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Research Report

Complex memories induced by intracranial electrical brain stimulation are related to complex networks

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ABSTRACT

The precise and fleeting moment of rich recollection triggered by an environmental cue is difficult to reproduce in the lab. However, epilepsy patients can experience sudden reminiscences after intracranial electrical brain stimulation (EBS). In these cases, the transient brain state related to the activation of the engram and its conscious perception can be recorded using intracerebral EEG (iEEG).

We collected various EBS-induced reminiscences for iEEG analysis, classifying them as follows: no or weak details (familiarity); moderate details and context (semantic and personal semantic memories); high details and context (episodic). Nine brain areas were selected within the temporal lobes (including the hippocampus and temporal neocortex, ipsi- and contralateral) and the insula, defining a network (each area as a node). Functional connectivity was measured by estimating pair-wise non-linear correlations between signals recorded from these brain regions during different memory events.

Seventeen reminiscences in six patients (2 episodic, 10 personal semantic, 2 semantic memories, 5 familiar objects, 1 déjà-rêvé) were compared to 18 control experiential phenomena (unrelated to reminiscence), 18 negative EBS (which failed to elicit memories or other phenomena) in the same locations, and pre-EBS baseline activity.

The global functional connectivity in the network was higher following EBS-induced reminiscences than during baseline activity, control phenomena, or negative EBS. The

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Abbreviations: AD, Afterdischarge; EBS, Electrical Brain Stimulation; CEP, Control Experiential Phenomenon; EP, Experiential phenomenon; iEEG, Intracranial (or intracerebral) electroencephalogram; MRI, Magnetic Resonance Imagery; MWW, Mann Whitney Wilcoxon test; NEG, Negative electrical brain stimulation; REM, Reminiscence (induced by EBS); SEEG, Stereoelectroencephalography.

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degree of connectivity increased with the complexity of memories; it was higher for detailed and contextualized memories like episodic memories. More significant links compared to baseline (edges with higher non-linear correlation relative to baseline) were observed for episodic memories than for less contextualized memories. These increases in connectivity occurred in all frequency bands, except the delta band.

Our results support understanding declarative memory retrieval as having a multiplexed organization. They also show that richer memories activated by intracranial EBS are related to more complex connectivity patterns across medial and neocortical temporal lobe structures.

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1. Introduction

"I had entered the courtyard of the Guermantes mansion [...]. And at the moment [...] I put my foot on a stone which was slightly lower than its neighbor, all my discouragement vanished [...] again the dazzling and indistinct vision fluttered near me [...] I recognised the vision: it was Venice, of which my efforts to describe it and the supposed snapshots taken by my memory had never told me anything, but which the sensation which I had once experienced as I stood upon the two uneven stones in the baptistery of St Marks's had, recurring a moment ago, restored to me complete with all the other sensations linked on that day to that particular sensation." A memory of a specific moment in a journey to Venice was suddenly awake in Proust's mind (Proust, 1927). This vivid experience was triggered by "uneven paving-stones in front of the coach-house."

Marcel Proust dissected the most influential examples of the precise fleeting moment when the rich recollection and vivid reinstatement of a past event is cued by a trigger, without any effort of mental retrieval (Frankland et al., 2019; Steinvorth et al., 2006; Tulving et al., 1983), such as cited above. He also presented the now famous image of how mouthful of a madeleine dipped in lime blossom tea led to a sudden feat of mental time travel back to his childhood. Such experiences can be observed in the course of what are called "involuntary autobiographical memories" (Barzykowski & Moulin, 2022; Bradley et al., 2013). These arise and "pop up" in our minds without explanation or when we unexpectedly encounter a stimulus in our environment (Curot et al., 2023). The absence of conscious effort involved is interesting, as this lack of intention might ensure the authenticity of the retrieved information and limit the distortions that tend to be inseparable from memory reconstruction (Conway & Pleydell-Pearce, 2000; Schacter, 1999).

Involuntary autobiographical memories involves the activation of an engram (Frankland et al., 2019), i.e., the reinstatement of "this specific pattern of connectivity between engram cell ensembles distributed in multiple brain regions" (Tonegawa et al., 2015), which has been instated during the encoding of the initial experience. The engram was initially defined as the neural substrate responsible for storing and recalling memories (Josselyn et al., 2017; Schacter et al., 1978). The sudden uncovering of an engram constitutes one of the most intense, although elusive, phenomenological experiences that link us to our own past.

Unfortunately, exploring the neural dynamics and the activation of the engram in humans remains a Holy Grail in research on the brain, seemingly being forever out of reach. How, that is, is it possible to capture such highly personal, transient, involuntary, autobiographical memories? Despite increasingly ecological experiments (Lemesle et al., 2022), the memory paradigms available to us cannot gather all the naturalistic characteristics of episodic memory, and even less so in the case of involuntary autobiographical memories. In any case, there is a pressing need for alternative ways to study memory in humans in conditions that are closer to real life, that is, at the same time that memory spontaneously unfolds.

Despite the elusive nature of such memories, some epileptic patients can experience sudden involuntary reminiscences after intracranial electrical brain stimulation (EBS) (Curot et al., 2017; Penfield & Perot, 1963). Penfield was the first researcher to artificially activate such engrams in epileptic patients while they were awake during surgery (Josselyn et al., 2015; Penfield & Perot, 1963), but the observation of epileptic patients spontaneously experiencing such reminiscence dates back to the pioneering work of Hughlings-Jackson (1888). Replacing environmental cues and without any effort on the part of the subject, EBS triggers a transient brain state, which can be recorded, or "trapped", by intracranial EEG (iEEG). The involuntary sudden projection in time and space induced by such EBS makes these memories phenomenological experiences that are very different from memories that have been retrieved using classic memory tasks. Instead, they bear greater resemblance with Proust's experiences (Bartolomei et al., 2016). Therefore, EBS is a unique method for 'uncovering the engram' and gaining a better understanding of how memories are stored and organized in the brain.

However, reminiscences are difficult to induce using EBS (Curot et al., 2017). Their scarcity and their low reproducibility have fueled a series of debates about their origin and about the nature of the engram that they can activate. According to one hypothesis, now considered a neuromyth (Loftus & Loftus, 1980; Yapko, 1994), the engram reactivated by EBS is literally a tape recording comprising every detail the subject had experienced in the past (Penfield & Perot, 1963). In the early 90's, Gloor contradicted the tape recorder hypothesis, since his own clinical experience of EBS had mainly resulted in fragmentary memories (Gloor, 1990). He theorized that the engram reactivated by EBS forms a matrix of neuronal networks "representing the substrate of a given experience", but not

the intact experience itself. A recent review of all reminiscences induced by EBS (Curot et al., 2017) showed that, in agreement with Gloor's suggestion, reminiscences can be induced by EBS applied to different areas of the medial temporal lobes, suggesting that activating any part of the matrix can activate the whole matrix. Such a matrix could tolerate a certain amount of degradation resulting from the passage of time and epileptic activities. This theory accords with data on the malleability of our memories (Conway, 2005) and their semanticization over time, associated with progressive decontextualization and loss of information (Cermak et al., 1984; Chrysanthidis et al., 2022; Tulving, 1972). It predicts that the whole matrix (i.e., the whole engram) would only rarely be activated, because of degradation over time. It also predicts, conversely, that the more nodes and connections between nodes are activated, the more complex the memory being retrieved should be, as the activated matrix should then resemble the original matrix (Gloor, 1990).

Since Gloor's research, a few case reports have focused on the functional coupling that occurs between different nodes of the network activated by EBS. They have revealed a higher functional coupling in distributed temporal and extratemporal areas (Bartolomei et al., 2016), including synchronization in the theta range (Barbeau et al., 2005). Recent reports of memories induced by EBS in the fornix also suggested that increasing the intensity of EBS could increase the details of induced memory, thus the completeness of the engram that was activated (Deeb et al., 2019). However, most EBS fail to activate a full engram that would be exactly the same as during the encoding experience (Curot et al., 2017), as predicted by Gloor.

Here, referring to Gloor's notion of a more or less "degraded matrix", we aimed test the hypothesis according to which the complexity of memories induced by EBS is related to the complexity of the connectivity pattern across brain areas following EBS. We collected a wide range of memory types induced by EBS, from poorly (semantic) to highly detailed and contextualized (episodic) memories. We analyzed functional connectivity between nine regions of interest in the medial and lateral bilateral temporal lobes as well as in the insula during involuntary memories and compared these with baseline state and 1) negative EBS (not inducing memories) and 2) EBS leading to other types of experiential phenomena, in this case experiential phenomena devoid of mental imagery, such as déjà vu.

2. Methods

2.1. Participants

We first identified EBS-induced experiential phenomena in the stereoelectroencephalography (SEEG) databases of two French epilepsy surgery centers (Marseille and Toulouse) between 2003 and 2016. All patients had suffered from focal epilepsy, and anticonvulsant drugs failed to control their seizures. The exact location of the epileptogenic zone could not be identified with confidence using non-invasive assessments (Isnard et al., 2018). The study was approved by the local ethics committees

(the Institutional Review Board of the Assistance Publique des Hôpitaux de Marseille, C3BHV2, and the Toulouse University Hospital Ethics Committee, CER No.47-0913). Each patient received detailed information about the objectives of the SEEG technique prior to electrodes being implanted, signed informed consent forms agreeing to the diffusion of their data for scientific purposes. EBS is a standard clinical procedure that is used for assessing the local propensity of the sampled brain areas to induce seizures and for functional mapping.

Patients were retrospectively selected if: (1) they reported experiential phenomena induced by EBS corresponding to reminiscences with the inclusion criteria defined below; (2) control experiential phenomenon induced by EBS and/or negative EBS were available on the same locations; (3) EEG data were of good quality; and (4) implantation included the nine selected nodes defined below. We did not necessarily have a reminiscence, a control experiential phenomenon, and a negative EBS for each EBS location for each patient. Patient CGT, for instance, experienced a reminiscence at one point and, at another time, experienced no symptom following rhinal EBS. No control experiential phenomenon was reported, however.

2.2. Electrode implantation, locations, and regions of interest

The choice of electrode locations was based solely on pre-SEEG clinical hypotheses about the location of the epileptogenic zone. Semi-rigid multilead clinical depth electrodes (DIXI Medical, France or Alcis, France) were implanted stereotactically according to Talairach's method (Talairach et al., 1962). Each electrode was .8 mm in diameter and contained 5–18 contacts (platinum/iridium) that were 2 mm long and 1.5 mm apart. The exact location of each contact was determined using post-operative CT scan/pre-operative MRI data fusion, whose resolution allows a visual control of its anatomical location in the gray or white matter (Bartolomei et al., 2004; Evangelista et al., 2015) (Fig. 1B).

As tailored implantations are performed for each SEEG, the global mapping of electrodes is specific to each patient. Our aim was to analyze the statistical interdependencies between bipolar signals exploring different regions of interest. To allow comparisons across patients, contacts in similar locations had to be selected. Therefore, we first selected nine locations (i.e., network nodes) a priori among the most frequently implanted brain areas across patients and known to be broadly involved in declarative memory networks (Figs. 1 and 2) (Cabeza & Jacques, 2007; Dickerson & Eichenbaum, 2010). Each node corresponds to a pair of adjacent macrocontacts located in the gray matter, allowing bipolar recordings of intracranial iEEG. As our aim was also to investigate specific interactions between the hippocampus and the temporal neocortex, the majority of nodes was located inside the temporal lobes. We added an insular node, as the insula may have a metacognitive role in memory, being involved in self-awareness (Cosentino et al., 2015; Craig, 2009). We considered hemispheric lateralization in relation to the EBS site for connectivity analyses (Fig. 1A): 7 nodes were retained ipsilateral to stimulation (amygdala, hippocampus, rhinal cortex, temporal

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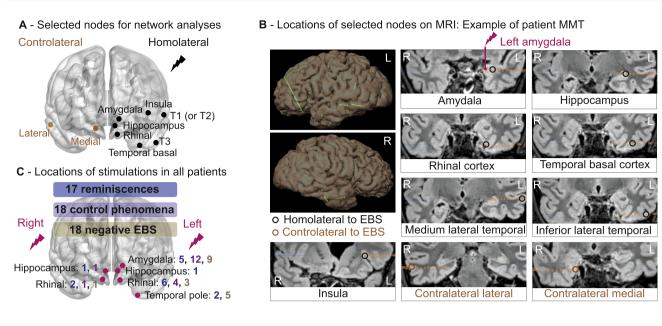


Fig. 1 – Selection of an a priori network of 9 nodes within homolateral and contralateral temporal lobes as well as the insula. A: schematic location of each of the 9 nodes. B: Example of the 9 nodes location in a single patient. C: Locations of the stimulations in all patients (EBS were pooled across patients). Numbers next to each node correspond to the number of EBS applied on the node that could be collected (in blue: reminiscences; in light purple: control experiential phenomena; in light brown: negative EBS). For instance, we could collect 5 reminiscences, 12 control experiential phenomena, and 9 negative EBS induced by left amygdala EBS across all the patients. Note that EBS on the temporal pole could induce reminiscences in several patients, but the temporal pole could not be included in the nodes because it had been implanted in patients inconsistently. We did not collect any insular or temporal basal EBS that induced reminiscence or control experiential phenomena.

basal cortex, inferior temporal gyrus [T3], superior and medium temporal gyrus [T1/T2], insula) and two nodes were contralateral (one node within medial temporal lobe, one node within lateral temporal neocortex). Right and left hemisphere nodes were pooled for connectivity analyses, and details of the hemispheric lateralization of EBS site are available in Fig. 1C.

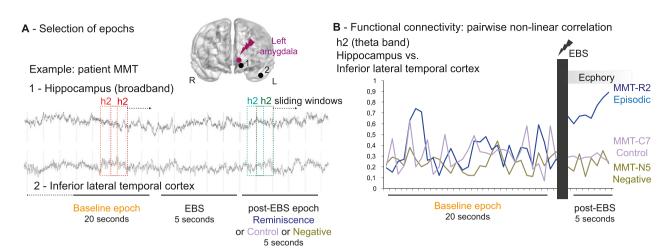
2.3. SEEG recordings and electrical brain stimulations

Signals were recorded on a 128-channel Deltamed™ (Marseille) or Micromed system (Toulouse), sampled at 256 Hz or 512 Hz with no digital filter. Two hardware filters (high-pass filter, cut-off frequency: .16 Hz at -3 dB; first-order low-pass filter, cut-off frequency: 97 Hz at -3 dB) were applied to avoid aliasing. During the clinical procedure, high frequency (50 Hz) or low frequency (1 Hz) EBS (pulse duration 1 msec) were applied in a bipolar fashion to most contacts in the gray matter and to some contacts in the white matter (according to the information required by the clinician), generally over a period of 5s for high-frequency EBS and 10s for low-frequency EBS. The current was gradually increased from .5 to 2.5 mA from one EBS to another (following standard clinical parameters in French epilepsy centers described in (Isnard et al., 2018)). Patients could be at rest or, for example, reading a magazine, and did not perform any specific cognitive tasks during EBS. They were not aware of when an EBS was applied. The standard protocol included mock trials in which patients were asked whether they had felt anything when no EBS was applied. Each site was stimulated a varying number of times depending on clinical constraints and initial EBS results. The phenomena reported in this study are those collected during this standard clinical procedure. We excluded EBS that triggered seizures and EBS exclusively in white matter. We reported whether an afterdischarge (AD) followed the EBS (Fig. 3, Tables 2 and 3, Supplementary Table). AD is defined as transient EEG changes after EBS, easily observed on intracranial recordings and corresponding to a burst of epileptiform activity induced by EBS (Kovac et al., 2016; Liu et al., 2017). AD can be confined to the electrodes that are stimulated, but can also spread to other brain areas, with or without clinical symptoms.

2.4. Classification of experiential phenomena

We analyzed the content of each memory, using detailed interviews of each patient reviews of the videos synchronized with EEG. We classified them as *reminiscence*, *control experiential phenomena* (CEP), or *negative* EBS (NEG). This classification was based solely on their semiology (their content and their phenomenology), and not on the EEG. We selected only EBS that induced a reminiscence in patients who also experienced at least one EBS inducing CEP and/or one NEG in the same location. *REM* was defined by the following criteria, as described in our previous studies (Curot et al., 2017, 2018) and relating to involuntary memories: (1) visual or auditory

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C - Example of functional connectivity across all nodes after different EBS (patient MMT, alpha band)

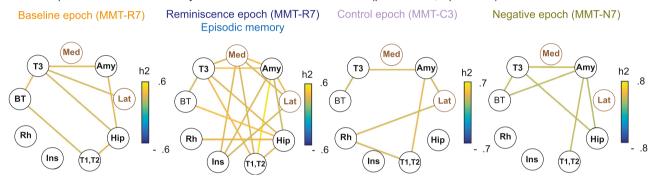


Fig. 2 — Illustration of how functional connectivity was computed. A- Illustration of the pre- and post-EBS epochs for iEEG recorded in the left hippocampus and left inferior lateral cortex after stimulation of the left amygdala. Two examples of overlapping sliding windows are illustrated. B- An example of the evolution of functional connectivity as assessed by the h2 value for each sliding window along each epoch between the iEEG recorded in the same regions as A, but here filtered in the theta band. MMT: anonymized label of the patient. C- Example of functional connectivity (h2 values) across all nodes after different EBS, for iEEG filtered in the alpha band (patient MMT). Amy: Homolateral amygdala; BT: Homolateral basal temporal cortex; Hip: Homolateral hippocampus; Ins: Homolateral insula; Lat: Contralateral temporal lateral neocortex; Med: Contralateral medial temporal lobe; Rh: Homolateral rhinal cortex; T1, T2: Homolateral superior and medium temporal gyri, respectively.

content or both, which could be more or less elaborate; (2) relation with memory; (3) induced by EBS. We then classified these memories according to the type of memory they belong to, based on modern conceptions of long-term memory, from non-contextualized and generic semantic memories to episodic memories that were highly detailed and contextualized in time and space (Moscovitch et al., 2005; Renoult et al., 2012; Tulving, 2002). We distinguished between autobiographical episodic memories, personal semantics, semantic memories, familiar elements, and déjà-rêvé (Curot et al., 2017, 2018) (Table 2). CEP included other experiential subjective phenomena that are not memories induced by EBS. They were all devoid of mental imagery and could not be defined as memories. In this category, we gathered: (1) déjà vu and déjà vécu (respectively, subjective sense of familiarity or feeling of recollection for an objectively new situation, without any content or mental imagery (Illman et al., 2012)); (2) feeling of strangeness; (3) transient amnesia; and (4) familiar odor devoid of any other mental content (no mental imagery, no sense of recollection, no accurate contextualization in time and space). NEG did not induce any particular experiential phenomena or clinical signs.

2.5. Selection of periods of interest (epochs)

For each EBS, two epochs were selected (Fig. 2A): (1) *a baseline epoch*, lasting 20 sec before the stimulation (ending at the onset of the EBS); (2) *a post-EBS epoch*, lasting 5 sec, beginning immediately after the end of the EBS artefacts and corresponding to either an REM, an NEG, or a CEP. Following previous studies (Barbeau et al., 2005; Bartolomei et al., 2012, 2016, 2019; Popa et al., 2019), we chose not to analyze EEG during EBS in order to avoid EBS artefacts. Baseline epochs with interictal epileptic discharges were not included. It is difficult to identify the precise onset of the memory and mental imagery in our patients, as it may start any time from the beginning of the EBS to some seconds after. However, even when reminiscences started during the EBS artefact, videos time-locked on the EEG strongly suggested that memory reinstatement persisted in the few seconds after EBS.

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			2 seconds

Fig. 3 - Examples of raw iEEG signals during three 50 Hz EBS instances lasting 5 sec of the medial amygdala in the same patient (Patient 6 - MMT). A - EBS of the left amygdala induced a semantic memory (MMT_R1). The patient reported, "I have nausea ... It made me think about a cartoon ... There was a little fish ... In a bowl ... " This description corresponds to a French TV advertisement for chocolate yogurts. The intensity of EBS was 1 mA. An afterdischarge occurred immediately after EBS within medial temporal areas before quickly propagating to the left lateral temporal cortex and insula. B - EBS of the left amygdala (same contacts as before) induced another semantic memory (MMT_R3). The patient described, "Oh ... A

2.6. Functional coupling (h2)

Computing non-linear correlations between the EEG signals allows us to estimate the statistical relationships between signals and interpreting results in terms of functional coupling, i.e., functional correlations, between neural assemblies. Non-linear regression analysis, i.e., h2 coefficient (Wendling et al., 2001), was used to study the functional connectivity between the nine nodes selected (Fig. 2B). The h2 method has been used efficiently for epileptic activity (Arthuis et al., 2009; Evangelista et al., 2015; Lagarde et al., 2018), experiential phenomena (Bartolomei et al., 2012, 2016) and other subjective phenomena (ecstatic hallucinations, body perception illusions) induced by EBS (Bartolomei et al., 2019; Popa et al., 2019; Scholly et al., 2022). It is a pair-wise approach that measures interdependency between 2 iEEG signals, X and Y, independently of the type of relation between them. It considers the amplitude of Y as a function of the amplitude of X using a non-linear (piecewise linear) regression curve and estimates the variance of Y that is explained, or predicted, by X according to this regression curve (Wendling et al., 2001). The h2 coefficient has values between 0 (no correlation) and 1 (maximal correlation) (Fig. 2B and C). Low h2 values denote that signals X and Y are independent, whereas high h2 values mean that both signals are dependent. To cope with the nonstationarity of iEEG signals and transient abrupt changes induced by EBS, the analysis of pre- and post-EBS epochs uses sliding windows (Fig. 2A). Sliding windows last 1 sec with an overlap of .5 sec. An h2 value is retained for each window sliding on the signal. Regression methods are robust methods for estimating functional relationships, validated in various forms of models (Wendling et al., 2009), especially on the SEEG signal (Bartolomei et al., 2016; Bratu et al., 2021; Liégeois-Chauvel et al., 2014).

The analyses were computed on bipolar signals recorded from two adjacent contacts located in each area, on the broadband iEEG (providing a global estimation of non-linear interdependencies) and on signals filtered in five fivefrequency bands (Hamming Finite Impulse Response (FIR) filters): delta (.5-3.4 Hz); theta (3.4-7.4 Hz); alpha (7.4-12.4 Hz); beta (12.4–24 Hz); and gamma (24–97 Hz) (example in the theta band in Fig. 2B, in the alpha band in Fig. 2C). We applied a 50 Hz notch filter. We thus obtained functional connectivity graphs where h2 values allow us to infer the strength of the link between two nodes in each frequency band. We used the Anywave software and its plugins to compute h2 coefficients (Colombet et al., 2015) and Matlab software (Natick, MA) for further analyses. Note that a bipolar montage may decrease the power in lower frequency bands (Parish, Michelmann, & Hanslmayr, 2023). Here, we chose a bipolar montage as in previous studies using a similar methodology (Bartolomei et al., 2016; Evangelista et al., 2015). The impact of different possible montages (7 possibilities were described in Parish, Michelmann, & Hanslmayr, 2023) is beyond the scope of this article.

2.7. Average power and wavelet coherence

In parallel to the connectivity analyses, we computed the mean power in five frequency bands using a wavelet transform across different epochs (Supplementary Figures). For each patient, the mean power (μV^2) was calculated separately for the pre-EBS and post-EBS epochs at each node, comparing reminiscence and non-reminiscence periods.

A grand average power spectrum was derived across all nodes during EBS-induced recollection, in comparison to baseline epochs and CEP. We also analyzed spectral coherence between each node for the reminiscence, CEP, and baseline conditions with a particular focus on key links between the rhinal cortex and hippocampus—regions commonly involved in reminiscences during EBS. These analyses were performed using Matlab software (Natick, MA), excluding patient 1 due to EEG format incompatibility.

2.8. Statistical and network analyses

A network is a mathematical representation of a complex system defined by a collection of nodes and links (or edges, i.e., functional or effective connections) between pairs of nodes (Rubinov & Sporns, 2010). We used different complementary measures from h2 computations to reflect the variations in connectivity between pairs of nodes induced by EBS inside the network. Details about these different measures are available in previous studies (Bartolomei et al., 2012, 2016, 2019; Popa et al., 2019).

As a first network measure, we estimated the mean functional connectivity of the network by computing the distribution of all h2 values across all nodes. We computed all pair-wise interactions from the nine nodes (72 connections). We computed a mean of all these h2 values across all pairs of nodes separately over the baseline epochs and the post-EBS epochs for each condition (reminiscence, CEP, and negative epochs), on broadband signals and in each frequency subband in order to assess whether variations in connectivity depended on the frequency and/or were specific to one frequency. We used paired Wilcoxon tests to compare baseline epochs with related post-EBS epochs, and an unpaired Mann Whitney Wilcoxon (MWW) test to compare the different types of post-EBS epochs (Python, sci.py library). A P-value of <.05 was considered significant. The dataset included a limited number of epochs despite drawing on the largest database of reminiscences compiled to date. We therefore treated each test in isolation and did not control for multiple comparisons. Note that we also provide several lines of results that all

memory of I don't know what ... It looks like cotton candy ... And a strange feeling in the throat ... An acidity ... " The intensity of EBS was .8 mA. No afterdischarge occurred. C – EBS of the left amygdala (same contacts as before) did not induce a memory phenomenon (MMT_C6). Instead, the patient felt anxious, nauseous, and experienced a subjective onset of a seizure. There was no memory content, and no afterdischarge was observed. The intensity of EBS was .8 mA. Note that EBS artifacts are not visible on the amygdala since the bipolar contact chosen for analysis within the amygdala was not the bipolar contact. Only the last seconds of baseline are depicted here.

Please cite this article as: Curot, J., et al networks, Cortex, https://doi.org/10.10	Table 1 – P	atients' cliv
l., Complex memor 016/j.cortex.2024.11	Patient	Age, Gender
memc 2024.1	Patient 1 MPM	48, F
ries ir 1.015	Patient 2 CCBM	30, F
ıduceo	Patient 3 MST	23, F
d by in	Patient 4 CGT	41, F
tracrania	Patient 5 SMT	37, M
l electrical b	Patient 6 MMT	33, F
rain s	B: Bilateral;	CEP: Contro
duced by intracranial electrical brain stimulation are related to complex		

Patient	Age, Gender	Epilepsy duration	Hand.	SOZ: Hemisphere, location	Lesion: MRI result, hemisphere	Locations of EBS: Locations, hemiphere	Reminiscences: Nb of EBS, type	CEP: Nb of EBS	NEG: Nb of EBS	Experiential phenomenon in usual seizures: yes/no (type)
Patient 1 MPM	48, F	34	R	Temporal, L	Normal	Entorhinal, L	6 (4 personal-sem, 2 familiarity)	4	2	Yes (déjà vu, prescience)
Patient 2 CCBM	30, F	10	R	Temporal, B	Periventricular heterotopia, B	Entorhinal, R	1 (déjà-rêvé)	1	1	Yes (déjà vu)
Patient 3 MST	23, F	7	R	Temporal, B	HS, R	Hippocampus, R	1 (personal-sem)	1	0	No
Patient 4 CGT	41, F	33	R	Temporal, L	Normal	Entorhinal- perirhinal, R	1 (personal-sem)	0	1	No
Patient 5 SMT	37, M	35	R	Temporal, B	Temporal Cavernoma, R/ Hippocampal dysmorphia, L	Hippocampus, L; Amygdala, L	2 (1 episodic, 1 personal-sem)	0	5	Yes (déjà vu, feeling of strangeness)
Patient 6 MMT	33, F	17	R	Temporal, L	HS, L	Entorhinal, R; Amygdala, L; Temporal pole, L	6 (1 episodic, 1 personal-sem, 3 familiarity, 1 semantic)	12	9	Yes (déjà vu)

Table 1 – Patients' clinical characteristics and number of reminiscences experienced.

B: Bilateral; CEP: Control experiential phenomena; Hand.: Handedness; HS: Hippocampal Sclerosis; L: Left; NEG: Negative EBS; nb: number; Perso-sem: Personal semantics; R: Right; y/n: yes/no.

Table 2 – Reminiscences induced by EBS.

Patient EBS	Reminiscence	Туре	EBS Location (bipolar microcontact)	Stimulated hemisphere	AD: hemisphere, location/duration (sec)	EBS frequency	EBS duration (sec)	Intensity (mA)
Patient 1 MPM_R1	Patient: I saw myself as if I was in a yellow room that I have already seen. [] A yellow room that reminds me of a hotel No, a hospital room. [] I saw a bed, a yellow wall. The same yellow color as in the 60s. Doctor: Did you see an image, a personal souvenir? Patient: Yes. [] it seems that it was a hospital room. There was an iron bed. [] it is old.	Personal semantics	Entorhinal (TB'1—2)	L	L, Hc, amygdala, temporal pole/4	50 Hz	5	1
Patient 1 MPM_R2	Patient: I saw something I have already seen. [] it was a building and a floor. [] I had the feeling of having already seen it, but I cannot say it was that building at that place. [] I saw the floor, I just saw the floor. It was a building from the 60s.	Familiarity	Entorhinal (TB'1—2)	L	L, Hc, amygdala, temporal pole, lateral temporal cortex/4	50 Hz	5	1
Patient 1 MPM_R3	Patient: Oh, this can't be! it comes back. It is the same room again. This can't be. But where was I? [] Doctor: Was it still a hospital room? Patient: Yes. Doctor: What color? Patient: Yellow.	Personal semantics	Entorhinal (TB'1—2)	L	L, Hc, amygdala, temporal pole/5	50 Hz	5	1
Patient 1 MPM_R4	Patient (reading a sentence about politics during the EBS): 2pm! 2 pm! [] That's still this story! [] The same. I saw the same corridor style. [] Doctor: Was it a memory? Patient: Yes, but which one? [] I said on purpose that it was 2 pm, because I felt it had taken place at 2 pm. [] Doctor: And was that corridor rather dark? Patient: No, the same: yellow.	Personal semantics	Entorhinal (TB'1—2)	L	L, Hc, amygdala, temporal pole/3	50 Hz	5	1.2
Patient 1 MPM_R5	Patient: It has returned to the room. Doctor: What has returned to the room? Patient: I have returned to the room. [] This one, with that pattern (showing the window of the hospital room), with grids. [] The first one, the hospital room. Doctor: Was it the same room as the one where you saw yourself? The one that was yellow? Patient: Yes.	Personal semantics	Entorhinal (TB'1—2)	L	L, Hc, amygdala, rhinal cortex temporal pole/9	50 Hz	5	1.2
Patient 1	Patient: The same [] The same room as earlier. [] It	Familiarity	Entorhinal (TB'1—2)	L	L, Hc/4	50 Hz	5	.8
MPM_R6 Patient 1	was visual, something I know. Patient: It's starting again. [] Like the other day. []	Familiarity	Entorhinal (TB'1–2)	L	L, Hc, amygdala,	50 Hz	5	.8
MPM_R7	The same room, the same style. Doctor: Was it yellow? Patient: Yes.	rannarity		Ľ	temporal pole/12	50 112	5	
Patient 2 CGT_R1	Patient: As if I had experienced something. I don't know why but it brought me back to work. [] As if it was something I had experienced earlier [] the feeling of having already experienced that at work. I sw myself in the hall.	Personal semantics	Entorhinal /Perirhinal (TB'2—3)	R	R, Hc, amygdala/6	50 Hz	5	1
							(cont	inued on next page)

Patient EBS	Reminiscence	Туре	EBS Location (bipolar microcontact)	Stimulated hemisphere	AD: hemisphere, location/duration (sec)	EBS frequency	EBS duration (sec)	Intensity (mA)
Patient 3 MST_R1	Patient: Here I feel pain (shows her epigastric region) [] And again, it makes me feel like when I have seizures: I mean, I'm physically in one place and then I'm not in the same place. I saw myself in Pibrac at my grandmother's place.	Personal semantics	Hc (A'2-3)	R	R, medial temporal lobe/3	50 Hz	5	.6
Patient 4 CCBM_R1	Patient (reading): Now, I had a reminiscence of a dream I had a few days ago. Doctor: What was this dream like? Patient: Well, I was like in a closed room and everything A kind of In a room, I felt It was very fleeting, I felt the atmosphere of the room in which I was in that dream Doctor: You felt the atmosphere but did you see the room? Patient: Yes. I saw the color. An orange color. [] It could be a dream I had yesterday or two days ago.	Déjà-rêvé	Entorhinal (T'B1-2)	R	R, Hc, rhinal cortex/2	50 Hz	5	Between 1 and 2
Patient 5 SMT_R1	Patient: Yeah, I feel something there. [] Something I have already seen. Doctor: Can you explain it to me better? Patient: An image already seen in another life. [] A picture of a place well, a place, a road where you have already been in your life. Doctor: Can you describe what you have seen? Patient: I saw Pibrac. Yeah, I saw Pibrac. The main street. [] Doctor: Where you "there"? Patient: Yeah. [] I am in front of the bar "St Germaine", that's what it's called. I Walk in front of the bar between the "Catalan" (the greengrocer) and St. Germaine (the cathedral) in Pibrac on the main street. Not far from the church and I walk. Doctor: Did it last long? Patient: No, five to 6 sec. Doctor: Was it associated with an emotion? Patient: Yes, a feeling of well-being.	Personal semantics	Amygdala (A'2–3)	L	_	50 Hz	5	1
Patient 5 SMT_R2	Patient: I feel pain there (showing her upper abdomen). Doctor: Pain and what else? Patient: Something I have already seen. [] A memory, an appointment. Images that come back in my head, of a place [] like the car park, close to here. [] I felt meeting people at a festival, in a car park, with all my friends, before getting to the place. Doctor: Would you be able to localize that car park? Patient: Yes, Purpan. Patient (pointing out of the window to the supermarket car park near the hospital which is called Purpan) [] It created an already-seen picture with the bus, with all the colleagues, the cars There was the bus, several cars We are going to leave But the more we talk of it the more I lose that image.	Episodic	Hc (B'2—3)	L	L, Hc, amygdala, rhinal cortex/40	50 Hz	5	.8
Patient 6 MMT_R1	Patient: I have nausea [] It made me think about a cartoon There was a little fish In a bowl it reminds me of another seizure Doctor: Does it remind you something of your life? Patient: No	Familiarity	Amygdala (A'2—3)	L	L, whole temporal lobe/40	50 Hz	5	1

CORTEX XXX (XXXX) XXX

Patient 6 MMT_R2	Patient: I have a memory of a bathroom you know, the faucets named Roca® [] with the writing on it. [] I saw the window of the bathroom furniture shop [] I used to pass often in front of it, when I lived in Lorca in		Amygdala (A'2–3)	L	-	50 Hz	5	.5
Patient 6 MMT_R3	Spain, between 13 and 21 years old. Patient: Oh A memory of I don't know what It looks like cotton candy And a strange feeling in the throat An acidity	Familiarity	Amygdala (A'2–3)	L	-	50 Hz	5	.8
Patient 6 MMT_R4	Patient: I've got a memory A memory that came back in my head A little girl who is spinning around herself Doctor: Like dancing? Patient: Yes, with her arm like that (she mimes her arms in the air). Doctor: Did you know her? Patient: I don't know. [] she had a pink dress. Doctor: Was she in a familiar place? [] patient: I Think I have already seen her. But I don't know where, when	Familiarity	Temporal pole (A′2 −3)	L	-	50 Hz	5	.8
Patient 6 MMT_R5	Patient: I have a feeling of déjà vécu like when I had an asthma attack [] I had tubes (showing her nose). I don't know how to explain This is a memory. [] I had tubes up my nose. I felt like tingling in the nose. Doctor: Was it a specific asthma attack or did it remind you of the usual sensation during asthma attacks? Patient (hesitating): A sensation		Entorhinal (A'2–3)	R	-	50 Hz	5	1.5
Patient 6 MMT_R6	Patient: I have a memory of having already heard something, a dialogue with an image that lasted a very short time. I think it was an image of "back to the future" with the same boy I think He was talking about hair Doctor: Is this a movie you know well? Patient: Not so much. I have seen it twice. [] The last time it was before going to the hospital.	Semantic	Temporal pole (TP'4 −5)	L	-	50 Hz	5	1.5
Patient 6 MMT_R7	Patient: F*** (grimacing, as if she felt nausea).Doctor: What do you feel? Patient: I don't know. [] I had like a memory of a seizure, a memory in my throat. It reminds me of something I experienced when I had a seizure, when my mum or my dad took me to the hospital I think it was in Toulouse or Agen I didn't know where I was and I had a lot of nausea I don't remember if it was my mum or my dad I remember a psychiatric hospital	Episodic	Amygdala (A'2–3)	L	L, temporal lobe/32	50 Hz	5	1.5

Patient_EBS	Reminiscence	Location	Hemisphere stimulated	AD: hemisphere, location/duration (sec)	EBS frequency	EBS duration (sec)	Intensit (mA)
Patient 1	Patient: Something but it is not déjà vécu.	Entorhinal (TB'1—2)	L	_	50 Hz	5	1
MPM_C1							
Patient 1	A feeling of déjà lu (already read).	Entorhinal (TB'1—2)	L	L, Hc, rhinal cortex/7	50 Hz	5	1
MPM_C2							
Patient 1	Déjà vu.	Entorhinal (TB'1—2)	L	L, Hc/4	50 Hz	5	.8
MPM_C3							
Patient1	Déjà vu.	Entorhinal (TB'1—2)	L	L, Hc, rhinal cortex,	50 Hz	5	.8
MPM_C4				temporal pole/6			
Patient 3 MST_C1	A feeling of anxiety without any reminiscence.	Hc (A'2—3)	R	_	50 Hz	5	.6
Patient 6 MMT_C1	Patient: Oh (grimacing) A burning smell	Amygdala (A'2–3)	L	-	50 Hz	5	.8
Patient 6 MMT_C2	Patient (reading a Harry Potter book): I had difficulty reading. I can feel this when I have a seizure.	Amygdala (A'2–3)	L	-	1 Hz	40	3
Patient 6	Patient (reading a Harry Potter book): I have difficulty	Amygdala (A'2–3)	L	_	1 Hz	40	3.5
MMT_C3	reading I feel tingling in my nose I see the words, I can read them but I don't understand what it means		2				010
Patient 6	Patient: I feel dizziness. I feel like a memory lapse No, like	Amygdala (A'2–3)	L	_	1 Hz	10	3
MMT_C4	a "white hole" … I was thinking about an old hospitalization for a video-EEG and suddenly I … I don't know I had the						
	feeling of forgetting						
Patient 6	Patient (talking about the movie she had watched the day	Amygdala (A'2–3)	L	_	1 Hz	40	3
MMT_C5	before): Forgetting! I know what I want to say but I can't. Like during a seizure. The story isn't coming back to me.	, , , , , , , , , , , , , , , , , , ,					
Patient 6	Patient: The same feeling as the beginning of seizure,	Amygdala (A'2–3)	L	_	50 Hz	5	.8
MMT_C6	anxiety, nausea	1111) guulu (112-0)	-		50112	5	
Patient 6	Patient: Nausea, a particular smell. I don't know what it is.	Amygdala (A'2–3)	L	_	50 Hz	5	.5
MMT_C7	[] It stinks. A DesTop® smell (caustic product).		_			-	
Patient 6	Patient: Nausea, an odor, a bad taste. [] An unpleasant	Amygdala (A'2–3)	L	L, Hc, rhinal cortex	50 Hz	5	1
MMT_C8	sensation	1111) guulu (112-0)	-	2, 110, 1111111 001001	50112	5	-
Patient 6	Patient: I feel nausea and a smell of alcohol a dizziness	Amygdala (A'2–3)	L	_	50 Hz	5	.5
MMT_C9	flashes in my eyes and a strange sensation.	1111) guulu (112-0)	-		50112	5	
Patient 6	Patient: I feel something light. The same thing I felt a	Amygdala (A'2–3)	L	_	50 Hz	5	.3
MMT_C10	moment ago, but lighter. Nausea	1111) guulu (112-0)	-		50112	5	
Patient 6	Patient: A strange sensation, dizziness, like the beginning of	Amygdala (A'2–3)	L	_	1 Hz	10	3
MMT_C11	a seizure.	1111) guulu (112-0)	-			10	5
Patient 6	Patient: F*** It's a sensation I've already had. It's It's	Amygdala (A'2–3)	L	L, Hc, amygdala, rhinal cortex	50 Hz	5	1
MMT_C12	disappearing. There is a smell mixed with nausea. [] There was no memory but a feeling of déjà vu.	·	2	2,, a, gaara,a. corten	50 112	5	-
Patient 6	Patient (reading the Harry Potter book): Ahhh! I want to	Amygdala (A'2–3)	L	L, Hc, amygdala,	50 Hz	5	1.5
MMT_C13	vomit. F*** [] I feel nauseous. I get the impression that I am in "Harry Potter" I'm nauseous I feel nervous very nervous A bad taste	niiyguala (n 2–3)	L	rhinal cortex, temporal pole	20 02	5	1.5

support the same conclusions. The unit of comparison in each test is individual trials.

As a second network measure, we analyzed the number of significant links (=edges) between nodes after EBS relatively to pre-EBS period. The number of significant links reflects the changes in functional coupling (higher coupling or decoupling) induced by EBS. For each pair of signals (X,Y), we retained the maximal h2 value across delays and across directions (X to Y or Y to X) and compared the h2 values of the post-EBS epochs relative to the h2 values of the pre-EBS epoch. For this, we calculated the Z-scores between the h2 sets during the post-EBS epochs and their respective baseline (pre-EBS epoch). Statistical significance was assessed using a Mann Whitney Wilcoxon nonparametric paired U-test between sets of responses with a threshold of p < .05. We only considered undertaking further analysis on significant links that corresponded to a higher connectivity during post-EBS epoch than during baseline epoch. The unit of comparison in each test is individual trials.

3. Results

We collected 43 EBS in 16 patients from our two epilepsy centers (transcripts are available in an open-source database, DOI: 10.6084/m9.figshare.4733026). Among these, 19 reminiscences in six patients met the inclusion criteria (Table 1). All were induced by medial temporal lobe EBS: 2 episodic memories, 10 personal semantics, 2 semantic memories, 5 related to familiar objects and 1 déjà-rêvé. Two of these were not processed further because of numerous EEG artefacts or owing to accidental suspension of iEEG recordings (MPM_R7 and MMT_R4). Eighteen EBS inducing control experiential phenomena, i.e., unrelated to memory, were selected (10 feelings of strangeness, 3 déjà vu, 3 familiar odor, 2 feelings of transitory memory loss). These were all gathered from only two patients, as none were available from other patients from the same patient group. Eighteen negative EBS, i.e., not inducing any phenomena, were also selected from five out of six patients from the same group. Details of EBS parameters and locations along with excerpts from patient statements are available in Tables 2 and 3, Supplementary table, and Fig. 1. Examples of raw iEEG signal during different EBS instances in the same patient are provided in Fig. 3. The mean power in each frequency band during reminiscence and non-reminiscence epochs is available in Supplementary Figs. 1 and 2.

3.1. Mean functional connectivity

In the broadband iEEG, the mean functional connectivity across the 9 nodes was significantly higher during reminiscence epochs than baseline (paired Wilcoxon test, T = 40, p = .048) and control experiential phenomenon epochs (unpaired Mann Whitney U-test, U = 88, p = .006). The observed difference exhibited only marginal significance (U = 111, p = .055). However, the mean functional connectivity across the nine nodes was significantly higher during reminiscence epochs than during negative epochs in the theta (U = 101, p = .027), alpha (U = 57, p = .0004), beta (U = 94, p = .01), and gamma bands (U = 98, p = .02). It was also significantly higher than during and control experiential phenomenon epochs in

the theta (U = 76, p = .003), alpha (U = 71, p = .002), beta (U = 94, p = .01), and gamma range (U = 98, p = .02) (Fig. 4, Table 4 for detailed h2 values and statistics).

In sum, reminiscences were associated with increased functional connectivity in a wide temporal network that included temporal regions, but also extra-temporal structures, such as the insular cortex.

3.2. Number of significant functional links

Next, we assessed whether there were changes in functional connectivity by assessing the number of connections between nodes that differed significantly from pre-EBS baseline, for different frequency bands. Mann Whitney Wilcoxon U-tests were used to determine whether the difference condition and the pre-EBS baseline were significant. As we were comparing the different types of memory, from the most complex to the simplest, with the control or negative EBS, we do not provide statistics regarding differences between the conditions themselves. Indeed, there were too few EBS in each case to do so in any meaningful way. An illustration of this approach for three different types of outcomes following EBS is provided in Fig. 5A. Functional correlation on filtered signals across all nodes varied according to the type of memory (Fig. 5B). It was higher for episodic memories than for personal semantics and even higher than for familiar memories.

As in the previous analysis, this result shows that functional connectivity is increased throughout a global network for reminiscences, especially during episodic memory.

3.3. Networks involving the hippocampus or neocortical structures

We then considered functional connectivity, as assessed by the mean h2 between nodes, within different substructures belonging to the temporal lobes, especially considering the hippocampus for its importance in episodic memory. We have not provided statistics comparing conditions, because there were too few EBS in each case. As illustrated in Fig. 6, a higher functional connectivity (mean h2 value) was observed between the hippocampus and the inferior temporal gyrus (T3), in the theta, alpha, and beta bands for episodic memories and personal semantics, compared to semantic memories, control experiential phenomena, and negative EBS (Fig. 6A). A higher functional connectivity for episodic memories was also observed between the hippocampus and the temporal basal neocortex (BT) in the theta and alpha bands (Fig. 6B) as well as with T1/T2 (Fig. 6C). Variable functional connectivity according to the type of reminiscence was also observed between neocortical structures themselves. In particular, greater connectivity was observed for episodic and personal semantic memories in the theta, alpha, and gamma bands, compared to semantic memories, control experiential phenomena, and negative EBS (Fig. 6D).

3.4. Functional networks operating across multiple frequency bands

The grand average power spectrum and coherence were computed across all contacts and patients during

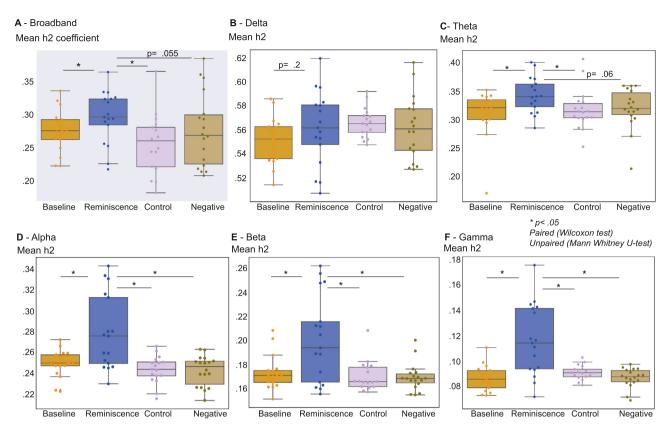


Fig. 4 – Mean functional connectivity across all 9 nodes (mean h2 coefficient). Increased functional connectivity was specific to reminiscences in the broadband iEEG and in different frequency bands, with the exception of the delta band. Each dot represents an experiential phenomenon.

Table 4 – Functional connectivity and statistics relative to reminiscences across the nine nodes for each type of epochs within all patients.

	H2 range in Broadband	Delta power	Theta power	Alpha power	Beta power	Gamma power
Reminiscence	.29+/.03	.56 ± .03	.34 ± .03	.27 ± .03	.20 ± .03	.11 ± .02
Baseline	.27 ± .03	.55 ± .01	.31 ± .04	.24 ± .01	.17+/.01	.08 ± .01
(versus reminiscence, Wilcoxon test)	$(T = 40, p = .048)^a$	(T = 52, p = .145)	$(T = 23, p = .006)^a$	$(T = 21, p = .005)^a$	$(T = 20, p = .004)^a$	$(T = 12, p = .001)^a$
Controls	.25 ± .04	.56 ± .01	.31 ± .02	.24 ± .01	.17+/.01	.08 ± .005
(versus reminiscence, Mann Whitney U-test)	(U = 88, p = .006) ^a	$(U = 158, p = .35)^a$	$(U = 76, p = .003)^a$	$(U = 71, p = .002)^a$	(U = 94, p = .01) ^a	$(U = 98, p = .02)^a$
Negative	.27 ± .05	.56 ± .02	.31 ± .03	.24 ± .01	.17+/.01	.08 ± .007
(versus reminiscence, Mann Whitney U-test)	(U = 111, p = .055) ^a	(U = 158, p = .35)	$(U = 101, p = .027)^a$	(U = 57, p = .0004) ^a	(U = 94, p = .01) ^a	(U = 98, p = .02)*
^a $p < .05$, uncorrected.						

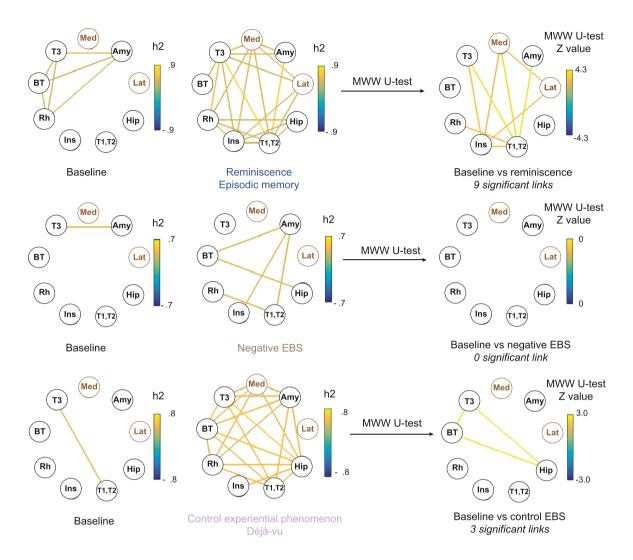
reminiscences, CEP, and baseline states, with the exception of patient 1 due to EEG format issues (Fig. 7, Supplementary Fig. 3). These analyses revealed an increase in power across multiple frequency bands during reminiscences (mean of all reminiscences), an effect not observed during CEP or baseline conditions (mean of all baselines) (Fig. 7A–B).

For example, coherence between the rhinal cortex and hippocampus (on the side homolateral to the EBS) was analyzed across all patients (excluding patient 1). This analysis demonstrated an enhancement in coherence across multiple frequency bands during reminiscences (mean of all reminiscences) (Fig. 7C, Supplementary Fig. 3). However, statistical tests were not conducted due to the limited number of trials.

4. Discussion

In the current study, we analyzed the iEEG recorded concomitantly with the largest reported collection of EBSinduced reminiscences in epileptic patients. Until we conducted our research, the analysis of functional connectivity

A - Examples of functional connectivity across all nodes after different EBS (patient MMT, theta band)



B - Significant links relative to baseline according to each type of EBS in different frequency bands (all patients)

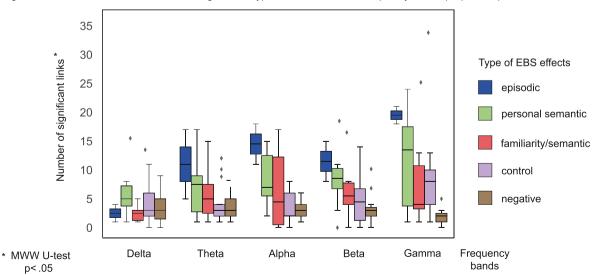


Fig. 5 – Functional connectivity varies according to memory type. A- Changes in h2 values obtained during the post-EBS epoch relative to the pre-EBS baseline epoch evaluated by calculating the variation of h2 values through Z-scores. On the left

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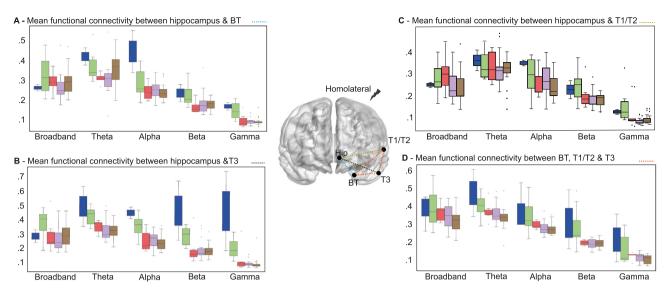


Fig. 6 – Functional coupling involving the hippocampus (A, B, C) and between temporal neocortical structures (D). We focused these illustrations on the analyses of the functional connectivity (broadband iEEG and different frequency bands) between several temporal nodes for all reminiscences (classified according to memory type), control experiential EBS, and negative EBS. A- Functional connectivity (mean h2) between the hippocampus (Hip) and the basal temporal (BT) cortex across different frequency bands and according to memory types. B– As above, but between the hippocampus and the inferior lateral temporal cortex (T3). C– As above, but between the hippocampus and the superior and medium lateral (T1 & T2) neocortex. D- As above, but between temporo-basal and lateral neocortical cortices (including superior [T1], medium [T2], and inferior [T3] temporal gyri).

during memories induced by EBS had only ever been performed in one patient at a time (Barbeau et al., 2005; Bartolomei et al., 2016a). We performed functional connectivity analyses during the moment related to the reactivation of the engram. Our sample included rich, vivid episodic memories as well as less contextualized semantic or personal semantic memories. Collecting this range of samples enables us to compare the functional networks related to each type of memory depending on their complexity. Through analyzing the mean connectivity of the number of significant connections, we obtained convergent evidence for specific connectivity changes during the reactivation of episodic memory, characterized by a broader and more richly connected network in several frequency bands.

4.1. Reminiscences induced by EBS: an original and unique way to uncover the engram

The study of memory is typically conducted using experimental tasks. While this approach has generated extensive data, memory assessed in this way may differ from how it is used in everyday, natural settings (Bruce, 1985). For instance, Neisser (American Association for Research into Nervous and Mental Diseases & Neisser, 1997) emphasized the distinction between memory as a storage system and memory actively utilized in the present.

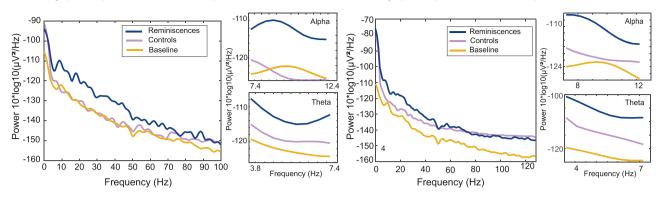
Additionally, studying the retrieval of "long-term" memories (older than a month) is challenging because most classical tasks involve a short delay of a few minutes between encoding and retrieval (Oedekoven et al., 2017). Autobiographical memory retrieval is typically assessed using word or photograph cues, or open-ended questions (Crovitz & Schiffman, 1974; Kopelman et al., 1989; Levine et al., 2002; Piolino, 2008). While these methods provide valuable information, they are susceptible to various distortions (Schacter, 2012). Virtual reality tasks (Pacheco Estefan et al., 2019) and video-clips (Bird et al., 2015; Chen et al., 2017) are more naturalistic often result in artificial or incomplete experiences of agency and autonoetic consciousness (Markowitsch & Staniloiu, 2011; Metcalfe & Son, 2012). Moreover, inducing

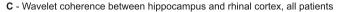
and middle panels, h2 values before MWW (Mann Whitney Wilcoxon) statistics. Only mean h2 values > .4 (high connectivity (Bartolomei et al., 2016; Scholly et al., 2022)) are reported on the graphs to simplify visualization. Statistics were, however, performed on every h2 value between every node. On the right panel, only significantly different connectivity after MWW statistics appear on the graph (p < .05). B- The mean number of significant links (MWW nonparametric paired U-test between functional connectivity during baseline and during reminiscence between two nodes, p < .05) varied according to the type of the reminiscence. It was higher for episodic memories than for personal semantics, and even higher than for familiar memories, for most frequency bands except in the delta band. Dots represent outliers. Amy: Homolateral amygdala; BT: Homolateral basal temporal cortex; Hip: Homolateral hippocampus; Ins: Homolateral insula; Lat: Contralateral temporal lateral neocortex; Med: Contralateral medial temporal lobe; Rh: Homolateral rhinal cortex; T1, T2: Homolateral superior and medium temporal gyri, respectively.

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A - Average power spectrum - All contacts, all patients

B - Average power spectrum - All contacts, patient MMT





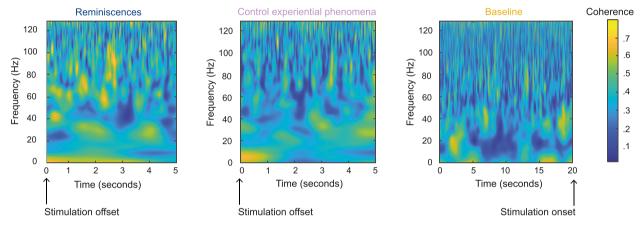


Fig. 7 — Grand average power and coherence during reminiscences, control experiential phenomena (CEP), and baseline state. A- The average power spectrum was computed across all contacts and patients (with the exception of patient 1 due to EEG format issues). This analysis demonstrated an increase in power across multiple frequency bands during reminiscences (mean of all reminiscences), an effect that was not observed during CEP or baseline conditions (mean of all baselines). A detailed view of the alpha and theta bands is provided to highlight these changes. B- A similar analysis was conducted in patient 6 (MMT), which also confirmed the power increases in multiple frequency bands during reminiscence epochs. C- Coherence between the rhinal cortex and hippocampus (on the side homolateral to the EBS) was analyzed across all patients (again, excluding patient 1). This analysis revealed an enhancement in coherence across multiple frequency bands during reminiscences (mean of all reminiscences). However, no statistical tests were conducted due to the limited number of trials. This figure is intended as an illustration, highlighting the involvement of various frequency bands during reminiscence episodes.

voluntary or incidental retrieval does not isolate the transient moment characteristic of involuntary autobiographical memory (Steinvorth et al., 2006). This brief moment is especially difficult to capture with techniques that have slow temporal resolution, such as fMRI (Bird et al., 2015; Chen et al., 2017).

Although not perfectly ecological, EBS that induces reminiscences provides an alternative method to study memory compared to classical experimental tasks. The involuntary memories we observe have unique characteristics: patients are unexpectedly and involuntarily overwhelmed by these "pop-up" memories, similar to involuntary autobiographical memories (Barzykowski & Moulin, 2022; Curot et al., 2023). Their attention is abruptly redirected inward. Furthermore, patients often report a strong sensation of temporal and/or spatial projection into their past, a feeling typically absent in most experimental memory tasks. It seems as if the stimulations directly activate the engram (Gloor, 1990). During these "pop-up" involuntary autobiographical memories, the intention to remember is absent, which minimizes bias in the processes being explored.

With this in mind, reminiscences induced by EBS represent an incomparable alternative way to trap the immediacy of the uncovering of the engram with a high spatio-temporal resolution. This method is, of course, also subject to a number of limitations, which will be discussed below.

4.2. A gradual complexity of the engram according to the memory type

In previous studies, memories were often mixed with other experiential phenomena, such as déjà vu, despite a different

phenomenology and probable specific networks (Curot et al., 2017; Bartolomei et al., 2004; Illman et al., 2012; Curot et al., 2019; O'Connor & Moulin, 2008; Moulin, 2017). Here, we classified memories according to their content and degree of contextual information. This original approach enables us to establish the existence of a connectivity gradient depending on the nature of the reminiscence.

The major result provided by the current study supports the idea that global functional connectivity varies according to the complexity of the content of memories. Global functional connectivity was higher for EBS that induced memories than for negative EBS. Global functional connectivity was, however, also higher for EBS that induced memories than for EBS that induced other control experiential phenomena. In this case, the subjects experienced a phenomenon, but this phenomenon was devoid of content, such as déjà vu. This reinforces the idea that EBS-induced memories are related to the activation of a more global and complex network, at least as defined in this study (a network made of nine nodes located mainly in the temporal lobes and also including the insula). In addition, we provide evidence (though not statistical analysis, owing to the low number of EBS in each case) that global functional connectivity was higher for more complex memories than for less complex ones, with a decreasing gradient of global complexity from episodic memories (memories that may include varying amounts of sensory and visual details, with an emotional content and located in time and space), to personal semantics (corresponding to autobiographical knowledge devoid of contextualization and sense of recollection) and to familiar memories. The complexity of functional connectivity in the networks activated during the brief period of reminiscence therefore seems to follow a gradient related to the richness of the memory that emerges.

Semantic and episodic memory has sometimes been considered as two systems relying on specific networks each. In our dataset, a relative gradual functional connectivity was evidenced, from semantic to episodic memories, between widespread temporal areas in both mean connectivity at the global network scale or in the number of connections between nodes. Such a gradation resonates with theories that assume a continuum between different memory systems (Barzykowski & Moulin, 2022; Greenberg & Verfaellie, 2010; Renoult et al., 2012, 2019) and the evidence of interactions between semantic and episodic memory during retrieval (Greve et al., 2007; Weidemann et al., 2019). It matches recent fMRI evidence that demonstrates a gradual magnitude of activation within a common network of brain regions, from general to autobiographical facts, from autobiographical facts to repeated events, and from repeated events to unique events (Tanguay et al., 2023). A progressive semanticization of episodic memories would lead to the gradual formation of generic episodes with loss of both information and specificity (Cermark et al., 1983; Piolino et al., 2006). Personal semantics integrates partial contextual information (Renoult et al., 2012), whereas semantic memories and familiar elements are devoid of it. Consequently, the amount of information, i.e., neural activity, they recruit, may be more significant for episodic than personal semantic or semantic memory.

4.3. The engram and largescale multiple interactions between medial temporal and neocortical areas

In his 2015 review, Tonegawa et al. proposed that "Engram cells' are a population of neurons that are activated by learning, have enduring cellular changes as a consequence of learning, and whose reactivation by a part of the original stimuli delivered during learning results in memory recall. 'Engram complex' refers to the whole engram for a given memory that is stored in a set of engram cell populations connected by an engram cell pathway" (Tonegawa et al., 2015). Intracranial EEG studies of induced reminiscences may be well suited to study the engram complex, by spanning large-scale networks within the human brain.

Our results confirm that interaction between medial temporal and neocortical regions takes place during the activation of the engram and recollection. It is only in these regions that reminiscences are induced. Functional connectivity at the global scale network increased during ecphory, both assessed through mean connectivity or a number of significant links compared to baseline. Likewise, the mean functional connectivity between the hippocampus and the temporal neocortex was higher during episodic memories in most frequency bands.

The comparison of the different types of memory also suggests that there may be variable functional connectivity between the hippocampus and neocortical structures, depending on the richness of the memories. These results are coherent with models (McClelland et al., 1995), electrophysiological data (Buzsáki, 1996; Fuentemilla et al., 2014; Griffiths et al., 2021; Köhler et al., 1998), and fMRI experiments (Steinvorth et al., 2006), which assume that recollecting episodic memories requires coordination between distributed brain areas, including medial temporal lobes, in particular the hippocampus and bilateral neocortical regions. The dense connections of the hippocampus with association cortices enables integrating multimodal sensory information (Andrews-Hanna et al., 2010; Kahn et al., 2008) and remembering through the reactivation of patterns of the sensoryspecific cortical regions that were engaged during encoding (Danker & Anderson, 2010; Polyn et al., 2005; Tanaka et al., 2014; Wheeler et al., 2004; Wing et al., 2015). In accordance with the description of distinct patterns of medial temporal lobe functional connectivity according to the vividness of reinstated autobiographical memories (Sheldon et al., 2016), vividness could modulate similarities and differences between the nodes that are recruited for ecphory. This is highly coherent with current network theories postulating that the emergence of a cognitive moment relies on the coordination of scattered mosaics of functionally specialized brain regions (Buzsáki, 2004; Eichenbaum et al., 2007; Sporns, 2014; Varela et al., 2001). EBS would recreate such mosaics, which are specific to the engram.

4.4. Multiple frequencies for one engram

Here, we demonstrated that connectivity increases in different frequency bands during ecphory. Mean connectivity after EBS was higher for reminiscences than other types of EBS and baseline states in the theta, alpha, beta, and gamma bands. A variation of the mean connectivity according to the

content of the memory was also observed in these frequency bands. This effect appears to be robust, as we observed power changes across different frequency bands in association with the increase in correlation. These power shifts reinforce the observation that frequency-specific interactions play a key role in modulating neural connectivity. By linking the power changes in these bands to the increase in correlation, we gain a clearer understanding of how diverse neural rhythms contribute to large-scale synchronization during brain activity. The involvement of changes in different frequencies between the same two structures during experiential phenomena has already been observed, such as increased correlations between the hippocampus and rhinal cortex in the theta and beta bands during déjà vu (Bartolomei et al., 2012).

Changes in several frequency bands converge with the findings of a wealth of literature that support that theta oscillations play a crucial role in binding distributed cortical representations and mediating a dynamic link between hippocampal and neocortical assemblies, allowing recollection (Griffiths et al., 2021; Guderian et al., 2005; Herweg et al., 2016; Klimesch et al., 2001; Nyhus & Curran, 2011; Steinvorth et al., 2010). We also observed a trend towards increased coherence between the hippocampus and rhinal cortex during reminiscences in the low frequencies and gamma band, in contrast to CEP and baseline. Higher phase synchrony in the theta band predicted more detailed visual imagery during the retrieval of vivid autobiographical memories (Fuentemilla et al., 2014). Theta-gamma coupling controls the transfer of information throughout the entorhinal-hippocampal network and temporally organizes sequences of events within each theta cycle (Colgin, 2015; Lisman & Idiart, 1995; Lisman & Jensen, 2013). Theta synchronization could reflect preferentially episodic memory processes, whereas alpha synchronization and desynchronization could be related to semantic longterm memory (Klimesch, 1999).

The power and phase at different frequencies would contribute to distinct neural representations during retrieval (e.g., spatial versus temporal information) (Siegel et al., 2012; Watrous et al., 2013). Electrophysiological studies have already suggested that episodic, semantic, and familiarity information are reflected by different frequencies (Gruber et al., 2008; Hanslmayr et al., 2009; Klimesch et al., 1994). Our results suggest that synchronization has a concomitant role in multiple frequency bands (not limited to theta/gamma) in supporting different types of information and handling the complexity of memories. They fit the hypothesis of "multiplexed" memories (Knight & Eichenbaum, 2013; Watrous & Ekstrom, 2014), even though our results do not allow us to specify what information is underpinned by each frequency.

We focused our analyses on increased functional connectivity between different brain areas, whereas the degree of desynchronization between the lateral temporal and medial nodes in these different frequency bands may also support specific information. In fact, neocortical alpha/beta desynchronization and hippocampal theta/gamma synchronization are thought to interact to enable the successful encoding and retrieval of episodic memories (Griffiths et al., 2021; Hanslmayr et al., 2016). The role of higher frequencies, or oscillations, such as ripples, should also be explored. It has been shown, for example, that sharp-wave ripples (70–180 Hz) activate the reinstatement of cortical representations during a free episodic memory retrieval task (Norman et al., 2019).

Unfortunately, because non-linear correlation analyses lack specificity about the nature of the coupling, they do not clarify whether the coupling relies on coupled oscillations, cross-region phase amplitude coupling, or any time lag between regions. Future work involving cross-regional coherograms, cross-frequency coupling, and phase synchronization analyses between pairs of nodes may help to address these relationships.

4.5. Access to the engram

The literature has long focused on a debate about how and from where the engram could be activated by EBS and has suggested a unique "entry" point from which the engram can be activated. Penfield suggested that it is the lateral neocortex (Penfield & Perot, 1963), whereas Bancaud et al. argued that this was located in the medial temporal lobe (Bancaud et al., 1994). Gloor (1990) put forward a more subtle view, namely that EBS has "the capacity to recreate the totality of a given experience when only a fragment of the network is activated". While Gloor may not have put enough emphasis on the neocortical-medial temporal dialogue, he theorized that the engram artificially reactivated by EBS is a matrix of neuronal networks that tolerate a certain amount of degradation resulting from the passage of time and epileptic activities. He hypothesized that the induction of memories by EBS should depend on the activation of a specific pattern of connectivity in widely distributed neural networks. This matrix may be composed of sparse activated and inhibited neuronal populations, representing the substrate of a specific previous event, but in a hazy version. This matrix could tolerate considerable amounts of degradation across time, equivalent to a reduction in connectivity and in the number of recruited nodes. Fragmentary but recognizable memories could arise from activating a degraded matrix. In the light of our results and of recent understandings, this finding could be expressed, in other words, by the fact that "low episodic" and "more semantic" memories emerge following the activation of a network with a lower connectivity. In this sense, our results fit with Gloor's hypothesis.

One of our previous studies confirmed that the engram can be artificially activated by various subcomponents or structures of the memory networks (Curot et al., 2017). A critical finding is that we observed more reminiscences following rhinal cortex EBS compared to other brain areas. This suggests that the rhinal cortex may serve as a primary gateway for inducing reminiscences through stimulation. However, EBS does not fully replicate a "complete" engram identical to the original encoding experience and the qualitative nature of memories largely depends on the site of stimulation: EBS of the rhinal cortex predominantly induces personal semantic reminiscences, whereas only hippocampal EBS elicits episodic memories. 20

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4.6. Limitations

By common standards, this study is underpowered. It was not possible to control for multiple comparisons and the distribution of the experiential or control conditions across patients was not equal, despite this study gathering the largest database of reminiscences to date. This is mainly due to the scarcity of reminiscences induced by EBS. EBS only rarely induce reminiscences and, when they do, not all epilepsy centers keep these data (testimonies of the reminiscence and iEEG), nor can all centers share them. For this reason, future progress in the field will rely on collective efforts being undertaken to create a shared database. Importantly, all our results went in the same direction and appeared to corroborate our hypothesis that more complex memories were related to more complex networks. We therefore believe that the study of reminiscences induced by EBS provides a valuable contribution to refining our understanding of how human memory works. It points towards valuable hypotheses that can be tested in future collaborative studies. Critically, despite current limitations, it is a novel way to study the electrophysiological correlates of memory as it spontaneously unfolds. To our knowledge, no other method is even close to achieving this.

It is also not always easy to fully characterize what patients experience. This requires both know-how and neuropsychologists trained in the field of memory. Moreover, these data were acquired from patients with drug-refractory epilepsy, and we have not yet explored how this patient group may have impacted our results. That said, the results we obtained are congruent with the literature in healthy subjects. The results obtained from cognitive iEEG studies are furthermore generally considered to agree with other studies (Fox et al., 2018; Han et al., 2023; Jonas & Rossion, 2023; Mercier et al., 2022; Parvizi & Kastner, 2018).

While we assessed differences between post-EBS and pre-EBS baseline periods, our data do not permit us to explore a hypothetical relationship between the endogenous coupling observed in the pre-stimulus baseline period and the likelihood of EBS triggering episodic recollection. It is conceivable that the subject's baseline state, potentially favoring introspective situations, may influence this process. One possibility is that reminiscences are induced only when EBS is applied during specific brain states (Curot et al., 2020), such as more introspective or relaxed states, or when the default mode network is already activated.

5. Conclusion

Reminiscences induced by EBS can be considered as snapshots of our memory engram. This study suggests that memories induced by EBS are not random artifacts: the higher the global connectivity and the number of temporal nodes that were recruited in different frequency bands, the more complex memories were. It supports a "multiplexed" view of connectivity related to the content of memories. Further analyses in larger collections of reminiscences are required to explore what type of information is underpinned by each frequency band.

CRediT authorship contribution statement

Jonathan Curot: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Vincent Dornier: Methodology, Formal analysis. Luc Valton: Writing – review & editing, Investigation, Data curation. Marie Denuelle: Writing – review & editing, Investigation, Data curation. Alexis Robin: Writing – review & editing, Visualization. Florence Rulquin: Writing – review & editing, Investigation. Jean-Christophe Sol: Resources, Investigation. Amaury De Barros: Resources, Investigation. Agnès Trébuchon: Resources, Investigation. Christian Bénar: Writing – review & editing, Software, Methodology. Fabrice Bartolomei: Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. Emmanuel J. Barbeau: Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

Data/code availability

The verbatim reports of experiential phenomena from our entire database are publicly accessible at https://figshare.com/articles/dataset/Memory_scrutinized_through_electrical_brain_stimulation_a_review_of_80_years_of_experiential_phenomena_Curot_et_al_2017_/4733026?file=17545268.

The code for h2 coefficient computation and related analyses is publicly available at https://meg.univamu.fr/wiki/AnyWave.

Due to ethical restrictions, anonymized EEG data cannot be publicly archived. Readers interested in accessing the data are encouraged to contact the lead author, Dr. Jonathan Curot. Access will be granted to identified individuals in compliance with ethical guidelines governing the reuse of sensitive data.

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None.

Conflict of Interest

The authors have no conflicts of interest.

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Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2024.11.015.

Appendix

This is among the last of the manuscripts which is passing through as the initial checklist was in place before STS and STR was introduced.

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