This "networked" conceptualization of functional specialization as proposed in the LUM model  
480 does not mean that all regions have a similar neuro-functional architecture or equal contribution.  
481 For example, the prefrontal cortex involved in FPN may be slightly biased in favor of control  
482 and monitoring operations. When actively engaged in verbal information processing, the IFG  
483 (pars opercularis in particular) could be an essential contributor to assembly operations (Merge;  
484 Zaccarella & Friederici, 2015). The hippocampus architecture is conducive to active links  
485 between multimodal information (Ekstrom & Yonelinas, 2020; Figure 5 for details). Together  
486 and integrated into a vast network, these regions actively link different elements, leading to an  
487 increasingly rich representational content. The global and local dynamics features put forward  
488 in the LUM framework can explain how such neurocognitive operations dynamically operate  
489 to unify language and memory contents into an internal multimodal representation (Figure 5 for

490 a demonstration). However, a more systematic and precise inventory of neurocognitive  
491 operations that may represent the cornerstone of understanding the interdependencies between  
492 different cognitive "domains" remains necessary. It thus constitutes one of the most important  
493 future challenges of cognitive neuroscience.

494

495 -----Insert Figure 5 here-----

496

#### 497 **4.2. LUM in clinical neuroscience**

498 The LUM model's fundamental specificity goes beyond the modular cognition vision by  
499 focusing on network dynamics and interactions. Doing so can provide an interesting angle of  
500 view on language and memory processes in healthy brains (e.g., development, plasticity due to  
501 learning, functional specialization or aging). It can also account for these functions'  
502 disturbances after brain injury (e.g., stroke, primary progressive aphasia, mild cognitive  
503 impairment, hippocampal hypoxia, epilepsy, or certain psychogenic disorders). Neuroplasticity  
504 (adaptive or maladaptive) does not follow random laws. For instance, unmasking a set of latent  
505 sub-circuits can take over operations sufficiently close to those normally required (Collignon  
506 et al., 2011). In this context, the simplified SAL-FPN-DMN network space of the LUM  
507 framework provides a taxonomy and guidance of where and how language and memory  
508 malfunctioning occur (see Figure 6 for an example of application in focal epilepsy). Rather than  
509 listing observable symptoms, the LUM connectivity-based and interactive model provides  
510 guidelines for evaluating and interpreting patients' dysfunctions. The framework allows  
511 reconsidering the pathology as affecting mechanisms that transcend the cognitive functions  
512 traditionally described.

513

514

-----Insert Figure 6 here-----

515

516 LUM dysfunctions may mainly result from the impairment of a particular network. For  
517 example, post-stroke cognitive dysfunctions tend to occur in the context of disruption of a  
518 specialized network, affecting preferentially areas sharing similar connectivity patterns of those  
519 of the lesion zone (intra-network dysfunction; e.g., Bayrak et al., 2019). This is in line with  
520 previous studies showing that the diaschisis preferentially affects functional connectivity  
521 between related areas within a given network (Baldassarre et al., 2016; Ovadia-Caro et al.,  
522 2013; Siegel et al., 2016). Other pathologies, such as mild cognitive impairment (MCI), could  
523 also primarily affect intra-network connectivity. The most frequently reported finding is  
524 decreased connectivity within the DMN (Krajcovicova et al., 2014). This hypothesis of DMN  
525 modifications is consistent with findings that patients with MCI often present amnesic MCI  
526 and show poor performances for naming, fluency, word definition, spontaneous descriptions  
527 (Ahmed et al., 2008; Oulhaj et al., 2009), all involving representations embedded in the **TA**  
528 dimension of the LUM model. Depending on the progression of the pathology (e.g., conversion  
529 from MCI to Alzheimer's disease), disruption may become more significant. They can impact  
530 other networks and inter-network integration (Badhwar et al., 2017; Chand et al., 2017, for a  
531 systematic review and a meta-analysis), altering cognition more widely. LUM perturbations  
532 could also be due to abnormal modulation of inter-networks dialogues. Even though this  
533 hypothesis has not been directly tested, possible abnormal FPN-DMN (or **CM-TA**) synchrony,  
534 in particular, could also be the cause of disorders such as psychogenic amnesia, for instance.  
535 The mechanism of involuntarily repressed memories in patients suffering from dissociative  
536 amnesia is reflected by the over-activation of prefrontal cortices leading to an under-activation  
537 of the hippocampal complex (Kikuchi et al., 2010).



538 Concerning local dynamics, several lines of evidence have shown that central hubs are highly  
539 prone to damage (Fornito et al., 2015). When neuropathology affects language-memory areas  
540 of convergence (damage to cortical connectors), as in certain forms of stroke or primary  
541 progressive aphasia (PPA), it results in a profound perturbation of inter-networks (LUM)  
542 integration and global modularity (Gratton et al., 2012; Power et al., 2013). Lesions or  
543 malfunctions of these areas lead to more severe deficits (e.g., Wilson et al., 2012), inducing  
544 symptoms of so-called Broca's or Wernicke's aphasia that could be translated, in computational  
545 terms, by interference in critical operations such as "Merge" or "Label".

546 In addition to acute injury, developmental neuropathology is also a privileged setting for  
547 identifying the resilience of the LUM system to cope with the constraints imposed by an atypical  
548 brain configuration. For example, dissociations between language and memory have been  
549 reported in amnesic patients with neonatal hypoxia and bilateral hippocampi damage (Vargha-  
550 Khadem et al., 1997; Vargha-Khadem & Cacucci, 2021, for a recent commentary). Despite  
551 apparent "autonetic" amnesia, these children who grew up without functional hippocampi show  
552 vast preservation of the verbal "semantic" learning and production-comprehension language  
553 abilities (Gadian et al., 2000). However, similar damage occurring in adulthood can lead to  
554 quantifiable disorders of naming or the social use of language (Duff et al., 2009; Hilverman &  
555 Duff, 2021). The idiosyncratic interdependencies and equilibria specific to an early atypical  
556 brain configuration have yet to be specified. In the LUM framework, this effort will help to  
557 understand how language-memory harmony can remain (relatively) preserved despite the  
558 disruption of essential operations as here, multimodal binding.

559 The timing, the type, and the extent of damage condition the degree of functional specialization  
560 and cognitive efficiency. The compensatory potential of the (developing) brain, however, can  
561 be highly impressive. Kliemann and colleagues found that childhood hemispherectomy patients  
562 may present remarkable preservation of their cognitive abilities, including language and

563 memory (Kliemann et al., 2019). Those patients, despite the absence of one hemisphere and  
564 thus of homotopic organization and interconnection, have nonetheless developed a close to  
565 typical pattern of functional connectivity in the remaining hemisphere, maintaining the  
566 segregation and specificity of specialized and intrinsic networks (see also Tyszka et al., 2011  
567 for similar observations in congenital agenesis of corpus callosum). The preservation of the  
568 global and local stereotypic LUM connectivity gradient thus appears to be an essential predicate  
569 for harmonious language and memory development. Other factors or neuroplasticity  
570 mechanisms such as degeneracy or pluripotentiality (Friston & Price, 2003; Noppeney et al.,  
571 2004) make the structure-function relationships complex need to be explored in the study of  
572 LUM disorders.

573 Overall, the application potential of the model is multiple. A focus on how LUM networks/brain  
574 regions are functionally modulated can bring new working hypotheses on the origin of  
575 (mal)adaptive plasticity, help diagnose clinical targets, and support the refinement of existing  
576 nosology. Conversely, testing the LUM model in various conditions  
577 (developmental/longitudinal, before/after neurosurgery, before/after cognitive rehabilitation)  
578 and pathologies represent an eminent source for enriching the model by helping, for example,  
579 to inventory LUM neurocognitive operations and associated critical  
580 regions/connections/dialogues.

### 581 **4.3. Cerebello-subcortico-cortical synchrony**

582

583 Although very comprehensive and detailed, the current language models (Duffau et al., 2014;  
584 Hickok & Poeppel, 2007; Indefrey, 2011; Price, 2012) do not incorporate mesial temporal  
585 structures that contribute to language processing (Bonhage et al., 2015; Hamamé et al., 2014;  
586 Piai et al., 2016). Although still under debate, the hippocampus's role in processing semantic  
587 memory and, more broadly, of language could be more important than previously considered

588 (Covington & Duff, 2016; Duff et al., 2020; Spiers, 2020) and should be studied further LUM  
589 context.

590 Moreover, the central place given to subcortical and cerebellar structures in higher-order  
591 cognitive functions, such as language and memory, remains relatively recent, probably owing  
592 to the implicit legacy left by the theory that the subcortical regions underlie primitive functions.  
593 Basal ganglia and striatum would be involved in sequencing (Leventhal et al., 2012) necessary  
594 for the working memory system (Parr & Friston, 2017) and in respect to language processing  
595 in the formulation of "syntactic complexity" (Santi et al., 2015). The parallel loops between the  
596 striatal complex and cortical region also engage the thalamus, a highly integrative hub of  
597 multimodal information, crucial for the language and long-term memory (Wolff & Vann, 2019;  
598 Figure 5B). Its anterior part, strongly linked to the hippocampus, would be notably engaged for  
599 in-memory recollection processes, constituting a "gateway to mental representations"  
600 (Aggleton et al., 2010; Johnson & Knight, 2015 for evidence coming from intracranial EEG).  
601 Finally, the cerebellum (or "little brain") is a complex structure whose involvement goes beyond  
602 language production's motor aspects. More precisely, Guell and Schmahmann (2020) have  
603 recently dissected its functional anatomy and have shown a specific functional ordering  
604 involving gradually motor, attentional/executive (mainly represented by working memory),  
605 default-mode (verbal task as story listening) aspects of cognition from the anterior to the  
606 posterior part of the cerebellum. The change from static to a dynamic view of cognition sheds  
607 light on the importance of these structures' roles in higher cognitive functions (Benítez-Burraco  
608 & Murphy, 2019). These regions' systematic functional connectivity investigation will ensure  
609 a more precise delineation of their involvement and specialization, which will enrich the current  
610 model.

#### 611 **4.4. Leveraging advances in functional connectomics**

612

613 Advances and methodological transfers in network sciences make it possible to propose new  
614 modeling to complex layouts (Bassett et al., 2018) and, in particular, to inter-function  
615 configurations (here LUM for language-memory relations). The multitude of new parameters  
616 offered for the study of networks (Lynn & Bassett, 2019) makes it possible to define, ever more  
617 precisely, the neuro-functional properties of certain cerebral regions or networks (e.g.,  
618 reflecting integration/segregation, flexibility/allegiance, hierarchies/heterarchies relationships).  
619 However, despite rapid progress, there is still no consensus on the number of network  
620 components that optimally describe brain function. The main networks we described in the  
621 LUM model could be effectively decomposed into several sub-networks or partitions (Akiki &  
622 Abdallah, 2019; Gordon et al., 2020; Yeo et al., 2011), and their implementation, therefore,  
623 represents one of the prospects for refining the model.

624 On the other hand, if functional connectivity has so far given a central place to nodes/brain  
625 regions, a new methodological approach based on the study of the properties of the connections  
626 themselves (an edge-centric approach; Faskowitz et al., 2020; Uddin, 2020) is an exciting  
627 perspective of added value for interactive models and framework. In addition, functional  
628 connectivity is now directly approaching dynamically (time-varying network representations;  
629 Medaglia & Bassett, 2018). Dynamical functional connectivity allows a better approach to the  
630 notion of "cognitive state" and thus provides crucial insights for investigating transient  
631 configurations and neurocognitive operations. In the near future, interactive models, such as the  
632 LUM model, will significantly benefit from developing and applying dynamical systems theory  
633 methods (see, in this perspective, Forseth et al., 2021). Moreover, the improvement of  
634 dynamical connectivity will also benefit the study of effective connectivity, causal relations  
635 between temporal signals, which should also greatly help clarify the "how" of language memory  
636 operations are performed by the brain and their failure. Finally, computational methods and  
637 artificial neural networks are also promising tools that, coupled with functional brain markers,

638 can allow a better understanding of the computations and algorithms involved in natural  
639 language processing as well as their neural implementation (e.g., Goldstein et al., 2021; Jain &  
640 Huth, 2018, for two examples on word prediction in natural context; Martin, 2020, for a  
641 proposed architecture of the hierarchical and compositional structure of language, based on  
642 neurobiological and neurocomputational modeling evidence).

643

## 644 **5 Conclusions**

645 Recent language or memory models emerged in recent years to improve our knowledge of  
646 neurocognitive processes and substrates underpinning these functions. The current paradigm  
647 tends to enrich these models and contribute parsimoniously to unify our vision of cognitive  
648 functioning, which, at this moment, remains fragmented. There is still a limited number of  
649 theories depicting relationships and dynamics between cognitive functions. We proposed the  
650 LUM model to address this issue and integrate the notable research findings with the more  
651 recent ones by considering the network theory perspective to provide useful benchmarks. Due  
652 to its interactive framework, LUM proposes a new **systems-based** taxonomy (**RT-CM-TA**  
653 neurobiologically supported by SAL-FPN-DMN) that can help understand normal development  
654 and aging and cognitive language and memory dysfunctions in patients with neuropsychiatric  
655 disorders. The model proposed goes beyond the traditional cognitive-centric approach. It is  
656 scalable and can thus be adapted to other cognitive domains. We present only a first theoretical  
657 step toward models that could design and help better understand the interactive dynamics of  
658 cognitive functions and meta-functions.

659

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1223

1224 **Box 1: Traditional "cognitive" definitions associated with language and memory**

1225

1226 **Language** is classically defined as a natural, intrinsic, and universal ability of human beings to construct  
1227 communication systems using codes (speech sounds or written symbols) and to use these codes.

1228 Language cognitively involves a semantic system (vocabulary and lexical access), specialized sensory-  
1229 motor capacities of perception and production (phonology), as well as capacities for decoding,  
1230 manipulating (grammar/syntax), and understanding these codes (shared symbolism; comprehension).

1231 **Language production** can be defined as the physical signal used to transmit language and share  
1232 thoughts. Speech production would require, among other capacities, syntactic and articulation processes.

1233 **Syntax** refers to the rules for organizing elements - word segments, words, sentences into a grammatical  
1234 discourse - to generate combinatorial and hierarchical structures.

1235 **Verbal comprehension** encompasses various processes helping to construct understandable and  
1236 meaningful speech productions (expressive language skills up to the pragmatics of language, for  
1237 instance) and to understand verbal productions (receptive language skills echoing vocabulary or  
1238 semantics).

1239 **Memory** represents the ability to maintain information or representations of past experience or  
1240 knowledge, arguing to be based on mental processes of encoding, retention and retrieval, or reactivation.  
1241 Several forms of memory have been proposed depending, for example, on the degree of consciousness  
1242 or attention given to the process (implicit *versus* explicit memorization) and/or the duration of retention  
1243 (short-term *versus* long-term memorization).

1244 **Working memory** is positioned between short and long-term memory and concerns the ability to  
1245 explicitly maintain and manipulate (re-)instantiated information to perform complex cognitive tasks of  
1246 learning, reasoning or comprehension. Working memory is generally considered to be part of executive  
1247 functioning (or central executive system), covering concepts such as planning, inhibition, and mental  
1248 flexibility.

1249 **Verbal working memory** involves a system for programming the utterance, scheduling verbal items at  
1250 several levels (words, phonemes and articulatory gestures), and maintaining what needs to be produced  
1251 (phonological loop and rehearsal); and appears conceptually close to the definition of syntax.

1252 **Declarative memory** is involved in maintaining information about facts/knowledge or events for a  
1253 significant period of time (long-term memory) and consciously recalling information. Declarative  
1254 memory is classically divided into two subtypes: semantic memory and episodic memory.

1255 **Semantic memory** includes general and factual knowledge about the world and abstract concepts  
1256 (noetic consciousness). It allows individuals to make sense of information and/or to engage in cognitive  
1257 processes such as object recognition or appropriate language use.

1258 **Episodic memory** evokes the memory of personally experienced events associated with a particular  
1259 time and place (spatiotemporal context), involving a sense of self-awareness (or autothetic  
1260 consciousness). In addition to the conscious recall of past events, episodic memory implies a "mental  
1261 journey through time" (mental time travel, i.e., a projection into the past and/or future).

1262 **Associative memory**: retrieval or activation of memories (stimulus, behaviors, facts, events...)  
1263 conceptually or contextually associated.

1264 **Note:** Definitions are extracted primarily from the dictionary of the American Psychological Association  
1265 (<https://dictionary.apa.org>). Definitions may vary from one theorist to another, but it is interesting to  
1266 note that there are overlaps and bridges between the different subfunctions described for language and  
1267 declarative memory. These interconnections can be expressed as a cognitive network (Figure Box 1).

1268 -----Insert Figure Box 1 here-----

1269

1270 **Box 2: LUM's fundamentals and outstanding questions**

1271  
1272 Brain mapping is traditionally delineated from psychological manifestations. This classical approach  
1273 restricts the field of study to inherited and intangible constructs often speculative, ambiguous, and/or  
1274 chimerical that compromise our understanding of neurocognitive functioning (blurred and unspecific  
1275 cognitive labels; Buzsáki, 2020). The brain-behavior discrepancy is of particular concern for complex  
1276 or high-level cognitive functions, such as language and memory. LUM (Language/union/Memory)  
1277 faces the problem by considering language and memory in a unified way and as a single behavior. We  
1278 formalize the unification of language and declarative memory by adopting a neuro-centric framework  
1279 (as opposed to mainstream cognitive-centric approaches) based on brain connectivity findings.

1280 **The main tenets can be outlined as follows:**

1281 (i) **Structure/Spatial:** cognitive processes initially defined distinctively are entangled (Box 1) and  
1282 share a mutual brain ground (see, e.g., Eisenberg et al., 2019). Three fundamental language-  
1283 memory overlapping dimensions can be considered in the LUM frame (Figure 2). See also Section  
1284 2.3 and Figure 3 for a specification of the structures at the language-memory intersection.

1285 (ii) **Dynamics/Temporal:** behavior emanates from the synergy of highly interactive functional brain  
1286 dynamics (e.g., Cocchi et al., 2013; Cocuzza et al., 2020; Hagoort, 2019 and its multi-network  
1287 perspective in language). LUM proposes a central architecture consisting of a triplet of main  
1288 networks whose interactions can underlie the latent dimensions of the language-memory behavior  
1289 (Section 3.2 and Figure 4).

1290 (iii) **Implementation/Processing:** the spectrum of observable behaviors depends on an embedding of  
1291 local (regional) and global (states) brain dynamics that support specialized operations  
1292 (neurooperations; Cowell et al., 2019). Figure 5 describes an example of these nested global and  
1293 local processes underpinning operations involved in the LUM context at the intersection of  
1294 language and memory (see also Section 4.1).

1295 (iv) **Equilibrium/Plasticity:** cognitive/behavioral efficiency is determined by states or states  
1296 equilibrium that is modulated by idiosyncratic factors of variability (see Herbet & Duffau, 2020,

1297 for instance). Section 4.2 describes several LUM disturbances in several brain affections. Figure  
1298 6 shows a concrete example in the case of chronic (epileptic) mesial temporal lobe damage.

1299 The fundamental principles underlying LUM are not limited to the processing of verbal information and  
1300 can be enriched in the future. This framework implies considering functional specialization or  
1301 perturbation under a different frame of reference, moving away from traditional cognitive concepts.

1302 **Some important questions remain open and need to be addressed in the future:**

- 1303 - What investigative methods/tools and level of granularity are optimal for identifying  
1304 elementary/primitive neurooperations?
- 1305 - Can computational sciences help to draw a parallel with brain operations? In other words, is the  
1306 language of the brain similar to that of (current) algorithms?
- 1307 - Can we envisage a common understanding of brain operations and a collective scientific  
1308 agreement on their definitions (vocabulary/repertoire/taxonomy)?

1309



1310 **Captions**

1311 **Figure 1: Main legacies of previous neurocognitive observations.**

1312 Simplified overview of the alleged functional role and specialization in language and/or memory  
1313 functions of: **A.** Brain regions and; **B.** Fascicles highlighted in previous neurocognitive meta-analyses  
1314 (Forkel et al., 2020; Walenski et al., 2019) or models (Duffau et al., 2014; Hagoort, 2016; Hickok &  
1315 Poeppel, 2007; Indefrey, 2011; Price, 2012), for language; (Duvernoy et al., 2013; Ranganath & Ritchey,  
1316 2012), for memory).

1317

1318 **Figure 2: Neurocognitive overlap between language and memory.**

1319 Meta-analytic functional maps (positive and thresholded fMRI maps) openly provided by the  
1320 Neurosynth initiative (<https://neurosynth.org/>; Yarkoni et al., 2011) and related to the cognitive terms  
1321 associated with declarative memory and language (PER = speech perception; PHON = phonological,  
1322 SYNT = syntactic; ART = articulatory; PROD = speech production; WM = verbal working memory;  
1323 COMP = language comprehension; LEX = lexical; ASSO = associative memory; EPI = episodic  
1324 memory; SEM = semantic memory) were analyzed using Principal Component Analysis to reveal the  
1325 factorial composition of underlying language-memory behavior.

1326 **A.** Three principal factors emerged from the PCA (elbow, dotted red line), explaining nearly 70% of the  
1327 variance (cumulative variance; scree plot).

1328 **B.** Projection of the cognitive constructs on the three detected components. The assignment is performed  
1329 on the basis of the functional representation (meta-analytic functional maps) and according to the factor  
1330 loadings associated with each principal factor (ternary plot).

1331 **C.** The main latent dimensions in the form of a Venn diagram. The diagram is composed of three subsets  
1332 that are both distinct (eigenvariance) and interrelated (common variance). The encapsulation of these  
1333 modules forms the union of language-memory (LUM) behaviors, while the overlaps form the language-  
1334 memory intersection ( $L \cap M$ ). The three dimensions have been labeled: “*Receiver-Transmitter (RT*  
1335 *System) - Controller-Manager (CM) - Transformer-Associative (TA)*”, according to their composition

1336 (i.e., according to the projection of the cognitive constructs; see the body of the text for a detailed  
1337 description). This 3-fold reformulation is supported by observations from functional connectivity (see  
1338 Figure 4), attesting to their neurobiological relevance.

1339

### 1340 **Figure 3: Neurocognitive conjunction of language and memory maps.**

1341 **A.** Meta-analytic language and memory functional maps openly provided by the Neurosynth initiative  
1342 (<https://neurosynth.org>; Yarkoni et al., 2011; see also Figure 2). The strength of intra- and inter-function  
1343 relationships (tanglegram) between fMRI meta-analytic maps of language (language, verbal production,  
1344 syntax, verbal comprehension) and memory (declarative memory, episodic memory, verbal working  
1345 memory, semantic memory) has been estimated using correlation coefficients. Only significant R-values  
1346 indicating strong similarity between the maps are reported.

1347 **B.** Cortical regions (AAL atlas), cognitive constructs (Neurosynth decoder), and brain white matter  
1348 fascicles (Natbrainlab atlas) associated with the language-memory intersection functional map ( $L \cap M$   
1349 mapping, computed from the functional maps included in A). The bigger the size of the words in the  
1350 word clouds, the more they are linked to the functional language-memory intersection map.

1351

### 1352 **Figure 4: Features and neural foundation of the LUM framework**

1353 **A.** LUM model: formalization of the dynamic links spanning language production and declarative  
1354 memory as an interactive oblique model (i.e., as a composite function). Latent dimensions (**RT-CM-**  
1355 **TA**) are individually associated with specific brain networks (SAL-FPN-DMN, respectively). In terms  
1356 of behavior, internal encoding implied in verbal comprehension, for example, consists of encoding  
1357 declarative inputs (engaging the **TA System**) via more or less attentive listening of verbal indications  
1358 (involving the **RT** and **CM** dimensions). Here, language "feeds" memory (MoL). Externalization, in its  
1359 most accomplished form, leads to the "production" of language involving a mapping of internal verbal  
1360 representations and thoughts (**TA System**) with the corresponding ordered output forms (thus involving

1361 manipulation of **Systems CM** and **RT** up to verbal evocation). Here, memory "feeds" language (LoM).  
1362 To ensure dynamics between language and memory, processes engage a synergy of **RT-CM-TA** latent  
1363 operations, supported by continuous interactions between networks, performed in parallel and executed  
1364 in a more or less controlled manner.

1365 **B.** Global functional topography of the links between brain regions belonging to different networks and  
1366 projected in a reduced space (n = 48 healthy controls, at rest). This global topology has been observed  
1367 in other recent studies (Barnett et al., 2020) and corroborates the dimensions and interactions proposed  
1368 in the LUM framework (i.e., the connectivity between high-level SAL-FPN-DMN networks supporting  
1369 **RT-CM-TA** linkages).

1370 **C.** Example of functional local SAL-FPN-DMN continuums (connector hubs). These functional  
1371 convergence zones correspond to structural convergence zones where the terminations of traditionally  
1372 described language and/or memory bundles are intertwined (Arcuate fascicle: AF; and branches II and  
1373 III of the superior longitudinal fascicle: SLF II-III). Together with peripheral hubs, these connector hubs  
1374 could play an important role in language-memory behavior (see description in the body text).

1375

1376 **Figure 5: Relational binding as one of the core neuro-mechanisms linking language and**  
1377 **memory**

1378 Illustration of the putative dialogues involved in the relational binding mechanism (global and local  
1379 LUM dynamics).

1380 **A.** Pattern separation and pattern completion neurocognitive operations engage online states manifested  
1381 by dialogs involving several connectors hubs. It pushes the brain to a multi-networks state between the  
1382 DMN and convergence zones. Several studies have highlighted an active role of connections between  
1383 the medial temporal lobe, IFG, and angular gyrus in these two processes and under the control of the  
1384 dorsolateral prefrontal cortex in the integration of multiple representations (Palacio & Cardenas, 2019  
1385 for a systematic review). Online activity recordings made at the cellular level (CA1 subfield of the rat

1386 hippocampus) show that the hippocampus engages in dynamic coordination of changes in rhythmic  
1387 profiles during associative learning (Rangel et al., 2016), allowing flexible dialogues in particular with  
1388 DMN regions and the convergence zones. The main difference between encoding and retrieval concerns  
1389 a change in modularity, especially between the two anterior and posterior subsystems of the DMN,  
1390 which are more inter-connected during memory retrieval (Cooper & Ritchey, 2020; Geib et al., 2017).  
1391 Thus, pattern completion probably engages the DMN in a more synchronized manner (dotted arrow)  
1392 than pattern separation.

1393 **B.** The "replay" operation entails an offline state with more or less long periods of spontaneous updating  
1394 of recently acquired information (Higgins et al., 2020). In terms of global LUM dialogues, consolidation  
1395 is linked to an anti-phasic system associated with a strong synchronization of the DMN and limbic  
1396 structures and a weaker synchronization between the DMN and other network components, such as  
1397 attentional-sensory networks (Sneve et al., 2017). At the local level, suppression of thalamic activity  
1398 could mediate these phase changes, reducing the transmission of external cognitive and sensory  
1399 information during consolidation and allowing neocortical regions to be more receptive to input  
1400 provided by peripheral hubs, mainly the hippocampus (e.g., Yang et al., 2019).

1401

## 1402 **Figure 6: Relevance of the LUM framework in temporal lobe epilepsy**

1403 Temporal lobe epilepsy (TLE) is frequently symptomatic, typically accompanied by language and  
1404 memory deficits (manifested in naming or verbal fluency assessment, spontaneous speech, immediate  
1405 and various memory tasks (Allone et al., 2017; Bartha-Doering & Trinkka, 2014; Benke et al., 2013;  
1406 Castro et al., 2013; Condret-Santi et al., 2014; Jaimes-Bautista et al., 2015; Metternich et al., 2014; Zhao  
1407 et al., 2014). While there is a plurality of profiles (Reyes et al., 2020), "pure" forms of language-memory  
1408 impairment are reported (Elverman et al., 2019), making TLE a relevant model for studying the LUM  
1409 framework in the pathological condition.

1410 **A.** Disruption of global LUM dynamics in patients (n = 37 patients compared to controls, at rest). Global  
1411 changes refer to how the connectivity of brain regions belonging to a particular network is altered, thus

1412 disrupting the overall topology and synchrony. The main character is a fragmentation of the FPN and  
1413 DMN networks (higher vectors of change, symbolized by the arrows), with reduced segregation between  
1414 specialized networks. The global integration of information by these networks (global efficiency) is also  
1415 particularly affected (boxplot). These observations are manifested by a reduction in connectivity within  
1416 and between DMN-FPN networks in patients (heatmap of connectivity change rates).

1417 **B.** Disruption of local LUM dynamics in patients. Global LUM connectivity changes are accompanied  
1418 by regional LUM disruption. At rest, patients present a significant functional disturbance of major  
1419 connector and provincial hubs (namely IFG and hippocampi), essential for relational binding (LUM  
1420 neurooperations; see Figure 5). These functional disturbances are indeed specifically related to poor  
1421 performance in cognitive indicators requiring the associative linking of verbal information (see our  
1422 previous works on TLE patients: Banjac et al., 2021; Roger et al., 2019, 2020). Moreover, the spatial  
1423 pattern of functional alterations largely coincides with the language-memory functional intersection map  
1424 (Neurosynth  $L \cap M$ , based on task-fMRI) and the alterations in structural connectivity (significant  
1425 decrease in tract-weighted fractional anisotropy in patients, estimated with high-resolution diffusion  
1426 MRI; Roger, 2020).

1427 Overall, TLE patients' analysis of intrinsic disturbances for both global and local dynamics leads to a  
1428 relational binding syndrome hypothesis, mainly manifests by DMN-FPN de-synchronizations and  
1429 essentially affecting the **CM-TA LUM Systems**. These observations, in the pathological context, also  
1430 confirm hypotheses about the potential interactive mechanisms involved in the relational binding  
1431 operation (as proposed in Figure 5).

1432

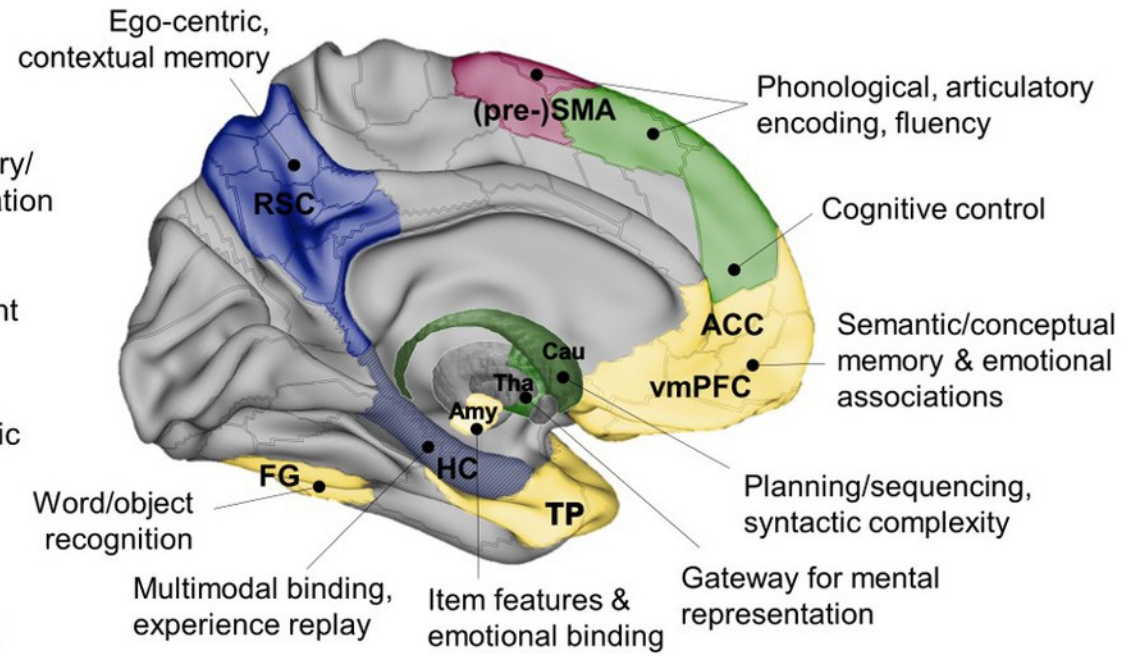
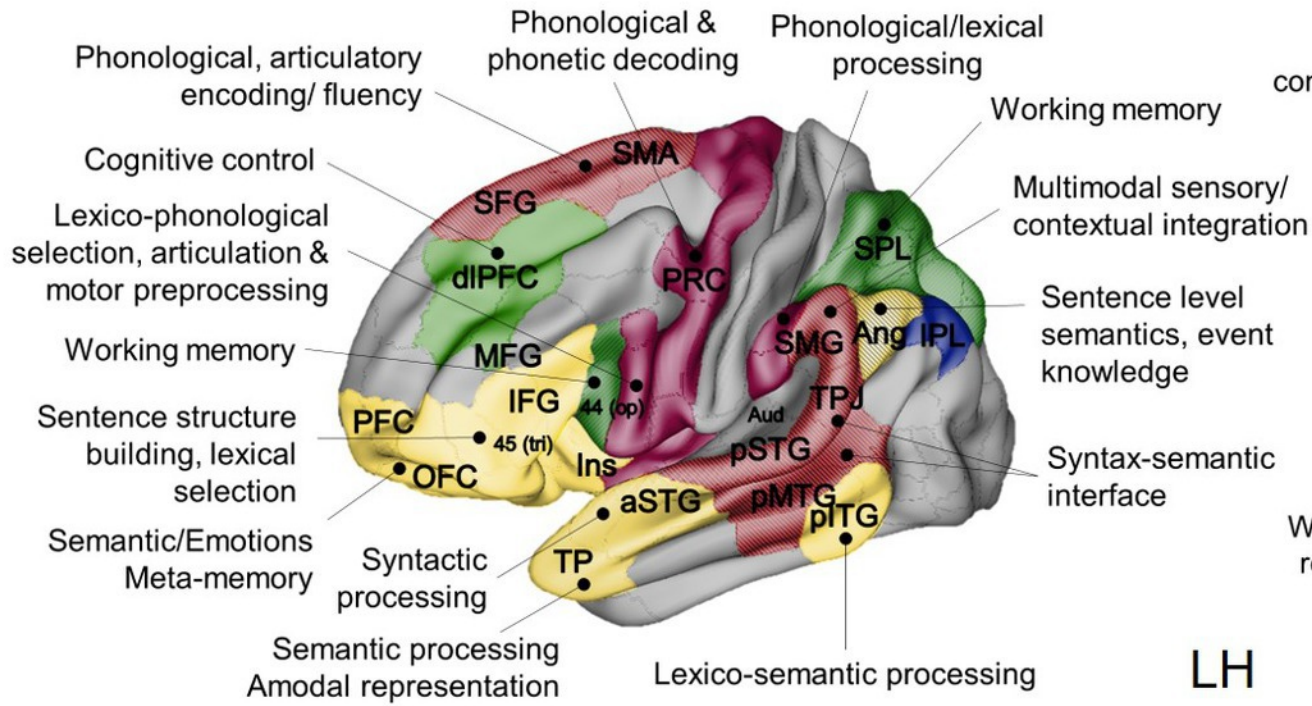
1433

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1437 0015-01]; and by NeuroCoG IDEX UGA in the framework of the “Investissements d’avenir”  
1438 program [grant number ANR-15-IDEX-02].

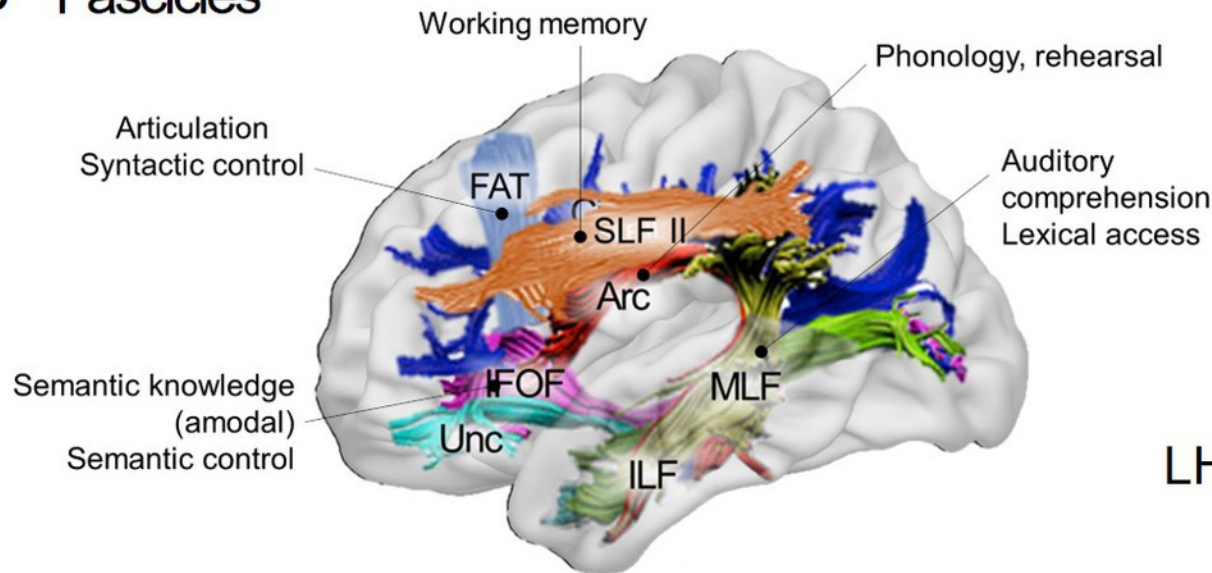
1439

# A Brain regions

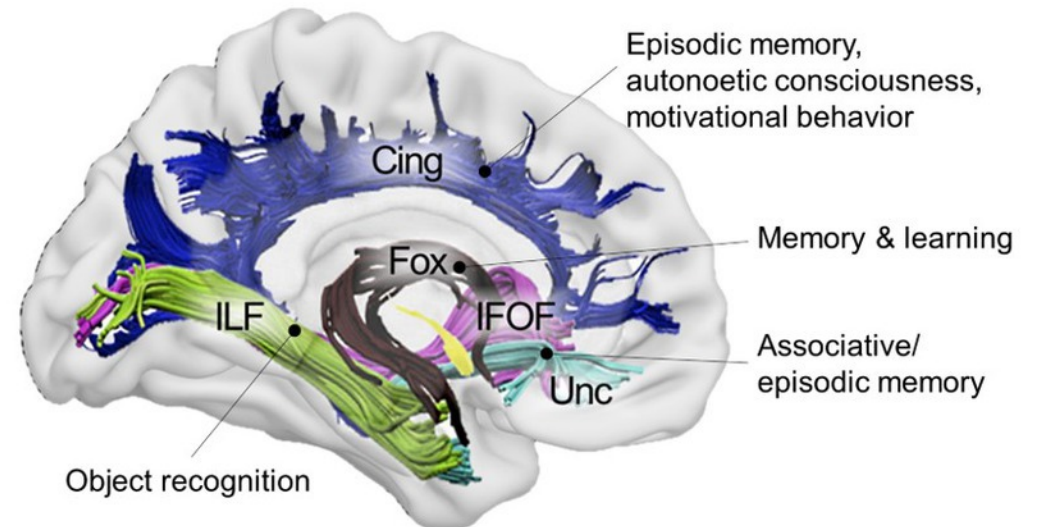


LH

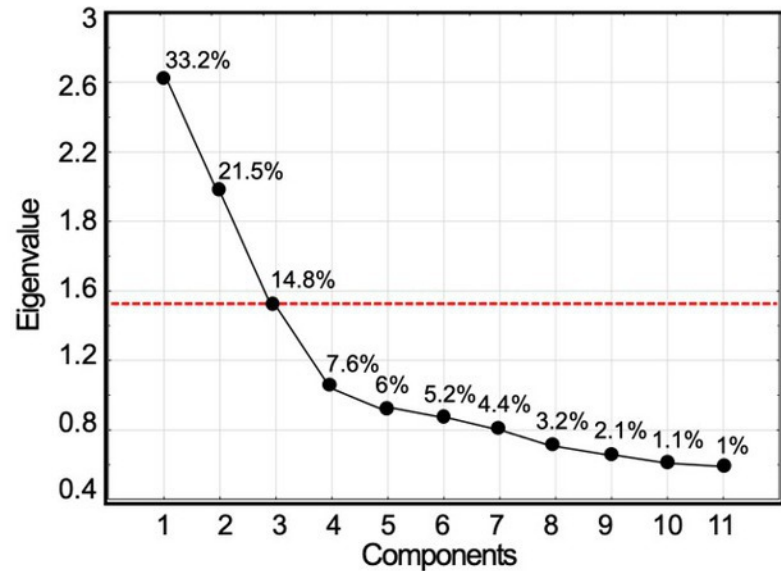
# B Fascicles



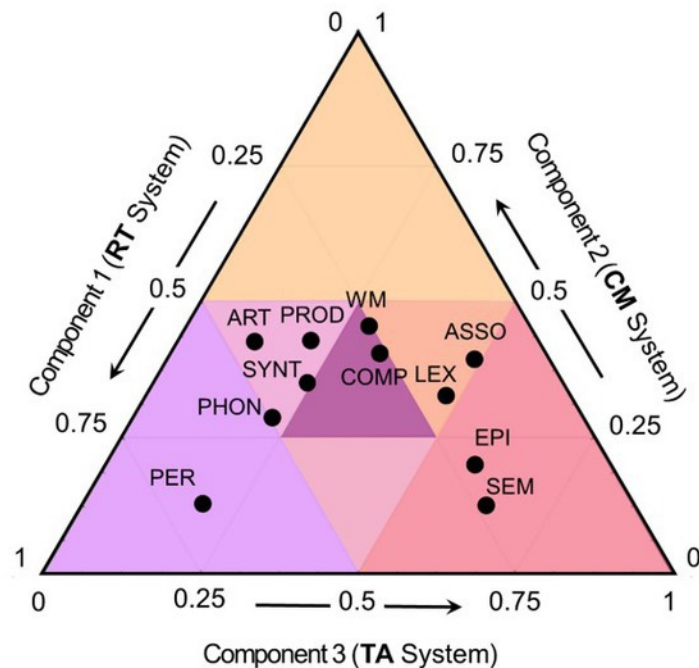
LH



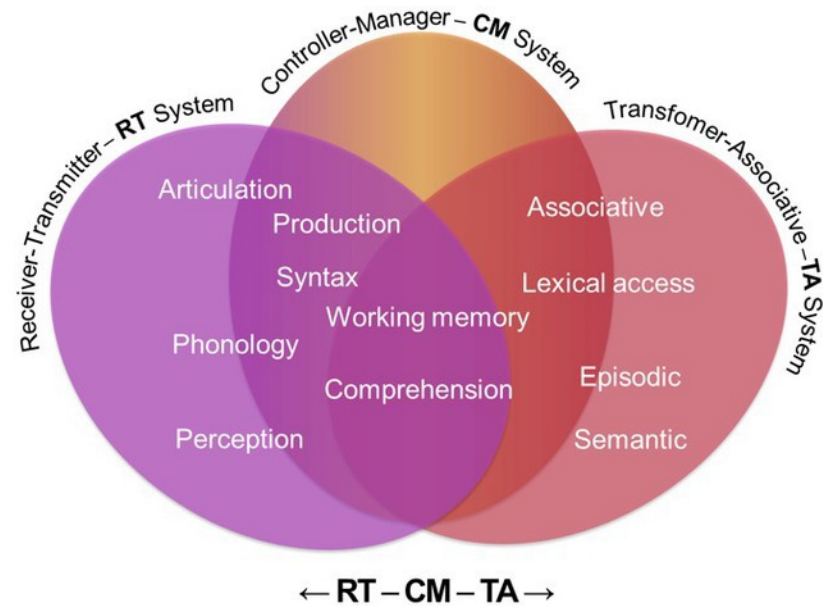
## A Fundamental dimensions



## B Cognitive mapping

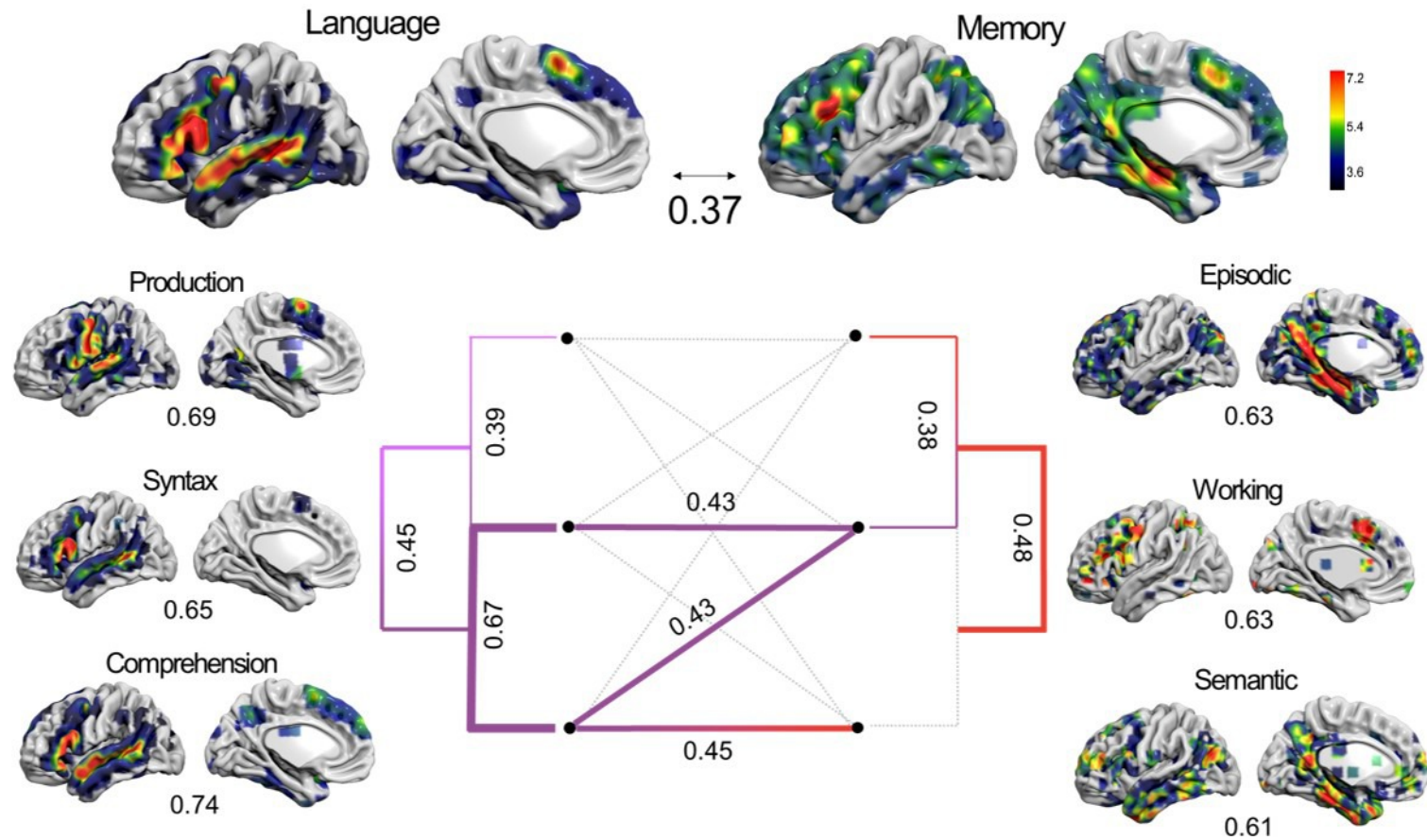


## C Language-memory continuum

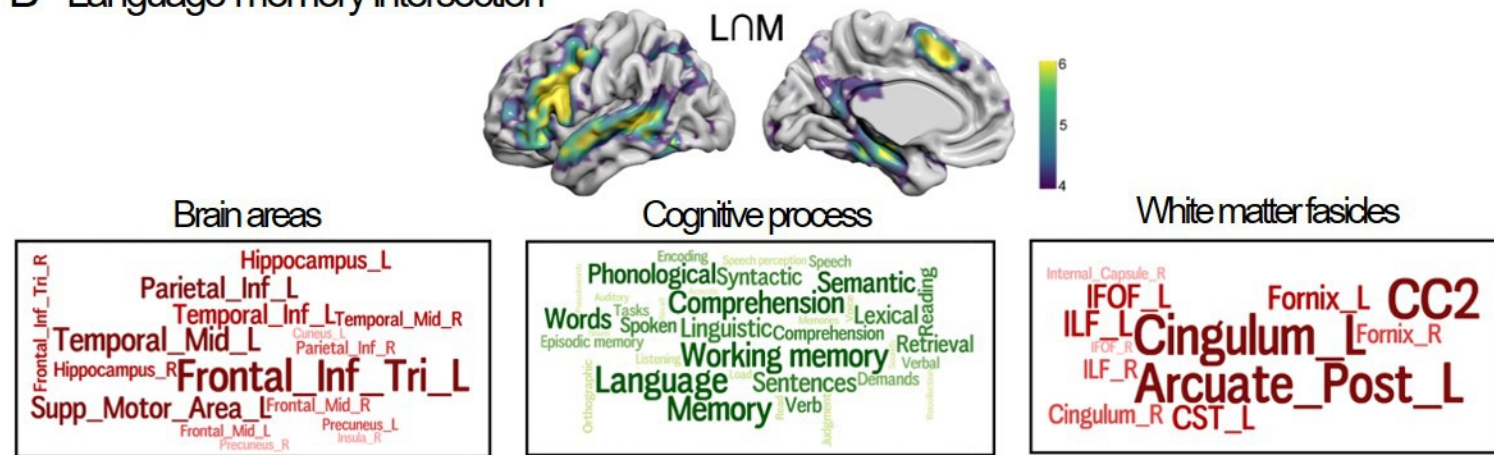




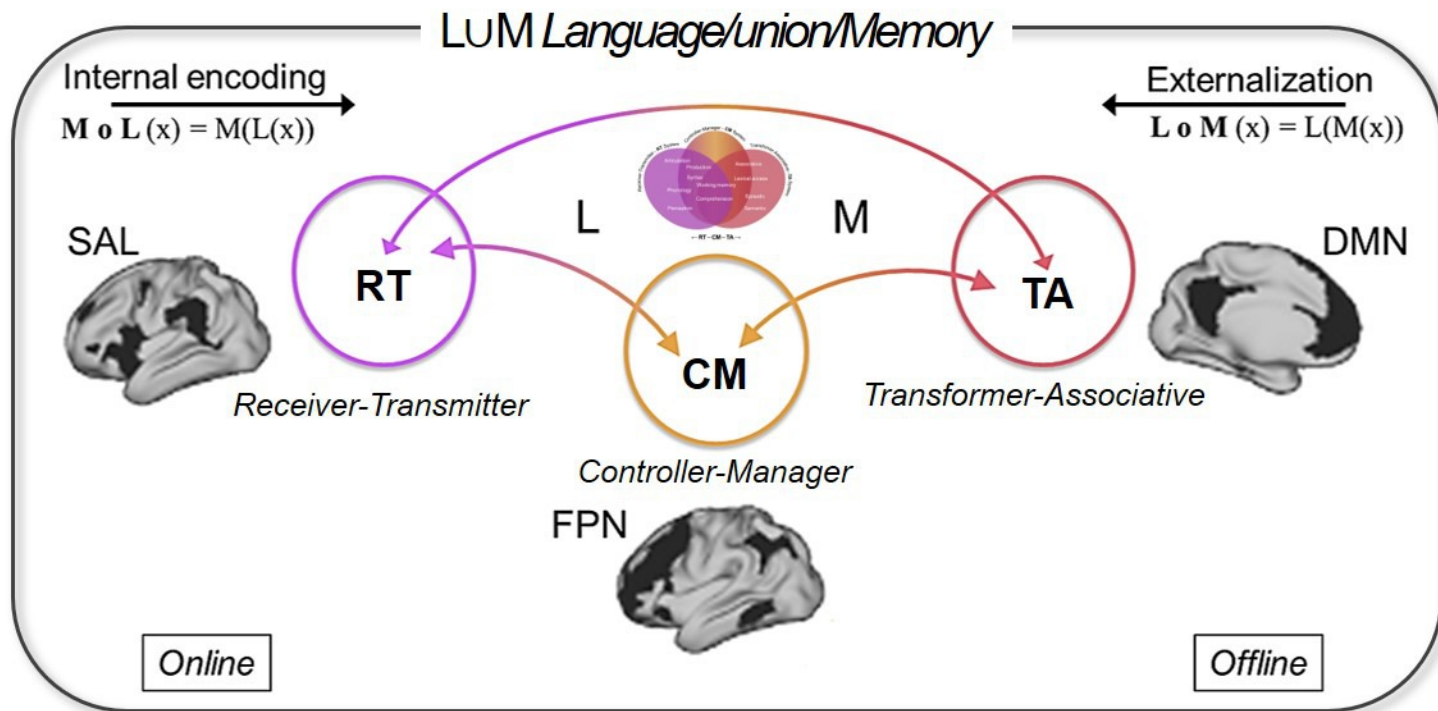
# A Language-memory correlations



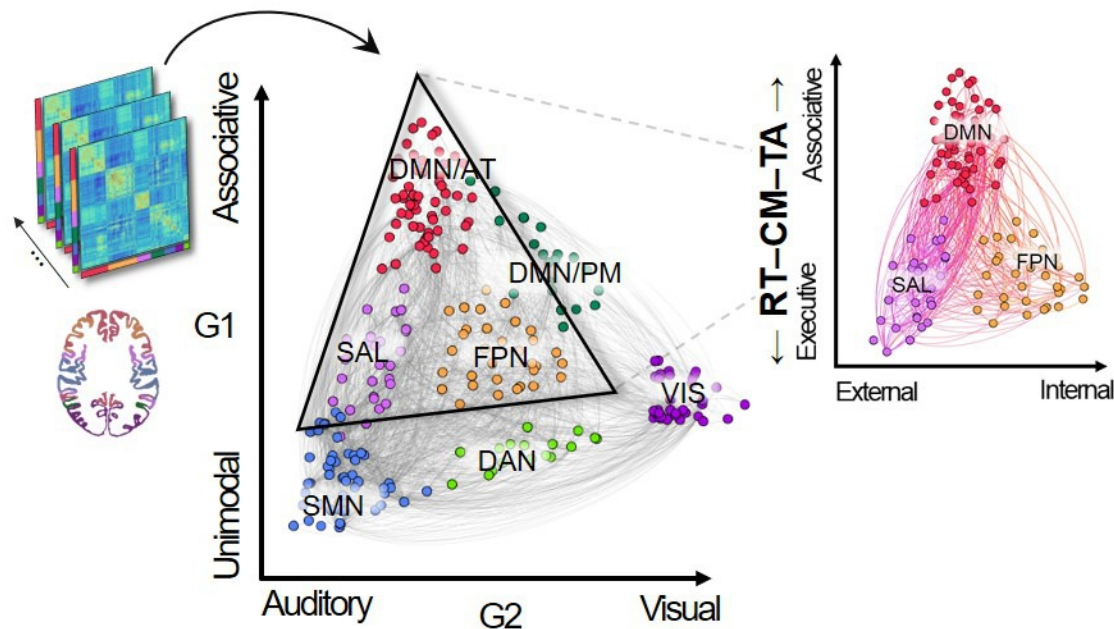
# B Language-memory intersection



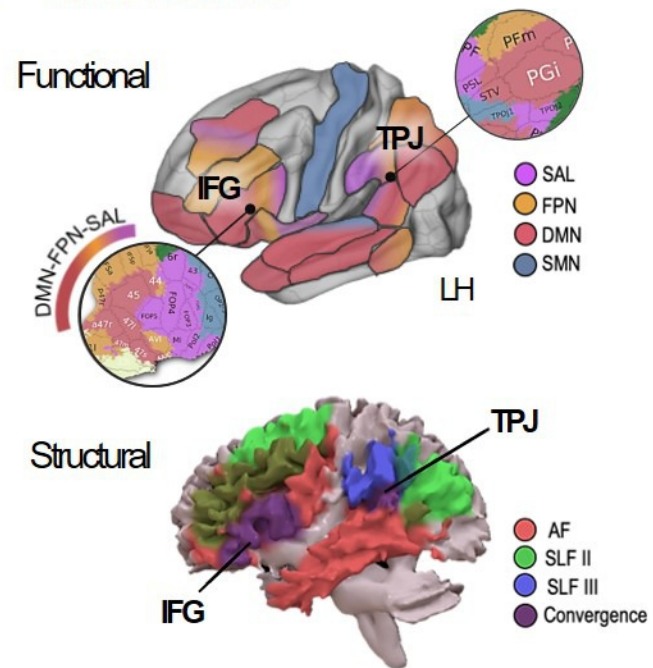
# A Overview of the LUM model



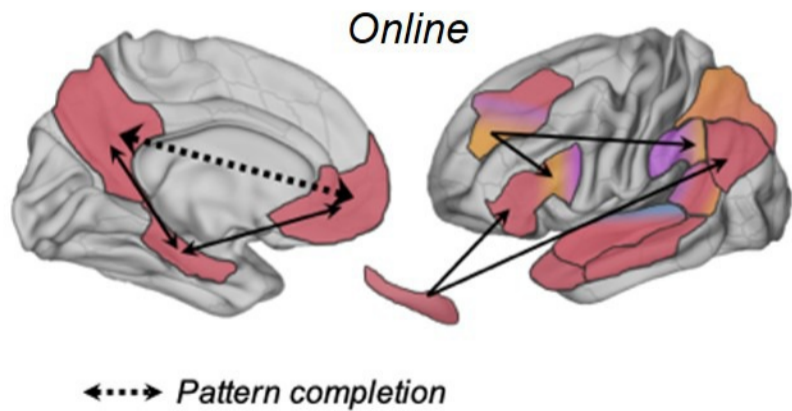
## B Global features



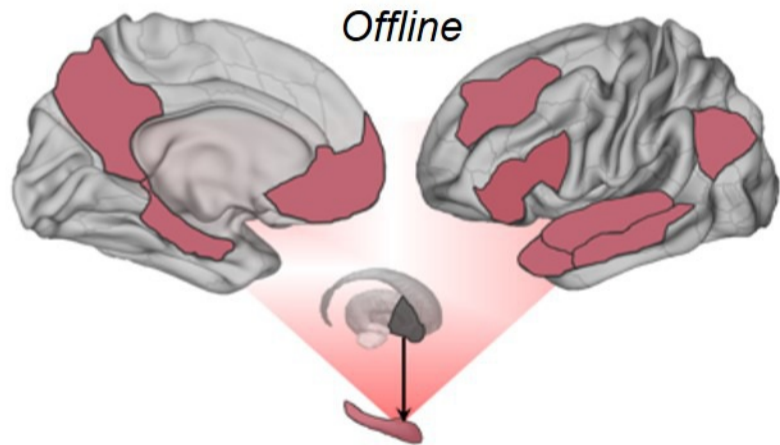
## C Local features



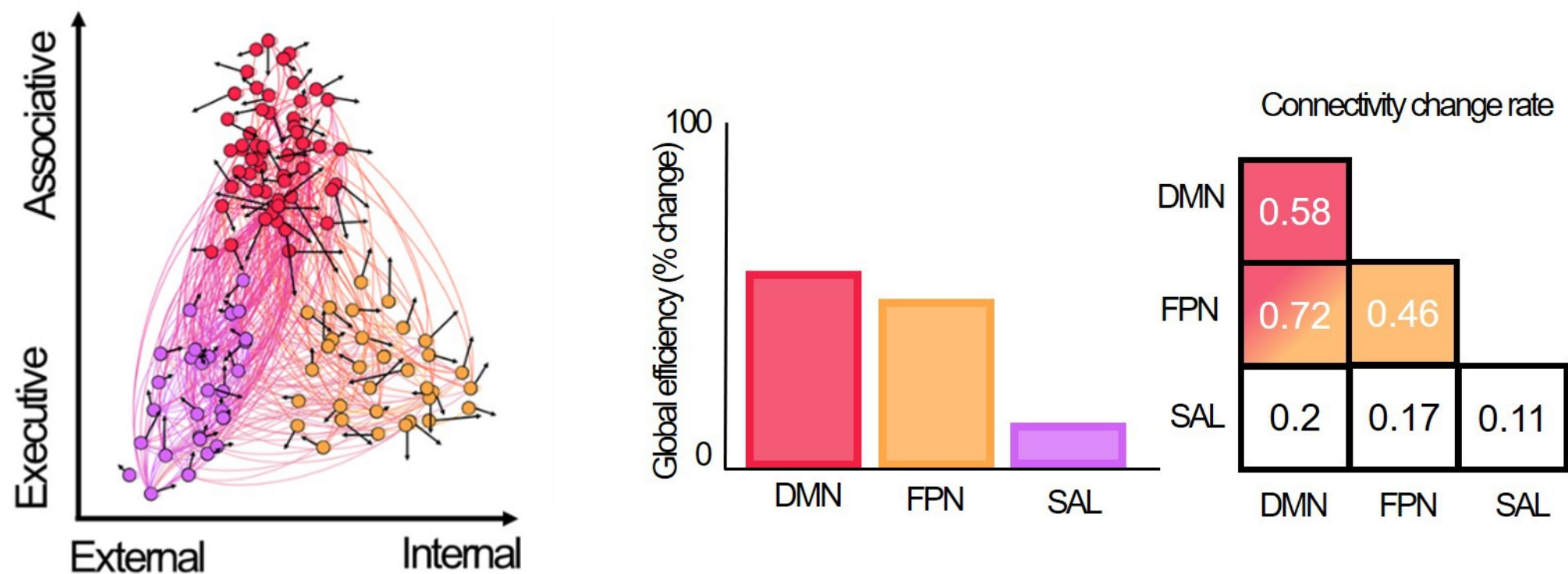
# A Pattern separation / completion



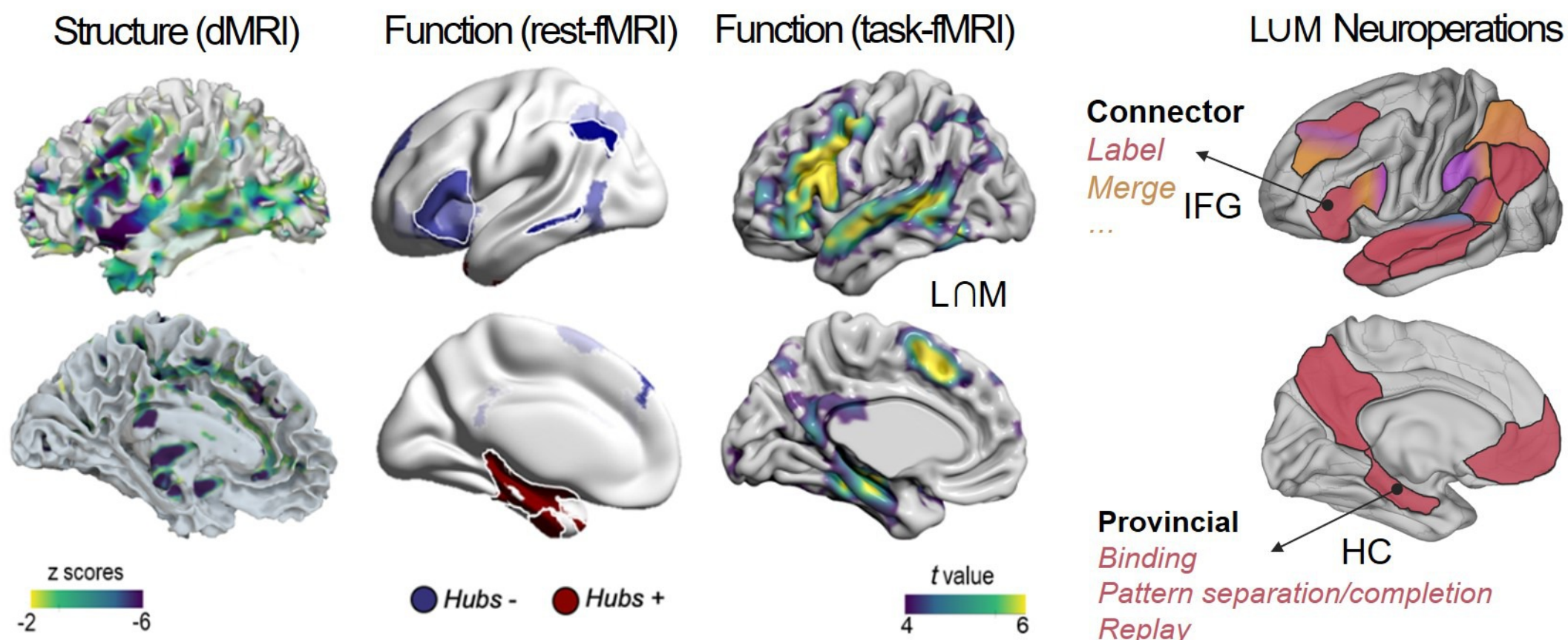
# B Replay



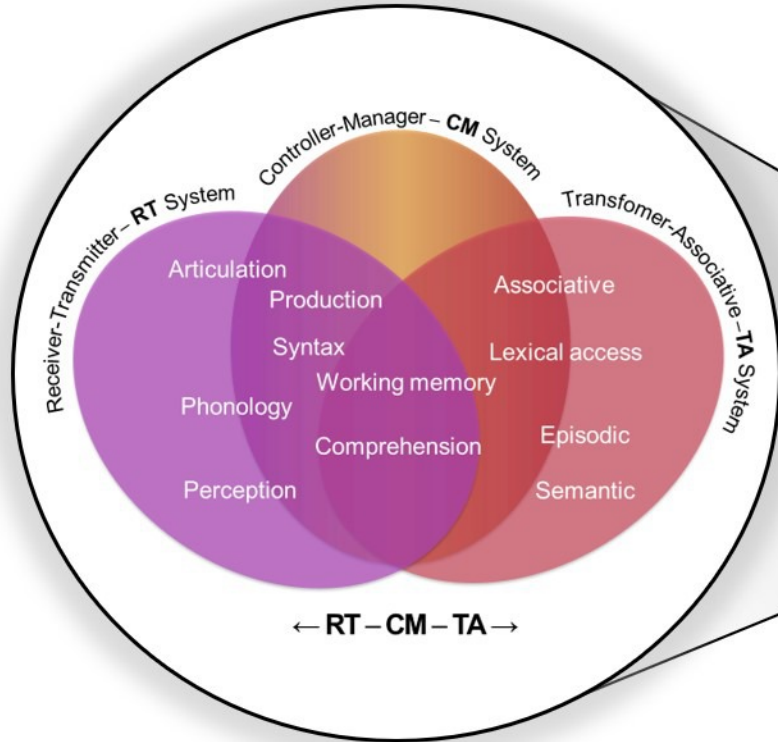
## A Disruption of the global dynamics



## B Disruption of the local dynamics



# Fundamental LUM dimensions



# Synergistic interactions between networks

