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Review article

Memory scrutinized through electrical brain stimulation: A review of 80 years of experiential phenomena

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ABSTRACT

Electrical brain stimulations (EBS) sometimes induce reminiscences, but it is largely unknown what type of memories they can trigger. We reviewed 80 years of literature on reminiscences induced by EBS and added our own database. We classified them according to modern conceptions of memory.

We observed a surprisingly large variety of reminiscences covering all aspects of declarative memory. However, most were poorly detailed and only a few were episodic. This result does not support theories of a highly stable and detailed memory, as initially postulated, and still widely believed as true by the general public.

Moreover, memory networks could only be activated by some of their nodes: 94.1% of EBS were temporal, although the parietal and frontal lobes, also involved in memory networks, were stimulated. The qualitative nature of memories largely depended on the site of stimulation: EBS to rhinal cortex mostly induced personal semantic reminiscences, while only hippocampal EBS induced episodic memories. This result supports the view that EBS can activate memory in predictable ways in humans.

1. Introduction

In 1934, Penfield reported that the application of low intensity electrical brain stimulation (EBS) on specific portions of the cortex of an epileptic patient undergoing awake neurosurgery made him/her relive an event of his/her past. Between the 30s and 60s, Penfield reported 40 epileptic patients who experienced psychic phenomena after application of EBS on the neocortex (Penfield, 1958; Penfield and Perot, 1963). Among them, several patients reported reminiscences of past experiences. Penfield assimilated these responses to the dreamy-state occurring spontaneously during seizures described half a century earlier by Hughlings Jackson (1880) and Hughlings Jackson and Colman (1898) (Box 1). Penfield considered that EBS were reactivating complete stored memory traces, these experiential phenomena being viewed as replays of engrams, like a "tape-recording": "*Past experience, when it is recalled electrically, seems to be complete including all the things of which an individual was aware at the time […]*" (Penfield and Perot, 1963).

Since Penfield's pioneering work, several studies have also reported experiential phenomena after EBS (see below for a complete list). However, some of them challenged Penfield's theory. For example, Gloor (1990) proposed the matrix theory, a reconstructive process whereby EBS leads to the elaboration of excitation and inhibition patterns in widely distributed neural networks, of which some are able to represent a given previous experience, albeit in a caricatured way. Hence, whereas Penfield thought that EBS could induce reminiscence exactly similar to the original event, a bit like playing a videotape at random, Gloor was of the view that only the gist of these memories could be activated. Penfield's hypothesis remains influential nowadays (Loftus and Loftus, 1980; Simons and Chabris, 2011). But although attractive, whether this conception of a highly stable memory is

Abbreviations: AD, afterdischarge; EBS, electrical brain stimulation; SEEG, stereoelectroencephalography

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Box 1
Definitions

We provide in this box a definition for some of the technical terms used in this review.

Afterdischarge: Transient EEG changes after electrical brain stimulation, easily observed on intracranial recording and corresponding to a burst of epileptiform activity induced by the electrical stimulation. Afterdischarge can be confined to the electrodes that are stimulated, but it can also spread to other brain areas, with or without clinical symptoms. When afterdischarge spreads to other adjacent and remote electrodes, it can be considered as a stimulation-EEG induced seizure. EBS applied during SEEG or electrocorticography do not systematically induced afterdischarges. (See Kovac et al., 2016 for review).

Déjà-vu: A transitory mental state whereby an objectively novel experience feels subjectively familiar. This experiential phenomenon is devoid of any content and has a short time course (Illman et al., 2012).

Dreamy-state: This terminology was originally used by Hughlings-Jackson (1880, 1888, 1898) to define a particular "elaborate and voluminous" mental state that occurs during some epileptic seizures: "*There is not always loss, but there is, I believe, always, at least defect, of consciousness co-existing with the over-consciousness*" (1898), "*I believe—there is a kind of double consciousness—a 'mental diplopia',"* (1899). He hypothesized that these mental states were "of different kinds". He paradoxically never referred specifically to dreams, but rather emphasized the fact that experiential phenomena following temporal lobe epilepsy felt like dreaming. Today, in clinical practice, experiential phenomena (see definition) related to temporal lobe epilepsy are often grouped under the term "dreamy-state", although reminiscences or experiential phenomena seem more appropriate because better defined.

Electrical Brain Stimulation: It is the application of electrical current directly to the cortex. It can be delivered temporarily: intra-operatively during awake surgery in patients with brain tumours or intractable epilepsy to identify critical areas for cognitive and motor functions; extra-operatively during stereoelectroencephalography and electrocorticography (see definition) in patients with intractable epilepsy in order to study connectivity, cortical excitability and to delineate the seizure onset zone. It can also be delivered chronically with implanted electrodes for treating various neurological (Parkinson disease, essential tremor, under development for intractable epilepsy) and psychiatric disorders (depression, obsessive compulsive disorders). They can sometimes induce unexpected behaviours and experiences, such as reminiscence (see definition).

Electrocorticography: Intracranial recording of EEG with similar indications and goals as the SEEG (see definition), but in this case subdural grids are placed directly on the surface of the cortex to record electrical activity from the cerebral cortex. A craniotomy is required to implant the grids. Recordings can be performed either in the operating room or extra-operatively during several days. Low intensity currents can be delivered between adjacent contacts to study local cortical excitability.

Experiential phenomena: This term is used in a broad sense and includes various types of transitory mental states, sensory and memory illusions, which the patients subjectively experience. They can occur during an epileptic seizure or following electrical brain stimulation. Penfield (1954) was the first to use the word "*experiential*": initially "*experiential flash-back*" referred to the "*random re-enactment of a conscious sequence from the patient's past"*. It was separated from "*interpretive illusions"* which referred to "*alteration of perception of the present"* such as auditory illusions and from "*interpretive signaling"* which were "*production of sudden interpretations of the present experience, such as familiar, strange, fearful…"*. Gloor gathered all these as "*experiential phenomena*" (Gloor et al., 1982; Gloor, 1990).

Reminiscence: Involuntary recall of a memory during a seizure or following electrical brain stimulation. This phenomenon has content such as visual mental images and/or other sensory characteristics contrary to déjà-vu. The time course of this phenomenon is supposed to be longer than déjà-vu. The content can refer to different type of information and thus to different types of memories: semantic memories, personal semantics, episodic memories but also reminiscences of dreams. Hughlings Jackson (1888) also used the word "*reminiscence*". But he assimilated it to the "*dreamy-state*" and he never defined it explicitely.

Stereoelectroencephalography (SEEG): Intracerebral and extra-operative recording of EEG during several days long, using depth electrodes surgically implanted into the brain. SEEG is used for drug-refractory epileptic patients, candidates for neurosurgery. Noninvasive presurgical assessment could not determine precisely the seizure onset zone. Intracerebral electrodes are thus implanted using a stereotaxic frame in circumscribed brain areas according to seizure semiology and hypothetical epileptic networks. The patient keeps these electrodes until seizures occur to determine the seizure onset zone. Low intensity currents can also be delivered along the different contacts of the electrodes to study local excitability (Talairach and Bancaud, 1965).

plausible or whether it is one of the numerous neuromyths that have been identified remains to be clarified (Lilienfeld et al., 2009; Dekker et al., 2012). This situation is largely due to the fact that it is unknown what type of memory EBS can exactly induce.

Furthermore, divergent views can be found in the literature about the influence of the localization of EBS (Penfield, 1958; Halgren et al., 1978; Vignal et al., 2007; Bartolomei et al., 2004). For example, some authors consider that the site of stimulation has no consequence on the type of memory induced, favouring the idea that what matters is the patients' personality (Halgren et al., 1978; Halgren and Chauvel, 1993; Chauvel, 2014), whereas others suggest that stimulation of specific sites could induce specific types of memories (Bartolomei et al., 2004; Barbeau et al., 2005). However, these reminiscences are nowadays the major source of inspiration for preliminary trials aiming at improving memory performances using EBS (Lee et al., 2013; Suthana and Fried, 2014). A series of reports demonstrated that EBS of the medial temporal lobes but also of the fornix could induce memories (Halgren et al., 1978; Gloor et al., 1982; Bancaud et al., 1994; Gloor, 1990; Hamani et al., 2008; Vignal et al., 2007). It is for this reason that stimulation of the rhinal cortex (Suthana et al., 2012, Fell et al., 2013), hippocampus (Fell et al., 2013) or fornix (Laxton et al., 2010; Smith et al., 2012; Fontaine et al., 2013) were chosen empirically as targets to modulate memory networks using chronic EBS. Whether the site of EBS really has no consequence on the type of memory; or whether there is a preferable localization to access specific types of memory is thus of crucial importance to determine how to modulate memory using EBS.

Moreover, an important variability of electrical stimulation parameters (electrode geometry, pulse amplitude, duration, frequency, monopolar or bipolar EBS, monophasic or biphasic pulses) can be found in the literature. This variability leads to differences in the electric field distribution (Kuncel and Grill, 2004; Winawer and Parvizi, 2016) and make it uncertain which neural elements are really targeted and modulated by EBS across studies. Fundamental questions remain about the effects of EBS on the neurons surrounding the electrode and on their large scale consequences (McIntyre et al., 2004; Borchers et al., 2012). Furthermore, contradictory effects are attributed to the afterdischarge (EEG changes after EBS artefacts, AD, see Box 1). Some authors postulated that a widespread AD is necessary to induce experiential phenomena (Halgren et al., 1978). Others insisted in contrast on an inhibitory role of AD, since an early spread of the discharge to the temporal neocortex could prevent the occurrence of reminiscences of memory (Vignal et al., 2007). Overall, much uncertainty about the conditions in which reminiscences of memory can be induced thus remains.

Surprisingly, given the theoretical importance of these data, no systematic review of reminiscences induced by EBS has been performed despite more than 80 years of production since Penfield's initial observations.

In this study, we performed a systematic review of all reminiscences, induced by EBS, we could find in the literature, with the addition of 45 cases from our own database for which we have precise localization. Penfield was referring to memory using the analogy of a videotape recorder. He was in fact referring to what would now be called autobiographical episodic memory (Tulving, 2002), as this concept had not been coined at his time. There has been little attempt to classify reminiscences following modern conceptions of memory, distinguishing, for example, episodic from semantic memory. Therefore, we classified all reminiscences induced by EBS depending on the type of memory. We also simultaneously analyzed the localization of the EBS, as well as the effects of the afterdischarge and the parameters of stimulation, to gather and synthesize as much information as possible for future studies.

2. Methods

2.1. Data collection

We did our best to collect all experiential reports related to memory induced by EBS, whether for severe epilepsy or other neurological disorders, available in the literature. Inclusion criteria were:

1. A content: visual or auditory content or both, which could be more or less elaborate.
2. A relation with memory.
3. Induced by EBS.

This implied the following exclusion criteria:

1. Déjà-vu and déjà-vécu phenomena: those that are devoid of any content or mental imagery and consist of a subjective sense of familiarity or a feeling of recollection for an objectively new situation (Bartolomei et al., 2004, 2012; O'Connor and Moulin, 2010; Illman et al., 2012).
2. Rudimentary visual or auditory hallucinations, such as a noise or a shape unrelated to memory.
3. All spontaneous phenomena and spontaneous memories reported during seizures.
4. Unrealistic and implausible events.

We surveyed all articles and studies published in scientific journals, book chapters and thesis manuscripts, published since Penfield's pioneering work, between 1958 and 2015 and indexed in Medline and Google Scholar. We searched these databases using combinations of the following keywords (no keyword was used in isolation): "Epilepsy", "memories" or "memory" (alone or combined with "autobiographical", "retrieval", "recollection"), "hallucination" (alone or combined with "visual" or "sound" or "auditory"), "dreamy-state", "souvenir", "reminiscence", "déjà-vu", "experiential phenomena", "mental imagery". These were furthermore combined with the keywords "electrical brain stimulation", "human brain stimulation", "brain stimulation", "electrocorticography", "deep brain stimulation", "depth electrodes", "stereo-electroencephalography". Pubmed search resulted in about 860 links to publications, and Google Scholar search in more than 5000 links (with overlaps between the 2 databases). Animal studies, explicit absence of reference to electrical stimulation in the title, explicit absence of experiential phenomenon in the title, explicit non-electrical stimulations (as TMS) in the title lead to rejection of the article. We scanned the abstracts of all the other reports. 188 publications were considered worth reading, and we ultimately selected 29 publications in English or in French dealing with EBS in human subjects. To be as comprehensive as possible, we also searched for relevant papers in the references provided in each of these publications and reviewed additional work.

We also added our own data, collected from three epilepsy surgery centres in France (Toulouse, Marseille, Nancy) covering the period between 2003 and 2015. All patients in this second category were explored using a similar Stereo-ElectroEncephalography (SEEG) technique (Box 1, Talairach and Bancaud, 1965). Each of these patients suffered from partial epilepsy and anticonvulsant drugs failed to control the seizures. The exact location of the epileptogenic zone could not be specified by a non-invasive assessment including MRI, video-EEG and functional imagery such as 18-FDG positron emission tomography in all patients and ictal single position emission cerebral tomography in some patients. SEEG recording was performed in order to precisely define the epileptogenic zone. All patients had a comprehensive evaluation including detailed history and neurological examination, neuropsychological testing, routine MRI, surface EEG and SEEG. SEEG was carried out as part of the patients' clinical care. SEEG recordings were performed using intracerebral multiple contacts depth electrodes implanted intracranially according to Talairach's stereotactic method (Talairach and Bancaud, 1965).

Each patient received detailed information about the objectives of the Stereo-ElectroEncephalography (SEEG) technique before intracerebral electrode implantation. They also received explanations about the objective of the stimulations, which is a standard clinical procedure and consists in stimulating the brain areas sampled with the intracerebral electrodes in order to assess the local propensity of these brain areas to induce seizures. They signed informed consent for the implantation. The reminiscence reported in this study are those collected during this standard clinical procedure. Patients were retrospectively selected if they reported reminiscence during the stimulations.

2.2. Data categorization

We distinguished EBS (e.g. application of electrical current on brain structures) and reminiscence (e.g. the reminiscence induced by EBS). Several EBS could indeed induce the same reminiscence in some patients. We thus identified a number of EBS and a number of reminiscences. Two publications needed special care. Bickford et al. (1958) reported a subject that would have felt a similar experiential phenomenon 62 times with the same electrode at the same place. However, the complexity of the phenomenon was variable depending on the parameters used, and only one single comprehensive debriefing that could fit into our classification is reported from their publication. Thus, we only considered one EBS and one reminiscence for this patient. Mahl et al. (1964) reported several experiential phenomena in one patient, including reminiscences. But due to a very specific methodology (targeted psychological examinations during EBS to assess the impact of EBS on psychological functioning and patient's discourse), we did not include the different EBS responses described in this publication in order to avoid any ambiguity.

Three evaluators (JC, TB, EB) working in the fields of neurology, psychology and cognitive neuroscience defined 8 different categories to classify memories according to their content. The aim was to classify the different reminiscences into various aspects of long-term declarative memory while staying as independent as possible without preconceptions. The categories were created in accordance with contemporary

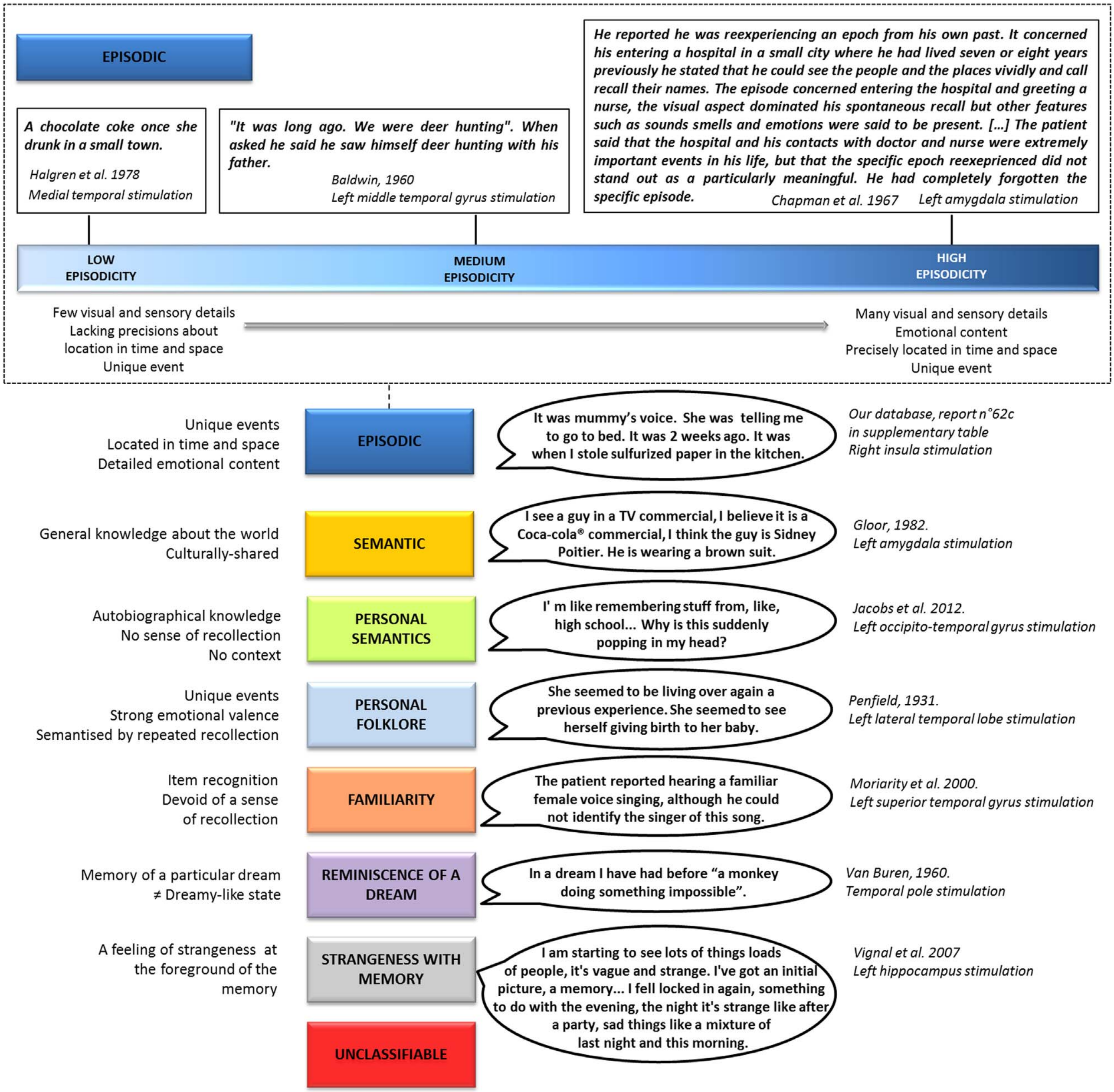

Fig. 1. Data categorization of memories induced by EBS. Examples are provided for each category.

memory systems (Tulving, 1972, 1995; Renoult et al., 2012). Reminiscences were then independently classified by each of the three evaluators, the final category corresponding to a consensus among the evaluators, after discussion in case of disagreement. If the three evaluators independently agreed on the same category, this category was automatically chosen. If one or more of the three evaluators disagreed, the content of the reminiscence was jointly re-analyzed. If the discussion led to a consensual category, this category was chosen. Reminiscences valued differently by the three evaluators and for which no consensus could be reached were classified in an "unclassifiable" category. The evaluators actually initially disagreed for 39% of the cases reported in the literature and in 13.3% of the cases reported in our database. The large disagreement for the cases from the literature is simply due to the poor description of many reminiscences. After discussion, 17.5% of the cases from the literature were classified in the "unclassifiable" category in contrast with 2.2% of the cases from our database. The categories were the following (see Fig. 1 for examples of each category).

1. **Autobiographical episodic memories:** An episodic response was defined as a unique personal event, detailed in space and time, including details and sometimes emotional content. Details of the debriefing were sufficient to conclude that this was a unique and plausible event from the patient's life. We divided this category in three subcategories, depending on the episodicity level (high, medium, low) based on the importance of the visual and sensory details and the state of consciousness reported by the patient. High episodic rating was given only if all the following components of the reminiscence were described: location, date and details. Medium episodic rating was given if the location or the date was given but not both and if the report lacked details. Low episodic rating was given if the debriefing allowed concluding to an episodic event while being poorly described and lacking date and place.
2. **General or pure semantic memories:** These were responses related to the general knowledge one has about the world, culturally-shared and devoid of spatial and temporal encoding context. We divided general semantics in visual or auditory semantic

depending of the content of the response.

3. **Personal semantics (or autobiographical semantic memories):** Personal semantics included all autobiographical knowledge devoid of any subjective sense of recollection and detailed temporal context.
4. **Personal folklore:** It was a category midway between autobiographical semantic memory and autobiographical episodic memory. These were unique events in a person's life but probably semanticised through repeated recollections because of their strong emotional valence and importance for the patient's identity (steps in life) (Cermak and O'Connor, 1983). The idea behind this category was that EBS could have triggered such reminiscences more than others given their importance for the subject.
5. **Familiarity:** Responses classified as familiar were reports of objects or sounds that were known by the subject but for which no further context could be retrieved. Visual familiarity and auditory familiarity were distinguished. Note that all these responses had content, i.e. feelings of familiarity without content were discarded.
6. **Reminiscence of a dream:** We noted that several patients reported the memory of a particular dream. It was not an EBS inducing a dreaming-like state, but an EBS inducing the memory of a dream already dreamed by the subject.
7. **Strangeness with memory:** Responses classified in this category were those for which the patient reported a relation with memory, but a feeling of strangeness was at the foreground of the experiential phenomenon and the content was too fragmentary to retain this phenomenon as an episodic or semantic memory.
8. We collected in **an unclassifiable category** all EBS that produced a phenomenon with a visual or auditory content that might be associated with memory. However, debriefing was too short and the authors did not provide enough information to reach a consensus between the evaluators for the phenomenon to be included in the preceding categories.

These categories were relatively exclusive of each other, as there are features belonging preferentially to one or the other. The only exception was the category "strangeness with memory", which could sometimes occur simultaneously with the others (we counted about 13 such occurrences and each time we classified the reminiscence not in the category "strangeness with memory" but in one of the other, thus resulting in some underestimation of this category).

2.3. Variables of interest

We separately analyzed the data from the literature and the data from our own SEEG database for which we know precisely the technique used, the different EBS parameters and the localization of the electrodes. We analyzed:

- Patients' clinical characteristics: age, gender, type of pathology, handedness, supposed lateralization of the epileptogenic zone.
- The prevalence of reminiscences induced by EBS when sufficient data were available in the articles.
- The localization of the different EBS to better understand which brain structures could be involved in the recall of such memories.
- Delay between encoding and EBS. Analysis of this period, when not clearly stated in the report of the patient, was carried out by an approximation based on the subject's age and the period of life that was referred to in the reminiscence. This analysis could indirectly inform us about consolidation mechanisms and the presence or absence of a temporal gradient in the type of memories recalled.
- All the information provided by the authors about the EBS parameters to analyze whether a combination of parameters preferentially allows the production of these reminiscences: types of electrodes (depth macro-electrodes, surface electrodes and subdural grids), monopolar or bipolar EBS, pulses (frequency in Hertz, duration and biphasic or monophasic stimulation), intensity (Ampere) or voltage (Volt) and duration. Very often, only the amplitude parameters or the intensity parameters were specified but not both. As the amplitude and intensity parameters vary widely between authors, we grouped them into ranges:
- Intensity of EBS: 0–1 mA, > 1–2 mA, > 2–3 mA, > 3 mA.
- Amplitude of EBS: 0–1 V, 1–5 V, 5 V. We also retained a range of 2–12 V due to a large number of EBS in this range, and because the authors did not provide more precise information.
- The presence or the absence of an afterdischarge (AD) after EBS. The AD corresponds to transient EEG changes (such as a burst of epileptiform activity) after EBS artefacts.

Note that in many instances, only partial information could be retrieved from the articles, in particular in the articles from the 60s to the 80s. For one patient in our database, data were too old to get all clinical and electrophysiological information, and for two patients we could not retrieve EBS intensity.

2.4. Localization of the EBS

The localizations of the EBS were represented on schematic brain maps according to the category of induced reminiscences. For the literature data, these brain maps were produced with the best approximation possible, since most publications provide a localization of EBS in terms of gyrus or Brodmann areas. Very few publications reported coordinates in a standardized referential atlas, however we report them in the on-line summary table when they were available.

We named "rhinal cortex" the brain area including the entorhinal and perirhinal cortices, with the aim to broadly make reference to anterior subhippocampal structures (Bartolomei et al., 2004, 2012). The entorhinal and perirhinal cortices border one another and it is sometimes difficult to know precisely which one was stimulated as stimulations are bipolar and likely partly spread to the neighbourhood. These structures belong to the visual ventral pathway and are involved in object, word and face recognition. The entorhinal cortex is also involved in the dorsal pathway and in space processing together with the parahippocampal cortex, which is located more posteriorly. Most reports don't provide these details and simply refer to stimulations of the medial temporal lobes or of the limbic system. However, as the different structures making the medial temporal lobes support different functions (e.g. Eichenbaum et al., 2012), it is important to be as precise as possible when these information are available to assess whether the reminiscence is related to the site of stimulation.

More specifically, literature data are often old and most reports were published before the current use of MRI. We therefore pooled these reports in a "medial temporal lobe" category. Some authors, however, specifically reported EBS in the parahippocampal gyrus (for instance Weingarten et al., 1977; Halgren et al., 1978; Gloor et al., 1982), which includes both the entorhinal, parahippocampal and part of the perirhinal cortex. As these authors explicitly mentioned this brain area, we maintained this localization.

We were much more precise with our own data. The post-implantation CT-scan was fused with the pre-implantation 3D T1 MRI. Approximate MNI coordinates of each bipolar contact leading to a reminiscence was then computed and a schematic overview of the contacts of interest was then generated using BrainNet Viewer (Xia et al., 2013).

2.5. Availability of the data

Reports of the patients, classifications of the reminiscences, main patients' clinical characteristics and EBS parameters are reported in a summary table available on the web for easier sorting and future research purpose: http://gpe.ups-tlse.fr/memstim.php. We also provide a permalink to the resource via figshare: https://figshare.com/s/

Table 1
All publications, available in the literature, relating memory phenomena with content, induced by EBS.

Author	Year	Study design	Patients (nb) in article	Population	Aim of EBS	Patients (nb) included in our review	EBS (nb) included in our review	EBS procedure	Brain areas explored	Reminiscences prevalence
Penfield	1958	Case-report	4 (also reported in the 1963 publication)	Epileptic patients	D	4	Cf. Penfield 1963	Awake surgery	Lateral and ventral temporal lobe	3% patients
Bickford	1958	Retrospective report	33	Epileptic patients	D	1	1	Depth macroelectrodes	Lateral and medial temporal lobe	
Baldwin	1960	Retrospective report	4	Epileptic patients	D	3	14	Awake surgery	Lateral and ventral temporal lobe	103 temporal explorations 2.9% patients
Sem-Jacobsen and Torkildsen	1960	Retrospective report	18	Schizophrenic and epileptic patients	T	1	1	Depth macroelectrodes	Lateral and medial temporal lobe	120 patients (6000 electrodes: 50% in frontal, 1/6 in temporal, 1/6 in occipital, 1/6 in parietal lobes), 0.83% patients
Van Buren	1961	Retrospective report	11	Epileptic patients	D	1	3	Depth macroelectrodes	Medial temporal lobe	
Penfield and Perot	1963	Retrospective report	40	Epileptic patients	D	25	96	Awake surgery	Lateral temporal lobe	520 temporal epilepsy patients (1132 total patients) 4.8% temporal epilepsy patients
Chapman et al.	1967	Retrospective report	25	Schizophrenic and epileptic patients, Chronic pain patients	D	1	7	Depth macroelectrodes	Medial temporal lobe	
Ferguson et al.	1969	Case-reports	5	Epileptic patients	D	1	1	Depth macroelectrodes	Medial temporal lobe	
Horowitz et al.	1968	Retrospective report	16	Epileptic patients	D	9	10	Depth macroelectrodes	Medial temporal lobe	1509 EBS – temporal epilepsy patients 0.59% EBS
Horowitz and Adams	1970	Retrospective report	16	Epileptic patients	D	-	-	Depth macroelectrodes	Medial temporal lobe	
Nashold and Wilson	1970	Case-reports	5	3 extrapyramidal sd., 1 thalamic pain sd., 1 chorea	T	1	1	Depth macroelectrodes	Thalamus	
Weingarten et al.	1977	Retrospective report	32	Epileptic patients	D	3 (+1 common with Halgren et al.'s study)	11	SEEG	Medial temporal lobe	
Halgren et al.	1978	Retrospective report	36	Epileptic patients	D	1	11	SEEG	Medial temporal lobe	3495 medial temporal EBS 267 "mental responses", 0.4% EBS
Gloor et al.	1982	Retrospective report	35	Epileptic patients	D	4	11	SEEG	Medial and lateral temporal lobe	
Morris et al.	1984	Case-report	1	Epileptic patients	D	1	4	Subdural grids	Lateral temporal lobe	
Brunet-Bourgin	1984	Retrospective report	16	Epileptic patients	D	4 (also reported in Bancaud et al.)	10 (also reported in Bancaud et al.)	SEEG	Medial and lateral temporal lobe Other cortical areas	
Gloor	1990	Review	1	Epileptic patients	D	1	4	SEEG	Medial and lateral temporal lobe	
Bancaud et al.	1994	Retrospective report	16	Epileptic patients	D	4	10	SEEG	Medial and lateral temporal lobe Other cortical areas	
Fried	1997	Review	1	Epileptic patients	D	1	4	Subdural grids	Lateral temporal lobe Other cortical areas	
Chauvel and Halgren	1997	Review	1	Epileptic patients	D	1	1	SEEG	Medial and lateral Temporal lobe Other cortical areas	
Blanke et al.	2000	Case-report	2	Epileptic patients	D	1	1	Subdural grids	Lateral temporal lobe Other cortical areas	
Moriarity et al.	2001	Case-report	1	Epileptic patients	D	4	8	Subdural grids	Lateral temporal lobe	

(continued on next page)

Table 1 *(continued)*

Author	Year	Study design	Patients (nb) in article	Population	Aim of EBS	Patients (nb) included in our review	EBS (nb) included in our review	EBS procedure	Brain areas explored	Reminiscences prevalence
									Other cortical areas	
Bartolomei et al.	2004	Retrospective report	24	Epileptic patients	D	4	4	SEEG	Lateral and medial temporal lobe Other cortical areas	101 SEEG (about 50% are temporal epilepsy) 3.96% patients
Barbeau et al.	2005	Case-report EEG analysis (linear correlation on AD)	1	Epileptic patients	D	1	2	SEEG	Lateral and medial temporal lobe Other cortical areas	
Vignal et al.	2007	Retrospective report	17	Epileptic patients	D	5	12	SEEG	Lateral and medial temporal lobe Other cortical areas	180 SEEG (mostly temporal epilepsy) 133 electrodes (83 temporal + 50 out of temporal lobe), 2.77% patients
Hamani et al.	2007	Case-report Cognitive tasks	1	Morbid obesity	T	1	6	Depth macroelectrodes	Hypothalamus Fornix	
Jacobs et al.	2012	Case-report Cognitive tasks EEG analysis (gamma power, phase amplitude coupling)	1	Epileptic patient	T	1	4	Subdural grids	Lateral and ventral temporal lobe Some contacts in medial temporal lobe Other cortical areas	
Mégevand et al.	2014	Case-report Cognitive tasks EEG analysis (gamma power, ERP), fMRI	1	Epileptic patient	D	1	7	SEEG	Lateral and medial temporal lobe Other cortical areas	

We specified the design of each study, the study population, the type of EBS (SEEG, depth macroelectrodes if used in a context which is not SEEG, awake surgery with surface electrodes, subdural grids for electrocorticography) and the number of memories reported matching the inclusion criteria of this review.
Nb: number; fMRI: functional MRI, sd.: syndrome; D: diagnostic purpose; T: therapeutic purpose, SEEG: stereo-electroencephalography (use of depth macroelectrodes for presurgical assessment of drug-refractory epilepsy).

923f93555a0ce51426e4. DOI: 10.6084/m9.figshare.4733026.

2.6. Statistics

Statistical analyses were performed with IBM SPSS Version 21.0 (Statistical Package for the Social Sciences) using binomial and χ^2 tests. Statistical analyses were carried out for all data (literature and our database) but also separately for our database. A p value < 0.05 was considered significant.

3. Results

3.1. Characteristics of the population

We collected 27 articles, 1 chapter and 1 thesis manuscript reporting reminiscences induced by EBS matching our inclusion criteria published between 1958 and 2015. 6 articles were single cases or case-reports, 3 were reviews, and they generally cited only one example of reminiscence (Table 1). Other publications consisted of retrospective studies from databases of epilepsy surgery centres. This set corresponded to a total of 73 patients, to which we added 18 patients from our own database. 5 had already been reported in previous publications (Bartolomei et al., 2004, 4 patients; Barbeau et al., 2005, 1 patient).

Patients were mostly epileptic patients undergoing presurgical assessment (88 patients). 40 had supposed unilateral temporal lobe epilepsy, 5 had bilateral temporal lobe epilepsy and 17 had temporal lobe epilepsy with unspecified localization. 5 patients had an epileptogenic zone outside the temporal lobe and for 3 it was not specified. 2 other patients suffered from other pathologies treated with depth macro-electrodes: an obese patient with bilateral macro-electrodes in the ventral hypothalamus (Hamani et al., 2008) and another suffering from chorea with an electrode in the right anterior thalamic nucleus (Nashold and Wilson, 1970). For one patient, the pathology was not clearly specified (Sem-Jacobsen and Torkildsen, 1960) but the study population to which he belonged consisted of schizophrenics and epileptic patients. In our database, all patients suffered from drug-refractory epilepsy and all excepted one suffered from temporal lobe epilepsy or epilepsy involving the temporal lobe. Overall, patients were relatively young (mean age 27.4 ± 9.8 years old, characteristics in Table 2).

Table 2
Patients' clinical characteristics and EBS localizations.

	Literature data	Our own database
Number of patients/number of EBS	73/228	18/45
Age of patients (yr.)	26.6 ± 9.1	28.3 ± 11.8
Gender (nb. patients) male/female/unspecified	28/26/19	6/12/–
Handedness (nb. patients) right/left/ambidextrous/unspecified	17/10/2/62	12/1/0/5
Type of epilepsy (number of patients)		
Unilateral temporal epilepsies	40	10
Bilateral temporal epilepsies	5	3
Temporal epilepsies (no precision)	17	4
Other area	5	1
Unspecified	3	–
Non epileptic patients	3	–
Dreamy-state during seizures/lacking data (nb patients (proportion of patients))	33 (45.2%)/8(10.9%)	8 (44%)/1(5.5%)
Hemisphere stimulated (nb. EBS) right/left/unspecified or lacking data	97/104/26	24/20/1
Technique of stimulation (nb. EBS)		
Surface electrodes/Subdural grids/SEEG/Depth therapeutic electrodes	109/21/90/7	–/–/45/–
Localizations of EBS inducing reminiscences		
Temporal cortex	214	42
-Superior temporal gyrus	85	3
-Medium temporal gyrus	30	0
-Inferior temporal gyrus	8	0
-Fusiform gyrus	10	3
-Temporal pole	7	1
-Amygdala	27	3
-Hippocampus	12	9
-Rhinal cortex	0	23
-Parahippocampal gyrus	16	0
-Deep/medial temporal lobe (unspecified)	19	0
Occipital cortex	3	0
Insula	0	3
Frontal cortex	2	0
Thalamus	1	0
Hypothalamus (fornix)	3	0
Unspecified	1	0

Nb.: number, yr.: year.

3.2. Dreamy-state during spontaneous seizures

45.2% patients from the literature and 44% in our database felt dreamy-state during their usual seizures (Table 1).

3.3. Stimulations

273 EBS inducing reminiscences were collected from the set of patients (228 from the literature, 45 from our database). 110 were performed with cortical electrodes during awake surgery, 21 with subdural grids, 135 with deep intra-cerebral electrodes implanted in the context of a SEEG and 7 depth electrodes implanted for therapeutic reasons (permanently or thermocoagulation). Characteristics of EBS are reported in Table 1.

Publications do not always specify the total number of patients in the source database or the total number of EBS. But in studies in which these data are available, the number of patients reporting reminiscence ranges from 0.8% to 4.8%, with from 0.3% to 0.59% EBS inducing reminiscences (Table 1).

3.4. Content of the reminiscences

Examples of reminiscences are presented in Figs. 1, 4 and 5. All reports and classifications of the reminiscences are reported in a table available on the web (see availability of the data in Section 2). Fig. 2 presents the proportion of induced reminiscences according to their contents.

In the literature data, only 14.0% ($n = 32$) of all induced responses were judged autobiographical episodic and only 4.3% met all criteria of strong episodicity (reports no. 3b, 12f, 20f, 27c, 32a, 32b, 32c, 47b in the table available on the web), including 3 EBS of the left amygdala reproducing the same memory in the same patient (Chapman et al., 1966). Reports were usually not sufficiently detailed to clarify whether these episodic reminiscences referred to frequently recalled memories, to know the perspective the subject had about the reminiscence (spectator or actor) or whether mental imagery was vivid or not. In our database, a similar rate of reminiscences was judged as episodic (13.3%, $n = 6$) and among them, only one met all criteria for high episodicity (report no. 62c in the table available on the web). There was no significant difference in the proportion of episodic memories ($\chi^2_1 = 0.15$, $p = 0.90$) in the literature data vs our database. Overall, only one patient reported what appeared to be a clearly detailed episodic memory for which he spontaneously specified that he had never thought about it (see example provided in Fig. 1, reports no. 32 in the table available on the web – the same reminiscence repeated 3 times, Chapman et al., 1966).

In contrast, the majority of reminiscences was classified as personal semantics in the literature (34.3%, $n = 78$) or in our database (35.5%, $n = 16$) with no difference between these proportions ($\chi^2_1 = 0.03$, $p = 0.86$). Most of the reminiscences classified in this category refer

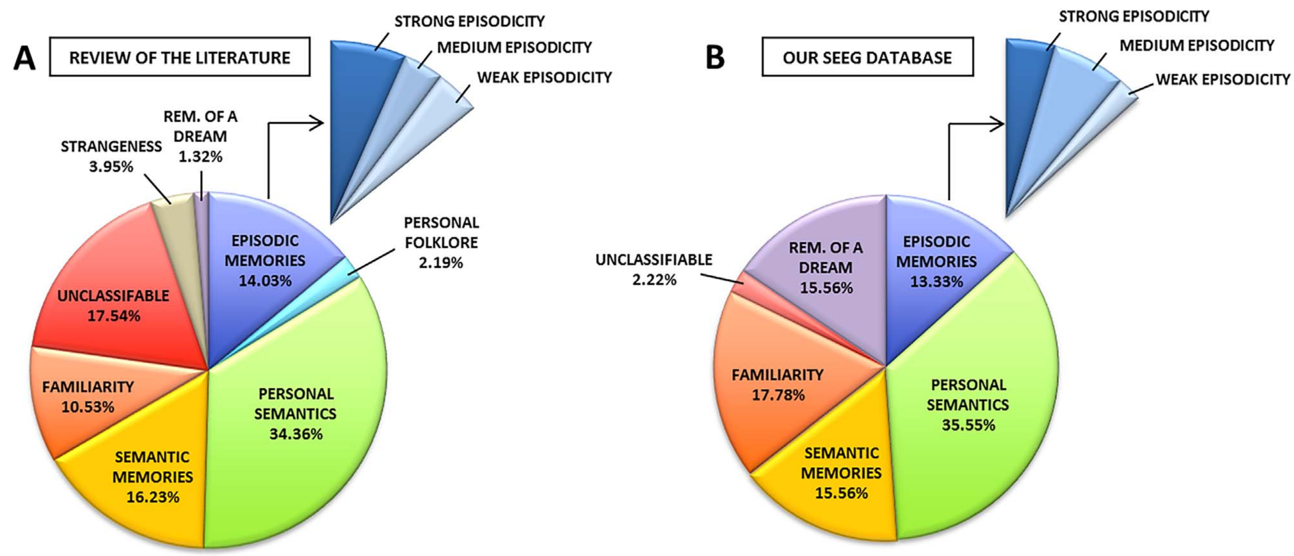

Fig. 2. Proportions of induced reminiscences according to their content in the literature and our own SEEG database.

to repeated, well-known or general personal situations such as being at home, with friends, etc. We also classified in this category occurrences of noteworthy projection in space (for example, "*You see I am in this room. However as soon as you press the button, I have the feeling that I am transferred over to this place…*" (Sem-Jacobsen and Torkildsen, 1960) or in time (for example, "*I had a young feeling*", "*I felt 6 years old again*", Baldwin, 1960). Although these reminiscences are clearly suggestive of mental space and time travel, they referred to events that were not unique. Some of these reminiscences were nice examples of the "mental diplopia" state occurring during some experiential phenomena that Huglings Jackson described in 1888. For example, one patient from our database wondered how it was possible that her body was there (Toulouse, France) and her mind elsewhere, the village of Pibrac in the South of France, where her grandmother was living (report no. 85a in the table available on the web).

A large proportion of memories was classified as pure semantic (16.3%, $n = 37$ in the literature, 15.5%, $n = 7$ in our database, $\chi_1^2 = 0.01$, $p = 0.91$). The content of semantic memories was predominantly auditory (26 in the literature, 3 in our database), mostly composed of famous songs (e.g., "Wish you were here" by the Pink Floyd, Moriarity et al., 2001), musical tracks (e.g., Star War theme, Fried, 1997) or advertising jingles (e.g., McDonald's jingle, in our database, report no. 62e in the table available on the web). In a lower proportion semantic memories were composed of visual content (9 in the literature, 3 in our database), mainly television programmes, movies (e.g. Gnomeo and Juliette, in our database, report no. 62h in the table available on the web) and for one EBS comic book characters (e.g. Philomene and Jacquot, Gloor et al., 1982). One from the literature was clearly audiovisual. We classified television programmes as visual semantic memory, if the report did not indicate whether the patient heard any sound.

10.6% ($n = 24$) reminiscences in the literature's database and 18% ($n = 8$) in our database were classified as familiarity ($\chi_1^2 = 1.9$, $p = 0.16$). In the literature, 17 were considered as auditory (mainly familiar voices or songs) and 4 as visual. We did not find memories classified as "familiarity" which were simultaneously visually and auditory familiar. 3 had olfactory content or were difficult to classify as visual or auditory. All familiarity reminiscences in our database were visual, mainly familiar rooms, places or objects.

Overall, the classification proportion was highly coherent between the literature and our own database excepted for the unclassifiable category (understandably much larger in the literature because reports were often oversimplified) and the dream category (patients reporting reminiscences of dreams they had, larger in our database).

3.5. "Age" of episodic memories

The delay between encoding and reminiscences for episodic memories was available for only 5 episodic memories in the literature. This delay varied from one day (example of patient 16 – Bancaud et al., 1994, report no. 55d in the table available on the web) to 14 years (a patient reported by Gloor in 1990 who was explored at 22 and recalled a picnic in Brewer Park in Ottawa when she was 8, report no. 57c in the table available on the web). We were able to estimate the delay between encoding and recall for 3 episodic memories in our database. It ranged from several months for one patient reliving a scene who took place the previous summer to several years for a patient hearing a reprimand from her father (reports no. 81a and 62b in the table available on the web).

3.6. Localizations of EBS inducing reminiscences

Localizations of EBS leading to reminiscences are detailed in Table 2 and Fig. 3. There was no statistical significant difference between the number of reminiscences obtained upon EBS of either the right (124 EBS) or left (121 EBS) hemisphere (binomial test, $p = 0.90$) considering all reminiscences (literature and our database).

A clear majority of EBS inducing memories resulted from EBS of the temporal lobes, whether in the literature (93.8%) or in our database (93.3%). However, in the literature reminiscences were more often induced by EBS of the lateral temporal lobes, largely due to Penfield's work. In contrast in our database, most reminiscences resulted from EBS of medial temporal structures (77.7% vs 8.9% on the lateral temporal cortex). More precisely, a clear majority of reminiscences in our database followed EBS to the rhinal cortex (51.1%, 11 following EBS to the entorhinal cortex, 12 following EBS to the perirhinal cortex) compared to 20% following stimulation to the hippocampus and only 6.6% to the lateral temporal cortex (Fig. 3A). Several regions (such as frontal cortex or medial parietal cortex) are frequently stimulated in each of our three centres. However, EBS in those regions never produced reminiscences.

We also analyzed more specifically, for one of our centres (Toulouse epilepsy unit), the number and localizations of all EBS applied (producing or not any experiential phenomenon) since the beginning of SEEG explorations (Fig. 3B). A similar rate of EBS was performed on the different structures of the medial temporal lobes: compared to the

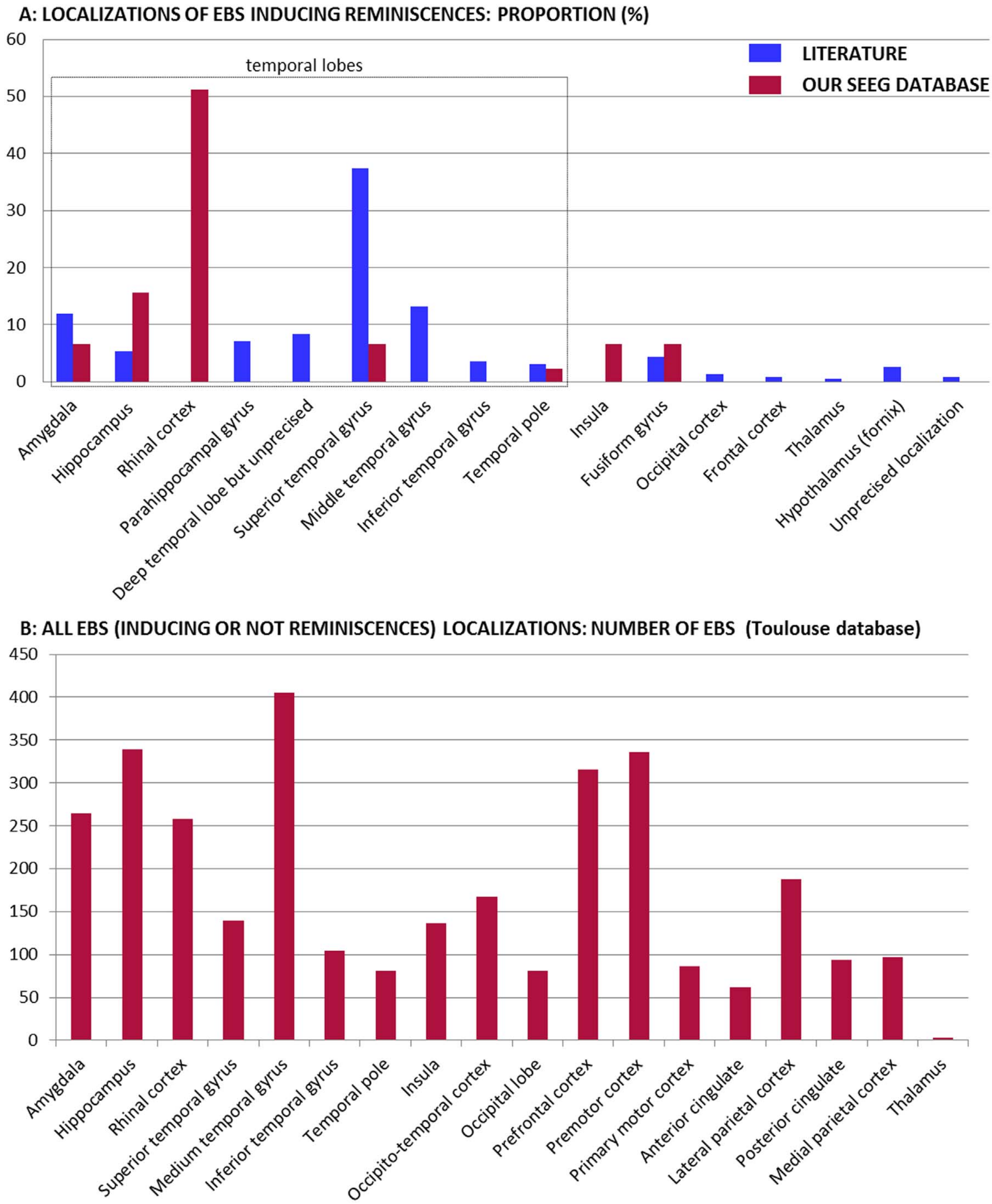

Fig. 3. Localizations of EBS inducing reminiscences. (A) Comparison of the localizations of EBS inducing reminiscences in the literature and in our database. (B) Total number of EBS (producing or not experiential phenomena) in the Toulouse epilepsy unit. This represents an amount of 3626 EBS, 2564 were 1 Hz single pulse shocks and 1062 were 50 Hz trains of 1 ms pulses.

amygdala or the hippocampus, the rhinal cortex (entorhinal and perirhinal cortices) was not more stimulated. Lateral temporal structures were also as frequently stimulated as medial temporal lobes.

3.7. Localizations of EBS and type of reminiscence

We next assessed whether some types of reminiscence were more likely triggered by EBS to specific brain localizations. We did not find any significant effect of hemispheric lateralization ($\chi^2_3 = 3.28$, $p = 0.34$) on the types of reminiscences considering all reminiscences (literature and our database): episodic (14 on right hemisphere, 17 on left hemisphere, 1 unspecified), personal semantics (48 on right hemisphere, 40 on left hemisphere, 6 unspecified) or semantic (21 on right, 18 on left hemisphere, 5 unspecified). One exception was noticed in our database for semantic memories, which were all obtained upon EBS of the right hemisphere ($n = 7$, due to one single subject).

Localization sites influenced the qualitative nature of memories (for details see Figs. 4 and 5). Taking together semantic memories and all data, auditory semantic memories were mostly obtained after EBS of the lateral temporal cortex while visual semantic memories were obtained after EBS of the medial temporal cortex (Fig. 4). Focusing on our own database for which we have more precision (Fig. 5), most

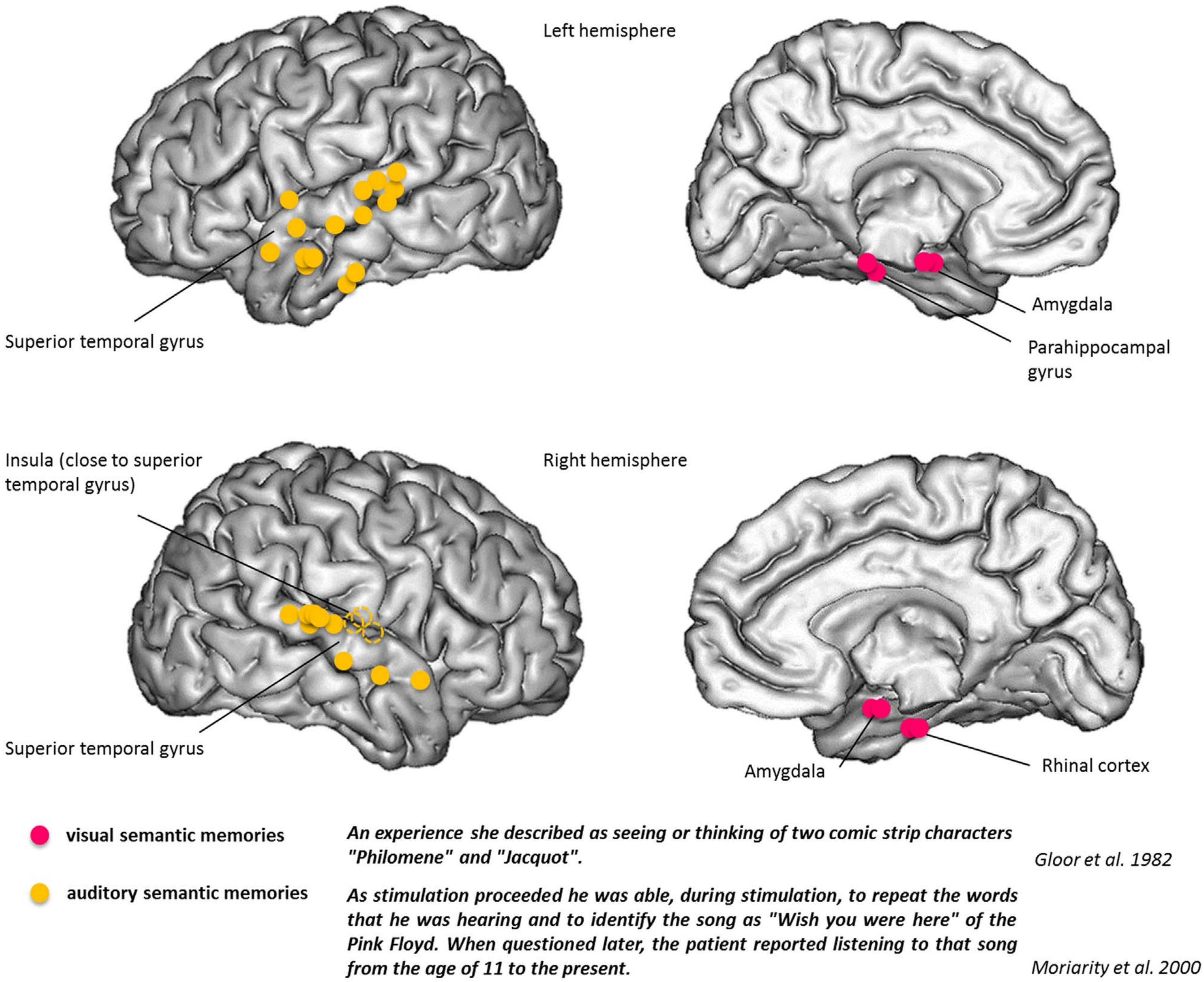

Fig. 4. Localizations of semantic memories according to their visual or auditory content, for all data. An example is provided for each category. Auditory semantic memories were mostly obtained after EBS of the lateral temporal cortex, most of them on the superior temporal gyrus. Visual semantic memories were obtained after EBS of the medial temporal lobes and the visual ventral stream.

episodic memories were obtained after EBS of medial temporal lobes. More specifically, episodic memories were induced only after EBS to the amygdala or hippocampus. Familiarity was induced after EBS to extra-hippocampal structures. Personal semantics were induced after amygdalo-hippocampal or rhinal EBS. EBS to the rhinal cortex, the clear majority in our database, produced mostly personal semantics and to a lesser extent familiarity, semantic or memories of dreams.

3.8. Reproducibility of the EBS

Different configurations were found (proportions provided in Fig. 6): EBS of the same localization could produce the same reminiscences (configuration A), EBS of the same localization could produce different reminiscences (configuration B) and EBS of different localizations could produce the same reminiscences with a similar content (configuration C). Finally, some reminiscences (configuration D) could not be classified since there was only one EBS inducing a reminiscence on one localization. Interestingly, a discrepancy between the literature and our database was found, since we did not find any configuration C in our database.

3.9. Stimulation parameters

Three main types of electrodes were used for EBS: intraoperative electrode during awake surgery, subdural grids or depth macro-electrodes (of different sizes, diameters and shapes). Most EBS were bipolar as only 10 monopolar EBS were identified in our review.

Intensity or amplitude of the electric current delivered varied considerably from one study to the other. Surveys with subdural grids used high intensity EBS between 4–8 mA (Jacobs et al., 2012), 1–15 mA (Morris et al., 1984) and 10–15 mA (Moriarity et al., 2001). Surveys using depth electrodes used mostly EBS between 0.8 and 3 mA, except for Halgren et al. (1978) and Horowitz et al. (1968), who used intensities which could reach up to 9.4 mA and 11 mA respectively. Bickford et al. (1958) obtained reminiscences for amplitudes higher than 5 V. Penfield used mostly EBS amplitudes in the range 1–5 V (but he used a Rahm stimulator, which intensity could be varied continuously from 0 to 20 V, Penfield and Jasper, 1954). In our database, average intensity of EBS was 1.2 (± 0.4) mA, 84.4% (n = 38) of EBS had intensity between 0.6 and 1.5 mA.

In the literature, a majority of high frequency EBS was used (40–100 Hz, 67.8%) compared to lower frequency EBS (1–20 Hz, 4.8%). A few used intermediate frequencies. Frequency and duration of pulses were not specified for about a quarter of EBS. Pulses were most of the time 2.5 ms long (41.8% of all EBS, mainly in Penfield's studies) but some were carried out with pulses 1 ms long. Pulse width can be very different: 0.3 ms for subdural grids EBS (Morris et al., 1984; Blanke et al., 2000; Moriarity et al., 2001) or 1 ms in SEEG studies. The

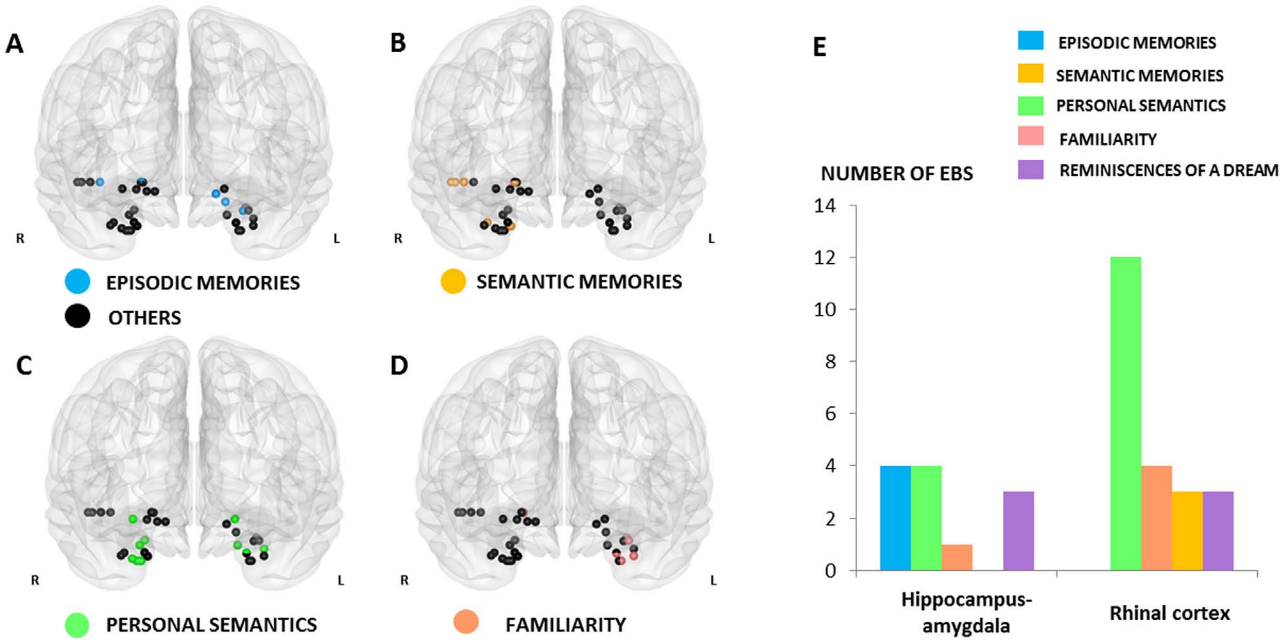

Fig. 5. Localizations of EBS inducing reminiscences in our SEEG database for the 4 main categories (episodic memories, semantic memories, personal semantics and familiarity). (A) Localization of the macrocontacts which stimulation induced reminiscences. (B) Proportion of the different kinds of memories collected in our database after EBS to medial temporal lobe structures. Episodic memories were only obtained after EBS of the amygdala or the hippocampus. EBS on rhinal cortex (which includes the entorhinal and perirhinal cortices) are more numerous and led to less contextualized memories. R: Right hemisphere. L: Left hemisphere.

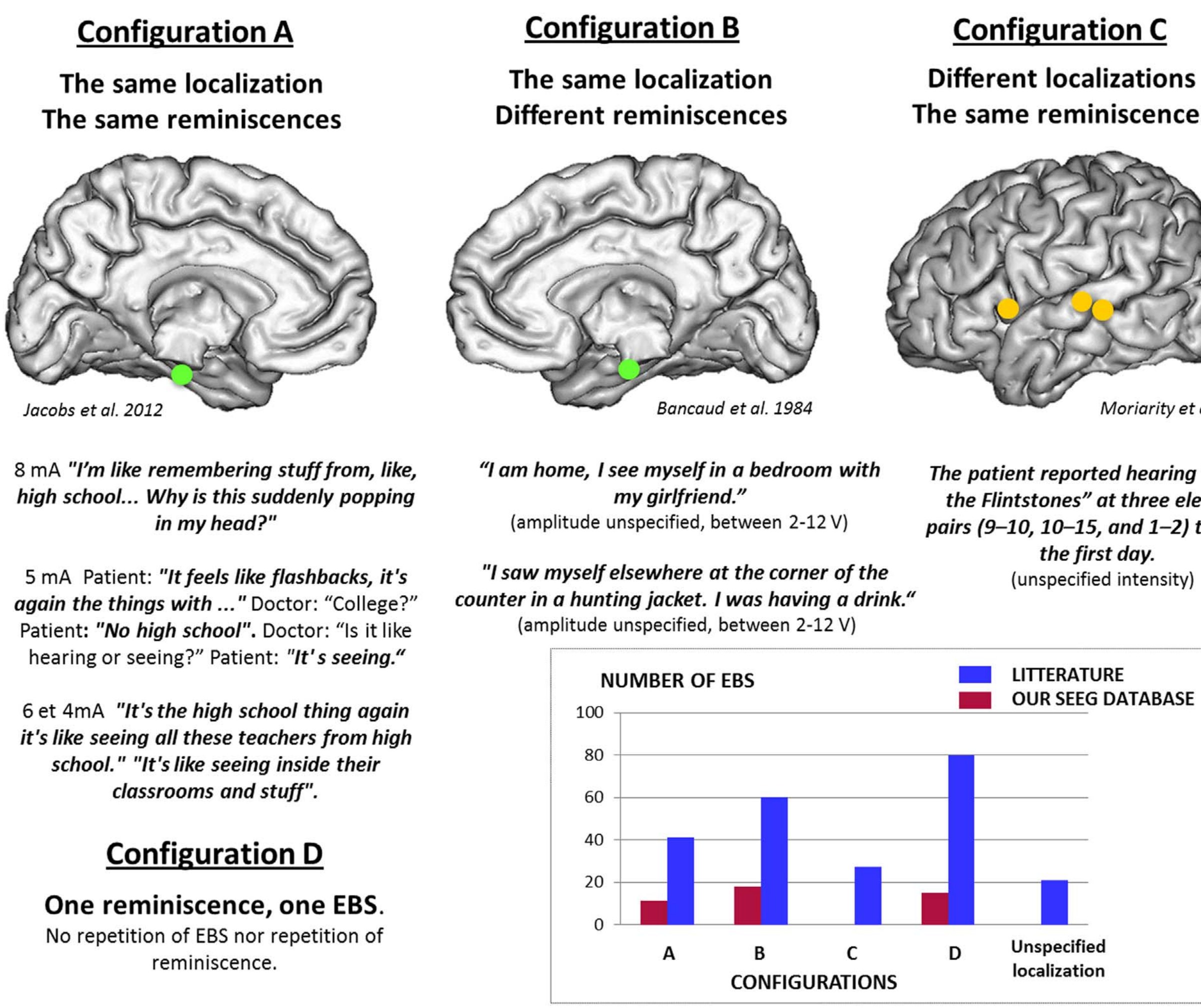

Fig. 6. Different configurations of localizations of EBS and variety of reminiscences. Graph represents the number of EBS for each configuration in the literature and in our database. Interestingly, configuration C has not been observed in our database.

majority of pulses were biphasic (95.6%). The duration of EBS is often not reported in the literature. Penfield in particular did not specify the duration of contact of the electrode with the cerebral cortex. But he probably used 1–4 s EBS (Szelényi et al., 2011). When this duration was specified (for 24.2% of all EBS), it was variable between 2 and 5 s. Some authors only specified a time range for the whole of their study, but do not report accurately the duration of EBS for each reminiscence (3–20 s for 3 EBS, Morris et al., 1984; 5–10 s for 2 EBS, Morris et al., 1984; 0.5–15 s for 8 EBS, Horowitz and Adams, 1970).

In our database, square wave pulses of alternating polarity were generated in 2–6 s trains: 55.5% of EBS lasted 5 s (n = 25) and 31.1% lasted 3 s (n = 14). All EBS were bipolar between two adjacent contacts. Interestingly, 43 EBS (95.5%) were trains of pulses (1 ms duration, 50 pulses/s), although 1 Hz single pulse are also commonly used during SEEG (Fig. 3).

3.10. Afterdischarge (AD)

Existence of an AD or not during reminiscences is poorly described in the literature, and when reported (38 EBS) descriptions are too heterogeneous for relevant analyses. Penfield specified in a footnote of his 1963 article (although he could use up to 8 electrodes on the surface of the brain for electrocorticography) that he did not observe any AD during experiential phenomena.

Focusing on our database, 23 EBS were followed by an AD and 21 were not (for one EEG data is lacking). For 9, the AD was limited to medial temporal lobes, for 13 the AD extended to all temporal lobe ± extra-temporal structures (cingulate, insula, fusiform gyrus or occipital cortex). Average duration of the AD was 24.1 s, but could vary from 2 s to 290 s. There was no influence of AD on the kinds of memories ($\chi^2_3 = 4.9$, $p = 0.17$), considering personal semantics (10 with AD, 6 without AD), episodic (3 with AD, 2 without AD, EEG data lacking for 1) and semantic memories (1 with AD, 2 without AD).

4. Discussion

Reviewing about 80 years of literature, we collected the largest series of reminiscences induced by EBS since Penfield seminal studies. Overall, this remains a rare phenomenon with from 0.3% to 0.59% EBS inducing reminiscences. We classified them according to modern conceptions of memory to shed light on the type of memories that can be induced by EBS.

4.1. Penfield's hypothesis and the meme of a permanent memory

Penfield thought that EBS were reactivating complete stored memory traces, like a “tape-recording” of our past experience. Any culture consists of *memes*, which are exchangeable cognitive units (ideas, behaviour or styles), which spread from an individual to another, enabling these memes to maintain throughout time (Dawkins, 1976). Penfield appeared to be relaying a secular meme: a conception of memory in which all experiences of an individual are stored in details but which, for various reasons, can no longer be accessed. This meme appears to have in its most extreme form three characteristics: infinite precision, infinite capacity and infinite permanence. Philosophers have long conveyed this meme: “*I believe indeed that all our past life is there, preserved even to the most infinitesimal details, and that we forget nothing*” (Bergson, 1920). A variant of this meme was also relayed by psychoanalysis. Freud concluded that the symptoms of hysteric patients make sense when they are connected to “forgotten” memories, sometimes coming back in dreams and symptoms (Freud, 1920; Wachtel, 1977).

Today, this meme is still deeply anchored. In the early 80s, 84% of psychologists believed that everything we learn is permanently stored in the mind, even though much of it cannot be retrieved (Loftus and Loftus, 1980). Multiple arguments are provided to support such a belief: personal experience with the occasional memory recovery (that had not been recalled for some time), hypnosis, psychoanalysis, repression, as well as the effect of pentothal and, of course, Penfield's work. 36% of the general public believe that our brain preserves permanent recordings of our past experiences (Alvarez and Brown, 2002). More recently, 63% of a large representative sample of the US population agreed that “*human memory works like a video camera, accurately recording the events we see and hear so that we can review and inspect them later.*” (Simons and Chabris, 2011).

What may be more surprising, recent neuroscientific literature provides clinical observations, which appear to lend some support to these ideas. About 30 subjects with Highly Superior Autobiographical Memory have been recently identified. These are apparently gifted with the ability to recall many details, even insignificant ones, of their lives (Parker et al., 2006; LePort et al., 2012; Ally et al., 2013; Patihis et al., 2013). Of course, only a limited part of the population is endowed with this ability. However, this suggests that the human brain has in some cases the ability for superior memory. Furthermore, cases of patients apparently experiencing involuntary resurgence of specific life periods have regularly been reported in retrograde, dissociative or transient global amnesia (Lucchelli et al., 1995; Kapur, 1996; Markowitsch et al., 1998; Laurent et al., 2012) or after removal of a tumour (Faber and Johnson, 2003). Though lacking a suitable review of the validity of these cases, they help maintain the idea that human memory may store much more of personal experiences than is usually believed.

4.2. Revising Penfield's hypothesis

EBS may induce in patients specific “brain states” (Posner, 2012) related to memory, difficult or impossible to reproduce with laboratory paradigms, such as sudden projection in space and time, mental diplopia or sudden synergetic ecphory (Tulving, 1982). As such, EBS is a fascinating method to study memory.

All types of reminiscences could be induced by EBS since were evoqued each of the major categories of declarative memory: semantic memory, episodic memory, personal semantics and familiarity. Induction of these types of reminiscences were found among different authors, but also to a similar rate between our review of the literature and our own database, suggesting that EBS can be at the origin of reproducible and non-random phenomena. EBS effects are not specific of one sensory modality as they can induce either visual (e.g., “Bugs Bunny cartoon”, Morris et al., 1984) or auditory memories (e.g., “War March of the Priests”, Penfield and Perot, 1963). When auditory memories are induced, it can be music but also verbal items and sentences (such as the voice of Richie Ashburn calling an unidentified game involving the Philadelphia Phillies, Moriarity et al., 2000). That EBS can induce so many distinct types of memories comes as a surprise. It means that reminiscences should be categorized and be studied as such rather than studying all reminiscences altogether.

However, all types of reminiscences are not evoked in the same proportion. Only a low number of EBS leads to purely episodic memories. A clear majority of EBS resulted in contrast in autobiographical semantic memories. Only 10 memories matched strong episodicity criteria, the only ones that could be considered as “movie tape-recordings” according to Penfield's proposal. These met the characteristics of autobiographical episodic memories: uniqueness, contextualized in space and time, sensory details (like odours), conceptual details such as names of present persons and an emotional content. A difficulty, however, is that it is unknown whether the patients had ever recalled these episodes and was re-experiencing them upon stimulation or whether they had been already recalled meaning that they could be partly semanticised. All in all only one patient (Chapman et al., 1966, see Fig. 1 and reports 32 in the table available on the web) reported a pure episodic memory in the sense that he gave the precision that he had not thought about it since it had occurred.

It is important to note that patients' reports are usually summed up in a few sentences, and most of the time in a few words in most studies. Furthermore, there is, most of the time, no suitable follow-up interview of the patient to assess precisely the type of memory that was induced. It is therefore possible that more episodic-like reminiscences were induced but that due to the simplification of the reports we judged them as semantic. This appears at present improbable since we do not find additional episodic reminiscences in our database, which contains more detailed reminiscences since they were videotaped. However, the possibility remains that the interview is not detailed enough to identify episodic memories because the medical staff is usually not aware that EBS can induce different types of memory.

Overall, these results do not support Penfield's idea of a highly stable memory that can be replayed randomly by EBS. Hence, results of EBS should not, at this stage, be taken as evidence for long-term episodic memories that can sometimes be retrieved. Coming back to the notion of the meme of a permanent memory, our results lend support to the idea that this meme is a neuromyth.

Overrepresentation of vaguely contextualized memories fits in contrast with the hypothesis of a progressive semantisation of episodic memories, with the gradual formation of generic episodes with loss of information and specificity in time (Cermak, 1984; Piolino et al., 2006). It fits perfectly with the assumption of a continuum or dynamic interactions between semantic and episodic systems, which proposes that personal semantic memory is derived from a process of abstraction of autobiographical episodic memories (Conway and Pleydell-Pearce, 2000; Conway, 2009; Renoult et al., 2012). Our results highlight the fragmentary, incomplete and vague composition of these reminiscences. This meets Gloor's position, who postulated that memories induced by EBS are fragmentary. According to him, the substrate of these memory phenomena is represented by matrices of connections between distributed neuronal populations. One of the properties of these matrices, or networks, is to tolerate a high degree of degradation with time: a matrix, having lost some of its connections or neuronal populations, would still be capable to support similar information with the same meaning and essence, but with a loss of details and specific properties (Gloor, 1990).

Interestingly however, EBS induced visual or auditory semantic memories but did not evoke factual, abstract and non-sensory, semantic memories such as “Venice is in the North of Italy” or “there are roughly 7 billion people on earth”. This reveals that, whilst episodic and semantic memory evocations and other states can be induced through stimulation, these memories all appear to have a sensory quality (in fact, this sensory quality has not been properly assessed most of the time and can only be inferred). This finding is important since it implies that these memories are activated through a specific mechanism that is sensitive to EBS. In contrast, it also implies that abstract non-sensory semantic memories do not have the same activation possibility. It further suggests that the taxonomy of semantic memory could take the difference between sensory and non-sensory knowledge into account.

4.3. Stimulation site and the content of the reminiscences

Halgren et al. (1978) and Chauvel (2014) postulated that the type of experience reported after EBS was related to patients' idiosynchratic factors, such as their personality and the “interpersonal situation” at the time of EBS. In contrast, Bartolomei et al. (2004) hypothesized that the anatomical situation of EBS was important for the content of reminiscences as in this study the qualitative nature of the reminiscences were different following EBS to the perirhinal cortex, the amygdala or the hippocampus.

A majority of EBS from the literature leading to reminiscences were located in the temporal lobes. Auditory memories were exclusively produced by lateral temporal EBS in or close to auditory cortex, and visual memories were exclusively produced by medial temporal EBS in the visual ventral stream.

In our database, for which we have precise coordinates of all EBS, contrary to the data from the literature, no pure semantic memory was obtained by EBS of the amygdala or the hippocampus. They were obtained only with EBS to the lateral temporal cortex, rhinal cortex and insula (close to superior temporal gyrus). In contrast, within the medial temporal lobes where we collected the large majority of our reminiscences, episodic memories were induced only by EBS to the amygdala and hippocampus. EBS of the rhinal cortex, in contrast, led mostly to personal semantics, familiarity and semantic memories, in other words to memories devoid of contextual information. These results fit well with the knowledge we have about the role of medial temporal lobe structures in memory. The hippocampus is thought to be critical for long-term detailed episodic memories (Vargha-Khadem et al., 1997), including after consolidation following the multiple trace theory (Moscovitch et al., 2005). The perirhinal region in contrast has been implicated in recognition memory and in context-free memory in general (Mishkin et al., 1997; Barbeau et al., 2011).

Our results support the neural substrate of declarative long-term memory currently known through lesion studies and functional imaging. This is critical since it clearly demonstrates that EBS does not activate memories randomly but following a relatively precise functional pattern. Hence, these reminiscences can be taken as mimics of true memories for further studies rather than simple objects of curiosity and open new perspectives to understand the architecture of memory.

4.4. Gateways to long-term memory network

Varela et al. (2001) proposed that the emergence of a unified cognitive moment (induced reminiscences could be considered as such) relies on the coordination of scattered mosaics of functionally specialized brain regions. Large-scale brain networks include different nodes and cores sharing large number of mutual connections (Varela et al., 2001; Mesulam, 2009; Bressler and Menon, 2010). Among these nodes, some are highly connected hubs, which make strong contributions to the global network (van den Heuvel and Sporns, 2013). We hypothesize that only long-range synchronization of functionally specialized brain regions can produce reminiscences after EBS, but that this synchronization is only made possible by the initial contribution of some of its functionally specialized hubs, which could be considered like gateways to that global network. These gateways could be different according to the qualitative nature of memories. This theory had already been proposed after rhinal cortex stimulation (Barbeau et al., 2005) and the induction of déjà-vu (Bartolomei et al., 2012).

Supporting this idea, no structure stimulated outside the supposed network of episodic autobiographical memory (Maguire, 2001; Svoboda et al., 2006; Cabeza and St Jacques, 2007) or the semantic network (Moscovitch et al., 2005; Binder and Desai, 2011) resulted in reminiscences. And within these networks, no stimulation of the autobiographical episodic memory network outside the MTL induced reminiscences. For example, the posterior cingulate region or the medial frontal lobes are part of the episodic memory network. Despite the fact that these regions are regularly stimulated in our epilepsy centres or in others (Ossandón et al., 2011; Dastjerdi et al., 2011; Foster and Parvizi, 2012; Foster et al., 2013), these stimulations do not seem to ever induce episodic reminiscence.

A critical result from our study is that we observed more reminiscences after rhinal cortex EBS than any other brain areas. This region thus seems to be one of these gateways, which stimulation is more prone to induce reminiscences. Bartolomei et al. (2004) have previously shown that not all structures of the temporal lobe contributed equally to the genesis of reminiscences; and that functional alteration of rhinal cortex physiology was an important contributor to these symptoms. Hence, déjà-vu was mostly associated with stimulation of the entorhinal cortex and reminiscences with the perirhinal cortex. Stimulation of the hippocampus or amygdala, however, accounted for much less déjà-vu. Supporting the idea of the rhinal cortex as a critical region to induce reminiscences, Fernández and Tendolkar (2006) hypothesized that the rhinal cortex could be a gatekeeper to the declarative memory system and act as an adaptable interface between the neocortex and the hippocampus. For example, an early perirhinal familiarity signal could trigger a source retrieval process for recollection in the hippocampus, which could in turn recruit perirhinal representations during episodic memory processes (Staresina et al., 2012). Furthermore, the rhinal cortex has prominent and convergent projections from sensory polymodal cortical areas and prominent interconnections with other MTL structures. The perirhinal cortex also tends to project back to a wider extent of the cortex than it receives input from, including some area that do not project to it at all (Lavenex et al., 2002; Suzuki and Naya, 2014). This striking asymmetrical reciprocity could contribute to its role as a gateway of information between neocortex and hippocampus.

4.5. Hemispheric lateralization

Taking together the literature and our database, a similar number of right and left EBS induced episodic memories, personal semantics and semantic memories. Based on these results, the gateways in memory network by EBS do not seem to be dependent of a hemispheric lateralization. Considering our database only, a predominant right laterality was found for semantic memories, however, all in the same patient. Reminiscences of dreams were mostly (6 out of 7 patients) obtained following right EBS. Several studies suggest a right hemispheric lateralization for successful dream recall (Marzano et al., 2011; Benedetti et al., 2015) or for dream material (Doricchi and Violani, 1992).

A few studies have shown a clear predominance of déjà-vu phenomena in right temporal lobe EBS (Weinand et al., 1994; Vignal et al., 2007). Another study demonstrated a predominance of déjà-vu in left-sided temporal lobe epilepsies (Guedj et al., 2010). Moreover, in Bartolomei et al.'s study (2004) a similar proportion of right and left temporal epilepsy was noticed, but reminiscences fall out of this framework as they have content. Recently, Heydrich et al. (2015) suggested a lateralizing value of spontaneous experiential hallucinations (during seizures). These authors related them to the left temporal lobe, while they did not identify any lateralizing value of déjà-vu. However, only 12 patients with experiential hallucinations were considered, without details about the content of their reminiscences. Data from the literature about a hemispheric lateralization during mnemonic recall remain patchy and inconsistent. Mental imagery could preferentially involve the right hemisphere (Conway, 2001). On the contrary, several recent studies have shown bilateral hemispheric activation during autobiographical recall (Cabeza and St Jacques, 2007; Steinvorth et al., 2006). In 2006, Lah et al. reported a deficit of autobiographical fluency in patients with temporal lobe epilepsy, regardless of the lateralization of epileptic focus, suggesting an involvement of both hemispheres in autobiographical memory. Involvement of both hemispheres appears therefore consistent, because memories are made of a variety of contents.

4.6. Role of the afterdischarges

The role of AD in reminiscences remains a subject of debate: necessary for reminiscences (Halgren et al., 1978) or having an inhibitory effect (Vignal et al., 2007). The results from our database demonstrate that AD is not necessary to induce reminiscences (nearly one half of reminiscences were devoid of any AD visible on EEG). The occurrence of an epileptiform discharge after EBS synchronizing different brain areas is thus not a required parameter for reminiscences. We do not believe this is a problem of sampling and partial covering of the brain by electrodes implantation. In Bartolomei et al.'s study (2012) an AD was not systematically associated with déjà-vu. This result supports prior results suggesting that EBS could evoke memories by recreating normal neural activation patterns (Jacobs et al., 2012), explaining apparent normal EEG activity. It reinforces the hypothesis that each location responsive to EBS may be an input gate in functional and physiological large-scale networks (David et al., 2010; Mandonnet et al., 2010) whether an AD occurred or not.

4.7. Optimal EBS parameters

EBS parameters do not appear to be directly predictive of the qualitative nature of memory. However, the technique used and stimulation parameters are probably crucial factors to induce reminiscences. Because of the heterogeneity of the literature or lacking data, it is difficult to determine the EBS parameters that would be optimal to increase the chance to induce reminiscences. For example, and intriguingly, awake surgery is a widespread technique (Duffau, 2010), but it remains unclear why no article in the field of awake surgery has reported reminiscences induced by EBS since Penfield. Interestingly, a larger number of reminiscences induced by depth macroelectrodes during SEEG was obtained compared to electrocorticography in the literature.

Nevertheless, some characteristics of the EBS leading to reminiscences emerge in our database such as a low intensity (around 1 mA seems sufficient), bipolar (which force the current to propagate in a single direction, Vincent et al., 2015), trains of pulses at 50 Hz and brief stimulations (between 3 and 5 s). This appears to match previous results which had suggested that trains were more prone to lead to clinical symptoms than 1 Hz shocks (Kahane et al., 1993; Kovac et al., 2016). Furthermore, we use biphasic pulses, which are generally recommended to limit local tissue damage (Piallat et al., 2009). Of course, prevalence of EBS leading to reminiscences, in our database, remains extremely low and not higher than in the literature, suggesting they may be other optimal parameters. Stimulus current waveform, pulses width, electrode properties (as shape), stimulator's output impedance, local temperature, electrode position with respect to the orientation of neurons and exact histologic nature of cerebral tissue under electrodes contacts may be other important factors (Vincent et al., 2016).

Finally, synchrony over multiple frequency bands, especially phase synchronization, appears to be fundamental for neural communication and memory formation (Fell and Axmacher, 2011). Weak EBS of the rhinal cortex and hippocampus synchronized to particular phases of EEG activity could modulate memory retrieval (Fell et al., 2013), but this has yet to be further analyzed.

5. Conclusion

EBS can induce different types of memories, including familiarity, semantic, autobiographical semantic and episodic memories. This variety may have been underappreciated and suggests that studies of the reminiscences induced by EBS should take this into account. Results from this study show that the type of reminiscence induced appear broadly consistent with current anatomo-functional models of declarative memory. However, the different types of reminiscence are not equally induced, the majority of them being autobiographical semantic, while autobiographical episodic memories appear to be relatively rare, in contrast to Penfield's tape-recorder hypothesis. The low prevalence of EBS inducing reminiscences suggests that a very particular combination of yet poorly understood factors is required. Future work should aim at improving our understanding of these factors.

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