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Research Report

The role of the basolateral amygdala in dreaming



Yvonne Blake ^{a,*,1}, David Terburg ^{b,c}, Ross Balchin ^d, Jack van Honk ^{b,c} and Mark Solms ^e

^a Department of Psychology, University of Cape Town, Cape Town, South Africa

^b Department of Experimental Psychology, Utrecht University, Utrecht, the Netherlands

 $^{
m c}$ Department of Psychiatry and Mental Health, University of Cape Town, Groote Schuur Hospital, Cape Town, South

Africa

^d Division of Neurosurgery, University of Cape Town, Groote Schuur Hospital, South Africa

^e Department of Psychology, University of Cape Town, Upper Campus, South Africa

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ABSTRACT

Neuroimaging studies have repeatedly shown amygdala activity during sleep (REM and NREM). Consequently, various theorists propose central roles for the amygdala in dreaming – particularly in the generation of dream affects, which seem to play a major role in dream plots. However, a causal role for the amygdala in dream phenomena has never been demonstrated. The traditional first step in determining this role is to observe the functional effects of isolated lesions to the brain structure in question. However, circumscribed bilateral amygdala lesions are extremely rare. Furthermore, the treatment of the amygdala as a unitary structure is problematic, as the basolateral and centromedial amygdala (BLA and CMA) may serve very different functions.

We analysed 23 dream reports collected from eight adult patients with bilateral calcification of the BLA as a result of a very rare genetic condition called Urbach-Wiethe Disease (UWD). We compared these dream reports to 52 reports collected from 17 matched controls. Given that the BLA has been implicated in various affective processes in waking life, we predicted that the emotional content of the patients' dreams would differ from that of controls. Due to the exploratory nature of this research, a range of different dream characteristics were analysed.

A principal components analysis run on all data returned three key factors, namely *pleasantness*, *length* and *danger*. The UWD patients' dream reports were significantly *more pleasant* and significantly *shorter* and *less complex* than control reports. No differences were found in levels of threat or danger.

The results support some current hypotheses concerning the amygdala's role in dreaming, and call others into question. Future research should examine whether these UWD patients show generally impaired emotional episodic memory due to BLA damage, which could explain some of the current findings.

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* Corresponding author.

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E-mail addresses: yvonne.c.blake@gmail.com (Y. Blake), d.terburg@uu.nl (D. Terburg), r.balchin@uct.ac.za (R. Balchin), j.vanhonk@uu.nl (J. van Honk), mark.solms@uct.ac.za (M. Solms).

¹ Present Address: Centre de Neurosciences Psychiatriques, Department of Psychiatry, University of Lausanne, Site de Cery, 1008 Prilly-Lausanne, Switzerland, email: <u>yvonne.blake@unil.ch</u>.

1. Introduction

The human amygdala is a small but complex brain structure deep in the medial temporal lobe which has been repeatedly linked with a range of affective processes during waking life, including fear conditioning, responses to salient stimuli and other aspects of emotional memory (e.g., Adolphs, Tranel, Damasio, & Damasio, 1994; Feinstein, Adolphs, Damasio, & Tranel, 2011; LeDoux, 2003; Phelps & LeDoux, 2005; Yang et al., 2002).

Various studies have indicated that the amygdala is highly active during both REM (e.g., Corsi-Cabrera et al., 2016; Dang-Vu et al., 2005; Maquet et al., 1996; Nofzinger, Mintun, Wiseman, Kupfer, & Moore, 1997) and NREM sleep (Nofzinger et al., 2002). Dreaming has been consistently observed during both REM and NREM sleep, although it appears to be more frequent and perhaps more emotionally charged during REM (e.g., Cipolli, Ferrara, De Gennaro, & Plazzi, 2017; Hobson, Pace-Schott, & Stickgold, 2000; Nir & Tononi, 2010; Solms, 2000).

Numerous authors have therefore drawn a speculative link between the high levels of amygdala activation during REM and the intensity of emotional experiences reported in dreams, and have also indicated that amygdala activity during REM may be linked to the processing and depotentiation of emotional memories (e.g., Dang-Vu et al., 2005; De Gennaro, Marzano, Cipolli, & Ferrara, 2012; Deliens, Gilson, & Peigneux, 2014; Deseilles, Dang-Vu, Sterpenich, & Schwartz, 2011; Maquet et al., 1996; Nielsen & Stenstrom, 2005; Nir & Tononi, 2010; Nishida, Pearsall, Buckner, & Walker, 2009; Pace-Schott, Germain, & Milad, 2015; Palagini & Rosenlicht, 2011; Perogamvros & Schwartz, 2012; Popa, Duvarci, Popescu, Lena, & Pare, 2010; Van Der Helm et al., 2011). The depotentiation of emotional memories by the limbic system during sleep is the neurophysiological side of the emotional regulation hypothesis of dreaming (e.g., Hartman 1996; Levin & Nielsen, 2007; Cartwright, 1991; Wright & Koulack, 1987; for a review see; Malinowski & Horton, 2015) and is supported by recent results showing that dreams temper the emotional intensity of emotional memories (Vallat, Chatard, Blagrove, & Ruby, 2017).

A number of influential dream theorists have proposed a central role for the amygdala in the production, modulation and recall of emotional dream experiences, especially those involving negative emotions such as fear (e.g., Domhoff, 2001; Hobson et al., 2000; Levin & Nielsen, 2007; Revonsuo, 2000). For instance, Revonsuo's (2000) threat simulation theory of dreaming (TST) pivots around the claim that dreams are an evolutionarily adapted form of threat and escape simulation (a safe form of fear conditioning) driven by the amygdala. Levin, Fireman, and Nielsen (2010) state that "the hippocampus and amygdala are now considered to be integral in basic dream production" (p. 235).

However, there is a distinct lack of empirical research supporting these strong theoretical claims. Possibly the largest body of available evidence concerns a general association between abnormal limbic activity on the one hand and nightmares and excessive negative dream emotion on the other, especially in temporal lobe epilepsy and post-traumatic stress disorder (e.g., Germain et al., 2013; Levin et al., 2010; Nielsen, 2005; Solms, 1997). However, these studies do not delineate a specific role for the amygdala.

To the best of our knowledge, only a handful of studies have thus far attempted to directly examine links between the amygdala and dream phenomena. Desseilles et al. (2006) showed a relationship between right amygdala activity during REM and heart rate variability, a variable that has been linked to emotional arousal. De Gennaro et al. (2011) reported that decreased micro-structural integrity of the left amygdala was linked to shorter dream reports and lower emotional load in the reports. However, decreased volume of the right amygdala was associated with *increased* emotional load. Subsequently, in a population of Parkinson's disease patients, De Gennaro et al. (2016) showed that increased visual vividness of dream reports was correlated with larger volume of the amygdala bilaterally.

Compounding the shortage of empirical evidence, a further problem with theoretical claims regarding the amygdala's role in dreaming is the fact that these theories tend to address the amygdala as if it were a unitary structure. The amygdala is in fact made up of several nuclei, which, in humans, are conventionally divided into two major functional groups: the centralmedial amygdala (CMA) and the basolateral amygdala (BLA).

Converging non-primate and, more recently, human evidence suggests that the various nuclei of the amygdala are so different in function, structure and connectivity that they should be considered separately. Simplistically speaking, the striatal-like CMA is thought to trigger the physiological expression of fear, whereas the more corticoid BLA is crucial to the conditioning of fear responses and plays a role in inhibiting and regulating CMA activity (e.g., Davis & Whalen, 2001; Hrybouski et al., 2016; Killcross, Robbins, & Everitt, 1997; Klumpers, Morgan, Terburg, Stein, & van Honk, 2015; Koen et al., 2016; LeDoux, 2007; Phelps & LeDoux, 2005; Royer, Martina, & Paré, 1999; Swanson & Petrovich, 1998; Terburg et al., 2012; 2018).

The study we report here aimed to address the lack of empirical evidence regarding the amygdala's role in dreaming by examining the dreams of a group of patients with a rare genetic condition known as Urbach-Wiethe Disease (UWD). Urbach-Wiethe Disease frequently results in the progressive development of lesions in the medial temporal lobes, which can be present without resulting in any disorders of the central nervous system (Appenzeller et al., 2006). In the sample of South African UWD patients examined in the current study, these lesions are localised almost exclusively to the BLA bilaterally. Not only is the specificity of damage to this brain area unique to our sample, the size of the South African UWD population is also unprecedented.

To date, the only published literature involving the dreams of UWD patients is Wiest and Brainin's (2010) neuropsychoanalytic study of a single UWD patient with selective lesions involving the entire amygdaloid complex. Wiest and Brainin (2010) noted in passing that this patient had difficulty recalling his dreams, but he did report three dreams to them. This constitutes the first and only lesion study concerning the role of the amygdala in dreaming. The only (tentative) conclusion that can reasonably be drawn from it is that the amygdala is not essential for the production of dreams. The central aim of the present study was to examine, as broadly as possible, the formal characteristics of UWD patients' dream reports by comparing them with reports collected from a closely matched control group. We thereby aimed to test the widely held, but empirically underinvestigated idea that the amygdala plays a central role in the development of dream plots, specifically in the intensity of negative (particularly threat related) experiences in dreams, but possibly also in dream affectivity more generally.

We focus specifically on the impact of BLA damage on dream plots (as opposed to the impact of damage to the amygdala as whole), mainly because the lesions in our patient group are predominantly localised to the BLA. However, in light of arguments that BLA and CMA functions are so dissimilar that the two complexes should be considered separately, it is also theoretically appropriate to investigate their specific contributions to dream phenomena. Furthermore, emotional episodic memory and other higher-order emotional processing functions appear to rely more on the BLA than the CMA (see Hortensius et al., 2017 and McGaugh, 2018 for recent commentaries). As such, one may speculate that the BLA is more likely to play a role in the development of the emotional narratives recounted in dream reports. Nevertheless, a potential role for the CMA in dreaming should not be dismissed.

Due to the paucity of existing data, and the unique opportunity presented by our clinical sample, this study assumed an exploratory approach and the dream reports were accordingly coded on a wide variety of dimensions. These dimensions were analysed by factor analysis in order to identify any patterns that emerged.

2. Methods

2.1. Participants

The sample comprised eight UWD patients and seventeen matched healthy controls. The inclusion criteria for the UWD group were a diagnosis of UWD and the presence of bilateral BLA lesions, alongside preservation of the CMA, as confirmed by MRI (see Fig. 1).

The lesions appeared to be entirely delimited to the BLA in five of the eight patients (however, participant UWD5 in particular showed evidence of some hippocampal extension²).

There was a high degree of homogeneity among the patients as they are all Afrikaans speaking women of low socioeconomic status living in rural communities in the Northern Cape province of South Africa, with low-to-average FSIQ scores (see Table 1).

The control group was matched on all these demographic measures, and two-tailed Mann–Whitney U tests showed no significant differences between the UWD patients and control participants on age, U = 68, p = 1.000, or FSIQ, U = 62.5, p = .763. We excluded participants who were younger than 18 years, or had a history of alcoholism or any psychiatric or neurological diagnoses other than UWD.

2.2. Procedure

Informed consent was obtained from all participants. Twentythree dream reports were collected from the eight UWD patients, and fifty-two reports were collected from the seventeen matched control participants. Dream reports were collected in the participants' homes using the Most Recent Dream (MRD) method. This method was used as it was considered ethically inappropriate to repeatedly require the participants to travel the long distance from their remote rural enclave to an urban university sleep laboratory. The MRD method is a reliable and valid alternative to the laboratory method of collecting dreams, and it yields reports of equivalent form and content to those collected in laboratory settings (Domhoff, 1999). The investigator asks each participant to recall the most recent dream they can remember, taking care to describe details such as settings, characters, and emotions (Avila-White, Schneider, & Domhoff, 1999). All the MRD interviews were conducted by a firstlanguage Afrikaans speaking nurse well known to the patients. This nurse was blind to our hypotheses but not to the patients' diagnostic status.

Three research assistants then coded the dream reports on seven different measures, namely: the Positive and Negative Dream Affect Scale (PANDAS), the Affective Dream Scale (ADS), a Wish-Fulfilment Scale, a Word and Narrative Item Count (all continuous measures); and Incidence of Nightmares, Incidence of Threat and Escape, and Classification of Approach versus Avoidance Behaviour (all categorical measures).

The coders were first language Afrikaans speakers blind to the study's hypotheses and the participants' diagnoses. All measures except the ADS were coded individually; the latter was coded by consensus. For the measures coded individually, a minimum inter-rater reliability of 80% perfect agreement or an intra-class correlation coefficient (ICC) of .8 was calculated for the categorical and continuous measures, respectively.

2.3. Materials

Below is a brief summary of each of the seven coding measures utilised, as well as a brief rationale for each and, where applicable, specific hypotheses.

2.3.1. The positive and negative dream affect scale (PANDAS) This scale was created for the purposes of the present study and is based on the affective dream scale (see below). It was designed to measure the intensity of positive affect (characterised as all pleasant emotion) and negative affect (characterised as all negative emotion) in the dreams reports. It uses the same 0-3 scale as the ADS, where 0 = these emotions were absent; 1 = very little of these emotions were present; 2 = a moderate amount of these emotions were present; and 3 = these emotions were very intense.

Rationale. Existing literature presents significant theoretical and empirical grounds to suppose that the amygdala may play a role in the generation of intense negative emotion in dreams (see section 1). Although the amygdala also plays a role in positive emotional processes, the nature of this role is less clear. Most neurobiological theories of dreaming focus on the amygdala's potential role in negative emotions such as fear during dreaming (e.g., Domhoff, 2001; Levin et al., 2010;

² Exclusion of participant UWD5 (on the basis of this extended damage) did not significantly change the results reported below.

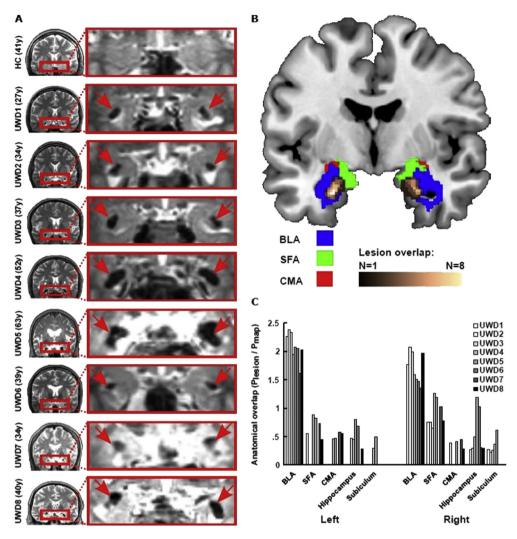


Fig. 1 – Calcifications are bilateral and focal to the BLA. (A) Coronal slices from the T2-weighted MRI scans and age at time of scanning for one healthy control and the eight UWD patients. The BLA lesions appear in black. (B) Lesion-overlap image in MNI space plotted within the amygdala sub-regions defined as voxels with sub-region probability >50%. (C) Bar graph representing bilateral excess probability (P_{excess}) values of the lesion volumes, whereby values >1 indicate a reliable match of volume and anatomical location of: BLA = Basolateral Amygdala, SFA = Superficial Amygdala, CMA = Central-Medial Amygdala.

Table 1 – Demograp	hic	data i	for	UWD	patients.
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	UWD 1	UWD 2	UWD 3	UWD 4	UWD 5	UWD 6	UWD 7	UWD 8
DOB	1985	1978	1974	1960	1948	1972	1979	1978
Age	28	35	38	52	64	40	33	35
FSIQ	98	84	87	81	83	83	73 ^a	90

Year of birth, age at time of dream interview, and Full Scale Intelligence Quotient are indicated for each participant.

^a Participant UWD7's FSIQ score is below the normal range (<80), however FSIQ is not an accurate reflection of intelligence in such socioeconomically deprived and undereducated communities (Wicherts, Dolan, & van der Maas, 2010). All of the FSIQ scores reported here are consequently likely to be underestimations. Excluding participant UWD7 did not significantly change the results reported below.

Revonsuo, 2000). Therefore, although this measure aimed to assess the role of the BLA in the generation of both positive and negative dream affect, an a priori directional hypothesis was made only for the effect of BLA damage on negative affect.

Hypothesis. The dreams of patients with UWD will show a significantly lower level of negative emotion than the dreams of control participants.

2.3.2. The affective dream scale (ADS)

This scale was developed to assess basic emotions in dreams over the course of a number of student projects in the Psychology Department at the University of Cape Town (UCT). The scale measures the intensity of the seven basic emotion systems, as identified by Panksepp (1998), on the 0-3 scale described above. These basic emotions,

FEAR, SEEKING, RAGE, GRIEF, PLAY, LUST and CARE, are capitalized as per Panksepp's (1998) taxonomy of basic emotions.

Rationale. Research regarding the amygdala's waking function has suggested that the structure might be particularly involved in FEAR processes. However, some research has also suggested that the amygdala may be involved in affective processes more generally. This study therefore aimed to assess the intensity of each of Panksepp's basic emotions in order to provide a broad understanding of the effects of bilateral basolateral amygdalae damage on dream affect, but an a priori directional hypothesis was made only for the effect of BLA damage on FEAR.

Hypothesis. The dreams of patients with UWD will show a significantly lower level of FEAR than the dreams of control participants.

2.3.3. The wish-fulfilment scale

This scale measured to what extent each dream report constituted the fulfilment of a wish, and was developed and refined during the pilot stages of the present study. It uses a similar 0–3 scale to the ADS, although in this case 0 = this dream includes no wish-fulfilling elements; 1 = this dream has some elements of wish fulfilment but is predominantly not a wish fulfilling dream; 2 = this dream includes a clear wish-fulfilment but also includes other aspects; and 3 = this dream is completely wish-fulfilling.

Rationale. An initial qualitative assessment of the dream reports collected led to the observation that there seemed to be a high degree of wish-fulfilment in the UWD patient dream reports. This scale was developed to test this observation.

Hypothesis. The dreams of patients with UWD will show a significantly higher level of wish fulfilment than the dreams of control participants.

2.3.4. Incidence of nightmares

This measure was included in order to investigate whether there was a difference between the frequencies of nightmares experienced by the UWD patients versus the controls. The incidence of nightmares was recorded by simply asking the research assistants to make a nominal judgement of whether or not the dream report in question could be labelled a nightmare. They were asked to make this decision based on a common-sense understanding of what nightmares are, and were provided with the following description in order to aid their decision: 'Nightmares are dreams marked by intensified feelings of dread or terror or other highly disturbing or unpleasant emotions, often with vivid visual imagery, these feelings are so intense that they typically cause the individual to wake up' Given that there has been a general failure in the nightmare literature to agree on a single definition of the term, the description provided to the raters consisted of a combination of a number of influential definitions (Levin et al., 2010; Nielsen, 2005).

Rationale. If patients with basolateral amygdala damage experience decreased negative emotions in their dreams, it may follow that they experience fewer nightmares. Furthermore, dream theorists have suggested that the amygdala plays a role in the generation of nightmares. The present study therefore aimed to test whether bilateral basolateral amygdala damage had any impact on the occurrence of nightmares. **Hypothesis**. Significantly fewer of the UWD patients' dreams than the control participants' dreams will be classified as nightmares.

2.3.5. Word and narrative item count

These two measures were developed for the purpose of previous dream research in the UCT Psychology Department and were adapted slightly for the present study. These scales require raters to count the number of words and the number of narrative items in the dream reports, thereby providing measures of the length (word count) and narrative complexity (narrative item count) of the dream reports.

Rationale. The literature provides some support for the idea that the amygdala is involved in the generation of dream plots. Most pertinently, De Gennaro et al. (2011) found that shorter dream reports were correlated with higher mean diffusivity of the left amygdala. Furthermore, given the BLA's apparently central role in emotional episodic memory (McGaugh, 2018), it seems feasible that BLA damage may result in shorter, less complex dream reports. The present study therefore aimed to test whether there was a difference in dream report length between UWD patients and control participants, and also to determine whether any difference in the narrative complexity of the dream reports.

Hypotheses. The dreams of patients with UWD will have a significantly lower word count than the dreams of control participants. The dreams of patients with UWD will have a significantly lower narrative item count than the dreams of control participants.

2.3.6. Incidence of threat and escape

This measure was included in order to test predictions based on Revonsuo's (2000) TST of dreaming. The measure has previously been applied by Malcolm-Smith and Solms (2004), and Malcolm-Smith, Solms, Turnbull, and Tredoux (2008). Raters are asked to make a series of five judgements concerning the presence and nature of threat and escape behaviour in each dream report: 1) Does the dream contain a realistic physical threat to the dreamer? If yes: 2) Is the threat life threatening? 3) Is the threat ancestral or modern? (Ancestral: ecologically valid threats – those present in our ancestral past, or similar to those present in our ancestral past, e.g., violent crime. Modern: Significant physical threats which have no equivalent in our ancestral past, e.g., major surgery, traffic accidents.) 4) Does the dreamer escape the threat? If yes: 5) Is the escape realistic?

Rationale. Revonsuo's (2000) TST would predict that patients with amygdala damage will exhibit fewer instances of threat and escape in their dreams. This study therefore aimed to test whether or not TST's predictions regarding the amygdala's role in threat-related dream activity hold true.

Hypotheses. There will be significantly fewer instances of threat in the dream reports of patients with UWD than in the dream reports of control participants. Patients with UWD will successfully escape significantly fewer of the threats in their dream reports than the control participants.

2.3.7. Classification of approach versus avoidance behaviour This method was employed by Malcolm-Smith, Koopowitz, Pantelis, and Solms (2012) to test another aspect of TST. It assesses the prevalence of threat-avoidance behaviours in dream reports by contrasting the incidence of threatavoidance to the incidence of a comparable instinctualemotional behaviour, namely approach behaviour.

Rationale. Revonsuo's (2000) TST views threat-avoidance behaviours as the cornerstone of dream behaviour, and the amygdala as being responsible for these behaviours. Approach behaviour, which is associated with the SEEKING system, provides a good contrast to threat-avoidance behaviour, which is associated with the FEAR system. This study therefore aimed to assess whether, in line with TST, patients with bilateral basolateral amygdala damage will display lower incidence of avoidance behaviour (relative to approach behaviour) than healthy individuals.

Hypothesis. The dreams of patients with UWD will show significantly fewer instances of avoidance behaviour than the dreams of control participants.

2.4. MRI methods

MRI scans were acquired with a Siemens Magnetom Allegra 3-T head-only scanner at the Cape Universities Brain Imaging Centre (CUBIC) in Cape Town, South Africa. For the lesion analysis we obtained whole brain T2-weighted images with 1 mm isotropic resolution, TR = 3500 msec, and TE = 354 msec.

2.4.1. Lesion analysis

To estimate extent and anatomical location of the lesions, T2weighted scans were normalized to MNI-space using unified segmentation, which is optimized for normalization of lesioned brains (Crinion et al., 2007). Lesion volumes were defined using the 3D volume-of-interest featured implemented in MRIcroN (http://www.mccauslandcenter.sc.edu/ mricro/mricron/index.html). The precise borders between amygdalae and neighbouring structures, or between the subregions of the amygdala, cannot be established based on MRI (Amunts et al., 2005; Solano-Castiella et al., 2011). To determine the precise location of the lesions in our UWD subjects we therefore assigned the lesion volumes to cytoarchitectonic probability maps according to the method described by Eickhoff et al. (2007). In this method, which is implemented in the SPM8 anatomy toolbox (http://www.fz-juelich.de/inm/ inm-1/spm_anatomy_toolbox), a volume of interest is superimposed onto a cytoarchitectonic probability map of the medial-temporal lobe (Amunts et al., 2005). This map is based on the microscopic analyses of postmortem human brains and follows a generally accepted division of the human amygdala in three sub-regions. The first is the CMA, which consists of the central and medial nuclei. The second is the BLA, which includes the lateral, basolateral, basomedial, and paralaminar nuclei, and the third is the superficial (or corticoid) amygdala (SFA), which includes the anterior amygdaloid area, amygdalopyrifom transition area, amygdaloidhippocampal area, and the cortical nucleus (Amunts et al., 2005). This method assigns to any given voxel a value representing the probability that the voxel belongs to an underlying structure. These values are derived from an overlap analysis of ten postmortem brains and are therefore divided into ten separate probability classes ranging from 10% to 100% probability.

To estimate how well the lesion volumes fit to the underlying structure, P_{excess} values are computed using the following equation:

$P_{\text{excess}} = P_{\text{lesion}} / P_{\text{map}}$

whereby P_{lesion} represents the average cytoarchitectonic probability of the voxels that are shared by the lesion and the cytoarchitectonic probability map, and P_{map} represents the average probability of the whole structure's cytoarchitectonic map. These values represent how much the average probability of the overlapping voxels exceed the overall probability distribution of that particular structure, thus indicating whether the lesion overlaps with relatively high or low probability classes of that structure. In other words, P_{excess} represents how 'central' the location of the lesion is relative to that structure's cytoarchitectonic map, whereby $P_{excess} > 1$ indicates a more central, and $P_{excess} < 1$ a more peripheral location (Eickhoff et al., 2007).

2.4.2. Lesion results

As depicted in Fig. 1A & B, calcified brain-tissue is localized in the BLA and the CMA appears to be unaffected. In a quantitative analysis these results are confirmed. Fig. 1C shows Pexcess values for the individual lesions and these lesions are, bilaterally, most central to the BLA as Pexcess values exceed 1.0 for each individual and hemisphere. Since this method is purely based on probability distributions, it is impossible to fully exclude that structures other than the BLA are affected by the calcifications. The fact that the lesionvolumes largely overlap with high probability classes in the bilateral BLA, and that Pexcess values greatly exceed the value of 1, can however be seen as strong support for our claim that these UWD-subjects have bilateral damage limited to the BLA. In three of the UWD subjects the calcifications might however extend into neighbouring structures. Namely, in subjects UWD4 and UWD5 the lesion might extend into the right SFA and in subjects UWD5 and UWD6 into the right hippocampus. However, we can safely conclude that the CMA is unaffected by the bilateral calcifications found in all of these UWDsubjects.

2.5. Data analysis

Given that three to four dream reports were collected from each participant, there was a possibility that this could threaten assumptions of independence of data. However, multilevel modelling showed that there was no significant variation at the level of the different participants. It was therefore appropriate to treat the data as independent (Bliese, 2016).

To determine whether the large number of independent variables measured could be reduced to a smaller number of common factors, and to control for inflation of the Type 1 error rate, we ran a principal components analysis with an oblique rotation, thereby improving the understanding of the data. Independent samples, two-tailed Mann–Whitney U tests (chosen as the data was not normally distributed) were then used to compare the UWD patients' scores to the control participants' scores on the components that emerged. Medians, range and effect size (Pearson's r) were calculated. For exploratory purposes, the data collected via each of the scales were also assessed by individual analyses. Two tailed Mann–Whitney *U* tests were used to compare the UWD patients to controls on each measure.

3. Results

3.1. Main results: principal components analysis

The original principal components analysis was conducted on 14 variables, namely: positive affect; negative affect; six of Panksepp's basic emotions (LUST was omitted as a score of 0 was recorded for every dream); wish fulfilment; nightmares; threat; approach versus avoidance behaviour; the narrative item count; and the word count. However, the solution was found to be more stable when RAGE, GRIEF and CARE were excluded from the analysis. This was due to these variables explaining very little variance, having low correlations with the other variables, and therefore also relating poorly to the components extracted by the analysis. In addition, these variables scored poorly on the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy.

The subsequent analysis was therefore run on the remaining 11 variables. The KMO score for this analysis as a whole was good, KMO = .73. The KMO scores for the individual variables were all greater than .6. Bartlett's test of sphericity was significant, χ^2 (55) = 638.98, p < .001, indicating that the correlations between the variables were sufficiently large for principal components analysis.

A principal components analysis with an oblique rotation (oblimin) was run, as there was reason to assume that the factors extracted were not totally independent. A three component solution was chosen based on Kaiser's criterion (three components had eigenvalues greater than one), as well as on the analysis of the scree plot.

Together, these three components explained 77% of the variance. The loadings of each variable on the three components after rotation are reflected in the pattern matrix (Table 2), and the structure matrix (Table 3) reveals the correlations between each variable and the three extracted components.

The first component reflected 'unpleasantness', or, if inverted, 'pleasantness' Positive affect, PLAY, and wish fulfilment all had large inverse loadings on this component, and the negative affect and nightmare variables showed strong positive loadings. FEAR also had a positive correlation with this component.

The second component seemed to reflect the 'length and complexity' of the dream report, as word and narrative item count, along with SEEKING, loaded most strongly onto this component, and an increase in each of these variables inevitably reflected an increase in the length of the dream report.

The third component could be described as 'danger'. Threat had a strong positive loading, and approach versus avoidance behaviour a strong negative loading on this component. FEAR and negative affect also showed strong correlations with this component.

The control participants had a higher median score on the 'unpleasantness' component than the UWD participants (see

Table 2 - Pattern matrix.

Variable	Component			
	Unpleasantness	Length	Danger	
Positive affect	965 [*]	.084	053	
Negative affect	.507 [*]	.400	.282	
PLAY	861 [*]	.122	174	
FEAR	.307	.328	.473	
SEEKING	.168	.618 [*]	.115	
Wish fulfilment	988 [*]	.021	.126	
Nightmare	.527*	.338	153	
Threat	071	.109	.912 [*]	
Approach vs avoidance	010	.117	884^{*}	
Word count	081	.945*	029	
Narrative count	102	.965*	001	

The loading, or individual contribution of each of the eleven included variables on the three extracted components. Factor loadings \geq .5 are indicated by * and presented in bold.

Table 3 - Structure matrix.

Variable	Component			
	Unpleasantness	Length	Danger	
Positive affect	950 [*]	280	324	
Negative affect	.738 [*]	.645*	.518 [*]	
PLAY	869 [*]	230	405	
FEAR	.568*	.540*	.633 [*]	
SEEKING	.428	.704 [*]	.295	
Wish fulfilment	942 [*]	314	164	
Nightmare	.605*	.499	.075	
Threat	.241	.275	.914 [*]	
Approach vs avoidance	231	073	863 [*]	
Word count	.256	.909 [*]	.145	
Narrative count	.250	.927*	.171	

The correlation of each of the eleven included variables with the three extracted components. Correlations \geq .5 are indicated by * and presented in bold.

Fig. 2). A two-tailed Mann–Whitney U test revealed that this difference was significant, U = 367, p = .007, r = -.31.

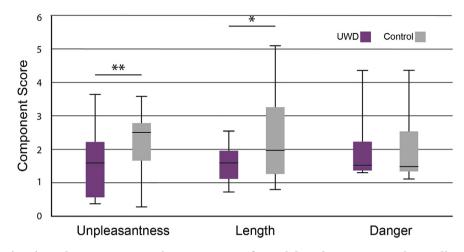
The control participants also had a higher median score on the 'length' component than the UWD participants (see Fig. 2). A two-tailed Mann–Whitney U test revealed that the difference between the groups was significant, U = 415, p = .035, r = -.24.

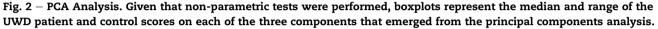
The UWD patients had a similar median score on the 'danger' component to the control group (see Fig. 2). A two-tailed Mann–Whitney U test showed no significant difference, U = 545, p = .549, r = -.07.

3.2. Descriptive results for individual coding measures

3.2.1. The positive and negative dream affect scale

The UWD patients had a higher median positive affect score than the control participants (see Fig. 3A). A two-tailed Mann–Whitney U test indicated that this difference was significant, U = 362.5, p = .005, r = .32. The UWD patients had a lower median negative affect score than the control





participants. However, this was not significant, U = 456, p = .100, r = -.19.

3.2.2. The affective dream scale

None of the reported dreams showed any instances of LUST, so this basic emotion was omitted from the analyses. As seen in Fig. 3B, no RAGE was observed in the UWD patients' dream reports, while a small number of the controls' dream reports did show RAGE. A two-tailed Mann–Whitney U test showed that this difference was significant, U = 483, p = .033, r = -.26. There were no significant differences for any of the other basic emotions.

3.2.3. The wish fulfilment scale

The UWD patients' dreams had a higher median wish-fulfilment score than the controls' dreams did (see Fig. 3C), and a two-tailed Mann–Whitney U test showed that this difference was significant, U = 377, p = .010, r = .30.

3.2.4. Incidence of nightmares

Only 1 of the 23 UWD patients' dream reports was classified as a nightmare, as were 12 of the 52 controls' dream reports (see Fig. 3D). A two sided chi-squared test just missed the threshold for significance; χ^2 (1) = 3.90, p = .055, ϕ_{Cramer} = .23. However, as the expected count for one of the cells in the contingency table was smaller than five, the chi-square statistic may be under-estimated. For this reason, Fisher's exact test statistic has been reported. The odds ratio indicated that the controls were 6.6 times more likely to report a nightmare than the UWD patients were.

3.2.5. Word and narrative item count

The UWD patients' dream reports had a lower mean word count than the dream reports from the control participants (see Fig. 3E). A two-tailed Mann–Whitney U test indicated a significant difference, U = 339.5, p = .003, r = -.37.

For the narrative item count a two-tailed Mann–Whitney U test indicated that the average narrative count of the UWD

patients' dream reports was significantly lower than the average narrative count of the controls' dream reports, U = 406, p = .027, r = -.28.

3.2.6. Incidence of threat and escape

A two sided chi-square test revealed that the incidence of threat in the dream reports was not contingent on whether the dreamer was an UWD patient or not, χ^2 (1) = .22, *p* = .766, ϕ Cramer = .05 (see Fig. 3F).

In the subsequent analyses concerning the nature of the threats as well as the participant's response to the threat, the contingency tables contained at least one cell with an expected count of less than five. Fischer's exact test statistic is reported in attempt to combat the resultant increase in the likelihood of coming to a false negative conclusion.

33.3% of the threats counted in the UWD patients' dream reports were life-threatening, as were 72.7% of the threats in the controls' dream reports. However, a two-sided chi-square test returned a non-significant result, χ^2 (1) = 2.49, p = .162, ϕ Cramer = .38.

The vast majority of the threats experienced by both the UWD patients and the controls were ancestral as opposed to modern (83.3% for the UWD patients and 90.7% for the controls). A chi-square test produced a non-significant result.

All of the UWD patients who reported a threat in their dream also reported an escape from the threat, as did 63.64% controls. According to the odds ratio, UWD patients were 3.25 times more likely than controls to report escaping the threat in their dreams; however, a two-sided chi-square test returned a non-significant result, χ^2 (1) = 2.85, p = .237, ϕ Cramer = .41.

Whether the escape was realistic or not was also not contingent on whether the dreamer was an UWD patient or not. In total, 2 of the 23 dream reports from UWD patients (8.7%), and 4 of the 52 dream reports from control participants (7.7%), contained a physical threat to the dreamer and a subsequent realistic escape.

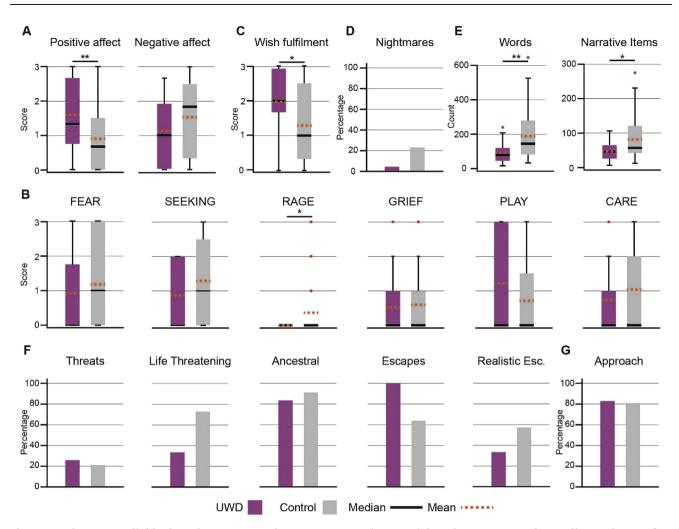


Fig. 3 – Exploratory Individual Analyses. For continuous measures (A–C & E), boxplots represent the median and range for the control and UWD patient scores. Outliers are indicated by red points and the mean is also indicated. (A) The range of scores for positive and negative dream affect scale. (B) The range of scores for the affective dream scale. (C) The range of scores for the wish fulfilment scale. (D) Percentage of dream reports coded as nightmares for UWD patients and controls. (E) The range of word and narrative item counts. (F) Incidence of threat and escape results for UWD patients and controls: the Threats plot indicates the percentage of dream reports which contained a threat. The Life Threatening plot indicates the percentage of threats which were coded as life threatening. The Ancestral plot indicates the percentage of threats which were coded as ancestral, as opposed to modern. The Escapes plot represents the percentage of threats which were escaped. The Realistic Esc. plot represents the percentage of escapes which were realistic. (G) The percentage of dream reports coded as consisting of predominantly approach as opposed to avoidance behaviour, for UWD patients and controls.

3.2.7. Classification of approach versus avoidance behaviour Both the UWD patients and the control participants showed considerably higher levels of approach as opposed to avoidance behaviour in their dream reports: 82.6% of the UWD patients' dream reports and 80.8% of the controls' dream reports were coded as constituting of predominantly approach behaviour (see Fig. 3G). A chi square analysis returned a nonsignificant result.

4. Discussion

Confirming Wiest and Brainin's (2010) single-case report, this study shows that patients without functioning basolateral amygdalae are clearly able to generate dreams and to remember their dreams. Therefore, despite high levels of activation during REM, and somewhat contrary to ideas put forth by many theorists, the BLA does not seem to be *indispensable* for the production of dreams or dream plots (unlike the medial forebrain bundle and parietococcipital cortex; Solms, 1997). The UWD patients in our study were able to recall a recent dream on each occasion they were requested to and they did not appear to struggle to recall dreams any more than the control participants did.

The convincing grouping of the various measures onto three underlying components is indicative of the measures' validity in that they seem to have probed consistent underlying characteristics of the dream reports. Correspondingly, three clear conclusions emerge from a comparison of the UWD patients' and the control participants' scores on these components, and they are reinforced by the subsequent analyses of each of the individual measures. Firstly, UWD patients scored significantly lower on the 'unpleasantness' component (or higher on 'pleasantness') than control participants. This indicates that UWD patients' dream reports were less emotionally negative than the controls' reports. Furthermore, and most convincingly, this score suggests that the dream reports of UWD patients are significantly more pleasant than the dream reports of control participants, as positive emotion, PLAY and wish fulfilment all had very strong negative loadings on this component.

Echoing this finding, the UWD patients' dream reports also showed a significantly higher mean intensity of positive emotion on the PANDAS scale than the control dream reports. Likewise, the UWD patients' dream reports showed a significantly higher level of wish fulfilment than the control dream reports. High levels of wish fulfilment in dream reports are most typically observed in children's dream reports (Colace, 2010), and in this sense the UWD patient dream reports could be seen as somewhat childlike.

The common current hypothesis regarding the effects of amygdala damage on dreaming is that it should lead to reduced negative dream affect (Domhoff, 2001; Hobson et al., 2000; Revonsuo, 2000) and possibly also to reduced dream affect in general (Corsi-Cabrera et al., 2016; Maquet & Franck, 1997; Nielsen & Stenstrom, 2005). As the UWD patients scored significantly lower on the unpleasantness component, our results do provide some support for the idea that the amygdala is involved in the intensity of negative emotions in dreams. In addition, the UWD patient dream reports showed significantly less RAGE than the control dream reports. However, due to the very infrequent observances of RAGE in the dream reports (indeed, RAGE was totally absent from all UWD dream reports), this result should be interpreted with caution.

Although the UWD dream reports had a lower mean score than control dream reports on the intensity of negative emotion, a two-tailed Mann–Whitney test returned a nonsignificant result. Moreover, based on the strength with which the various variables loaded on this first component, it may be that increased positive emotion in UWD patients' dream reports, as opposed to decreased negative emotion, is mostly driving the strong between group difference on the 'unpleasantness' component. Certainly, the notion that the amygdala is critical for the production of dream emotion in general is called into question by our finding that the UWD patients' dream reports in fact show increased positive emotion relative to the controls' dream reports.

Nevertheless, our results echo those by De Gennaro et al. (2011) in that they do implicate a role for the amygdala in determining the intensity of dream affect. De Gennaro et al. (2011) showed that decreased volume of the right amygdala was associated with increased emotional intensity, which may fit with our finding that BLA damage was associated with increased intensity of positive emotion. However, they found that decreased structural integrity of the left amygdala was associated with decreased emotional intensity. It is difficult to interpret exactly how this relates to our results, as our study cannot speak to the possibility of laterality effects in amygdala function. Moreover, De Gennaro et al. (2011) did not differentiate between positive or negative valence of dream affect in their analysis, whereas we found divergent associations between positive and negative dream affect and BLA damage. The second component to emerge from the factor analysis demonstrated that the UWD patients' dream reports were significantly shorter and less complex than those of the controls. Not only did the patients differ significantly from controls on this 'length' component, the difference in word count was also significant and the narrative item count revealed that the UWD patients' dream reports contained significantly fewer meaningful units of information, and less detail, leading to simpler dream narratives. These results are apparently consistent with De Gennaro et al's (2011) finding that increased diffusivity of the left amygdala is associated with shorter dream reports.

However, it is difficult to determine whether reduced length reflects a quality intrinsic to the UWD patients' dreams, as it might be influenced by impaired emotionally relevant narrative memory in general. Although affective narrative memory has not been systematically assessed in these patients, it seems reasonable to assume that it may well be impaired, considering the widespread finding that the amygdala (and particularly the BLA) is implicated in emotional memory (e.g., Adolphs, Tranel, & Buchananan, 2005; Cahill, Babinsky, Markowitsch, & Mc Gaugh, 1995; McGaugh, 2018; Phelps & LeDoux, 2005). Of course, this possibility in no way precludes the UWD patients' actual dreams from being shorter and simpler than the norm, and indeed, disentangling dream from dream memory will always be a complex (if not impossible) process.

Thirdly, the dream reports of the UWD patients showed similar levels of 'threat' to those of the control participants. This may be surprising, given the vast literature linking the amygdala to fear processing. It appears that although there were similar levels of threatening situations and appropriate FEAR responses among both groups' dream reports, the threatening situations may have been experienced with less intense negative emotion, and may have been more frequently resolved in the UWD patients' reports than in the controls' reports. Indeed, UWD patients were 3.25 times more likely than controls to escape from a threat in their dream report. Although this difference was not significant, this is unsurprising considering that only a small number of dream reports contained any threat at all.

A plausible interpretation of these results is that, although dangerous situations occur with normal frequency in the dream reports of UWD patients, their negative emotional *experience* of these situations tends to be less intense than that of controls. Furthermore, the threats in the UWD dream reports could be seen as more manageable than the threats in control dream reports, as they seem to be resolved more frequently. For example, one of the UWD patients reported dreaming that she was lost in a big city among crowds of people, feeling tense and a bit frightened – until her brother came up to her and told her she had taken a wrong turn, and showed her which way to go. This outcome left her feeling "happy" and "excited". However, considering the scarcity with which significant threats and subsequent escapes were observed in our sample, this interpretation cannot be conclusive.

It is also interesting that the UWD patients were 6.6 times less likely to report a nightmare than the control participants were. This seems to be consistent with research linking elevated prevalence and severity of nightmares to overactivation of the limbic system in patients with posttraumatic stress disorder (Levin et al., 2010). Although a chisquare test just missed significance, this result still provides a degree of support for the hypothesis that the amygdala is involved in the generation of nightmares (Domhoff, 2001; Levin & Nielsen, 2007; Revonsuo, 2000).

Once again, the lack of significance can surely be attributed to the low numbers of nightmares observed in our sample over-all. Indeed, the frequency of nightmares in the adult population is typically very low (Sandman et al., 2013), and a small sample such as ours is therefore inappropriate for properly assessing nightmare frequency. Nevertheless, this apparent difference in frequency of nightmares, but not in 'danger' or FEAR levels, does fit with the interpretation that, although there can be negative and threatening aspects to UWD patients' dreams, they may not respond as emotively to these aspects as control participants.

The lack of significant difference between UWD and control dream reports on the 'danger' component or on FEAR is in line with a shift away from viewing the amygdala as a simple fear centre in the brain (e.g., Barrett & Satpute, 2017; LeDoux & Pine, 2016). Indeed, preserved fear responses, and even hyperreactivity to certain fear cues, have been demonstrated in this same population of UWD patients during waking (Terburg et al., 2012; 2018). It is likely that the preservation of the CMA, alongside degeneration of the BLA, leads to a disinhibition of the CMA and is responsible for the hyper-reactivity observed in these patients in waking. Whether CMA preservation is also responsible for the preserved levels of threat and FEAR observed in the present study is plausible but remains difficult to say. The generation of threatening situations in dreams, as indeed the generation of any dream content, may well depend on a much larger network of dream production.

This absence of a significant difference on the 'danger' component, and also between specifically measured levels of threat and approach versus avoidance behaviour, does not support Revonsuo's (2000) threat simulation theory of dreaming. According to this theory, dreaming primes the fearconditioning network (which centres on the amygdala) and should therefore be impaired in patients with BLA lesions. However, only a small percentage of the dream reports collected (from both controls and UWD patients) included a significant threat and subsequent realistic escape, and BLA damage thus appeared to have no significant impact on this tendency. This replicates previous studies showing low levels of threat and escape in dreams (Malcolm-Smith et al., 2008; Malcolm-Smith & Solms, 2004; Zadra, Desjardins, & Marcotte, 2006). In addition, we replicated Malcolm-Smith et al. (2012)'s finding that dream reports contain more approach than avoidance behaviour, and showed that bilateral BLA damage likewise has no significant impact on this tendency.

The finding of preserved ability to generate dream emotions despite bilateral BLA damage is consistent with research which suggests that the amygdala is involved in modulating reactions to perceived affective stimuli, and not in the generation of affects per se (Adolphs, 2010; Sander, Grafman, & Zalla, 2003). This is also consistent with preserved, and indeed at times enhanced, emotional reactivity in this same population of UWD patients during waking (Terburg et al., 2012; 2018). The present findings suggest that the amygdala does play a role in the subjective emotional *experience* of dreams, as bilateral BLA damage was associated with increased positive dream affect, and some analyses also point towards decreased negative dream affect.

These results provide some support for the idea that the BLA's role chiefly relates to analysing the valence of emotionally charged stimuli and modulating central medial amygdala responses (De Gelder et al., 2014; Pessoa, 2010; Pessoa & Adolphs, 2010; Sander et al., 2003). Such a hypothesis would be in line with our findings which suggest that, despite equivalent levels of threat in UWD patients' dream reports when compared to controls' dream reports, the patients may demonstrate less negative emotion in response to these threats, and instead show more persistent positive emotion.

It is unclear how this relates to the narrative simplicity of the UWD patients' dream reports. However, in line with emotion regulation theories of dreaming (see Van Der Helm et al., 2011), we may tentatively speculate that dream narratives are reactions to dream affects (perhaps negative affects in particular), rather than the other way around. Narrative simplicity, like wish fulfilment, is typical of children's dream reports (Colace, 2010), and it may be interesting to consider that the UWD patients' dream reports appear to resemble children's dream reports in this characteristic as well. Furthermore, the reduced length of the UWD patients' dream reports is likely to be related to the role of the BLA in emotional episodic memory consolidation during both REM sleep and wakefulness.

Lastly, it is important to bear in mind that the intensity of dream emotion may have important implications for dream recall. The salience hypothesis of dreaming (Cohen & MacNeilage, 1974) put forward the idea that the salience of dream material is an important determinant of dream recall, and that the emotional intensity of a dream is one of the central aspects of its salience. Subsequent investigations have provided support both for (Parke & Horton, 2009; Watson, 2003) and against (Schredl, 2000) this hypothesis. The current results do not support the salience hypothesis, especially regarding negative emotion, as dream recall was preserved despite lesions to the BLA (a structure which is thought to mediate the effect of emotion on memory), and despite the reduced intensity of negative emotion in the UWD patient's dream reports relative to those of controls. However, the intensity of positive emotion was significantly higher in the UWD patients' dream reports than in those of controls.

5. Limitations

Some limitations should be addressed here, in addition to the various limiting factors which have come forward thus far. Firstly, it is true that the sample of dream reports collected from the UWD patients is relatively small, and unequal to the sample collected from the control participants (twenty-three dream reports from eight UWD patients and fifty-two dream reports from seventeen controls). Although this reduces the power of the statistical analyses we report, it should be noted that most prominent studies to have been published with such patients have involved single case studies or samples of only a couple of patients.

Secondly, it was not possible to test the dream reports of the UWD patients before the development of the BLA lesions, and as such we have no intra-subject comparison point. It should also be noted that these lesions develop progressively, and some corresponding brain adaptation is therefore likely. In addition, the lesions are not entirely limited to the BLA in all our patients, nor are we able to totally eliminate the possibility of some remaining BLA function in our patients, though the structure is certainly significantly deteriorated. Furthermore, the possibility of a general deficit in emotional episodic memory in the UWD patients has not yet been empirically explored, and could play a role in the current findings.

6. Future directions and conclusion

To better understand the possible role that abnormalities in the UWD patients' memory functioning might play in the present findings, a systematic assessment of emotional narrative memory in these patients versus matched controls would be enlightening. In addition, although it was not possible to collect dream reports in a sleep laboratory for the present study, this possibility should be explored with UWD patients who are more accessible to such investigations. This would entail waking participants from REM sleep and asking them to recall their dreams immediately, thereby reducing the risk of forgetting and other memory confounds. Another potentially useful methodological approach, which should be explored in the future but was not feasible in the present group of patients, would be to investigate the dream frequency and content evolution before and after 1 month of dream diary. As dream diaries are known to increase dream recall frequency and dreams length (Schredl, 2002), such an experiment could further elucidate the role of the amygdala in dream production or dream recall. However, these approaches would potentially entail a trade-off in sample size, since the large (but socioeconomically disadvantaged and geographically isolated) community of UWD patients that participated in our study is highly unusual, if not unique.

It would be worth testing whether the emotional intensity of waking life memories is attenuated in UWD patients' dreams as in healthy subjects' dreams (Vallat et al., 2017). This would improve our understanding of the role of the amygdala in emotion depotentiation during sleep. It would also be of interest to further explore the apparent similarities between the UWD patient's dream reports and children's dream reports, along with the implications that this could have for contemporary Freudian dream theory in terms of a potential role for the BLA in this theory. Finally, in order to learn more about the potential contribution of other amygdala regions to dreaming, it would be revealing to examine dream reports in patients with lesions to the entire amygdaloid complex.

In summary, our results suggest that bilateral BLA damage leads to dream reports that are shorter, simpler, and more pleasant than those of controls (see the Supplementary Materials for the English translations of all the UWD patient dream reports). Nevertheless, threatening experiences occur with unaltered frequency in the dream reports of patients with bilateral BLA lesions. This study thereby provides the first empirical evidence that the BLA plays an important role in the production of dream affect and dream narratives, while calling into question dream theories which imply that the amygdala is indispensable to dreaming.

Declarations of interest

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Supplementary data

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