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REVIEW ARTICLE

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Neural bases of the bodily self as revealed by electrical brain stimulation: A systematic review

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Abstract

An increasing amount of recent research has focused on the multisensory and neural bases of the bodily self. This pre-reflective form of self is considered as multifaceted, incorporating phenomenal components, such as self location, body ownership, first-person perspective, agency, and the perceptual body image. Direct electrical brain stimulation (EBS) during presurgical evaluation of epilepsy and brain tumor resection is a unique method to causally relate specific brain areas to the various phenomenal components of the bodily self. We conducted a systematic review of the literature describing altered phenomenal experience of the bodily self evoked by EBS. We included 42 articles and analyzed self reports from 221 patients. Three-dimensional density maps of EBS revealed that stimulation in the middle cingulum, inferior parietal lobule, supplementary motor area, posterior insula, hippocampal complex/amygdala, and precuneus most consistently altered one or several components of the bodily self. In addition, we found that only EBS in the parietal cortex induced disturbances of all five components of the bodily self considered in this review article. These findings inform current neuroscientific models of the bodily self.

KEYWORDS
self consciousness, bodily self, electrical brain stimulation, epilepsy, parietal cortex

1 | INTRODUCTION

The functionality, morphology, and state of our body have shown to play a major role in many cognitive, affective, and social processes and crucially define our self consciousness. Such bodily self is considered to result from a constant multisensory integration and fine-tuning of bottom-up signals (visual, somatosensory, interoceptive, and vestibular signals) and top-down expectancy (Blanke, 2012; Lenggenhager & Lopez, 2015; Park & Blanke, 2019; Tsakiris, 2010). Various phenomenal components of the bodily self have been described in the literature, of which five main components will be differentiated in the present review article: self location, body ownership, the first-person perspective, the sense of agency, and the perceptual body image (Table 1). Self location refers to the experience of occupying a volume of space, typically localized within one's own physical body boundaries (Blanke & Metzinger, 2009). Body ownership is the experience of owning a physical body (Tsakiris et al., 2007). The first-person perspective refers to "the experience from where I perceive the world" (Blanke, 2012). The first-person perspective is usually centered on the body and corresponds to an egocentric perspective/viewpoint (Vogeley & Fink, 2003). Agency is the sense of being in control of one's own actions (Jeannerod, 2006). The

TABLE 1 Five core phenomenal experiences underlying the bodily self

Bodily experiences	Definition	Exemplary experimental paradigm in healthy participants	Exemplary cases in neurology and psychiatry
Self location	A volume of space, normally localized within the physical boundaries of one's body	Rubber-hand illusion (Botvinick & Cohen, 1998), full-body illusion (Lenggenhager et al., 2007)	Out-of-body experience, heautoscopy
Body ownership	The feeling that our body and its parts belong to us	Rubber hand illusion, full-body illusion (Petkova et al., 2011), real hand illusion (Kannape et al., 2019)	Somatoparaphrenia, hemiasomatognosia, body integrity dysphoria
First-person perspective	The experience from where I perceive the world	Mental imagery perspective-taking tasks (Vogeley et al., 2004), full-body illusion (Ehrsson, 2007)	Heautoscopy, out-of-body experience
Agency	The feeling of being at the origin of our actions	Rubber hand illusion, full body illusion, arm agency illusions (Farrer et al., 2003), full-body agency illusions (Kannape & Blanke, 2013)	Schizophrenia, alien hand syndrome
Perceptual body image	Own body perceptions that can be verbalized: size, weight, body shape, etc.	Body shape distortions in the full-body illusion (Piryankova et al., 2014), rubber hand illusion (Linkenauger et al., 2013), Pinocchio illusion (Lackner, 1988)	Macro/microsomatognosia, supernumerary phantom limb, depersonalization, body integrity dysphoria, anorexia, Alice in Wonderland syndrome

Note: Definition of the bodily experiences, examples of experimental paradigms used to alter and study the respective component in healthy participants, and examples of neurological and psychiatric conditions leading to alterations in these bodily experiences.

perceptual body image refers to the perceptual experience of one's own body, such as the perceived size and shape of one's own body (Gallagher, 2005).

An increasing amount of research has investigated the neural mechanisms underlying the bodily self and its different phenomenal aspects (Blanke, 2012; Blanke et al., 2015). Such research includes investigations in neurological and psychiatric patients with specific alterations in the bodily self, as well as functional and structural neuroimaging in healthy participants (reviewed in Berlucchi & Aglioti, 2010; Blanke, 2012; Park & Blanke, 2019; see Table 1 for a summary). Results point to a widely distributed cerebral network, encompassing particularly the temporo-parietal, premotor, posterior parietal, and extrastriate cortices, underlying the stable sense of a bodily self. In neurological patients, for example, it has been proposed that lesion to the posterior insula and parietal operculum can lead to a sense of loss of ownership for one's own hand or arm (e.g., somatoparaphrenia; Gandola et al., 2012). Disembodied self location, on the other hand, has been linked to lesion or seizure involving the temporo-parietal junction (Blanke et al., 2004), or the posterior insula (Heydrich & Blanke, 2013). Lesions to the posterior parietal and the prefrontal cortex have been shown to distort own-body representations, for example the sense that the body is split in two (Heydrich et al., 2010), or the experience of having an additional limb (Hari et al., 1998).

Most studies in healthy participants combined functional neuroimaging with experimental manipulations of the bodily self through synchronous, but mismatching, multisensory stimulation, altering specific components of the bodily self (reviewed in Blanke, 2012; Dieguez & Lopez, 2017). Illusory ownership of a fake hand (Botvinick & Cohen, 1998; Ehrsson et al., 2004), self identification with a virtual body and altered self location (Ionta et al., 2011; Lenggenhager et al., 2007; Nakul, Orlando-Dessaints, et al., 2020), altered sense of agency (Farrer et al., 2003), or distortions in the structure and size of the felt body (de Vignemont et al., 2005; Ehrsson, Kito, Sadato, Passingham & Naito, 2005) have been induced using such techniques in healthy participants (see Table 1 for a summary). Functional neuroimaging studies revealed an involvement of the premotor cortex, primary somatosensory cortex, extrastriate body area, insula, the putamen, and intraparietal sulcus in illusory self identification with a rubber hand or with a virtual body (Chancel et al., 2022; Ehrsson et al., 2004; Ehrsson, Holmes, & Passingham, 2005; Gentile et al., 2015; Guterstam, Björnsdotter, Bergouignan, et al., 2015; Ionta et al., 2011; Limanowski et al., 2014; Limanowski & Blankenburg, 2015; Petkova et al., 2011). Other studies found that the temporo-parietal junction, primary somatosensory cortex, premotor cortex, cingulate cortex, and the posterior superior temporal gyrus are related to illusory changes in the self location (Guterstam, Björnsdotter, Gentile, & Ehrsson, 2015; Ionta et al., 2011). The sense of agency on the other hand, has been related to the insula and inferior parietal cortex (Chambon et al., 2013; Farrer et al., 2003; Farrer, Frey, et al., 2008, Farrer, Bouchereau, et al., 2008; Farrer & Frith, 2002), whereas experimentally-induced changes in the perceptual body image (perceived shape and size or posture of the body) have been related to the postcentral sulcus, intraparietal sulcus, insula, and inferior parietal lobule (Ehrsson et al., 2005; Kavounoudias et al., 2008; Naito et al., 2017). While the neural networks revealed by these neuroimaging studies are typically based on a correlative approach, a more causal link has been suggested by non-invasive transcranial direct current stimulation (de Boer et al., 2020; Lira et al., 2018; van Elk et al., 2017), or even more directly by invasive, intracranial electrical brain stimulation (EBS) (Arzy et al., 2006; Blanke et al., 2002; Bos et al., 2016; Desmurget et al., 2009; Schaller et al., 2021).

EBS is typically used during presurgical evaluation of focal intractable epilepsy to define as accurately as possible the seizure onset zone and perform functional brain mapping (Trebuchon et al., 2020; Trébuchon & Chauvel, 2016), or in awake patients during brain tumor resection (Duffau, 2015). During EBS an electrical current of several mA is directly delivered to the brain through intracerebrally implanted electrodes (stereoelectroencephalography, SEEG) or through subdural grids and strips of electrodes placed at the surface of the cerebral cortex (electrocorticography, ECoG; Grande et al., 2020; Isnard et al., 2018; Lesser et al., 2010). SEEG electrodes are implanted either unilaterally or bilaterally, and each electrode has multiple contacts to record activity from several brain regions and/or to apply EBS (Isnard et al., 2018). The electrodes allow to stimulate and record activity in deep brain regions such as the insular, cingulate, and orbitofrontal cortex, or the amygdala. During EBS, clinicians record the patients' phenomenal experience (including perceived disturbances of the bodily self), behavioral responses (e.g., muscle contraction), and electroencephalographic activity (i.e., SEEG and ECoG). During brain tumor resection, electrical current is applied through electrodes directly on the cortex or on subcortical fibers. Under local anesthesia, patients perform various cognitive and motor tasks to identify the resection boundaries, while largely preserving functionally significant areas and pathways. Since the pioneering work from neurosurgeon Wilder Penfield (e.g., Penfield & Rasmussen, 1950), clinicians have increasingly used EBS, providing functional maps (Duffau et al., 2003; Salanova et al., 1995a, 1995b) and connectivity maps (Duffau, 2015) of the human cerebral cortex. Given these advantages, EBS during awake surgery might be a particularly interesting perspective to assess the sense of self (Schaller et al., 2021).

EBS offers some advantages for mapping brain functions (reviewed in Mercier et al., 2022). EBS enables three-dimensional recordings of epileptic discharges, changes in cortical excitability and in brain connectivity evoked by EBS with a high temporal resolution (Isnard et al., 2018). Furthermore, EBS is usually considered to provide *causal* rather than just *correlative* evidence for a link between neural structures and phenomenal experience, such as somatosensory, visual, auditory, vestibular, emotional, and autonomic perceptions (reviewed in Selimbeyoglu & Parvizi, 2010), or more complex sensations, like reminiscence of past experience, déjà-vu, dreamy state and memory illusions (Curot et al., 2017; Penfield, 1955).

While in his seminal investigations Penfield did not investigate specifically disturbances of the bodily self, he reviewed 190 cases of surgery for focal epilepsy in awake patients under local anesthesia carried out during a nine-year period and described "psychical responses," during which the patient is conscious and usually capable of introspection (Penfield, 1947, 1955). Psychical responses include experiential responses, defined as psychical hallucinations of past experience (e.g., flash back, dream), and interpretive responses, defined as psychical illusion about the present experience (e.g., *déjà-vu*, fear, disembodiment). Interestingly, both experiential and interpretive responses encompass distortions of the bodily self as defined in the present study, as they refer to illusions about the experienced state of the body (posture, weight, size, shape) and self (location, connection to the body). Penfield (1955) identified 10 relevant cases and concluded that psychical responses "result from the stimulation principally of the lateral and superior surfaces of either temporal lobe. The superior surface is that portion of the temporal lobe that is hidden within the Sylvian fissure and in the circular sulcus that surrounds the insula beneath it" (see areas highlighted in pink in Figure 1). In line with earlier work by Penfield, more recent EBS studies confirmed the role of the superior temporal cortex and temporo-parietal junction in self location and embodiment. For example, an especially spectacular phenomenon reported during EBS in the temporo-parietal junction is an out-of-body experience (OBE), during which the self is perceived as located outside of the physical body, resulting in alterations of several components of the bodily self, especially self location and first-person perspective (Blanke et al., 2002; Bos et al., 2016; De Ridder et al., 2007; reviewed in Nakul & Lopez, 2017). However, full-blown OBEs seem very rare in the context of EBS, and investigations of the neural bases of other components of the bodily self have been poorly described in earlier EBS studies, have attracted less attention, and have not been systematically reviewed.

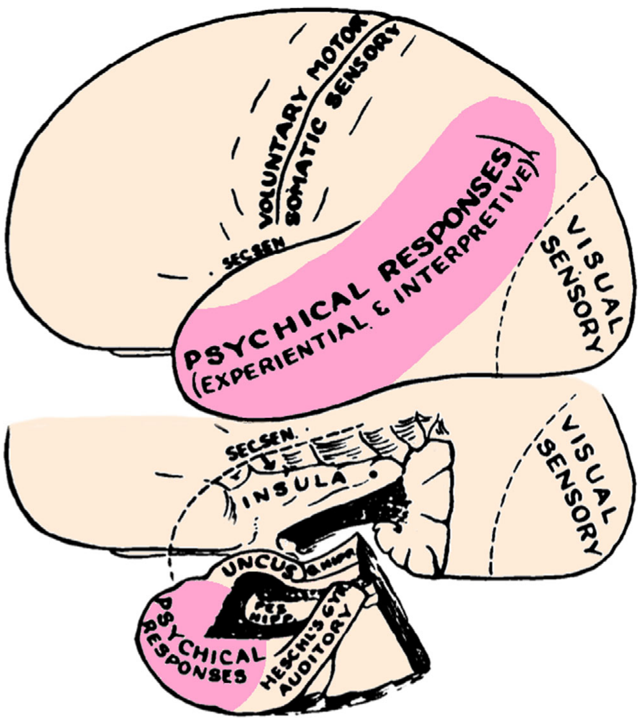

FIGURE 1 Brain areas responsible for psychical responses identified by Penfield. In this anatomical description of the left cerebral hemisphere, Penfield has represented the temporal lobe cut and turned down in order to show the superior and mesial surface of the temporal lobe. Modified from Penfield (1955) "The Twenty-Ninth Maudsley Lecture: The Role of the Temporal Cortex in Certain Psychical Phenomena" with the permission from Cambridge University Press

Here, we provide a systematic review of the literature on the neural bases of the bodily self as revealed by EBS in neurological patients, following the preferred reporting items for systematic reviews and meta-analyses (PRISMA) guidelines (Page et al., 2021). We focus on disturbances in the five core phenomenal components of the bodily self described above—self location, body ownership, first-person perspective, agency and perceptual body image—and aim at identifying the underlying brain areas.

2 | MATERIALS AND METHODS

2.1 | Search strategy

This systematic literature review is reported in accordance with the PRISMA guidelines (Page et al., 2021; Tables S1 and S2). We searched articles published in English in PubMed up to March 23, 2022 without date restriction using keywords in all available fields (title, abstract, keywords). The full search strategy is detailed in Table S3. Keywords searched included several synonyms for the stimulation and recording methods: "SEEG," "stereo-EEG," "electrical cortical stimulation," "stereoencephalography," "electrical stimulation," "direct electrical stimulation," "direct stimulation," "stereo EEG," "intracranial electroencephalography," "stereo-electro-encephalography," "epilepsy," "awake," "craniotomy," "glioma." For the bodily self disturbances, keywords included various disorders of self and own body perception: "embodiment," "disembodiment," "doppelgänger," "feeling of a presence," "heautoscopy," "depersonalisation," "self location," "derealisation," "autoscopy," "bodily self," "out of body experience," "self consciousness," "out-of-body illusion," "body schema," "body image," "ownership," "agency," "vestibular," "posture," "proprioception."

2.2 | Study selection

We included only primary articles (original research articles, case reports, prospective and retrospective case series) but not review articles. Inclusion criteria were studies reporting patients who received EBS with implanted depth electrodes (SEEG), subdural grids and strips of electrodes (EcOG), or during awake brain surgery. Studies were included in our review only if they reported a disturbance of one or several phenomenal components of the bodily self that could be related to the direct effect of EBS. Inclusion criteria were defined as follows:

- *Disturbances of self location* include (1) *OBE*, that is, full-blown illusory perception of being disembodied; (2) *vestibular sensations*, that is, illusory self motion without disembodiment, including illusory translations of the entire body, sensation of falling, floating in the air, rocking, and being tilted; and (3) *proprioceptive sensations*, that is, illusory motion of a body part without disembodiment, such as illusory elevation of an arm.
- *Disturbances of body ownership* correspond to the inability to recognize a body part as one's own, or to sensation of disownership, estrangement or disembodiment of a body part or of the whole body.
- *Disturbances of first-person perspective* correspond to a change in the multisensory perspective, or viewpoint on the world, which may be allocentric instead of egocentric, distanced and elevated.
- *Disturbances of agency* correspond to the sensations of not being at the origin of the bodily actions, of not controlling and generating them, or when one feels the urge to execute actions, or when one experiences a resistance to planned actions.
- *Disturbances of the perceptual body image* correspond to own body perceptions that can be verbalized, including sensations of lightness or heaviness of a body part (without illusory or real motion of this body part), sensations that a body part is absent or lost, or a perceived body size distortion.
- *Other disturbances of the bodily self*, which did not clearly fit into the above categories were also considered. This category encompasses the sense of depersonalization, that is, a dissociative experience combining sensations of being detached from the body, of losing control over the body, actions, or thoughts (Simeon & Abugel, 2006). This category also includes the feeling of a presence, the vivid sensation that somebody is present nearby (Fénelon et al., 2011), as it has been proposed that a sensed presence is a sensorimotor double of the patient's own body (Arzy et al., 2006; Bernasconi et al., 2021).

2.3 | Data extraction

The characteristics of the publications were extracted (authors, year of publication, region in the world), as well as information about the clinical population (sample size, number of patients reported, disease), methods of the applied EBS (brain areas explored, stimulation parameters). For each EBS-evoked bodily self disturbance, we identified the category of bodily self disturbance and the location of the stimulation (cerebral hemisphere, lobe, brain area, and coordinates of electrode location). Only four publications reported coordinates in a standardized atlas (14 cases from 2 studies in Talairach coordinates; 14 cases from 2 studies in MNI coordinates). Authors from recent studies were contacted by email to require coordinates of activation if they were not reported in their original publication. Six authors provided additional electrode coordinates (71 cases from 6 studies in MNI coordinates). All data are summarized in Table S4.

2.4 | Analysis of the neuroanatomical localization of EBS

The localizations of the EBS evoking different types of bodily self disturbances were summarized on a 3D rendering of the right cerebral hemisphere on the MNI brain template from FreeSurfer (Fischl et al., 2004). We used 3Dviewer tool for the visual

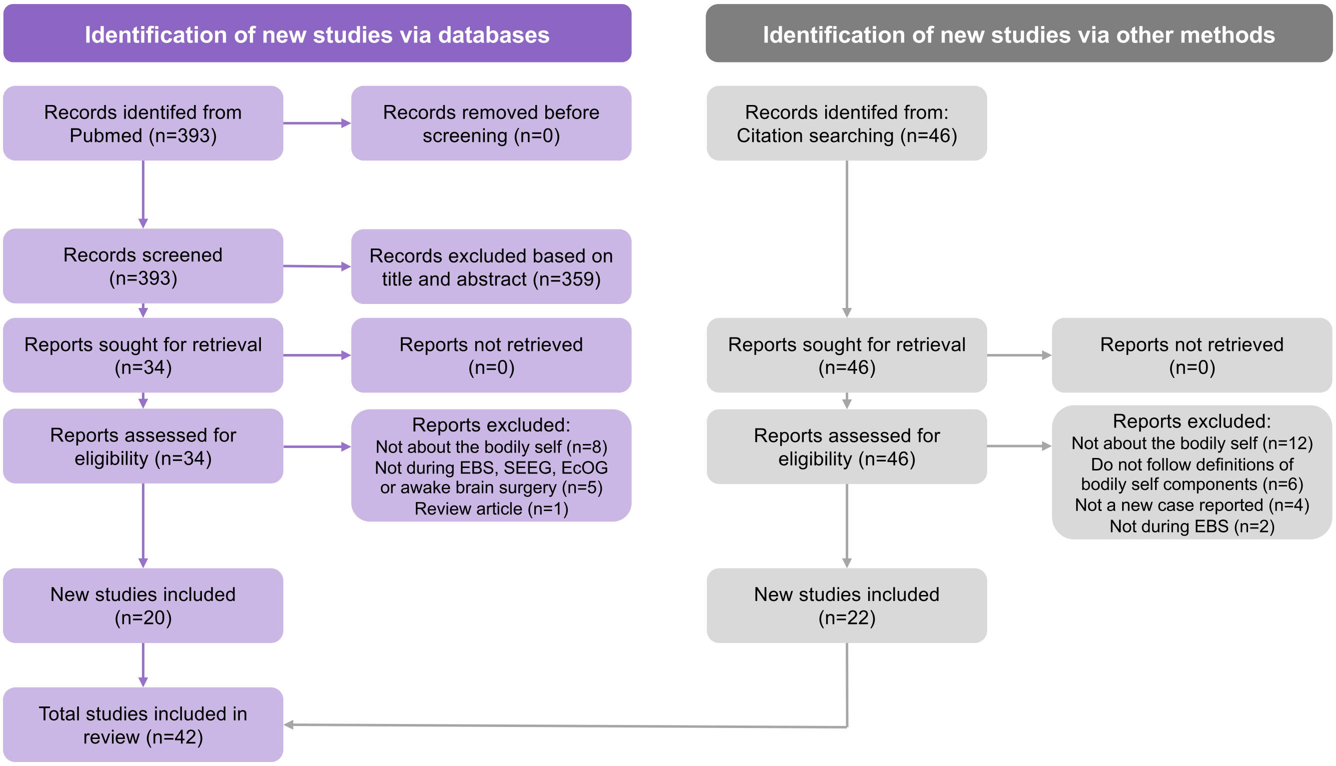

FIGURE 2 Flow diagram for the preferred reporting items for systematic reviews and meta-analyses (PRISMA)

representation (Medina Villalon et al., 2018) available at https://meg.univ-amu.fr/wiki/3DViewer. We converted the coordinates from Talairach to MNI coordinates when necessary, using custom-based scripts in MATLAB 2020 (The MathWorks, Inc., USA). When possible, we reported the other EBS localizations with the best approximation possible on the MNI template, considering the published MRI or implantation schema, and considering the original description of EBS localizations in terms of gyrus, sulcus, and Brodmann area. Sites of EBS were plotted on a single right cerebral hemisphere surface, by projecting coordinates on its closest mesial or lateral parts. Each point was projected on the surface, except for the amygdala, hippocampus, and insula, for which we created a mesh on which points were projected.

2.5 | Statistical analysis

To identify the core areas underpinning the bodily self, we calculated 3D spatial density of electrode contacts evoking disturbances of the bodily self using custom-based scripts in MATLAB 2020 and projected the spatial density maps on a 3D rendering of the right cerebral hemisphere on the MNI template. We also analyzed the proportion of evoked responses per brain region, as well as the hemispheric dominance of EBS for each component of the bodily self, using the Fisher's Exact test and *z*-tests (SPSS 26, IBM, USA).

3 | RESULTS

3.1 | Literature review

We identified 393 articles in the database, of which 20 were eligible to be included in the systematic review. We also searched for relevant studies in the references provided in each of these publications and included 22 other articles on the effects of EBS on the bodily self. In total, 42 articles were included in the systematic review. Figure 2 presents the PRISMA flow diagram of the study selection.

3.2 | Characteristics of the studies

The 42 articles included in the systematic review were published between 1937 and 2022. More than half of the studies were from Europe (52.3%; $n = 22$), 33.3% ($n = 14$) were conducted in North America, and 14.3% ($n = 6$) in Asia. Twenty-three articles were retrospective studies (sample size: 33–1132 patients; mean ± *SD*: 196 ± 231 patients), 7 articles were case series (13–47 patients; 21 ± 16 patients), and 12 studies were single case reports. Table 2 summarizes the study characteristics, as well as clinical population, stimulation parameters, location of electrodes, and phenomenal experience.

TABLE 2 Summary of the publications included in the systematic review reporting bodily self disturbances evoked by electrical brain stimulation

Publication	Region	Clinical population and EBS procedure	Type of study: Sample size	Number of patients included in the review	Prevalence of bodily self disturbances (%)	Category of bodily self disturbance reported	Brain areas explored by EBS
Penfield and Boldrey (1937)	N. America	Epilepsy (ABS)	RS: 163	3	1.8	SL (vest), Ag.	Frontal, parietal, temporal
Penfield (1947)	N. America	Epilepsy (ABS)	RS: 190	1	0.5	SL (vest), Other	Temporal
Penfield (1955)	N. America	Epilepsy (ABS)	RS: 190	1	0.5	SL (OBE)	Temporal
Penfield (1957)	N. America	Brain tumor and epilepsy (ABS)	RS: 108	1	0.9	SL (vest)	Temporal, central
Mullan and Penfield (1959)	N. America	Epilepsy (ABS)	RS: 217	4	1.8	Other	Temporal
Penfield and Perot (1963)	N. America	Epilepsy (ABS)	RS: 1132	1	0.1	SL (vest)	Whole brain
Halgren et al. (1978)	N. America	Epilepsy (ABS)	CS: 36	15	–	SL (prop), Ag., SL (vest)	Temporal
Fried et al. (1991)	N. America	Epilepsy (subdural grid)	CS: 13	7	–	Ag., SL (prop)	Fronto-parietal
Richer et al. (1993)	N. America	Epilepsy (SEEG)	RS: 40	3	7.5	SL (prop), SL (vest)	Rolandic, parietal
Salanova et al. (1995a)	N. America	Epilepsy (ABS)	RS: 82	6	7.3	SL (vest), BI, Other	Parietal
Salanova et al. (1995b)	N. America	Epilepsy and brain tumor (ABS, subdural grid)	RS: 34	1	2.9	BI	Parietal
Blanke et al. (2000)	Europe	Epilepsy (subdural grid)	CR: 1	1	–	SL (vest)	Frontal, temporal, parietal
Kremer et al. (2001)	Europe	Epilepsy (SEEG)	CR: 1	1	–	Ag.	Cingulate
Blanke et al. (2002)	Europe	Epilepsy (subdural grid)	CR: 1	1	–	SL (vest), BI, 1PP, SL (OBE)	Frontal, temporal, parietal
Ostrowsky et al. (2002)	Europe	Epilepsy (SEEG)	CS: 30	2	–	BI	Temporal
Kahane et al. (2003)	Europe	Epilepsy (SEEG)	RS: 260	13	5	SL (vest)	Whole brain
Wiest et al. (2004)	Europe	Epilepsy (subdural grid)	CR: 1	1	–	SL (vest)	Parietal
So and Schaüble (2004)	N. America	Epilepsy (subdural grid)	CR: 1	1	–	Own.	Fronto-central
Isnard et al. (2004)	Europe	Epilepsy (SEEG)	RS: 50	12	24	SL (vest), Other	Temporal, insular
Arzy et al. (2006)	Europe	Epilepsy (subdural grid)	CR: 1	1	–	Other	Frontal, temporal, parietal
Vignal et al. (2007)	Europe	Epilepsy (SEEG)	RS: 180	3	1.7	Other, SL (OBE)	Temporal
De Ridder et al. (2007)	Europe	Tinnitus (paddle electrode)	CR: 1	1	–	SL (OBE)	Temporo-parietal
Mulak et al. (2008)	Europe	Epilepsy (SEEG)	RS: 339	5	1.5	Other	Whole brain
Desmurget et al. (2009)	Europe	Brain tumor (ABS)	CS: 7	3	–	Ag., SL (prop)	Parietal, premotor

TABLE 2 (Continued)

Publication	Region	Clinical population and EBS procedure	Type of study: Sample size	Number of patients included in the review	Prevalence of bodily self disturbances (%)	Category of bodily self disturbance reported	Brain areas explored by EBS
Mazzola et al. (2014)	Europe	Epilepsy (SEEG)	RS: 219	13	5.9	SL (vest)	Insula
Blanke et al. (2014)	Europe	Epilepsy, brain tumor (subdural grid)	CS: 5	3	–	Other	Insular, temporal, fronto-parietal
Balestrini et al. (2015)	Europe	Epilepsy (SEEG)	RS: 274	16	5.8	BI, Other, SL (vest)	Parietal
Bos et al. (2016)	Europe	Brain tumor (ABS)	CR: 1	1	–	SL (prop), SL (OBE), 1PP	Parietal, temporal, Sylvian fissure
Caruana et al. (2018)	Europe	Epilepsy (SEEG)	RS: 329	25	7.6	SL (vest)	Cingulate
Yu, Liu, et al. (2018)	Asia	Epilepsy (SEEG)	CR: 1	1	–	SL (OBE), 1PP	Frontal, temporal, parietal
Yu, Yu, et al. (2018)	Asia	Epilepsy (SEEG)	RS: 43	3	7	BI, SL (vest)	Operculo-insular
Popa et al. (2019)	Europe	Epilepsy (SEEG)	RS: 110	11	10	BI, SL (vest), SL (prop), 1PP	Cingulate
Mandonnet et al. (2020)	Europe	Brain tumor (ABS)	CR: 1	1	–	BI	Superior parietal
Fornia et al. (2020)	Europe	Brain tumor (ABS)	CS: 12	8	–	Ag.	Premotor and S1
Andelman-Gur et al. (2020)	Asia	Epilepsy (subdural grid)	RS: 62	23*	–	Ag., SL (vest), SL (OBE)	Frontal, parietal, occipital, temporal
Oane et al. (2020)	Europe	Epilepsy (SEEG)	CS: 47	6	–	SL (vest)	Whole brain
Fox et al. (2020)	N. America	Epilepsy (SEEG, subdural grid, strip of electrodes)	RS: 67	7	10.4	SL (vest)	Frontal, temporal, parietal, cingulate
Sun, Zhang, Ren, et al. (2021)	Asia	Epilepsy (SEEG)	RS: 20	1	–	BI	Parietal (S1)
Sun, Zhang, Yu, et al. (2021)	Asia	Epilepsy (SEEG)	RS: 33	9	27.3	Ag.	Parietal (S1)
Parvizi et al. (2021)	N. America	Epilepsy (SEEG)	CR: 1	1	–	Other	Frontal, temporal, parietal
Bratu et al. (2021)	Europe	Epilepsy (SEEG)	CR: 1	1	–	SL (OBE)	Whole brain
Hao et al. (2022)	Asia	Epilepsy (SEEG)	RS: 376	3	0.8	BI	Whole brain

Note: Publications are sorted by year of publication. Region of the sample: North America (N. America). Procedures for electrical brain stimulation (EBS): stimulation during awake brain surgery (ABS) for resection of brain tumor or epileptic zone, and stimulation during presurgical evaluation of epilepsy (stereoelectroencephalography [SEEG] or subdural electrodes), or implantation to treat tinnitus. Type of study: retrospective study (RS), case report (CR), and case series (CS). To avoid bias, the prevalence of bodily self disturbance (in % of the patients sample) is reported only when sample size is above 30. Categories of bodily self disturbance: SL (vest): self location (vestibular); SL (OBE): self location (out-of-body experience); SL (prop): self location (proprioceptive); Ag: agency; BI: body image; 1PP: first-person perspective; Own: ownership; Other (feeling of a presence, depersonalization, derealization). S1: primary somatosensory cortex. *Individual EBS evoking bodily self disturbances were reported as different cases as the number of patients was not indicated.

3.3 | Characteristics of clinical populations

Together, the studies included in this systematic review analyzed the EBS responses of a total of 4680 patients, of which 51.7% ($n = 2421$) received EBS during the presurgical evaluation of intractable epilepsy, 48.2% ($n = 2258$) received EBS during awake brain surgery for epilepsy or brain tumor, and 0.02% ($n = 1$) received EBS for intractable tinnitus. Out of these, we identified 221 patients (4.7% of all reported patients) who experienced a disturbance of one or several components of the bodily self during EBS. Eighty percent of the patients who reported a disturbance of their bodily self ($n = 176$) received EBS through SEEG, ECoG or strips of electrodes, whereas 20% ($n = 45$) received EBS during awake brain surgery.

3.4 | Prevalence of bodily self disturbances during EBS

When considering only the retrospective studies with a sample above 30 patients in order to avoid bias related to small samples (for similar procedures, see Dai et al., 2022), we observed that the prevalence of bodily self disturbances ranged from 0.1% to 27.3% (mean ± *SD*: 6.2% ± 7.3%; Table 2).

3.5 | Categories of bodily self disturbances evoked by EBS

Figure 3 compares the number of EBS-evoked disturbances of the different components of the bodily self and Table S4 summarizes the individual phenomenal reports.

The by far most commonly reported disturbance of the bodily self was a change in the perceived self location (163 responses representing 55.8% of all responses). Disturbances in the perceived self location were evoked significantly more often than any other component of the bodily self (all $z > 9.05$, and all p-values $< .0001$). The most common responses within this category included a perceived change in self location with vestibular sensations ($n = 131$; 44.9% of all responses; all $z > 6.55$ and $p < .0001$) characterized by illusory translation of the entire body (reported by 43 patients, e.g., Case 43 in Table S4: "Sliding towards the lower end of the bed"; Blanke et al., 2000), sensation of falling (in 39 patients, e.g., Case 45: "The patient reported that she was 'sinking into the bed' or 'falling from a height'."; Blanke et al., 2002), or feeling of floating in the air (in 31 patients, e.g., Case 34: "Feeling their whole body floating just above the bed"; Richer et al., 1993), without the sense of disembodiment.

The second most frequent EBS-evoked disturbance of the bodily self affected the sense of agency ($n = 57$; 19.5% of all responses). Disturbance in the sense of agency was also significantly more frequently evoked than other components of the bodily self, excluding self location (all $z > 2.13$ and all p-values $< .05$). Disorders of agency included the sensation an external agent moving (parts of) the body (reported by 17 patients, e.g., Cases 11–19: "The patients perceived all the above movements as being induced by an agent outside themselves"; Halgren et al., 1978), an "urge to move" for 8 patients (Andelman-Gur et al., 2020; Sun, Zhang, Yu, et al., 2021), an intention to move (5 patients, e.g., Case 85: "A pure intention, that is, a felt desire to move without any overt movement being produced"; Desmurget et al., 2009), or a resistance to perform an action (10 patients, e.g., Cases 171–180: "I feel resistance to anything I am told to do […] the possibility of continuing in any action is blocked"; Andelman-Gur et al., 2020).

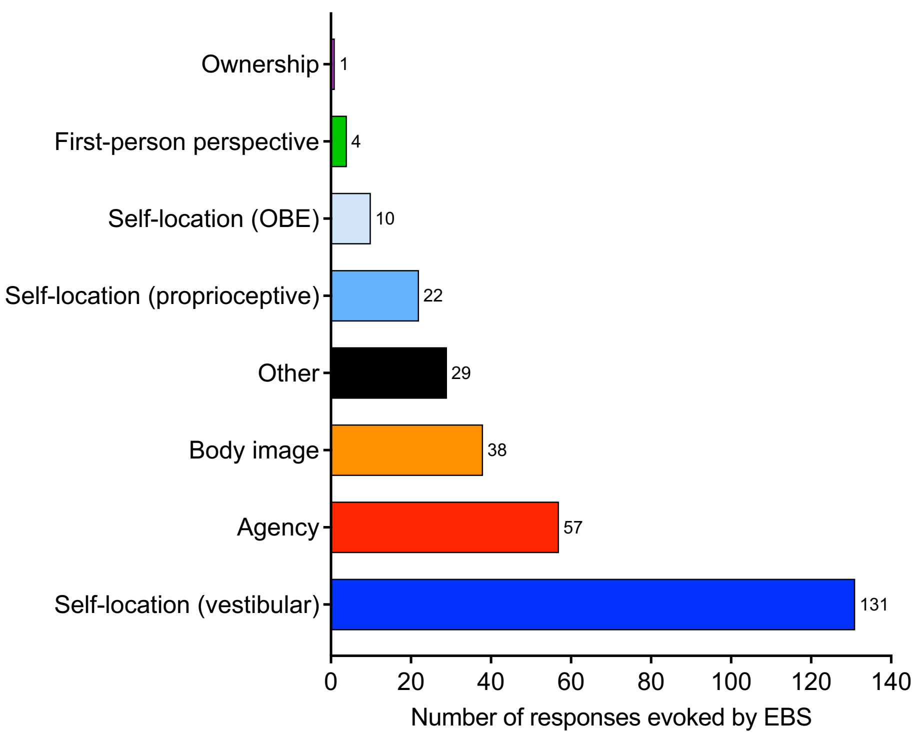

FIGURE 3 Distribution of the EBS-evoked disturbances in the different components of the bodily self. Disturbances of self location are plotted separately for vestibular illusions, proprioceptive illusions, and out-of-body experiences (OBE). Note that the number of responses reported exceeds the number of patients: when patients reported disturbances in several components of the bodily self for a given EBS, all components were counted separately

Disturbances of the perceptual body image represented 13% (n = 38) of the bodily self related responses. The cases included sensations that a body part was larger (in 15 patients, e.g., Cases 104–117: "He feels his right hand larger and swollen"; Balestrini et al., 2015), sensations that a body part was smaller (only in Case 45: "She reported seeing her legs 'becoming shorter'."; Blanke et al., 2002), or heavier (in 6 patients, e.g., Case 151: "Sensation that the upper right limb is heavier"; Popa et al., 2019), that a body part was missing (in 11 patients, e.g., Case 146: "The patient reported that he could not feel the existence of his right hand"; Yu, Yu, et al., 2018); Case 40: "Feeling that the leg is absent" (Salanova et al., 1995b), or the sensation that a body part was distorted (in 4 patients, e.g., Case 42: "My hand feels as if it is going around like a screwdriver"; Salanova et al., 1995a). There was no reported case of a supernumerary limb.

Other disturbances represented 9.9% (n = 29) of all bodily self related responses after EBS, a proportion of responses that did not differ from that of the perceptual body image (z = 1.17, p = .24). They included the sense of depersonalization (in 22 patients, e.g., Case 217: "This feeling of being disconnected from something. […] It's like being weightless in your own mind as a personality"; Parvizi et al., 2021) and the feeling of a presence (in 5 patients, e.g., Case 75: "He is behind me, almost at my body, but I do not feel it"; Arzy et al., 2006).

There were 22 cases of disturbances of self location with proprioceptive illusion, which represented 7.5% of all responses (e.g., Case 45: "The patient felt her right leg being drawn towards the opposite wall of the operating theatre"; Blanke et al., 2002); Case 159: "Sensation that the upper part of the body moves upwards" (Popa et al., 2019).

We found only very rare cases of full-blown OBEs, which include changes in the first-person perspective and body ownership during EBS. We identified 10 cases of illusory self location during OBEs, representing 3.4% of all responses. OBE included the perception that the self was disembodied with autoscopy (e.g., Case 120: "She felt as if she floated just below the ceiling and saw her own body lying on the operating table"; Bos et al., 2016) or disembodiment without autoscopy (e.g., Case 5: "Oh God! I am leaving my body, an altered relationship to his own person as though he were outside of his body"; Penfield, 1955). We identified three responses of changes in the first-person perspective, associated with OBE, which represented 1% of all responses (e.g., Case 45: "I see myself lying in bed, from above, but I only see my legs and lower trunk"; Blanke et al., 2002). However, we found only one case of altered sense of body ownership during EBS in a patient with epilepsy (Case 62: "Sudden estrangement of the left lower extremity from the rest of his body"; So & Schaüble, 2004).

3.6 | Localization of EBS evoking disturbances of the different components of the bodily self

3.6.1 | Effect of EBS in the different lobes

Figure 4a summarizes the localization of EBS evoking disturbances of the bodily self and Figure 4b quantifies the different categories of bodily self disturbances separately for each lobe and the cingulum. Disturbances of the bodily self were evoked by EBS in the parietal lobe (n = 90 responses evoked by EBS, representing 32.1% of all evoked responses in all brain regions stimulated), cingulum (n = 60, 21.4%), temporal lobe (n = 54, 19.3%), frontal lobe (n =39, 13.9%) and insular lobe (n = 32, 11.4%). EBS in the occipital lobe only rarely evoked disturbances of the bodily self (n = 5, 1.8%). Statistical analyses indicated a significantly higher proportion of responses in the parietal lobe (32.1%) than in all other regions stimulated (all z > 2.86 and all p-values <.01). The proportion of responses did not differ between the cingulate and temporal cortex (z = 0.63, p = .53), but was higher in the cingulate than in the frontal cortex (z = 2.32, p < .05).

Figure 4b shows that only EBS in the parietal lobe evoked disturbances of all five phenomenal components underlying the ordinary and healthy sense of the bodily self that were considered in the present systematic review (including all three subcategories of self location, agency, perceptual body image, first-person perspective, body ownership).

3.6.2 | Localization of EBS changing the perceived self location

Vestibular sensations were evoked by EBS in the cingulate (36% of self location responses), parietal (27%), insular (16%) and temporal (15%) cortex (Figure 4b). Although the proportion of vestibular sensations did not differ significantly between the cingulate and parietal cortex (z = 1.51, p = .12), the proportion of vestibular responses in each of these areas was significantly higher than in the insular cortex (all z = 2.01 and p < .05) and temporal cortex (all z = 2.36 and p < .05). Stimulation in the anterior, middle and posterior cingulate cortex induced an illusory displacement of entire body. Similar sensations were evoked by insula stimulation, especially during EBS in the posterior insula. Illusory whole-body displacements were also evoked by temporal cortex stimulation, mostly in the hippocampal/amygdala complex (e.g., Cases 20–25), superior temporal gyrus, as well as less frequently by EBS in the middle and inferior temporal gyri. In the parietal cortex, EBS in the parietal operculum, angular gyrus or precuneus predominately evoked feelings of body elevation and illusions that the body moved toward one side (e.g., Case 54).

Proprioceptive sensations were evoked by EBS in the parietal (36% of the proprioceptive responses), temporal (32%), and cingulate (18%) cortex (statistical tests on proportions were not conducted due to the low number of responses). Responses including illusory translation of a body part (e.g., Case 159) occurred after stimulation of the right angular and supramarginal gyri, subcortical white matter in the temporo-parietal junction or middle cingulate cortex.

Ten OBEs were evoked during EBS in the temporal (50% of all OBE responses), parietal (20%), occipital (10%), frontal (10%) and insular (10%) cortex (statistical tests on proportions were not conducted due to the low number of responses). More precisely, OBE was evoked by EBS in the angular gyrus, the posterior part of the superior

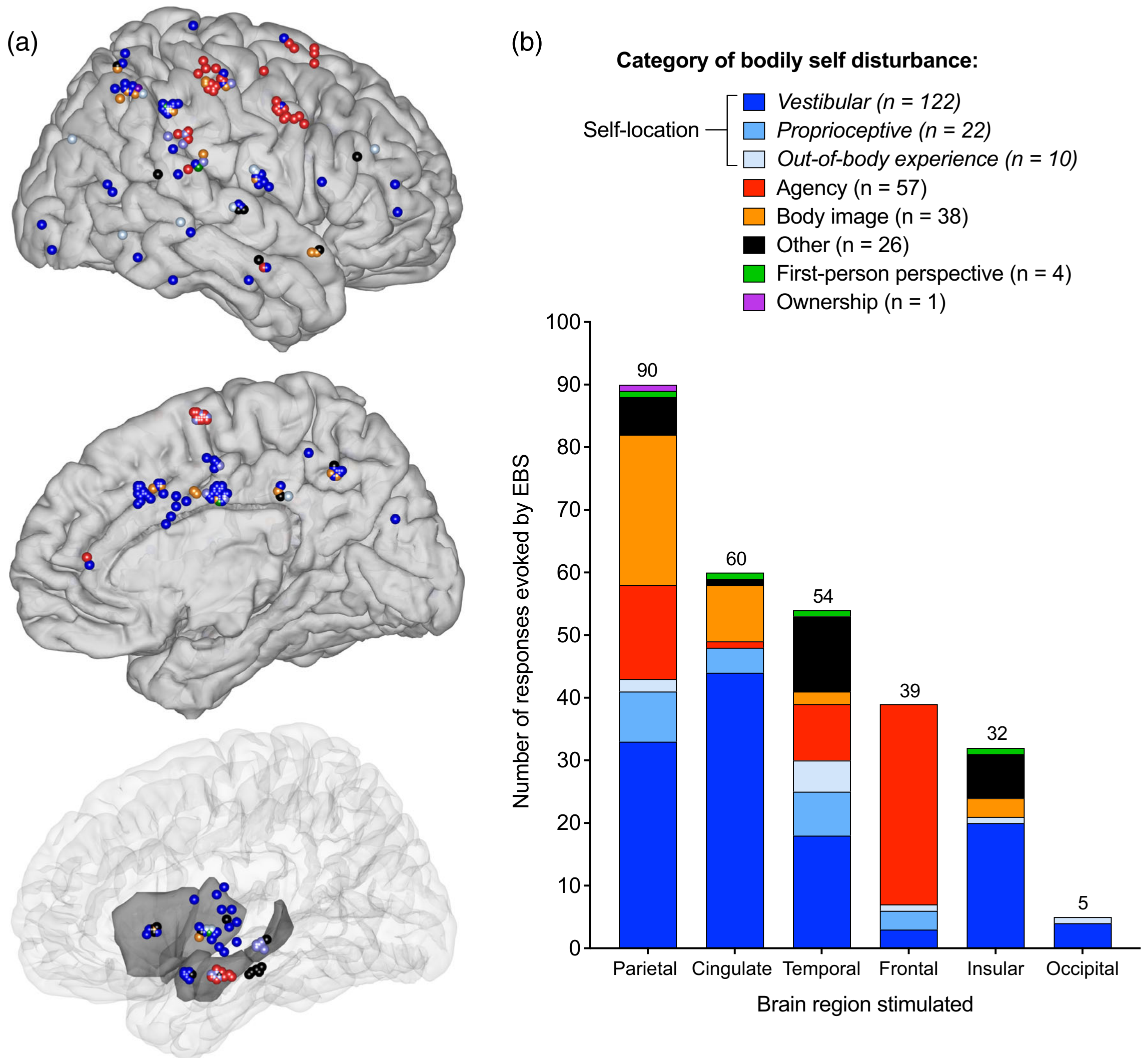

FIGURE 4 Localization of EBS evoking bodily self disturbances. (a) EBS sites are summarized on 3D views of the right cerebral hemisphere, with a color code indicating the category of bodily self disturbances. The lower part shows EBS in the insula and mesio-temporal region. (b) Number of disturbances in the different components of the bodily self according to the brain region stimulated. 292 EBS could be located based on the anatomical data available in the articles considered in the review. Changes in the experience of self location are plotted separately for vestibular illusions, proprioceptive illusions and out-of-body experiences (OBE). Note that patients may report disturbances of several components of the bodily self for a given stimulation, which was coded in several categories

temporal gyrus at the junction with the angular gyrus, the subcortical white matter in the temporo-parietal junction, the anterior insula and in middle frontal gyrus and middle occipital gyrus.

3.6.3 | Localization of EBS changing the sense of agency

Fifty-six percent of the sensations to urge movements or sensations of a resistance to move were reported after EBS in the frontal cortex, whereas 26% of the responses were reported after parietal lobe stimulation, such as in the angular gyrus or somatosensory cortex. There was a significantly higher proportion of responses in the frontal cortex than in all other regions stimulated (all $z > 3.23$ all p-values $< .01$). Disturbances in the sense of agency were especially evoked by EBS in the superior frontal gyrus (mesial and lateral parts) and precentral gyrus, including the supplementary motor area and the premotor cortex (e.g., Cases 171 and 172; "feeling a strong resistance to performing the task"). Stimulation in the mesial temporal lobe (hippocampus; 16% of the response) induced, for example, the sensation that the patient's movements were "induced by an agent outside themselves" (e.g., Cases 11–19).

3.6.4 | Localization of EBS changing the perceptual body image

Disturbance of the perceptual body image was reported after EBS in the parietal (63% of all body image responses), cingulate (24%) and insular (8%) cortex. There was a significantly higher proportion of responses in the parietal cortex than in all other regions stimulated (all $z > 3.47$ and p-values $< .001$). Sensation that a body part becomes heavier or lighter was induced, for example, after EBS in the angular gyrus or middle cingulate cortex (e.g., case 151). Illusory distortions of the body size (e.g., Case 45) occurred after EBS in the precuneus, postcentral gyrus, posterior cingulum, and superior parietal lobule. Finally, sensations that a body part is absent (e.g., Case 161) was reported when the superior part of the anterior insular long gyrus, middle cingulate cortex, superior parietal lobule and postcentral gyrus were stimulated.

3.6.5 | Localization of EBS changing the first-person perspective

Patients reported observing their environment from a viewpoint outside their body (together with a feeling of disembodiment, OBE) after stimulation in the parietal (25% of the responses), temporal (25%), cingulate (25%), and insular (25%) cortex (e.g., Cases 45, 120, 149, 153; statistical tests on proportions were not conducted due to the low number of responses). More precisely, changes in the first-person perspective were found after EBS in the angular gyrus, subcortical white matter in the temporo-parietal junction, anterior insula, and middle cingulate cortex. EBS at similar location evoked an OBE and a change in the first-person perspective, but OBE could also be evoked without a change in the first-person perspective.

3.6.6 | Localization of EBS changing the sense of body ownership

One case was identified during which EBS in the superior parietal lobule evoked an estrangement of the left lower extremity from the rest of the patient's body (Case 61).

3.6.7 | Localization of EBS evoking other disorders of the bodily self

Cases of depersonalization-derealization were reported during EBS in the superior temporal gyrus (12%), posterior cingulate cortex (4%), parahippocampal gyrus (19%), hippocampus (8%), insula (27%), and amygdala (4%; statistical tests on proportions were not conducted due to the low number of responses). The feeling of a presence was for example evoked by EBS in the left temporo-parietal junction (Case 75: "The patient had the impression that somebody was behind her").

3.7 | Identification of the main areas underpinning the bodily self

Two quantifications helped determine the main areas underpinning the bodily self. First, we plotted the histograms showing the number of bodily self disturbances as a function of the main gyri and areas reported in the articles considered in our review. 280 EBS could be localized using this method (Figure 5). We found that disturbances of the bodily self were consistently evoked by EBS in the middle cingulum ($n = 50$, 18% of all responses evoked in all brain regions), inferior parietal lobule (angular and supramarginal gyrus, $n = 34$, 12%), mesial and lateral parts of the superior frontal gyrus (supplementary motor area and premotor cortex, $n = 23$, 8%), posterior insula ($n = 21$, 7.5%) and hippocampus ($n = 19$, 6.8%). EBS in these regions induced disturbances in one or more phenomenal components of the bodily self.

Second, we calculated 3D density maps of EBS for which coordinates were available, irrespective of the category of bodily self disturbance. Figure 6 revealed that six brain areas seem crucially involved in the bodily self as their stimulation most consistently altered the bodily self across the different studies. This approach revealed the predominant implication of the inferior parietal lobule, middle cingulum, supplementary motor area, posterior insula, hippocampal complex/amygdala, and the precuneus.

3.8 | Hemispheric laterality of EBS and category of bodily self disturbances

As not all information about the lateralization was available, we only listed the EBS where the lateralization was clearly indicated (203 responses; Figure 7). The statistical analysis of the effect of the stimulation side could only be carried out for self location, agency, body image and other sensations, for which there were enough cases reported. When considering these four experiences, we found a significant association between the hemisphere stimulated and the evoked responses ($\chi^2(3) = 55.84$, $p < .001$). The Bayes factor strongly supports the hypothesis for this association ($BF_3 = 1.23 \times 10^{11}$). Results of the z-tests indicated that for self location, the proportion of response after EBS in the right hemisphere was significantly higher than the proportion of response after EBS in the left hemisphere (77.6% of all responses evoked by EBS of the right hemisphere vs. 33.3% of all responses evoked by EBS of the left hemisphere, respectively). By contrast, for agency we found that the proportion of response in the left hemisphere was significantly higher than the proportion of response in the right hemisphere (32.1% vs. 0.8%, respectively). There was no statistically significant difference for the body image and other sensations.

4 | DISCUSSION

This systematic review of the literature presents the largest series of EBS in awake patients reporting disturbances of the bodily self. We describe below the nature of the phenomenal experience reported by the patients and the role of the stimulated brain areas in generating the sense of a bodily self.

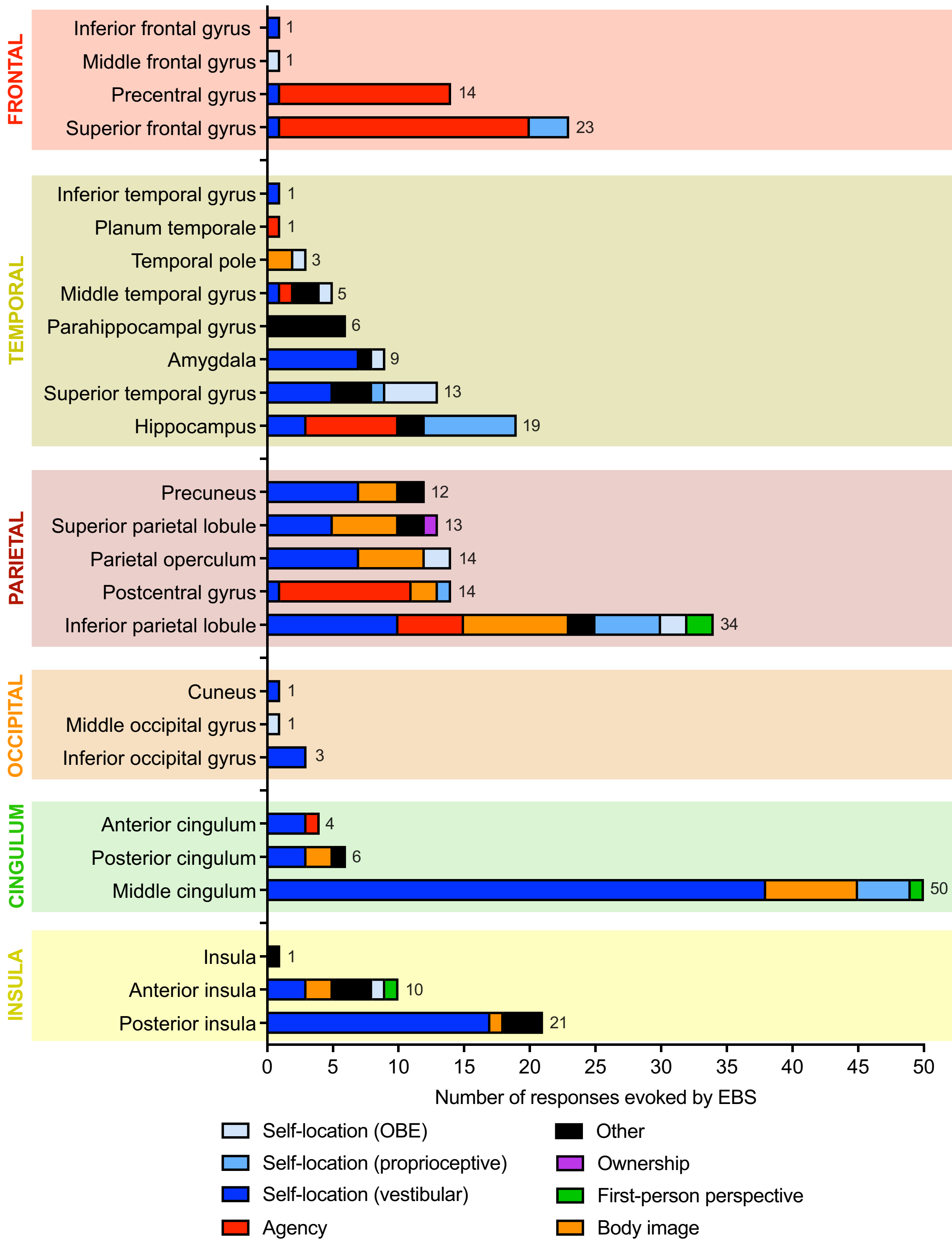

FIGURE 5 Number of disturbances of the different components of the bodily self as a function of EBS location. 280 EBS could be localized according to the main gyri for each lobe and the cingulum

4.1 | Nature and frequency of distorted components of the bodily self during EBS

The present systematic review of the literature shows that not all components of the bodily self were equally altered by EBS in awake patients.

The high prevalence of illusory self location in space (vestibular illusions of floating, levitation or translation and proprioceptive illusions such as illusory movement of a body part) that do not involve the sense of disembodiment is likely related to the relatively simple and unisensory nature of these illusions. They are also commonly experienced during hypnagogic and hypnopompic states in

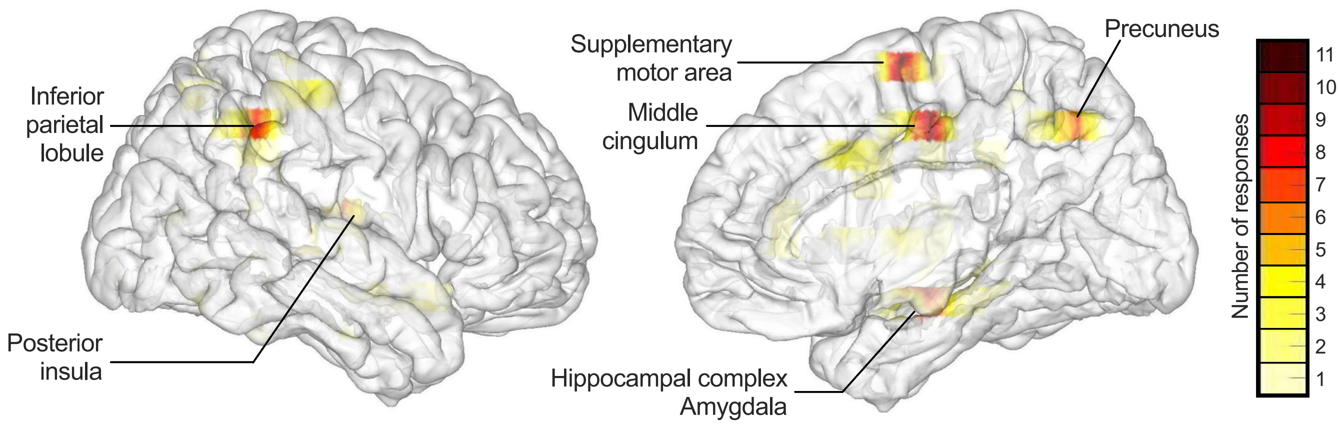

FIGURE 6 Color-coded density maps showing the number of EBS evoking disturbances of the bodily self. This analysis, conducted irrespective of the category of bodily self disturbances, revealed 6 main areas underlying the bodily self

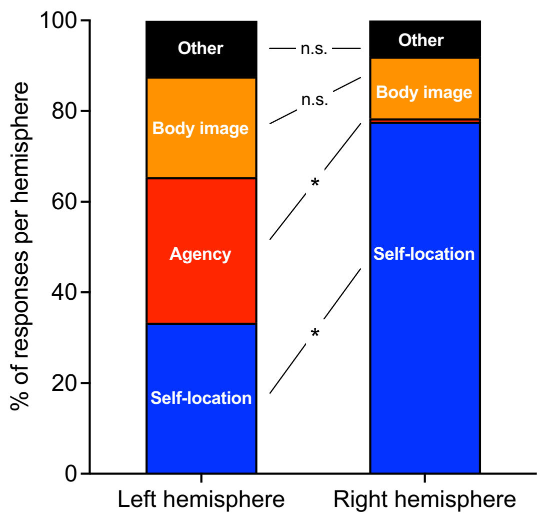

FIGURE 7 Percentage of all reported responses according to the stimulation side. * Statistically significant differences ($p < .05$) for the *z*-tests comparing the number of responses evoked by the stimulation of the right *vs.* left cerebral hemisphere

neurotypical populations (reviewed in Windt, 2015). A high prevalence of illusory self location can also be accounted by the widespread cortical vestibular network, encompassing a large number of multisensory areas in the parietal, temporal, insular, and cingulate cortex (Dieterich et al., 2003; Kahane et al., 2003; Lopez, Blanke, & Mast, 2012; Zu Eulenburg et al., 2012), which are strongly and reciprocally interconnected (Raiser et al., 2020). Similarly, illusory self location with proprioceptive illusions are in line with a large fronto-parietal network processing signals from muscle spindle afferents (Cignetti et al., 2014; Kavounoudias et al., 2008; Naito et al., 2017). In addition, there is evidence that the intrinsic cortical network architecture can predict the frequency of responses elicited by EBS in patients with epilepsy (Fox et al., 2020; McGonigal et al., 2021). EBS in "unimodal brain networks at the base of the cortical hierarchy elicited frequent and simple effects," such as EBS in somatomotor and visual networks (Fox et al., 2020).

Abnormal sense of agency was the second most frequent type of EBS-evoked disturbances of the bodily self, whereas distortions of the perceptual body image and other disturbances were the third most frequent disturbances of the bodily self. One should note that this is in part related to the high prevalence of the reported "urge" to perform an action (Fried et al., 1991), which we included as disturbance of agency, defined in a non-restrictive way. Full-blown disturbance of agency, such as the feeling that someone else is controlling the action, an experience sometimes reported by patients with schizophrenia or depersonalization disorders, was however rarely found. Disturbances of the body image were mostly experiences that the body shape was distorted, usually involving the sense of a larger body part or a loss of a body part. Although we report of few cases of asomatognosia (missing limb, estrangement of body part) during EBS, the feeling of an additional body part seems to be rarely evoked by EBS. We found only one case of supernumerary phantom limb due to EBS of the motor cortex for treating central pain (Canavero et al., 1999), which did not follow our inclusion criteria. The patient reported once every 1–2 weeks the presence of a painful supernumerary left arm. However, this illusion was reported about 6 weeks after the stimulator implantation, and could not be causally related to the direct effect of EBS, when compared to the immediate effects of EBS in patients with epilepsy or during awake brain surgery. Consistent with our observations on the effects of EBS, supernumerary phantom limbs are also rare during seizures (Hari et al., 1998) or stroke (Khateb et al., 2009; Miyazawa et al., 2004). Other types of disturbances of the bodily self reported here were mainly related to depersonalization, which combines various sensations of being detached from the body, or losing control over the body, actions, or thoughts, or a feeling of a presence.

It is interesting to note that in our analysis OBE including changes in the first-person perspective and body ownership were very rarely found. While the rare cases have revealed important insights on the fundaments of the bodily self (Blanke & Metzinger, 2009) and have been widely discussed in the scientific and general literature, there is no clear answer as to why these phenomena are so rare during EBS.

The low prevalence of OBE, changes in the first-person perspective and body ownership does not seem to be related to different excitability of the underlying intrinsic brain network (Fox et al., 2020), as these illusions were mostly triggered by EBS in the network where the most frequent disorders of the bodily self were also triggered. All these three disturbances of the bodily self are much more complex illusions than simple illusory elevation of the body, or illusory flexion of a body part, as they involve interpreting the experience from several senses together, and/or require a breakdown of a larger brain network. At a first glance, this low prevalence seems in contrast with the fact that 5%–10% of individuals from the general population have had at least an OBE in their lifetime, sometimes including changes in the visuospatial perspective (Blanke & Dieguez, 2009; Lopez & Elzière, 2018). On the other hand, experimentally-induced conflicts between senses in healthy participants have to date never evoked full-blown OBEs, but rather illusory self location toward an avatar and self identification with an avatar, without overt disembodiment (Ionta et al., 2011; Lenggenhager et al., 2007; Nakul, Orlando-Dessaints, et al., 2020). Alternatively, EBS may be effective only in populations prone to these illusory changes in embodiment, first-person perspective, and body ownership. Indeed, disturbances of self location and the perceptual body image, together with mental imagery abilities about the own body and spatial perspective, have been related to several factors and personality traits, including anxiety, migraine, depersonalization (Braithwaite et al., 2017; Lopez & Elzière, 2018), and schizotypy (Arzy et al., 2007; Mohr et al., 2006), or to different reliance on interoceptive and visual signals (Nakul, Dabard, et al., 2020; Pfeiffer et al., 2013; Tsakiris et al., 2011). It is therefore speculated that illusory disembodiment and changes in ownership were evoked mostly or only in these subpopulations of participants. Finally, it is also possible that the conditions to evoke such illusions require a particular involvement of the synchrony of the underlying neural systems (Hsu et al., 2022), as it is the case for complex phenomena such as memory reminiscence (Barbeau et al., 2005; Bartolomei et al., 2017).

4.2 | Prevalence of bodily self disturbances among experiential phenomena during EBS

Despite the increasing use of SEEG in clinical practice for presurgical evaluation of epilepsy (Parvizi & Kastner, 2018), there are only few retrospective studies in large samples of patients, and no prospective studies available, to correctly estimate the prevalence of EBS-evoked bodily self disturbances. A previous review article summarized the effects of EBS reported in the literature up 2010 (Selimbeyoglu & Parvizi, 2010). Based on their data, we calculated that out the 566 responses evoked after EBS, 9% were disturbances of the bodily self as defined in our present review article.

In the sample of patients included in our systematic review of the literature, we estimated that the prevalence of bodily self disturbances averaged 6.2% (of the patients receiving EBS) based on retrospective studies with a sample size above 30 patients. However, there was a very large variability in the prevalence across studies, ranging from 0.1% to 27.3%, depending on the stimulated brain regions. The highest prevalence was found in the parietal cortex (primary somatosensory cortex: 27.3%; Sun, Zhang, Yu, et al., 2021) and temporo-insular cortex (24%; Isnard et al., 2004), whereas the lowest prevalence was found for early whole-brain or temporal cortex mapping by Penfield and colleagues (0.1%–1.8%; Penfield & Perot, 1963; Penfield, 1947, 1955, 1957).

The generally comparatively low occurrence of bodily self responses during EBS might have several causes. It has been argued that EBS is not ideal to investigate complex cognitive functions and perceptions due to the nature of the brain networks involved and because of methodological limitations pertaining to EBS procedures during SEEG and awake brain surgery (Herbet, 2021; Mandonnet, 2021). While low-level sensorimotor perceptions rely on rather local and unimodal neural networks, with limited spatial variability between brains, high-level cognitive and perceptual functions are based on more distributed networks of multisensory cortical and subcortical brain areas, which present with larger variability between individuals. There is recent evidence to suggest that EBS in network that are heteromodal and higher in the cortical hierarchy evoke rare and more variable perceptions (such as stimulation of the limbic and default mode network; Fox et al., 2020), which may render particularly difficult the study of higher cognitive functions. This may also account for the intra-individual and inter-individual variability of the responses during EBS in a same network (e.g., Halgren et al., 1978), sometimes given as a limitation of EBS procedures (Borchers et al., 2011). In addition to the nature of the networks involved, EBS procedures may limit the investigation of high-level cognitive functions and perceptions, such as distortions of the bodily self. Indeed, EBS is often applied during cognitive tasks such as reading, picture naming, memory tasks or motor tasks. Accordingly, the self reports and clinical responses collected are oriented toward the performance of these tasks, rather than toward detailed introspective analysis from the patients about their sense of self.

4.3 | Neural network underpinning the bodily self

The disturbances in the bodily self reported in the present review of the literature fall into the category of interpretive responses and psychical illusions defined by Penfield (1955), as they are illusions about the current state of the body and self. In contrast to Penfield's description of a core area for psychical responses in the temporal cortex (Figure 1), we identified a much larger network involved in the sense of self, encompassing mainly the inferior parietal lobule, middle cingulum, supplementary motor area, posterior insula, precuneus, and hippocampus (Figure 6). As reviewed in details elsewhere, all these areas belong to brain networks related to the sense of self in functional neuroimaging in healthy participants or in brain lesion studies (Berlucchi & Aglioti, 2010; Blanke, 2012; Blanke & Metzinger, 2009; Lenggenhager & Lopez, 2015; Park & Blanke, 2019; Serino et al., 2013; Seth, 2013; Tsakiris, 2010; Vogeley & Fink, 2003). These areas have also been related to phantom perceptions in general

(De Ridder et al., 2011). This might explain why EBS within areas belonging to this network can trigger various illusory contents about the self and body, either in relation to the perceptual and emotional state of the body (through cingulate, prefrontal, parietal, and precuneus activation), or to memories through activation of the hippocampus, parahippocampal area, and amygdala (De Ridder et al., 2011). Interestingly, the areas reported here as underpinning the bodily self overlap to a great degree with the posterior brain networks underlying conscious experience in general (Koch, 2018; Raccah et al., 2021). However, the bodily self, as a minimal and immediate form of self (Blanke & Metzinger, 2009; Gallagher, 2000), does not seem to involve the prefrontal cortex, which is more implicated in higher cognitive functions and reflective aspects of consciousness (Boly et al., 2017; Dehaene & Changeux, 2011; Odegaard et al., 2017) and is in general less likely to evoke responses and perceptions during EBS (Fox et al., 2020).

4.3.1 | Inferior parietal lobule

The present review revealed that only stimulation of the parietal cortex induced a modification of all components of bodily self and that the proportion of responses evoked by EBS in the parietal cortex was higher than in any other brain area stimulated. Except for disturbance of body ownership, which was only evoked once by EBS in the superior parietal lobule, EBS applied in the inferior parietal lobule resulted in a change in all other core components of the bodily self. Moreover, the analysis of EBS spatial density indicates a strong overlap of stimulation sites in the inferior parietal lobule (angular gyrus and supramarginal gyrus). This result from EBS studies showing causal implication of the inferior parietal lobule in the bodily self is in line with results from previous functional neuroimaging studies in healthy participants and brain lesion studies. Studies found that all areas within the inferior parietal lobule were strongly connected to the inferior frontal, insular and posterior temporal cortex, as well as to a broad network of other posterior brain regions, such as the somatosensory cortex and superior parietal areas, as well as with the auditory and visual cortex (Caspers et al., 2011). Results from diffusion tensor imaging and tractography studies (reviewed in Seghier, 2013) showed that the angular gyrus is especially strongly connected to areas that we identified as underpinning the bodily self, such as the precuneus, supramarginal gyrus, the hippocampus and parahippocampal gyrus, the middle temporal gyrus, the superior frontal gyrus, and the inferior frontal gyrus (Catani et al., 2005; Makris et al., 2007; Rushworth et al., 2006; Uddin et al., 2010). Because of this extensive pattern of connection, the inferior parietal lobule belongs to and interact with fronto-temporal systems, or the default mode network.

4.3.2 | Middle cingulate cortex

We found that EBS in the middle cingulate cortex evoked mostly sensations of illusory self location (vestibular illusions) and distortions of the body image. The middle cingulate cortex has been involved in a very large range of functions, including "feedback processing, pain, salience, action-reward association, premotor functions, and conflict monitoring" in humans and in non-human primates (reviewed in Procyk et al., 2016; p. 467). More posterior stimulation during awake brain surgery have been related to altered states of consciousness (Herbet et al., 2016). A large retrospective analysis of the effects of EBS in the cingulate cortex indicates that the majority of vestibular responses—in relation to illusory self location in the present review article—were evoked by stimulation of the caudal part of the middle cingulate cortex (Caruana et al., 2018). In general, EBS in the posterior regions of the cingulate cortex (caudal part of the middle cingulate cortex and posterior cingulate cortex) were characterized by sensory illusions concerning the vestibular, interoceptive, somatosensory, and visual systems (Caruana et al., 2018). The role of the middle and posterior cingulate cortex in self location is also confirmed by their activation in fMRI studies that have used optokinetic stimulation or galvanic vestibular stimulation, evoking illusory self motion perception (Cardin & Smith, 2010; Smith et al., 2011), or experimentally-induced illusions of self location and body ownership (Guterstam, Björnsdotter, Gentile, & Ehrsson, 2015). Given the importance of these senses for the experienced bodily self, the posterior regions of the cingulate cortex may play an important role in the bodily self.

4.3.3 | Supplementary motor area

The supplementary motor area was mostly involved in changes in the sense of agency, as broadly defined in the present review article, although a few EBS also evoked illusory self location. The medial frontal cortex has consistently been involved in action monitoring in various fMRI studies (Yomogida et al., 2010), studies using transcranial magnetic stimulation and transcranial direct current stimulation (Cavazzana et al., 2015; Moore et al., 2010) and using SEEG recordings (Bonini et al., 2014). Here, we provide further causal evidence of the role of the mesial frontal cortex in the sense of agency.

4.3.4 | Insula

The insula has attracted a lot of attention recently in neuroscience. Functional MRI and PET studies have linked the insula to a large range of sensory, emotional and cognitive functions (Craig, 2002, 2009; Kurth, Zilles, et al., 2010, Kurth, Eickhoff, et al., 2010). The posterior insula has more specifically been involved in the processing of somatosensory, thermosensory, nociceptive, and vestibular information (Bottini et al., 1994, 2001; Dieterich et al., 2003; Mazzola et al., 2019; Ostrowsky et al., 2002). Recent meta-analyses of functional neuroimaging data revealed that the posterior insula is more particularly involved in sensorimotor processing, whereas the anterior insula is more involved in cognitive and socio-emotional functions (Kurth, Zilles, et al., 2010). Of note, the posterior insula contains neurons responding to somatosensory stimuli to various body parts, and also to the entire body, making it a crucial area for whole-body integration and perception (Coq et al., 2004; Evrard, 2019; Schneider et al., 1993). The posterior insula also overlaps with the human equivalent of the monkey parieto-insular vestibular cortex, as revealed by functional neuroimaging and electrophysiological data (Bense et al., 2001; Bottini et al., 2001; Dieterich et al., 2003; Frank et al., 2014; Frank & Greenlee, 2018; Guldin & Grüsser, 1998; Lopez, Blanke, & Mast, 2012; Nakul et al., 2021). This area, which is considered the core of the vestibular cortical network, is involved in processing signals about self motion, and should therefore be important for the bodily self, given the recognized role of vestibular information for the neural underpinning of the bodily self (Lenggenhager & Lopez, 2015; Lopez, 2013, 2016; Lopez & Elzière, 2018; Lopez, Schreyer, et al., 2012). The fact that EBS evoked mostly changes in the bodily self during stimulation of the posterior rather than the anterior insula, is in line with the sensorimotor foundations of the bodily self, a minimal and immediate form of self (Blanke & Metzinger, 2009; Gallagher, 2000).

4.3.5 | Hippocampal complex

Stimulation of the hippocampus and parahippocampal gyrus evoked illusory self location (proprioceptive and vestibular), depersonalization, and distorted sense of agency. There is a large body of neurophysiological and neuroimaging evidence demonstrating that the hippocampus is crucially involved in self location and spatial memory, as it contains place cells coding the specific location of an animal (Barry & Burgess, 2014; Burgess & O'Keefe, 2003; O'Keefe & Conway, 1978; Poucet et al., 2003; Wiener et al., 2002) or a human (Ekstrom et al., 2003; Miller et al., 2013) within a real or virtual space. A seminal intracranial EEG study in patients with epilepsy identified place selectivity in the hippocampus in patients immersed in a virtual environment (Ekstrom et al., 2003). In addition, an MRI study during experimentally-induced OBE-like illusion teleporting the participants in another location of the room showed that activity in the hippocampus predicted the perceived location of the bodily self in the room (Guterstam, Björnsdotter, Gentile, & Ehrsson, 2015). Accordingly, EBS in the hippocampus may disturb the neural underpinnings of self location and/or disturb the encoding of sensory afferents to the hippocampus. There is indeed evidence that the hippocampus processes vestibular signals, which are crucial for self location (Hitier et al., 2021; Horii et al., 2004; O'Mara et al., 1994; Smith, 1997; Suzuki et al., 2001; Vitte et al., 1996). Moreover, the hippocampus is well-known for its role in episodic memory. EBS in the hippocampus has been shown to evoke various psychical experiences (Halgren et al., 1978; Penfield, 1958; Penfield & Perot, 1963), including episodic memories, personal semantics, familiarity and reminiscences of a dream (reviewed in Curot et al., 2017). This could explain the feelings of unreality reported by some patients during stimulation of the hippocampus.

4.3.6 | Precuneus

We found that stimulation of the precuneus also evoked disturbances of the body image, self location, and depersonalization. There is a large body of evidence indicating that the precuneus is involved in self processing, self awareness and consciousness (Cavanna & Trimble, 2006). Functional MRI and PET studies showed precuneus activations during numerous self related tasks, such as during visuospatial tasks conducted from a first- versus a third-person perspective, when participants attribute seen actions to self versus others, or judgment of personality traits pertaining to self versus others (David et al., 2006; Farrer & Frith, 2002; Kircher et al., 2000; Lambrey et al., 2012; Ruby & Decety, 2001; Vogeley et al., 2004). Interestingly, a PET study in a patient receiving EBS at the temporo-parietal junction, which triggered an OBE, revealed that the disembodied experience was related to activation of a brain network encompassing the right precuneus (De Ridder et al., 2007). The precuneus also receives vestibular information (Dieterich et al., 2003), which may explain the illusory self location reported during EBS. Tracer studies in animals indicate that the precuneus is interconnected with most of the brain areas that we found involved in the bodily self, including the supplementary motor area, the cingulate cortex, the inferior parietal lobule, and more generally the temporo-parieto-occipital cortex (Cavanna & Trimble, 2006). Accordingly, EBS in the precuneus may activate a large parieto-temporo-frontal network underlying self experience.

4.4 | Hemispheric dominance for the neural bases of the bodily self

Here, we found a right hemisphere dominance for self location and a left hemisphere dominance for the sense of agency, and no significant dominance for the perceptual body image and the other types of bodily self disturbances. The right dominance for self location is congruent with the dominance in the right cerebral hemisphere of vestibular information processing, which is crucial for the sense of self location, and represents the majority of the distortions of the bodily self collected in our systematic review. This right hemispheric dominance of the vestibular cortex has consistently been shown in right-handed individuals by a series of functional neuroimaging, anatomical and clinical studies (Dieterich et al., 2003; Dieterich et al., 2017; Janzen et al., 2008; Kirsch et al., 2016, 2018), as well as by a meta-analysis of functional neuroimaging data (Lopez, Blanke, & Mast, 2012). The right hemispheric dominance for self location is also in line with the right dominance of the proprioceptive networks (e.g., Naito et al., 2017). Overall, self awareness in a broad sense has long been associated with a right hemispheric dominance (Devinsky, 2000; Feinberg & Keenan, 2005; Keenan et al., 2005). Previous studies showed that the right hemisphere is specialized in own-body recognition and motor awareness (Antoniello & Gottesman, 2017; Martinaud et al., 2017), as well as in first-person perspective (Vogeley et al., 2004) and the experience of an embodied self location (Ionta et al., 2011).

We found that the sense of agency was mostly disturbed when EBS was applied on the left side. While this result is in line with the large number of feeling of the "urge" to move and execute an action and the dominance of the motor areas in the left cerebral hemisphere of right-handed participants, it is not congruent with the implication of the mostly right insula and angular gyrus in the conscious sense of agency. However, these areas are more likely involved in the conscious sense of agency for ongoing actions (i.e., "monitoring intentional fluency" and "the subjective sense of control"; Haggard & Chambon, 2012) manipulated experimentally in fMRI studies, rather than in the feeling of urge to move evoked by EBS in otherwise immobile individuals.

4.5 | Limitations of EBS studies for neuroscientific investigations of the bodily self

Despite the recognized clinical advantages of EBS (George et al., 2020; Grande et al., 2020; Mandonnet et al., 2010), functional brain mapping using EBS has several limitations related to procedures and clinical constraints, which have been discussed in details elsewhere (Borchers et al., 2011; Parvizi & Kastner, 2018; Ritaccio et al., 2018).

First, EBS is limited by the unequal implantation of electrodes in the different cortices, which could be a bias for the results reported here. Most of focal epilepsies originate from the temporal and frontal lobes, which explains that the majority of electrodes was implanted in the temporal and frontal lobes (Parvizi & Kastner, 2018). In addition, there is an overrepresentation of some regions which have intensively been mapped and reported during the last years in retrospective studies, such as the effects of EBS in the insula (Mazzola et al., 2009, 2014, 2019; Ostrowsky et al., 2002; Yu, Yu, et al., 2018), cingulate cortex (Balestrini et al., 2015; Herbet et al., 2016; Oane et al., 2020; Popa et al., 2019), and frontal cortex (Fornia et al., 2020; Fox et al., 2018). We also note that because subcortical structures are only rarely implanted (with the exception of the hippocampus and amygdala) when compared to the cortex, we currently lack descriptions of the cerebellar and subcortical (brainstem, basal ganglia, thalamus) contributions to the bodily self, a spatial sampling bias which has been referred to as "corticocentric myopia" (Parvizi, 2009).

Second, EBS allows to investigate functions in various areas of the brain and create a causal link between neural activity and behavior (Borchers et al., 2011; Parvizi & Kastner, 2018) and is considered "the gold standard" for brain mapping (Mandonnet et al., 2010). However, distant and undirect effects of EBS have also been described and the causal effect of EBS is deemed controversial (Borchers et al., 2011; Desmurget et al., 2013). The effects of EBS are the result of inhibition and excitation of population of neurons at local and/or distant sites (Borchers et al., 2011; Ritaccio et al., 2018). Accordingly, locations of electrodes reported here may represent the effect of EBS on a larger brain network rather than the action on the neural populations close to the stimulation electrode only. There is indeed evidence that local stimulation, evoking for example ecstatic sensations, autobiographical memories and own-body perceptions, were associated with increased or decreased pattern of functional connectivity within larger cerebral networks (Bartolomei et al., 2012, 2017, 2019; Popa et al., 2019).

Third, EBS is by definition applied to the brain of patients who have abnormal brain tissue functioning and/or tumors, which may hamper the generalization of findings to non-neurological individuals. Patients with long-lasting epilepsy exhibit changes in functional connectivity in epileptogenic networks (Besson et al., 2017; Bettus et al., 2008, 2009; Lagarde et al., 2022; Wirsich et al., 2016). We note that recent EBS studies report only the effects of stimulation in non-epileptic tissue and/or the effects of stimulation not followed by epileptic discharges. In the case of low-grade glioma, brain reorganization before EBS may have modified the structure and function of the brain networks investigated (Duffau, 2015). Of note, only 20% of the patients reported in the present review underwent awake brain surgery. The advantage of a systematic review like ours is to identify the brain areas and phenomenal responses that are consistent across studies and patients, despite differences in the stimulation methods and paradigms (frequency, duration, intensity…).

With respect to the study of the sense of self, another limitation is related to the way clinical assessments are done during EBS. Neuropsychological and sensorimotor assessments performed during EBS in patients with epilepsy or during awake brain surgery typically focus on language, memory and visuo-spatial abilities, whereas self and own-body perceptions may not be spontaneously reported by the patients and not recorded. Patients may also have difficulty expressing what they are feeling or be afraid to say what is happening to them, resulting in a reporting bias. Regarding spontaneous self reports, the lack of structured questionnaires or interview, rarely compatible with clinical routine during EBS, limits the detailed description that would be needed to fully describe the often complex phenomenal experience associated with changes in the sense of self. For example, structured questionnaires and scales have shown to be helpful for screening emotional responses during EBS in the amygdala (Lanteaume et al., 2007).

Finally, a limitation of systematic reviews of the literature is the efficiency of online search and citation searching in published articles to identify all published cases related to the sense of self. We note that our online search was not able to identify articles published before 1993, including the work by Penfield and colleagues, probably due to the lack of keywords and referenced abstract. The large number of keywords used to define the various facets of the bodily self in our review should have allowed a comprehensive identification of the cases of bodily self disturbances published until 2022.

5 | CONCLUSIONS AND PERSPECTIVES

This systematic review of the literature reveals that EBS can evoke a large variety of phenomenal content related to the bodily self, including a disturbed sense of self location (regarding the whole-body, body parts, or disembodiment) and agency, change in the first-person perspective, altered body ownership, distorted body image, or symptoms of depersonalization. While these different phenomenal components of the bodily self are relatively rare and were not equally altered by EBS, they were all evoked by the stimulation of the parietal cortex. We also identified a network of six main areas that were most consistently involved in disturbances of the bodily self, including the inferior parietal lobule, middle cingulum, supplementary motor area, posterior insula, precuneus, and hippocampus. This seems in contrast with earlier work by Penfield (1955, 1947), who found that "psychical responses" (i.e., experiential and interpretive responses) were mostly evoked by EBS in the lateral and superior surfaces of the temporal lobes. Future electrophysiological studies should endeavor to determine how changes in neural network electrophysiology, such as dynamics of functional connectivity between distant brain areas, underpin the bodily self. The possibility to use sensory and cognitive tasks during EBS and SEEG recordings open interesting avenues, such as the simultaneous experimental manipulation of the bodily self (e.g., using the rubber hand illusion or the full-body illusion) and recordings of intracranial EEG signals (Guterstam et al., 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in this article are available in Table S4.

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