

Missing links: The functional unification of language and memory $(L \cup M)$

Elise Roger, Sonja Banjac, Michel Thiebaut de Schotten, Monica Baciu

► To cite this version:

Elise Roger, Sonja Banjac, Michel Thiebaut de Schotten, Monica Baciu. Missing links: The functional unification of language and memory (L \cup M). Neuroscience and Biobehavioral Reviews, 2022, 133, pp.104489. 10.1016/j.neubiorev.2021.12.012 . hal-03624908

HAL Id: hal-03624908 https://hal.univ-grenoble-alpes.fr/hal-03624908

Submitted on 8 Jan 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

Running title: Language and memory unification (LUM)

Elise Roger^{1 CA}, Sonja Banjac¹, Michel Thiebaut de Schotten^{2,3} & Monica Baciu¹

¹LPNC, Univ. Grenoble Alpes, CNRS UMR 5105, Grenoble, France

² Brain Connectivity and Behaviour Laboratory, Sorbonne Universities, Paris, France

³ Groupe d'Imagerie Neurofonctionnelle, Institut des Maladies Neurodégénératives-UMR

5293, CNRS, CEA University of Bordeaux, Bordeaux, France

CA, Corresponding Author Elise Roger LPNC, UMR CNRS 5105 BSHM, BP 47 38040 Grenoble Cedex 09, France Phone: +33 456 52 97 21 Fax: +33 456 52 97 21 Email: <u>elise.roger@univ-grenoble-alpes.fr</u>

1 1 Introduction

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

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

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

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

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

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

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

52

53 2 Main legacies of neurocognitive observations

54 **2.1. Language and memory coevolution**

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

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

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

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

As with the semantic processing, mental time travel, and episodic memory, often referred to as
declarative or "declarable" memory (Squire, 2004; Tulving, 1972; Box 1), have co-evolved with
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 exchanges of information necessary for the production and understanding of language (Figure 108 109 1 for the putative role of brain regions and fascicles in language processing). This advanced language representation has challenged the modular and serial views and demonstrated that 110 semantic, phonological, and syntactic processing pertains to parallel large-scale cortico-111 subcortical sub-networks. These specialized systems would be dynamically interconnected 112 (Duffau et al., 2014), allowing rich and flexible language skills. 113

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

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

132

2.2.2. Declarative memory

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

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

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

- 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

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

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

From a neurocognitive point of view, the first latent dimension – which we propose to call "*Receiver-Transmitter*" (RT System) – mainly encompasses aspects related to speech perception, phonology, articulation, and syntax. In addition, and even if to a lesser extent, working memory and comprehension saturate this dimension. This suggests that RT comprises processes related to the externalization of verbalizable outputs, implying "spell-out" and sensory inputs influencing all cognitive processes and the outputs. RT may involve perceptuomotor information processing operations (Giraud & Poeppel, 2012; Poeppel & Assaneo, 2020,
for an example of computational principles associated with speech perception) – *selection/detection, segmentation, concatenation/linearization, conjunctive binding.* To
simplify and caricatured, RT could proceed at the computational level as an active in and out
cognitive "Receiver-Transmitter" system.

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

The third dimension covers neurocognitive aspects related to language comprehension, associative memory, lexical access/retrieval, verbal semantic, episodic, and working memories. In a simplistic way, it can be described as a "**Transformer-Associative**" computational component (**TA System**) as it includes computations to build and maintain mental, conceptual, and multimodal representations. The operations underlying TA encompass, for instance,
 abstraction/dimensionality reduction, multimodal/relational binding, pattern separation/completion, and *replay* (Cowell et al., 2019).

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

- 243
- 244

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

- 245
- 246

247 2.3.2. Shared substrate

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

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

269

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

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

278

279

2.3.3. Synergistic networks interactions

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

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

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

311

312

3 Towards a unified view of language and memory

313

3.1. LUM formalism and main principles

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

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

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

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

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

353

3.2.2. FPN, the "Controller-Manager"

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

364 3.2.3. DMN, the "Transformer-Associative"

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

384

385 3.3. LUM interactions: global and local dynamics

386

3.3.1. Non-stationary global dynamics of networks

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

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

407

3.3.2. Local dynamics of integrative hubs

By attempting to locate the language within the organization of intrinsic networks, DiNicola et al. (2020) showed that language-associated regions exhibit a similar pattern of juxtapositions of several networks. These cortical sites, located at the crossroads of the leading networks, thus present essential properties to act as "connector hubs" that are core regions able to integrate information from the different networks locally (see also Braga et al., 2013 for a description of the local multi-networks echo phenomenon). Among these convergence areas, the inferior frontal gyrus (IFG complex) follows a SAL-FPN-DMN gradient during the transition from *pars* *opercularis* to *pars orbitalis* (Figure 4C). The IFG complex could functionally and gradually
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 region per se, the connections to and from the IFG confer this role of assembling linguistic 419 representations. These observations fit with the MUC model proposed by Hagoort (Hagoort, 420 421 2016), describing a tripartite "Memory-Unification-Control" hierarchy within the IFG, maintained by structural connections with other areas of functional convergence such as the 422 temporoparietal junction (TPJ) or the posterior part of the mean temporal gyrus (pMTG). 423 Indeed, anatomically, these connector hubs receive the projection of crucial structural pathways 424 (e.g., the arcuate and branches II-III of the superior longitudinal fascicle; Figure 4C) and thus 425 426 constitute essential convergence zones for inter-network integration. Similar local gradients exist in the insula, the supramarginal and angular gyrus, the posterior upper/mid temporal gyrus, 427 the supplementary motor area, the dorsolateral prefrontal cortex, the cerebellum, and the basal 428 ganglia. These local integrators could serve as interfaces to interconnect the different LUM 429 dimensions by manipulating external information and internal mental representations. Their 430 431 role could be particularly crucial when the demand for inter-network connection is reinforced, e.g., during online activity. 432

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

440

Relevance and future directions 4

441

442

4.1. Functional specialization

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

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

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

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

This "networked" conceptualization of functional specialization as proposed in the LUM model 479 does not mean that all regions have a similar neuro-functional architecture or equal contribution. 480 481 For example, the prefrontal cortex involved in FPN may be slightly biased in favor of control and monitoring operations. When actively engaged in verbal information processing, the IFG 482 483 (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 in the LUM framework can explain how such neurocognitive operations dynamically operate 488 to unify language and memory contents into an internal multimodal representation (Figure 5 for 489

a demonstration). However, a more systematic and precise inventory of neurocognitive 490 491 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 future challenges of cognitive neuroscience. 493

- 494
- 495

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

- 496

4.2. LUM in clinical neuroscience 497

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

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

514

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

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

546 In addition to acute injury, developmental neuropathology is also a privileged setting for identifying the resilience of the LUM system to cope with the constraints imposed by an atypical 547 brain configuration. For example, dissociations between language and memory have been 548 549 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 vast preservation of the verbal "semantic" learning and production-comprehension language 552 abilities (Gadian et al., 2000). However, similar damage occurring in adulthood can lead to 553 554 quantifiable disorders of naming or the social use of language (Duff et al., 2009; Hilverman & Duff, 2021). The idiosyncratic interdependencies and equilibria specific to an early atypical 555 556 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.

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

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

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

581

4.3. Cerebello-subcortico-cortical synchrony

582

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

(Covington & Duff, 2016; Duff et al., 2020; Spiers, 2020) and should be studied further LUM
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. Basal ganglia and striatum would be involved in sequencing (Leventhal et al., 2012) necessary 593 for the working memory system (Parr & Friston, 2017) and in respect to language processing 594 in the formulation of "syntactic complexity" (Santi et al., 2015). The parallel loops between the 595 596 striatal complex and cortical region also engage the thalamus, a highly integrative hub of multimodal information, crucial for the language and long-term memory (Wolff & Vann, 2019; 597 598 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" (Aggleton et al., 2010; Johnson & Knight, 2015 for evidence coming from intracranial EEG). 600 Finally, the cerebellum (or "little brain") is a complex structure whose involvement goes beyond 601 602 language production's motor aspects. More precisely, Guell and Schmahmann (2020) have recently dissected its functional anatomy and have shown a specific functional ordering 603 604 involving gradually motor, attentional/executive (mainly represented by working memory), default-mode (verbal task as story listening) aspects of cognition from the anterior to the 605 606 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 a more precise delineation of their involvement and specialization, which will enrich the current 609 610 model.

611

4.4. Leveraging advances in functional connectomics

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

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

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

643

644 5 <u>Conclusions</u>

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

660 **References**

- Aboitiz, F. (2012). Gestures, Vocalizations, and Memory in Language Origins. *Frontiers in Evolutionary Neuroscience*, 4. https://doi.org/10.3389/fnevo.2012.00002
- Aboitiz, F., Aboitiz, S., & García, R. R. (2010). The Phonological Loop : A Key Innovation in Human
 Evolution. *Current Anthropology*, *51*(S1), S55-S65. https://doi.org/10.1086/650525
- Achard, S., & Bullmore, E. (2007). Efficiency and Cost of Economical Brain Functional Networks.
 PLOS Computational Biology, 3(2), e17. https://doi.org/10.1371/journal.pcbi.0030017
- Acheson, D. J., Hamidi, M., Binder, J. R., & Postle, B. R. (2010). A Common Neural Substrate for
 Language Production and Verbal Working Memory. *Journal of Cognitive Neuroscience*, 23(6),
 1358-1367. https://doi.org/10.1162/jocn.2010.21519
- Aggleton, J. P., O'Mara, S. M., Vann, S. D., Wright, N. F., Tsanov, M., & Erichsen, J. T. (2010).
 Hippocampal-anterior thalamic pathways for memory : Uncovering a network of direct and indirect
- 672 actions: Hippocampal-thalamic pathways for memory. European Journal of Neuroscience, 31(12),
- 673 2292-2307. https://doi.org/10.1111/j.1460-9568.2010.07251.x
- Ahmed, S., Arnold, R., Thompson, S. A., Graham, K. S., & Hodges, J. R. (2008). Naming of objects,
 faces and buildings in mild cognitive impairment. *Cortex*, 44(6), 746-752.
 https://doi.org/10.1016/j.cortex.2007.02.002
- Akiki, T. J., & Abdallah, C. G. (2019). Determining the Hierarchical Architecture of the Human Brain
 Using Subject-Level Clustering of Functional Networks. *Scientific Reports*, 9(1), 19290.
 https://doi.org/10.1038/s41598-019-55738-y
- Allone, C., Lo Buono, V., Corallo, F., Pisani, L. R., Pollicino, P., Bramanti, P., & Marino, S. (2017).
 Neuroimaging and cognitive functions in temporal lobe epilepsy : A review of the literature. *Journal of the Neurological Sciences*, 381, 7-15. https://doi.org/10.1016/j.jns.2017.08.007
- Anderson, B. (2011). There is no Such Thing as Attention. *Frontiers in Psychology*, 2.
 https://doi.org/10.3389/fpsyg.2011.00246
- Andrews-Hanna, J. R., Smallwood, J., & Spreng, R. N. (2014). The default network and self-generated
 thought: Component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences*, 1316(1), 29-52. https://doi.org/10.1111/nyas.12360
- Assem, M., Blank, I. A., Mineroff, Z., Ademoğlu, A., & Fedorenko, E. (2020). Activity in the frontoparietal multiple-demand network is robustly associated with individual differences in working memory
 and fluid intelligence. *Cortex*, 131, 1-16. https://doi.org/10.1016/j.cortex.2020.06.013
- Badhwar, A., Tam, A., Dansereau, C., Orban, P., Hoffstaedter, F., & Bellec, P. (2017). Resting-state
 network dysfunction in Alzheimer's disease : A systematic review and meta-analysis. *Alzheimer's & Dementia: Diagnosis, Assessment & Disease Monitoring, 8, 73-85.*https://doi.org/10.1016/j.dadm.2017.03.007
- Baldassano, C., Chen, J., Zadbood, A., Pillow, J. W., Hasson, U., & Norman, K. A. (2017). Discovering
 Event Structure in Continuous Narrative Perception and Memory. *Neuron*, 95(3), 709-721.e5.
- 697 https://doi.org/10.1016/j.neuron.2017.06.041

Baldassarre, A., Ramsey, L. E., Siegel, J. S., Shulman, G. L., & Corbetta, M. (2016). Brain connectivity
and neurological disorders after stroke: *Current Opinion in Neurology*, 29(6), 706-713.
https://doi.org/10.1097/WCO.0000000000396

701 Banjac, S., Roger, E., Pichat, C., Cousin, E., Mosca, C., Lamalle, L., Krainik, A., Kahane, P., & Baciu, 702 M. (2021). Reconfiguration dynamics of a language-and-memory network in healthy participants and 703 patients temporal lobe epilepsy. NeuroImage. Clinical, 102702. with 31. 704 https://doi.org/10.1016/j.nicl.2021.102702

- Barnett, A. J., Reilly, W., Dimsdale-Zucker, H., Mizrak, E., Reagh, Z., & Ranganath, C. (2020, juin 10).
 Organization of cortico-hippocampal networks in the human brain. *BioRxiv*, 2020.06.09.142166.
- Barry, D. N., & Maguire, E. A. (2019). Remote Memory and the Hippocampus : A Constructive Critique. *Trends in Cognitive Sciences*, 23(2), 128-142. https://doi.org/10.1016/j.tics.2018.11.005
- Bartha-Doering, L., & Trinka, E. (2014). The interictal language profile in adult epilepsy. *Epilepsia*, 55(10), 1512-1525. https://doi.org/10.1111/epi.12743
- Bassett, D. S., Zurn, P., & Gold, J. I. (2018). On the nature and use of models in network neuroscience. *Nature Reviews Neuroscience*, *19*(9), 566-578. https://doi.org/10.1038/s41583-018-0038-8
- Bayrak, Ş., Khalil, A. A., Villringer, K., Fiebach, J. B., Villringer, A., Margulies, D. S., & Ovadia-Caro,
 S. (2019). The impact of ischemic stroke on connectivity gradients. *NeuroImage: Clinical*, 24, 101947.
 https://doi.org/10.1016/j.nicl.2019.101947
- Benedek, M., Jauk, E., Beaty, R. E., Fink, A., Koschutnig, K., & Neubauer, A. C. (2016). Brain
 mechanisms associated with internally directed attention and self-generated thought. *Scientific Reports*, 6(1), 22959. https://doi.org/10.1038/srep22959
- 719 Benítez-Burraco, A., & Murphy, E. (2016). The Oscillopathic Nature of Language Deficits in Autism:
 720 From Genes to Language Evolution. *Frontiers in Human Neuroscience*, 10, 120.
 721 https://doi.org/10.3389/fnhum.2016.00120
- Benítez-Burraco, A., & Murphy, E. (2019). Why Brain Oscillations Are Improving Our Understanding
 of Language. *Frontiers in Behavioral Neuroscience*, *13*. https://doi.org/10.3389/fnbeh.2019.00190
- Benke, T., Kuen, E., Schwarz, M., & Walser, G. (2013). Proper name retrieval in temporal lobe
 epilepsy: Naming of famous faces and landmarks. *Epilepsy & Behavior*, 27(2), 371-377.
 https://doi.org/10.1016/j.yebeh.2013.02.013
- Berwick, R. C., Friederici, A. D., Chomsky, N., & Bolhuis, J. J. (2013). Evolution, brain, and the nature of language. *Trends in Cognitive Sciences*, *17*(2), 89-98. https://doi.org/10.1016/j.tics.2012.12.002
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, 15(11), 527-536. https://doi.org/10.1016/j.tics.2011.10.001
- 731 Bloom, P. (2000). *How Children Learn the Meanings of Words*. MIT Press.
- Boeckx, C. A., & Benítez-Burraco, A. (2014). The shape of the human language-ready brain. *Frontiers in Psychology*, 5, 282. https://doi.org/10.3389/fpsyg.2014.00282
- Bolhuis, J. J., Tattersall, I., Chomsky, N., & Berwick, R. C. (2014). How Could Language Have
 Evolved? *PLoS Biol*, *12*(8), e1001934. https://doi.org/10.1371/journal.pbio.1001934

- Bonhage, C. E., Mueller, J. L., Friederici, A. D., & Fiebach, C. J. (2015). Combined eye tracking and
 fMRI reveals neural basis of linguistic predictions during sentence comprehension. *Cortex*, 68, 33-47.
- 738 https://doi.org/10.1016/j.cortex.2015.04.011
- Boyer, P. (2008). Evolutionary economics of mental time travel? *Trends in Cognitive Sciences*, *12*(6),
 219-224. https://doi.org/10.1016/j.tics.2008.03.003
- Braga, R. M., DiNicola, L. M., Becker, H. C., & Buckner, R. L. (2020). Situating the left-lateralized
 language network in the broader organization of multiple specialized large-scale distributed networks. *Journal of Neurophysiology*, 124(5), 1415-1448. https://doi.org/10.1152/jn.00753.2019
- Braga, R. M., Sharp, D. J., Leeson, C., Wise, R. J. S., & Leech, R. (2013). Echoes of the Brain within
 Default Mode, Association, and Heteromodal Cortices. *Journal of Neuroscience*, *33*(35), 14031-14039.
 https://doi.org/10.1523/JNEUROSCI.0570-13.2013
- Broca, P. (1865). Sur le siège de la faculté du langage articulé. *Bulletins de la Société d'anthropologie de Paris*, 6(1), 377-393. https://doi.org/10.3406/bmsap.1865.9495
- Brown-Schmidt, S., & Duff, M. C. (2016). Memory and Common Ground Processes in Language Use. *Top Cogn Sci*, 8(4), 722-736. https://doi.org/10.1111/tops.12224
- 751 Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network : Anatomy,
- function, and relevance to disease. In A. Kingstone & M. B. Miller (Éds.), Annals of the New York
- 753 Academy of Sciences : Vol. 1124. The year in cognitive neuroscience 2008 (p. 1-38). Blackwell
- 754 Publishing. http://doi.wiley.com/10.1196/annals.1440.011
- Buckner, R. L., Krienen, F. M., & Yeo, B. T. T. (2013). Opportunities and limitations of intrinsic
 functional connectivity MRI. *Nature Neuroscience*, *16*(7), 832-837. https://doi.org/10.1038/nn.3423
- Bullock, D., Takemura, H., Caiafa, C. F., Kitchell, L., McPherson, B., Caron, B., & Pestilli, F. (2019).
 Associative white matter connecting the dorsal and ventral posterior human cortex. *Brain Structure and Function*, 224(8), 2631-2660. https://doi.org/10.1007/s00429-019-01907-8
- Buzsáki, G. (2020). The Brain–Cognitive Behavior Problem: A Retrospective. *eNeuro*, 7(4).
 https://doi.org/10.1523/ENEURO.0069-20.2020
- Campbell, K. L., & Tyler, L. K. (2018). Language-related domain-specific and domain-general systems 762 763 in the human brain. Current **Opinion** in Behavioral Sciences, 21, 132-137. https://doi.org/10.1016/j.cobeha.2018.04.008 764
- 765 Carruthers, P. (2013). Mindreading in Infancy. *Mind & Language*, 141-172.
- Carstairs-McCarthy, A. (1999). The origins of complex language : An inquiry into the evolutionary
 beginnings of sentences, syllables, and truth. Oxford University Press on Demand.
- Castro, L. H., Silva, L. C. A. M., Adda, C. C., Banaskiwitz, N. H. C., Xavier, A. B., Jorge, C. L., Valerio,
 R. M., & Nitrini, R. (2013). Low prevalence but high specificity of material-specific memory
 impairment in epilepsy associated with hippocampal sclerosis. *Epilepsia*, 54(10), 1735-1742.
 https://doi.org/10.1111/epi.12343
- Catani, M., & Dawson, M. S. (2017). Chapter 31—Language Processing, Development and Evolution.
 In P. M. Conn (Éd.), *Conn's Translational Neuroscience* (p. 679-692). Academic Press.
 https://doi.org/10.1016/B978-0-12-802381-5.00049-X

- 775 Chand, G. B., Wu, J., Hajjar, I., & Qiu, D. (2017). Interactions of the Salience Network and Its
- 776 Subsystems with the Default-Mode and the Central-Executive Networks in Normal Aging and Mild
- 777 Cognitive Impairment. *Brain Connectivity*, 7(7), 401-412. https://doi.org/10.1089/brain.2017.0509
- 778 Chomsky, N. (1995). *The Minimalist Program*. MIT Press.
- 779 Clark, H. H., & Marshall, C. R. (1981). Definite Reference and Mutual Knowledge. In A. K. Joshi, B.
- L. Webber, & I. A. Sag (Éds.), *Elements of discourse understanding* (p. 10-63). Cambridge University
 Press.
- Cocchi, L., Zalesky, A., Fornito, A., & Mattingley, J. B. (2013). Dynamic cooperation and competition
 between brain systems during cognitive control. *Trends in Cognitive Sciences*, 17(10), 493-501.
 https://doi.org/10.1016/j.tics.2013.08.006
- Cocuzza, C. V., Ito, T., Schultz, D., Bassett, D. S., & Cole, M. W. (2020). Flexible Coordinator and
 Switcher Hubs for Adaptive Task Control. *Journal of Neuroscience*, 40(36), 6949-6968.
 https://doi.org/10.1523/JNEUROSCI.2559-19.2020
- Collignon, O., Champoux, F., Voss, P., & Lepore, F. (2011). Sensory rehabilitation in the plastic brain.
 In *Progress in Brain Research* (Vol. 191, p. 211-231). Elsevier. https://doi.org/10.1016/B978-0-444-53752-2.00003-5
- 791 Condret-Santi, V., Barragan-Jason, G., Valton, L., Denuelle, M., Curot, J., Nespoulous, J.-L., &
- 792Barbeau, E. J. (2014). Object and proper name retrieval in temporal lobe epilepsy : A study of difficulties
- and latencies. *Epilepsy Research*, 108(10), 1825-1838. https://doi.org/10.1016/j.eplepsyres.2014.09.001
- Constantinescu, A. O., O'Reilly, J. X., & Behrens, T. E. J. (2016). Organizing conceptual knowledge in
 humans with a gridlike code. *Science*, *352*(6292), 1464-1468. https://doi.org/10.1126/science.aaf0941
- Conway, M. A., & Loveday, C. (2015). Remembering, imagining, false memories & personal meanings.
 Consciousness and Cognition, *33*, 574-581. https://doi.org/10.1016/j.concog.2014.12.002
- Cooper, R. A., & Ritchey, M. (2020). Progression from Feature-Specific Brain Activity to Hippocampal
 Binding during Episodic Encoding. J. Neurosci., 40(8), 1701-1709.
 https://doi.org/10.1523/JNEUROSCI.1971-19.2019
- 801 Corballis, M. C. (2019). Minimalism and Evolution. *Front. Commun.*, *4*, 46.
 802 https://doi.org/10.3389/fcomm.2019.00046
- Corkin, S. (2013). *Permanent present tense : The unforgettable life of the amnesic patient, H. M.* (p. xix, 364). Basic Books.
- 805 Covington, N. V., & Duff, M. C. (2016). Expanding the Language Network : Direct Contributions from
 806 the Hippocampus. *Trends in Cognitive Sciences*, 20(12), 869-870.
 807 https://doi.org/10.1016/j.tics.2016.10.006
- Cowell, R. A., Barense, M. D., & Sadil, P. S. (2019). A Roadmap for Understanding Memory:
 Decomposing Cognitive Processes into Operations and Representations. *ENeuro*, 6(4), ENEURO.012219.2019. https://doi.org/10.1523/ENEURO.0122-19.2019
- Banker, J. F., & Anderson, J. R. (2010). The ghosts of brain states past: Remembering reactivates the
 brain regions engaged during encoding. *Psychological Bulletin*, 136(1), 87-102.
 https://doi.org/10.1037/a0017937
- de Boer, B. (2011). Self-organization and language evolution. In K. R. Gibson & M. Tallerman (Éds.), *The Oxford Handbook of Language Evolution* (p. 612-620). Oxford University Press.

- de Vanssay-Maigne, A., Noulhiane, M., Devauchelle, A. D., Rodrigo, S., Baudoin-Chial, S., Meder, J.
- F., Oppenheim, C., Chiron, C., & Chassoux, F. (2011). Modulation of encoding and retrieval by
 recollection and familiarity: Mapping the medial temporal lobe networks. *NeuroImage*, 58(4),
 1131-1138. https://doi.org/10.1016/j.neuroimage.2011.06.086
- Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the
 medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, 11(9), 379-386.
- 822 https://doi.org/10.1016/j.tics.2007.08.001
- DiNicola, L. M., Braga, R. M., & Buckner, R. L. (2020). Parallel Distributed Networks Dissociate
 Episodic and Social Functions Within the Individual. *Journal of Neurophysiology*, *123*(3), 1144-1179.
- Bohmatob, E., Dumas, G., & Bzdok, D. (2020). Dark Control: The Default Mode Network as a
 Reinforcement Learning Agent. *Human Brain Mapping*, 38.
- B27 Doucet, G. E., Lee, W. H., & Frangou, S. (2019). Evaluation of the spatial variability in the major
 resting-state networks across human brain functional atlases. *Hum Brain Mapp*, 40(15), 4577-4587.
 https://doi.org/10.1002/hbm.24722
- Buff, M. C., & Brown-Schmidt, S. (2012). The hippocampus and the flexible use and processing of
 language. *Frontiers in Human Neuroscience*, 6. https://doi.org/10.3389/fnhum.2012.00069
- Buff, M. C., Covington, N. V., Hilverman, C., & Cohen, N. J. (2020). Semantic Memory and the
 Hippocampus : Revisiting, Reaffirming, and Extending the Reach of Their Critical Relationship. *Frontiers in Human Neuroscience*, *13*. https://doi.org/10.3389/fnhum.2019.00471
- B35 Duff, M. C., Hengst, J. A., Tranel, D., & Cohen, N. J. (2009). Hippocampal amnesia disrupts verbal
- play and the creative use of language in social interaction. *Aphasiology*, 23(7-8), 926-939.
 https://doi.org/10.1080/02687030802533748
- Buffau, H., Moritz-Gasser, S., & Mandonnet, E. (2014). A re-examination of neural basis of language
 processing : Proposal of a dynamic hodotopical model from data provided by brain stimulation mapping
 during picture naming. *Brain and Language*, *131*, 1-10. https://doi.org/10.1016/j.bandl.2013.05.011
- Buvernoy, H. M., Cattin, F., & Risold, P.-Y. (2013). *The Human Hippocampus*. Springer, Berlin Heidelberg. http://link.springer.com/10.1007/978-3-642-33603-4
- Eisenberg, I. W., Bissett, P. G., Zeynep Enkavi, A., Li, J., MacKinnon, D. P., Marsch, L. A., & Poldrack,
 R. A. (2019). Uncovering the structure of self-regulation through data-driven ontology discovery. *Nature Communications*, 10(1), 2319. https://doi.org/10.1038/s41467-019-10301-1
- Ekstrom, A. D., & Yonelinas, A. P. (2020). Precision, binding, and the hippocampus : Precisely what
 are we talking about? *Neuropsychologia*, *138*, 107341.
 https://doi.org/10.1016/j.neuropsychologia.2020.107341
- Elverman, K. H., Resch, Z. J., Quasney, E. E., Sabsevitz, D. S., Binder, J. R., & Swanson, S. J. (2019).
 Temporal lobe epilepsy is associated with distinct cognitive phenotypes. *Epilepsy & Behavior*, 96,
- 851 61-68. https://doi.org/10.1016/j.yebeh.2019.04.015
- Epstein, R. A. (2008). Parahippocampal and retrosplenial contributions to human spatial navigation.
 Trends in Cognitive Sciences, *12*(10), 388-396. https://doi.org/10.1016/j.tics.2008.07.004
- Eriksson, J., Vogel, E. K., Lansner, A., Bergström, F., & Nyberg, L. (2015). Neurocognitive
 Architecture of Working Memory. *Neuron*, 33-46.

- Everts, R., Simon Harvey, A., Lillywhite, L., Wrennall, J., Abbott, D. F., Gonzalez, L., Kean, M.,
 Jackson, G. D., & Anderson, V. (2010). Language lateralization correlates with verbal memory
 performance in children with focal epilepsy. *Epilepsia*, *51*(4), 627-638. https://doi.org/10.1111/j.15281167.2009.02406.x
- Fabre-Thorpe, M. (2003). Visual categorization : Accessing abstraction in non-human primates. *Phil. Trans. R. Soc. Lond. B*, 358(1435), 1215-1223. https://doi.org/10.1098/rstb.2003.1310
- Faskowitz, J., Esfahlani, F. Z., Jo, Y., Sporns, O., & Betzel, R. F. (2020). Edge-centric functional
 network representations of human cerebral cortex reveal overlapping system-level architecture. *Nature Neuroscience*, 23(12), 1644-1654. https://doi.org/10.1038/s41593-020-00719-y
- Ferreira, F., & Engelhardt, P. E. (2006). Chapter 3—Syntax and Production. In M. J. Traxler & M. A.
- Gernsbacher (Éds.), *Handbook of Psycholinguistics (Second Edition)* (p. 61-91). Academic Press.
 https://doi.org/10.1016/B978-012369374-7/50004-3
- ffytche, D. H., & Catani, M. (2005). Beyond localization : From hodology to function. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360(1456), 767-779.
 https://doi.org/10.1098/rstb.2005.1621
- Fitch, W. T. (2010). *The Evolution of Language*. Cambridge University Press.
- Forkel, S., Friedrich, P., Thiebaut de Schotten, M., & Howells, H. (2020). White matter variability,
 cognition, and disorders : A systematic review. *medRxiv*.
- Fornito, A., Zalesky, A., & Breakspear, M. (2015). The connectomics of brain disorders. *Nature Reviews. Neuroscience*, 16(3), 159-172. https://doi.org/10.1038/nrn3901
- Forseth, K., Pitkow, X., Fischer-Baum, S., & Tandon, N. (2021). *What The Brain Does As We Speak*[Preprint]. Neuroscience. https://doi.org/10.1101/2021.02.05.429841
- Friederici, A. D., Chomsky, N., Berwick, R. C., Moro, A., & Bolhuis, J. J. (2017). Language, mind and
 brain. *Nature Human Behaviour*, *1*(10), 713-722. https://doi.org/10.1038/s41562-017-0184-4
- Friston, K. J., & Price, C. J. (2003). Degeneracy and redundancy in cognitive anatomy. *Trends in Cognitive Sciences*, 7(4), 151-152. https://doi.org/10.1016/S1364-6613(03)00054-8
- Gadian, D. G., Aicardi, J., Watkins, K. E., Porter, D. A., Mishkin, M., & Vargha-Khadem, F. (2000).
 Developmental amnesia associated with early hypoxic–ischaemic injury. *Brain*, *123*(3), 499-507.
 https://doi.org/10.1093/brain/123.3.499
- Gaffan, D. (1997). Episodic and semantic memory and the role of the not-hippocampus. *Trends in Cognitive Sciences*, 1(7), 246-248. https://doi.org/10.1016/S1364-6613(97)01074-7
- Geib, B. R., Stanley, M. L., Wing, E. A., Laurienti, P. J., & Cabeza, R. (2017). Hippocampal
 Contributions to the Large-Scale Episodic Memory Network Predict Vivid Visual Memories. *Cerebral Cortex*, 27(1), 680-693. https://doi.org/10.1093/cercor/bhv272
- Genon, S., Reid, A., Langner, R., Amunts, K., & Eickhoff, S. B. (2018). How to Characterize the
 Function of a Brain Region. *Trends in Cognitive Sciences*, 22(4), 350-364.
 https://doi.org/10.1016/j.tics.2018.01.010
- Giraud, A.-L., & Poeppel, D. (2012). Cortical oscillations and speech processing: Emerging
 computational principles and operations. *Nature neuroscience*, 15(4), 511-517.
 https://doi.org/10.1038/nn.3063

- Goldstein, A., Zada, Z., Buchnik, E., Schain, M., Price, A., Aubrey, B., Nastase, S. A., Feder, A.,
 Emanuel, D., Cohen, A., Jansen, A., Gazula, H., Choe, G., Rao, A., Kim, C., Casto, C., Fanda, L., Doyle,
 W. E. J. D., U. M. (2021), *The distribution of the second states of th*
- W., Friedman, D., ... Hasson, U. (2021). Thinking ahead: Spontaneous prediction in context as a
 keystone of language in humans and machines (p. 2020.12.02.403477).
- 900 https://doi.org/10.1101/2020.12.02.403477
- Gordon, E. M., Laumann, T. O., Marek, S., Raut, R. V., Gratton, C., Newbold, D. J., Greene, D. J.,
 Coalson, R. S., Snyder, A. Z., Schlaggar, B. L., Petersen, S. E., Dosenbach, N. U. F., & Nelson, S. M.
 (2020). Default-mode network streams for coupling to language and control systems. *Proceedings of the National Academy of Sciences*, *117*(29), 17308-17319. https://doi.org/10.1073/pnas.2005238117
- Goucha, T., Zaccarella, E., & Friederici, A. D. (2017). A revival of Homo loquens as a builder of labeled
 structures : Neurocognitive considerations. *Neuroscience & Biobehavioral Reviews*, *81*, 213-224.
 https://doi.org/10.1016/j.neubiorev.2017.01.036
- Graham, K. S., Simons, J. S., Pratt, K. H., Patterson, K., & Hodges, J. R. (2000). Insights from semantic dementia on the relationship between episodic and semantic memory. *Neuropsychologia*, 38(3), 313-324. https://doi.org/10.1016/S0028-3932(99)00073-1
- 911 Gratton, C., Nomura, E. M., Pérez, F., & D'Esposito, M. (2012). Focal Brain Lesions to Critical
- 912 Locations Cause Widespread Disruption of the Modular Organization of the Brain. *Journal of Cognitive*
- 913 *Neuroscience*, 24(6), 1275-1285. https://doi.org/10.1162/jocn_a_00222
- Guell, X., & Schmahmann, J. (2020). Cerebellar Functional Anatomy : A Didactic Summary Based on
 Human fMRI Evidence. *Cerebellum*, 19(1), 1-5. https://doi.org/10.1007/s12311-019-01083-9
- Hagoort, P. (2013). MUC (Memory, Unification, Control) and beyond. *Frontiers in Psychology*, *4*, 416.
 https://doi.org/10.3389/fpsyg.2013.00416
- Hagoort, P. (2014). Nodes and networks in the neural architecture for language: Broca's region and
 beyond. *Current Opinion in Neurobiology*, 28, 136-141. https://doi.org/10.1016/j.conb.2014.07.013
- Hagoort, P. (2016). MUC (Memory, Unification, Control) : A Model on the Neurobiology of Language
 Beyond Single Word Processing. In G. Hickok & S. L. Small (Éds.), *Neurobiology of Language* (p. 339-347). Elsevier. https://doi.org/10.1016/B978-0-12-407794-2.00028-6
- Hagoort, P. (2019). The neurobiology of language beyond single-word processing. *Science*.
 https://www.science.org/doi/abs/10.1126/science.aax0289
- 925 Hamamé, C. M., Alario, F.-X., Llorens, A., Liégeois-Chauvel, C., & Trébuchon-Da Fonseca, A. (2014).
- High frequency gamma activity in the left hippocampus predicts visual object naming performance. *Brain and Language*, 135, 104-114. https://doi.org/10.1016/j.bandl.2014.05.007
- Hasson, U., Chen, J., & Honey, C. J. (2015). Hierarchical process memory : Memory as an integral
 component of information processing. *Trends in Cognitive Sciences*, 19(6), 304-313.
 https://doi.org/10.1016/j.tics.2015.04.006
- Herbet, G., & Duffau, H. (2020). Revisiting the Functional Anatomy of the Human Brain : Toward a
 Meta-Networking Theory of Cerebral Functions. *Physiological Reviews*.
 https://doi.org/10.1152/physrev.00033.2019
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8(5), 393-402. https://doi.org/10.1038/nrn2113

Higgins, C., Liu, Y., Vidaurre, D., Kurth-Nelson, Z., Dolan, R., Behrens, T., & Woolrich, M. (2020).
Replay bursts coincide with activation of the default mode and parietal alpha network. *BioRxiv*, 2020.06.23.166645. https://doi.org/10.1101/2020.06.23.166645

Hilgetag, C. C., & Goulas, A. (2020). 'Hierarchy' in the organization of brain networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1796), 20190319.
https://doi.org/10.1098/rstb.2019.0319

- Hilverman, C., & Duff, M. C. (2021). Evidence of impaired naming in patients with hippocampal
 amnesia. *Hippocampus*, *31*(6), 612-626. https://doi.org/10.1002/hipo.23325
- Hinzen, W. (2013). Narrow syntax and the language of thought. *Philosophical Psychology*, 26(1), 1-23.
 https://doi.org/10.1080/09515089.2011.627537

Hogan, T. P., Adlof, S. M., & Alonzo, C. N. (2014). On the importance of listening comprehension. *International Journal of Speech-Language Pathology*, 16(3), 199-207.
https://doi.org/10.3109/17549507.2014.904441

- Horton, W. S. (2007). The influence of partner-specific memory associations on language production :
 Evidence from picture naming. *Language and Cognitive Processes*, 22(7), 1114-1139.
 https://doi.org/10.1080/01690960701402933
- Hula, W. D., Panesar, S., Gravier, M. L., Yeh, F.-C., Dresang, H. C., Dickey, M. W., & Fernandez-
- Miranda, J. C. (2020). Structural white matter connectometry of word production in aphasia : An
 observational study. *Brain*, 143(8), 2532-2544. https://doi.org/10.1093/brain/awaa193
- Humphreys, G. F., & Lambon Ralph, M. A. (2015). Fusion and Fission of Cognitive Functions in the
 Human Parietal Cortex. *Cereb. Cortex*, 25(10), 3547-3560. https://doi.org/10.1093/cercor/bhu198
- Indefrey, P. (2011). The Spatial and Temporal Signatures of Word Production Components : A Critical
 Update. *Frontiers in Psychology*, 2. https://doi.org/10.3389/fpsyg.2011.00255
- 959 Jaimes-Bautista, A. G., Rodríguez-Camacho, M., Martínez-Juárez, I. E., & Rodríguez-Agudelo, Y.
- 960 (2015, juillet 16). Semantic Processing Impairment in Patients with Temporal Lobe Epilepsy [Review
- Article]. Epilepsy Research and Treatment; Hindawi. https://doi.org/10.1155/2015/746745
- Jain, S., & Huth, A. (2018). Incorporating Context into Language Encoding Models for fMRI. Advances
 in Neural Information Processing Systems, 31.
 https://papers.nips.cc/paper/2018/hash/f471223d1a1614b58a7dc45c9d01df19-Abstract.html
- Jeong, W., Chung, C. K., & Kim, J. S. (2015). Episodic memory in aspects of large-scale brain networks.
 Front. Hum. Neurosci., 9. https://doi.org/10.3389/fnhum.2015.00454
- Ji, J. L., Spronk, M., Kulkarni, K., Repovš, G., Anticevic, A., & Cole, M. W. (2019, 15). Mapping the
 human brain's cortical-subcortical functional network organization. *NeuroImage*, 35-57.
- Johnson, E. L., & Knight, R. T. (2015). Intracranial recordings and human memory. *Current Opinion in Neurobiology*, *31*, 18-25. https://doi.org/10.1016/j.conb.2014.07.021
- 971 Jonin, P.-Y., Calia, C., Muratot, S., Belliard, S., Duché, Q., Barbeau, E. J., & Parra, M. A. (2019).
- 972 Refining understanding of working memory buffers through the construct of binding : Evidence from a
- 973 single case informs theory and clinical practise. *Cortex; a Journal Devoted to the Study of the Nervous*
- 974 System and Behavior, 112, 37-57. https://doi.org/10.1016/j.cortex.2018.08.011
- Kempe, V., & Brooks, P. J. (2016). Modern Theories of Language. In V. Weekes-Shackelford, T. K.
 Shackelford, & V. A. Weekes-Shackelford (Éds.), *Encyclopedia of Evolutionary Psychological Science*

- 977 (p. 1-12). Springer International Publishing. http://link.springer.com/10.1007/978-3-319-16999 978 6_3321-1
- Kikuchi, H., Fujii, T., Abe, N., Suzuki, M., Takagi, M., Mugikura, S., Takahashi, S., & Mori, E. (2010).
 Memory Repression: Brain Mechanisms underlying Dissociative Amnesia. *Journal of Cognitive Neuroscience*, 22(3), 602-613. https://doi.org/10.1162/jocn.2009.21212
- Kintsch, W., & Kintsch, E. (2005). Comprehension. In S. G. Paris & S. A. Stahl (Éds.), *Children's reading comprehension and assessment* (p. 71-92). Routledge.
- Klemfuss, J. Z. (2015). Differential Contributions of Language Skills to Children's Episodic Recall.
 Journal of Cognition and Development, 16(4), 608-620. https://doi.org/10.1080/15248372.2014.952415
- Kliemann, D., Adolphs, R., Tyszka, J. M., Fischl, B., Yeo, B. T. T., Nair, R., Dubois, J., & Paul, L. K.
 (2019). Intrinsic Functional Connectivity of the Brain in Adults with a Single Cerebral Hemisphere. *Cell Reports*, 29(8), 2398-2407.e4. https://doi.org/10.1016/j.celrep.2019.10.067
- Konishi, M., McLaren, D. G., Engen, H., & Smallwood, J. (2015). Shaped by the Past: The Default
 Mode Network Supports Cognition that Is Independent of Immediate Perceptual Input. *PLOS ONE*,
- 990 Mode Network Supports Cognition that is independent of inimediate Per 991 I0(6), e0132209. https://doi.org/10.1371/journal.pone.0132209
- Krajcovicova, L., Marecek, R., Mikl, M., & Rektorova, I. (2014). Disruption of Resting Functional
 Connectivity in Alzheimer's Patients and At-Risk Subjects. *Current Neurology and Neuroscience*
- 994 Reports, 14(10), 491. https://doi.org/10.1007/s11910-014-0491-3
- Krienen, F. M., Tu, P.-C., & Buckner, R. L. (2010). Clan Mentality: Evidence That the Medial
 Prefrontal Cortex Responds to Close Others. *Journal of Neuroscience*, 30(41), 13906-13915.
 https://doi.org/10.1523/JNEUROSCI.2180-10.2010
- 998 Larsen, S. F., Schrauf, R. W., Fromholt, P., & Rubin, D. C. (2002). Inner speech and bilingual
 999 autobiographical memory: A Polish-Danish cross-cultural study. *Memory*, 10(1), 45-54.
 1000 https://doi.org/10.1080/09658210143000218
- Lau, E. F., Gramfort, A., Hämäläinen, M. S., & Kuperberg, G. R. (2013). Automatic Semantic
 Facilitation in Anterior Temporal Cortex Revealed through Multimodal Neuroimaging. *J. Neurosci.*, *33*(43), 17174-17181. https://doi.org/10.1523/JNEUROSCI.1018-13.2013
- 1004 Levelt, W. J. M. (1989). *Speaking : From intention to articulation*. MIT Press.
- Levelt, W. J. M. (1993). Lexical Access in Speech Production. In E. Reuland & W. Abraham (Éds.),
 Knowledge and Language : Volume I From Orwell's Problem to Plato's Problem (p. 241-251). Springer
- 1007 Netherlands. https://doi.org/10.1007/978-94-011-1840-8_11
- Leventhal, D. K., Gage, G. J., Schmidt, R., Pettibone, J. R., Case, A. C., & Berke, J. D. (2012). Basal
 Ganglia Beta Oscillations Accompany Cue Utilization. *Neuron*, 73(3), 523-536.
 https://doi.org/10.1016/j.neuron.2011.11.032
- Libby, L. A., Hannula, D. E., & Ranganath, C. (2014). Medial Temporal Lobe Coding of Item and
 Spatial Information during Relational Binding in Working Memory. *Journal of Neuroscience*, *34*(43),
 14233-14242. https://doi.org/10.1523/JNEUROSCI.0655-14.2014
- Luo, C., Makaretz, S., Stepanovic, M., Papadimitriou, G., Quimby, M., Palanivelu, S., Dickerson, B. C.,
 & Makris, N. (2020). Middle longitudinal fascicle is associated with semantic processing deficits in
 primary progressive aphasia. *NeuroImage: Clinical*, 25, 102115.
 https://doi.org/10.1016/j.nicl.2019.102115

- Lynn, C. W., & Bassett, D. S. (2019). The physics of brain network structure, function and control.
 Nature Reviews Physics, 1(5), 318-332. https://doi.org/10.1038/s42254-019-0040-8
- Margulies, D. S., Ghosh, S. S., Goulas, A., Falkiewicz, M., Huntenburg, J. M., Langs, G., Bezgin, G.,
 Eickhoff, S. B., Castellanos, F. X., Petrides, M., Jefferies, E., & Smallwood, J. (2016). Situating the
 default-mode network along a principal gradient of macroscale cortical organization. *Proceedings of the*
- 1023 National Academy of Sciences, 113(44), 12574-12579. https://doi.org/10.1073/pnas.1608282113
- Marian, V., & Neisser, U. (2000). Language-Dependent Recall of Autobiographical Memories. *Journal of Experimental Psychology: General*, *126*(3), 361-368.
- Marr, D. (1982). Vision : A computational investigation into the human representation and processing
 of visual information.
- Martin, A. E. (2020). A Compositional Neural Architecture for Language. *Journal of Cognitive Neuroscience*, 32(8), 1407-1427. https://doi.org/10.1162/jocn a 01552
- Matthen, M. (2005). Seeing, Doing, and Knowing : A Philosophical Theory of Sense Perception. Oxford
 University Press.
- 1032 Mazoyer, B., Zago, L., Mellet, E., Bricogne, S., Etard, O., Houdé, O., Crivello, F., Joliot, M., Petit, L.,
- 1033 & Tzourio-Mazoyer, N. (2001). Cortical networks for working memory and executive functions sustain
- 1034 the conscious resting state in man. Brain Research Bulletin, 54(3), 287-298.
- 1035 https://doi.org/10.1016/S0361-9230(00)00437-8
- 1036 McCormick, C., Protzner, A. B., Barnett, A. J., Cohn, M., Valiante, T. A., & McAndrews, M. P. (2014).
- Linking DMN connectivity to episodic memory capacity : What can we learn from patients with medial
 temporal lobe damage? *NeuroImage: Clinical*, 5, 188-196. https://doi.org/10.1016/j.nicl.2014.05.008
- Medaglia, J. D., & Bassett, D. S. (2018, septembre 26). Network Analyses and Nervous System
 Disorders. Oxford Research Encyclopedia of Neuroscience.
 https://doi.org/10.1093/acrefore/9780190264086.013.121
- Mesulam, M.-M. (1990). Large-scale neurocognitive networks and distributed processing for attention,
 language, and memory. *Annals of Neurology*, 28(5), 597-613. https://doi.org/10.1002/ana.410280502
- Metternich, B., Buschmann, F., Wagner, K., Schulze-Bonhage, A., & Kriston, L. (2014). Verbal fluency
 in focal epilepsy: A systematic review and meta-analysis. *Neuropsychology Review*, 24(2), 200-218.
 https://doi.org/10.1007/s11065-014-9255-8
- 1047 Milner, B. (1970). Memory and the medial temporal regions of the brain. *Biology of Memory*, 23, 31-59.
- Moscovitch, M., Cabeza, R., Winocur, G., & Nadel, L. (2016). Episodic Memory and Beyond: The
 Hippocampus and Neocortex in Transformation. *Annu. Rev. Psychol.*, 67(1), 105-134.
 https://doi.org/10.1146/annurev-psych-113011-143733
- Moscovitch, M., Nadel, L., Winocur, G., Gilboa, A., & Rosenbaum, R. S. (2006). The cognitive neuroscience of remote episodic, semantic and spatial memory. *Current Opinion in Neurobiology*, 1053 16(2), 179-190. https://doi.org/10.1016/j.conb.2006.03.013
- Murphy, E. (2015a). The brain dynamics of linguistic computation. *Frontiers in Psychology*, *6*, 1515.
 https://doi.org/10.3389/fpsyg.2015.01515
- Murphy, E. (2015b). Labels, cognomes, and cyclic computation: An ethological perspective. *Front. Psychol.*, 6. https://doi.org/10.3389/fpsyg.2015.00715

Noppeney, U., Friston, K. J., & Price, C. J. (2004). Degenerate neuronal systems sustaining cognitive
functions. *Journal of Anatomy*, 205(6), 433-442. https://doi.org/10.1111/j.0021-8782.2004.00343.x

Oulhaj, A., Wilcock, G. K., Smith, A. D., & de Jager, C. A. (2009). Predicting the time of conversion
to MCI in the elderly: Role of verbal expression and learning. *Neurology*, 73(18), 1436-1442.
https://doi.org/10.1212/WNL.0b013e3181c0665f

1063 Ovadia-Caro, S., Villringer, K., Fiebach, J., Jungehulsing, G. J., van der Meer, E., Margulies, D. S., &
1064 Villringer, A. (2013). Longitudinal Effects of Lesions on Functional Networks after Stroke. *J Cereb*1065 *Blood Flow Metab*, 33(8), 1279-1285. https://doi.org/10.1038/jcbfm.2013.80

- Palacio, N., & Cardenas, F. (2019). A systematic review of brain functional connectivity patterns
 involved in episodic and semantic memory. *Reviews in the Neurosciences*, 30(8), 889-902.
 https://doi.org/10.1515/revneuro-2018-0117
- Parr, T., & Friston, K. J. (2017). Working memory, attention, and salience in active inference. *Sci Rep*,
 7(1), 14678. https://doi.org/10.1038/s41598-017-15249-0
- Piai, V., Anderson, K. L., Lin, J. J., Dewar, C., Parvizi, J., Dronkers, N. F., & Knight, R. T. (2016).
 Direct brain recordings reveal hippocampal rhythm underpinnings of language processing. *Proceedings* of the National Academy of Sciences, 113(40), 11366-11371. https://doi.org/10.1073/pnas.1603312113
- 1073 *of the National Academy of Sciences*, *113*(40), 11366-11371. https://doi.org/10.1073/pnas.1603312113
- 1074 Pidgeon, L. M., & Morcom, A. M. (2016). Cortical pattern separation and item-specific memory
 1075 encoding. *Neuropsychologia*, 85, 256-271. https://doi.org/10.1016/j.neuropsychologia.2016.03.026
- Poeppel, D., & Assaneo, M. F. (2020). Speech rhythms and their neural foundations. *Nature Reviews Neuroscience*, 21(6), 322-334. https://doi.org/10.1038/s41583-020-0304-4
- Power, J. D., Schlaggar, B. L., Lessov-Schlaggar, C. N., & Petersen, S. E. (2013). Evidence for hubs in human functional brain networks. *Neuron*, 79(4), 10.1016/j.neuron.2013.07.035.
 https://doi.org/10.1016/j.neuron.2013.07.035
- Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and brain sciences*, 1(4), 515-526.
- Price, C. J. (2012). A review and synthesis of the first 20years of PET and fMRI studies of heard speech,
 spoken language and reading. *NeuroImage*, 62(2), 816-847.
 https://doi.org/10.1016/j.neuroimage.2012.04.062
- 1086 Raichle, M. E. (2015). The Brain's Default Mode Network. *Annual Review of Neuroscience*, 38(1),
 1087 433-447. https://doi.org/10.1146/annurev-neuro-071013-014030
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L.
 (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences*, 98(2),
 676-682. https://doi.org/10.1073/pnas.98.2.676
- Ranganath, C., & Ritchey, M. (2012). Two cortical systems for memory-guided behaviour. *Nature Reviews Neuroscience*, 13(10), 713-726. https://doi.org/10.1038/nrn3338
- Rangel, L. M., Rueckemann, J. W., Riviere, P. D., Keefe, K. R., Porter, B. S., Heimbuch, I. S., Budlong,
 C. H., & Eichenbaum, H. (2016). Rhythmic coordination of hippocampal neurons during associative
 memory processing. *ELife*, *5*, e09849. https://doi.org/10.7554/eLife.09849
- 1096 Reuland, E. (2017). Language and imagination: Evolutionary explorations. *Neuroscience & Biobehavioral Reviews*, 81, 255-278. https://doi.org/10.1016/j.neubiorev.2016.12.017

Reyes, A., Kaestner, E., Ferguson, L., Jones, J. E., Seidenberg, M., Barr, W. B., Busch, R. M., Hermann,
B. P., & McDonald, C. R. (2020). Cognitive phenotypes in temporal lobe epilepsy utilizing data- and
clinically driven approaches : Moving toward a new taxonomy. *Epilepsia*, 1211-1220.

Richter, F. R., Cooper, R. A., Bays, P. M., & Simons, J. S. (2016). Distinct neural mechanisms underlie 1101 1102 vividness of episodic memory. the success. precision, and ELife, 5. e18260. 1103 https://doi.org/10.7554/eLife.18260

Rilling, J. K. (2014). Comparative primate neuroimaging : Insights into human brain evolution. *Trends in Cognitive Sciences*, 18(1), 46-55. https://doi.org/10.1016/j.tics.2013.09.013

Ritchey, M., Montchal, M. E., Yonelinas, A. P., & Ranganath, C. (2015). Delay-dependent contributions
of medial temporal lobe regions to episodic memory retrieval. *eLife*, 4, e05025.
https://doi.org/10.7554/eLife.05025

Roger, E. (2020). Neurocognitive reorganizations of language and memory in temporal lobe epilepsy:
A multimodal connectivity-based approach [Doctoral thesis, Grenoble Alpes University].
http://www.theses.fr/2020GRALS011

- 1112 Roger, E., Pichat, C., Torlay, L., David, O., Renard, F., Banjac, S., Attyé, A., Minotti, L., Lamalle, L.,
- 1113 Kahane, P., & Baciu, M. (2019). Hubs disruption in mesial temporal lobe epilepsy. A resting-state fMRI

1114 study on a language-and-memory network. *Human Brain Mapping*, 41(3), 779-796.
1115 https://doi.org/10.1002/hbm.24839

- Roger, E., Torlay, L., Gardette, J., Mosca, C., Banjac, S., Minotti, L., Kahane, P., & Baciu, M. (2020).
 A machine learning approach to explore cognitive signatures in patients with temporo-mesial epilepsy.
- 1118 *Neuropsychologia*, 142, 107455. https://doi.org/10.1016/j.neuropsychologia.2020.107455
- 1119 Rosazza, C., & Minati, L. (2011). Resting-state brain networks : Literature review and clinical applications. *Neurological Sciences*, *32*(5), 773-785. https://doi.org/10.1007/s10072-011-0636-y
- Santi, A., Friederici, A. D., Makuuchi, M., & Grodzinsky, Y. (2015). An fMRI study dissociating distance measures computed by Broca's area in movement processing: Clause boundary vs. identity. *Front. Psychol.*, 6, 654. https://doi.org/10.3389/fpsyg.2015.00654
- Schaeffer, J. D. (1990). Sensus Communis: Vico, Rhetoric, and the Limits of Relativism. Duke
 University Press.
- Schwering, S. C., & MacDonald, M. C. (2020). Verbal Working Memory as Emergent from Language
 Comprehension and Production. *Frontiers in Human Neuroscience*, 14, 68.
 https://doi.org/10.3389/fnhum.2020.00068
- Scoville, W. B., & Milner, B. (1957). Loss Of Recent Memory After Bilateral Hippocampal Lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, 20(1), 11-21.
- Sheldon, S., Farb, N., Palombo, D. J., & Levine, B. (2016). Intrinsic medial temporal lobe connectivity
 relates to individual differences in episodic autobiographical remembering. *Cortex*, 74, 206-216.
 https://doi.org/10.1016/j.cortex.2015.11.005
- Siegel, J. S., Ramsey, L. E., Snyder, A. Z., Metcalf, N. V., Chacko, R. V., Weinberger, K., Baldassarre,
 A., Hacker, C. D., Shulman, G. L., & Corbetta, M. (2016). Disruptions of network connectivity predict
 impairment in multiple behavioral domains after stroke. *Proc Natl Acad Sci USA*, *113*(30),
 E4367-E4376. https://doi.org/10.1073/pnas.1521083113

- 1138 Silbert, L. J., Honey, C. J., Simony, E., Poeppel, D., & Hasson, U. (2014). Coupled neural systems 1139 underlie the production and comprehension of naturalistic narrative speech. *Proceedings of the National*
- 1140 Academy of Sciences, 111(43), E4687-E4696. https://doi.org/10.1073/pnas.1323812111
- Simony, E., Honey, C. J., Chen, J., Lositsky, O., Yeshurun, Y., Wiesel, A., & Hasson, U. (2016).
 Dynamic reconfiguration of the default mode network during narrative comprehension. *Nat Commun*, 7(1), 12141. https://doi.org/10.1038/ncomms12141
- Sneve, M. H., Grydeland, H., Amlien, I. K., Langnes, E., Walhovd, K. B., & Fjell, A. M. (2017).
 Decoupling of large-scale brain networks supports the consolidation of durable episodic memories. *NeuroImage*, 153, 336-345. https://doi.org/10.1016/j.neuroimage.2016.05.048
- Spiers, H. J. (2020). The Hippocampal Cognitive Map: One Space or Many? *Trends in Cognitive Sciences*, S1364661319303158. https://doi.org/10.1016/j.tics.2019.12.013
- Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2013). Intrinsic
 Architecture Underlying the Relations among the Default, Dorsal Attention, and Frontoparietal Control
 Networks of the Human Brain. *Journal of Cognitive Neuroscience*, 25(1), 74-86.
 https://doi.org/10.1162/jocn_a_00281
- Squire, L. R. (2004). Memory systems of the brain: A brief history and current perspective.
 Neurobiology of Learning and Memory, 82(3), 171-177. https://doi.org/10.1016/j.nlm.2004.06.005
- Squire, L. R. (2009). The Legacy of Patient H.M. for Neuroscience. *Neuron*, 61(1), 6-9.
 https://doi.org/10.1016/j.neuron.2008.12.023
- Squire, S., L. R. (1984). The Neuropsychology of Memory. In P. Marler & H. S. Terrace (Éds.), *The Biology of Learning. Dahlem Workshop Reports (Life Sciences Research Reports)* (Vol. 29, p. 667-686).
 Springer.
- Sreekumar, V., Nielson, D. M., Smith, T. A., Dennis, S. J., & Sederberg, P. B. (2018). The experience
 of vivid autobiographical reminiscence is supported by subjective content representations in the
 precuneus. *Sci Rep*, 8(1), 14899. https://doi.org/10.1038/s41598-018-32879-0
- Studdert-Kennedy, M. (2005). How did language go discrete. In M. Tallerman (Éd.), *Language origins : Perspectives on evolution* (p. 48-67). Oxford University Press.
- Thiebaut de Schotten, M., Dell'Acqua, F., Ratiu, P., Leslie, A., Howells, H., Cabanis, E., Iba-Zizen, M.
 T., Plaisant, O., Simmons, A., Dronkers, N. F., Corkin, S., & Catani, M. (2015). From Phineas Gage
 and Monsieur Leborgne to H.M. : Revisiting Disconnection Syndromes. *Cerebral Cortex (New York,*NY), 25(12), 4812-4827. https://doi.org/10.1093/cercor/bhv173
- Tulving, E. (1972). Episodic and semantic memory. In *Organization of memory*. (p. xiii, 423-xiii, 423).
 Academic Press.
- Tyszka, J. M., Kennedy, D. P., Adolphs, R., & Paul, L. K. (2011). Intact Bilateral Resting-State
 Networks in the Absence of the Corpus Callosum. *Journal of Neuroscience*, *31*(42), 15154-15162.
 https://doi.org/10.1523/JNEUROSCI.1453-11.2011
- 1174 Uddin, L. Q. (2020). An 'edgy' new look. *Nature Neuroscience*, 23(12), 1471-1472.
 1175 https://doi.org/10.1038/s41593-020-00741-0
- 1176 Vargha-Khadem, F., & Cacucci, F. (2021). A brief history of developmental amnesia.
 1177 *Neuropsychologia*, 150, 107689. https://doi.org/10.1016/j.neuropsychologia.2020.107689

- 1178 Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Paesschen, W. V., & Mishkin, M.
 1179 (1997). Differential Effects of Early Hippocampal Pathology on Episodic and Semantic Memory.
 1180 Science. https://www.science.org/doi/abs/10.1126/science.277.5324.376
- Walenski, M., Europa, E., Caplan, D., & Thompson, C. K. (2019). Neural networks for sentence
 comprehension and production : An ALE-based meta-analysis of neuroimaging studies. *Human Brain Mapping*, 40(8), 2275-2304. https://doi.org/10.1002/hbm.24523
- Wang, S., Van der Haegen, L., Tao, L., & Cai, Q. (2019). Brain Functional Organization Associated
 With Language Lateralization. *Cerebral Cortex*, 29(10), 4312-4320.
 https://doi.org/10.1093/cercor/bhy313
- Wang, X., Margulies, D. S., Smallwood, J., & Jefferies, E. (2020). A gradient from long-term memory
 to novel cognition : Transitions through default mode and executive cortex [Preprint]. Neuroscience.
 https://doi.org/10.1101/2020.01.16.908327
- Waxman, S. R. (2004). Everything had a name, and each name gave birth to a new thought: Links
 between early word-learning and conceptual organization. In G. D. Hall & S. R. Waxman (Éds.), *Weaving a lexicon* (p. 295-335).
- 1193 Wernicke, C. (1874). Der aphasische Symptomencomplex: Eine psychologische Studie auf 1194 anatomischer Basis. Cohn.
- Wilson, S. M., Galantucci, S., Tartaglia, M. C., & Gorno-Tempini, M. L. (2012). The neural basis of
 syntactic deficits in primary progressive aphasia. *Brain and Language*, 122(3), 190-198.
 https://doi.org/10.1016/j.bandl.2012.04.005
- Wolff, M., & Vann, S. D. (2019). The Cognitive Thalamus as a Gateway to Mental Representations. J.
 Neurosci., 39(1), 3-14. https://doi.org/10.1523/JNEUROSCI.0479-18.2018
- Xu, Y., He, Y., & Bi, Y. (2017). A Tri-network Model of Human Semantic Processing. *Frontiers in Psychology*, 8. https://doi.org/10.3389/fpsyg.2017.01538
- Yang, M., Logothetis, N. K., & Eschenko, O. (2019). Occurrence of Hippocampal Ripples is Associated
 with Activity Suppression in the Mediodorsal Thalamic Nucleus. *Journal of Neuroscience*, *39*(3),
 434-444. https://doi.org/10.1523/JNEUROSCI.2107-18.2018
- Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C., & Wager, T. D. (2011). Large-scale
 automated synthesis of human functional neuroimaging data. *Nature Methods*, 8(8), 665-670.
 https://doi.org/10.1038/nmeth.1635
- Yassa, M. A., & Stark, C. E. L. (2011). Pattern separation in the hippocampus. *Trends in Neurosciences*, 34(10), 515-525. https://doi.org/10.1016/j.tins.2011.06.006
- Yeo, T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., Roffman, J. L.,
 Smoller, J. W., Zöllei, L., Polimeni, J. R., Fischl, B., Liu, H., & Buckner, R. L. (2011). The organization
- 1212 of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*,
- 1213 106(3), 1125-1165. https://doi.org/10.1152/jn.00338.2011
- Yonelinas, A. P., & Ritchey, M. (2015). The slow forgetting of emotional episodic memories : An
 emotional binding account. *Trends in Cognitive Sciences*, 19(5), 259-267.
 https://doi.org/10.1016/j.tics.2015.02.009
- 1217 Zaccarella, E., & Friederici, A. D. (2015). Merge in the Human Brain : A Sub-Region Based Functional
 1218 Investigation in the Left Pars Opercularis. *Frontiers in Psychology*, 6.
 1219 https://doi.org/10.3389/fpsyg.2015.01818

- Zhao, F., Kang, H., Llbo, Y., Rastogi, P., Venkatesh, D., & Chandra, M. (2014). Neuropsychological deficits in temporal lobe epilepsy: A comprehensive review. *Ann Indian Acad Neurol*, *17*(4), 374-382.
- https://doi.org/10.4103/0972-2327.144003

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

1225

Language is classically defined as a natural, intrinsic, and universal ability of human beings to construct communication systems using codes (speech sounds or written symbols) and to use these codes. Language cognitively involves a semantic system (vocabulary and lexical access), specialized sensorymotor capacities of perception and production (phonology), as well as capacities for decoding, manipulating (grammar/syntax), and understanding these codes (shared symbolism; comprehension).

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

Syntax refers to the rules for organizing elements - word segments, words, sentences into a grammatical
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).

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

Working memory is positioned between short and long-term memory and concerns the ability to explicitly maintain and manipulate (re-)instantiated information to perform complex cognitive tasks of learning, reasoning or comprehension. Working memory is generally considered to be part of executive functioning (or central executive system), covering concepts such as planning, inhibition, and mental flexibility. Verbal working memory involves a system for programming the utterance, scheduling verbal items at
several levels (words, phonemes and articulatory gestures), and maintaining what needs to be produced
(phonological loop and rehearsal); and appears conceptually close to the definition of syntax.

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

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

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

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

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

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

- 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 (as opposed to mainstream cognitive-centric approaches) based on brain connectivity findings. 1279

1280 The main tenets can be outlined as follows:

(i) Structure/Spatial: cognitive processes initially defined distinctively are entangled (Box 1) and
 share a mutual brain ground (see, e.g., Eisenberg et al., 2019). Three fundamental language memory overlapping dimensions can be considered in the LUM frame (Figure 2). See also Section
 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).

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

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

for instance). Section 4.2 describes several LUM disturbances in several brain affections. Figure
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:

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

1310 Captions

1311 Figure 1: Main legacies of previous neurocognitive observations.

Simplified overview of the alleged functional role and specialization in language and/or memory
functions of: A. Brain regions and; B. Fascicles highlighted in previous neurocognitive meta-analyses
(Forkel et al., 2020; Walenski et al., 2019) or models (Duffau et al., 2014; Hagoort, 2016; Hickok &
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.

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

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

B. Projection of the cognitive constructs on the three detected components. The assignment is performed
on the basis of the functional representation (meta-analytic functional maps) and according to the factor
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 subsets1332 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

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

1339

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

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

B. Cortical regions (AAL atlas), cognitive constructs (Neurosynth decoder), and brain white matter fascicles (Natbrainlab atlas) associated with the language-memory intersection functional map ($L \cap M$ mapping, computed from the functional maps included in A). The bigger the size of the words in the 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 memory as an interactive oblique model (i.e., as a composite function). Latent dimensions (RT-CM-1354 1355 TA) are individually associated with specific brain networks (SAL-FPN-DMN, respectively). In terms of behavior, internal encoding implied in verbal comprehension, for example, consists of encoding 1356 declarative inputs (engaging the TA System) via more or less attentive listening of verbal indications 1357 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.

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

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

1375

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

1378 Illustration of the putative dialogues involved in the relational binding mechanism (global and local1379 LUM dynamics).

A. Pattern separation and pattern completion neurocognitive operations engage online states manifested by dialogs involving several connectors hubs. It pushes the brain to a multi-networks state between the DMN and convergence zones. Several studies have highlighted an active role of connections between the medial temporal lobe, IFG, and angular gyrus in these two processes and under the control of the dorsolateral prefrontal cortex in the integration of multiple representations (Palacio & Cardenas, 2019 for a systematic review). Online activity recordings made at the cellular level (CA1 subfield of the rat hippocampus) show that the hippocampus engages in dynamic coordination of changes in rhythmic
profiles during associative learning (Rangel et al., 2016), allowing flexible dialogues in particular with
DMN regions and the convergence zones. The main difference between encoding and retrieval concerns
a change in modularity, especially between the two anterior and posterior subsystems of the DMN,
which are more inter-connected during memory retrieval (Cooper & Ritchey, 2020; Geib et al., 2017).
Thus, pattern completion probably engages the DMN in a more synchronized manner (dotted arrow)
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 structures and a weaker synchronization between the DMN and other network components, such as 1396 attentional-sensory networks (Sneve et al., 2017). At the local level, suppression of thalamic activity 1397 1398 could mediate these phase changes, reducing the transmission of external cognitive and sensory information during consolidation and allowing neocortical regions to be more receptive to input 1399 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

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

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

disrupting the overall topology and synchrony. The main character is a fragmentation of the FPN and
DMN networks (higher vectors of change, symbolized by the arrows), with reduced segregation between
specialized networks. The global integration of information by these networks (global efficiency) is also
particularly affected (boxplot). These observations are manifested by a reduction in connectivity within
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 neuroperations; see Figure 5). These functional disturbances are indeed specifically related to poor performance in cognitive indicators requiring the associative linking of verbal information (see our 1421 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).

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

- 1432
- 1433

1434 **Funding**

- 1435 This work has been supported by the French program "AAP GENERIQUE 2017" run by
- 1436 the "Agence Nationale pour la Recherche" grant 'REORG' [grant number ANR-17-CE28-
- 1437 0015-01]; and by NeuroCoG IDEX UGA in the framework of the "Investissements d'avenir"
- 1438 program [grant number ANR-15-IDEX-02].

A Brain regions

Production Comprehension/semantic Episodic/Associative

Executive control



Fundamental dimensions A



B Cognitive mapping

ART PRODWM

SYNT

PHON

PER

0.25

0.25

Controlon 1 (AT System)

0.75

0

0.

Son

0.5

ponent 2 (CM System)

0.25

0

0.75

ASSO

EPI

SEM

COMP LEX

 $-0.5 \longrightarrow 0.75$

Component 3 (TA System)

Language-memory continuum



A Language-memory correlations Language Memo





7.2 5.4 3.6



B Language-memory intersection



Overview of the LUM model A







A Pattern separation / completion





<---> Pattern completion



A Disruption of the global dynamics



B Disruption of the local dynamics



Fundamental LUM dimensions

