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Imagetic and affective measures of memory reverberation diverge at sleep onset in association with theta rhythm

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ABSTRACT

The 'day residue' - the presence of waking memories into dreams - is a century-old concept that remains controversial in neuroscience. Even at the psychological level, it remains unclear how waking imagery cedes into dreams. Are visual and affective residues enhanced, modified, or erased at sleep onset? Are they linked, or dissociated? What are the neural correlates of these transformations? To address these questions we combined quantitative semantics, sleep EEG markers, visual stimulation, and multiple awakenings to investigate visual and affect residues in hypnagogic imagery at sleep onset. Healthy adults were repeatedly stimulated with an affective image, allowed to sleep and awoken seconds to minutes later, during waking (WK), N1 or N2 sleep stages. 'Image Residue' was objectively defined as the formal semantic similarity between oral reports describing the last image visualized before closing the eyes ('ground image'), and oral reports of subsequent visual imagery ('hypnagogic imagery). Similarly, 'Affect Residue' measured the proximity of affective valences between 'ground image' and 'hypnagogic imagery'. We then compared these grounded measures of two distinct aspects of the 'day residue', calculated within participants, to randomly generated values calculated across participants. The results show that Image Residue persisted throughout the transition to sleep, increasing during N1 in proportion to the time spent in this stage. In contrast, the Affect Residue was gradually neutralized as sleep progressed, decreasing in proportion to the time spent in N1 and reaching a minimum during N2. EEG power in the theta band (4.5-6.5 Hz) was inversely correlated with the Image Residue during N1. The results show that the visual and affective aspects of the 'day residue' in hypnagogic imagery diverge at sleep onset, possibly decoupling visual contents from strong negative emotions, in association with increased theta rhythm.

Introduction

The term 'day residue' refers to the persistence of waking contents into sleep mentation (Freud, 1900). While this concept has many potential neurophysiological correlates in animal models (Pavlides and Winson, 1989; Wilson and McNaughton, 1994; Ribeiro et al., 1999; van de Ven et al., 2016; Li et al., 2017) as well as humans (Maquet et al., 2000; Laureys et al., 2001; Huber et al., 2004; Eichenlaub et al., 2018; Murphy et al., 2018), the actual quantification of 'day residues' in dream reports remains a major challenge. The use of blind raters to score the overall similarity between experimental stimulus and subsequent dreaming has confirmed the influence of daytime events on the contents and emotional tone of dreaming (Foulkes and Rechtschaffen, 1964;

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Rechtschaffen and Foulkes, 1965; Arkin and Antrobus, 1991), but direct incorporation of experimental stimuli is low even after highly engaging visuomotor tasks (Stickgold et al., 2000; Wamsley et al., 2010a).

A further difficulty is the wide range of possible dream contents without relevant affective impact (Revonsuo, 2000; Valli et al., 2005). Given the large number of daily events with mild affective impact in a typical dreamer's experience, the contents possibly replayed during subsequent sleep are bound to be highly variable. Not surprisingly, the relationship between sleep and affect is quite complex. People stressed during waking show physiological stress signs during ensuing sleep, increasing heart rate, and decreasing heart rate variability (Hesameddin et al., 2016). At present, it is unknown whether the visual contents and affective valences of the stimuli experienced during waking reverberate continuously from waking to sleep onset and onwards, or rather get reactivated *de novo* at later sleep stages, with further filtering, linking, editing, and distortion. Consequently, the many conflicting theories of dream function lack common ground for objective confrontation, and despite the abundance of results, a dispute persists on whether dreams reflect the enhancement, inhibition ("censorship") or transformation of waking memories (Freud and Breuer, 1895; Stickgold et al., 2000; Wagner et al., 2004; Stickgold and Walker, 2007; Valli and Revonsuo, 2009; Baran et al., 2010; Wamsley et al., 2010a; Wamsley et al., 2010b; Sara, 2010; Fischer et al., 2011; Kröner-Borowik et al., 2013; Solms, 2013; Kouider et al., 2014; Malinowski, 2015; Noreika et al., 2015; Solms, 2015; Llewellyn, 2015; Murphy et al., 2018). Since sleep is a sequential process that involves very different types of mentation, the investigation of memory reverberation at sleep onset is crucial to understand the sequence of transformations undergone by the 'day residue'.

The study of brain function during dreaming is intrinsically challenging. For decades it was debated whether dream reports obtained from awakenings performed across full nights of sleep were related to brain activity immediately before awakening, immediately after awakening (Malcolm, 1956; Dennett, 1976; Noreika et al., 2015) or were, in fact, a carry-over from previous REM sleep episodes (Kales et al., 1966; Nielsen, 2000). Progress was achieved by studying EEG recordings and comparing sleep trials with or without dream recall (Chellappa et al., 2011; Marzano et al., 2011). In general, dream recall is associated with high-frequency theta power during REM sleep, and low-frequency alpha power during NREM sleep. Awareness of specific dream contents correlates with high-frequency EEG activity in posterior cortical regions (Siclari et al., 2017), and visual imagery during sleep correlates best with posterior fMRI BOLD signals recorded within ten seconds of awakening (Horikawa et al., 2013).

Part of the difficulty relates to the inherently subjective, "private" nature of dreams. The notion that the latent meaning of a dream may only be interpretable by the dreamer itself makes it even harder to objectively assess dream contents (Freud, 1900). However, a similar problem has begun to be successfully addressed in the case of psychiatric evaluations, which historically were also considered inherently subjective but are becoming more objective due to quantitative speech analysis (Elvevåg et al., 2001; Cabana et al., 2011; Mota et al., 2012; Mota et al., 2014; Bedi et al., 2015; Mota et al., 2017). The estimation of semantic similarity between terms (words) or sets of terms (reports) represented in a semantic space based on the co-occurrence of words in a large set of documents (Mikolov et al., 2013) is a powerful tool not only for psychiatry but also to study dream contents (Altszyler et al., 2017).

A deeper understanding of the 'day residue' requires a clear definition of distance between waking stimulus and residue. Just like it is pointless to measure voltage without a ground, no residue can be measured without a reference for comparison. Here we show that the neural basis of the 'day residue' can be objectively studied through the combination of semantic measures, EEG sleep markers and a multiple awakenings protocol with affective images as pre-sleep ground stimuli (Fig. 1). This protocol effectively grounds each measure to a reference stimulus, creating a consistent and precise metric for the estimation of visual and affective day residues. Our strategy allowed us to tackle important questions: What happens to the visual content and affective valence of the memory that lingers from the last image visualized before falling asleep? Are specific sleep oscillations or spectral measures related to the residual persistence of waking stimuli into hypnagogic imagery? As sleep begins, what neural phenomena contribute to the preservation or distortion of day residues?

We hypothesized that recall would be enhanced in N1 (Stickgold et al., 2000; Wamsley et al., 2010a). We also aimed to verify whether the time elapsed between image and imagery influenced recall and Image Residue, with the hypothesis of decay over time in both cases (Stickgold et al., 2000; Wamsley et al., 2010a). Furthermore, we assessed whether specific sleep EEG oscillations would be related to the production of imagery, irrespective of the similarity to the image used as stimulus. Here, the hypotheses were that slow oscillations such as K complexes and vertex waves would be associated with decreased recall (Chugh et al., 1996; Pace-Schott et al., 2009), while faster oscillations such as cortical spindles would be associated with increased recall (Nielsen et al., 2015). Finally, we hypothesized that Image Residues would correlate positively with cortical spindles (Nielsen et al., 2015; Schabus et al., 2004) and high-frequency EEG power in posterior cortical regions (Siclari et al., 2017).

Material and Methods

Participants

A sample of 28 adults (16 males and 12 females, age range 20-43 years; mean ± SD = 30.99 ± 7.25, all native Portuguese speakers) was assessed (Suppl. Table S1). Participants were first interviewed by a psychiatrist (NBM, first author) to screen for mental, neurological or sleep disorders, and excluded when symptoms were observed. Those approved to participate in the research were instructed to keep a dream diary for two weeks before the recording session. On the day before the experiment, participants were requested not to drink alcohol or caffeine and were instructed to reduce their habitual sleep period at night by 50% (sleep deprivation in the second half of the night), hence resulting in higher sleep pressure the next morning, during the recording session. On the day of the experiment, participants arrived at the sleep laboratory approximately one hour before their habitual awakening time. The study was approved by the UFRN Research Ethics Committee (permit # 650.714/2014) and all the participants provided written informed consent. The sample size was estimated based on a pilot study (3 experiments, image residue correlated to PSD in the theta frequency with Rho = 0.505) using an alpha error level of 5% and a beta error level of 20%, resulting in N = 28.

EEG recordings

Preparation for the recording sessions usually began at 7:30, and recordings typically ran from 9:40-14:00. Upon the arrival of a participant in the laboratory, the electrode cap was positioned, and adequate impedances were set. Participants were instructed to lay reclined over an articulated sofa that allowed for comfortable sleep. A computer monitor for stimulus presentation was positioned one meter away from the participant. Recordings were performed with a 64-channel EEG system comprising two BrainAMP amplifiers (Brain Products GmbH, Gilching, Germany), at a sample rate of 1 kHz. Signals including bipolar electrooculogram (EOG) and electro-myogram (EMG) were re-referenced offline to the average reference. Lights were kept off throughout the recordings.

Experimental design

To get sufficient data from the same individuals, we collected 36 pairs of wake-sleep reports (Fig. 1a). Participants were asked to attempt to sleep at the beginning of each trial and, upon being woken up by a

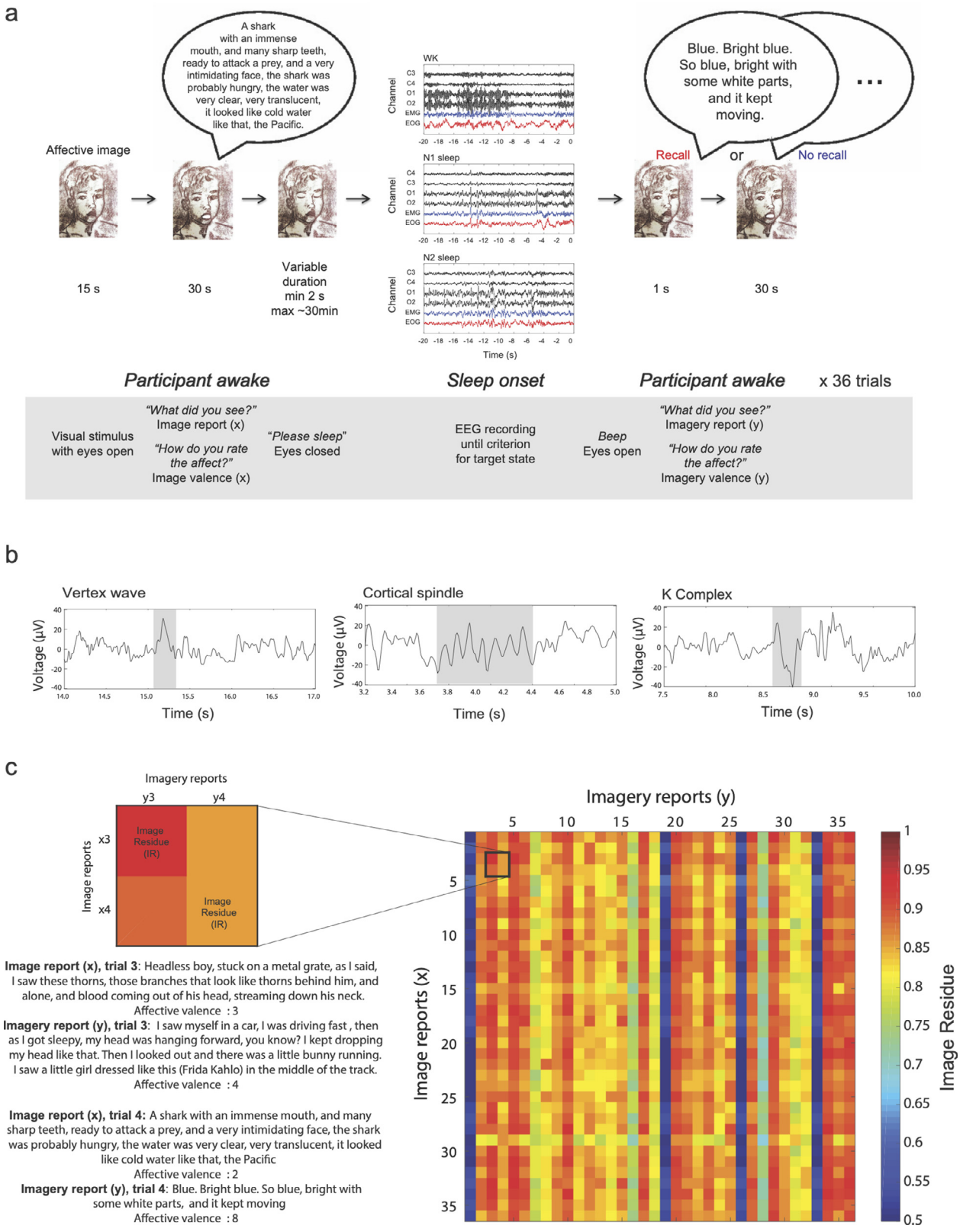

Fig. 1. Study design and semantic analysis of the oral reports. (a) Each trial comprised stimulus display, image report, eyes closure, an interval of variable length, and imagery report. Representative examples of EEG traces within WK, N1 or N2 are shown. Image report refers to the description of the visual stimulus with eyes open (x), imagery report refers to the description of the visual imagery with eyes closed (y). When the participant was able to recall any visual imagery, the trial was considered a 'recall' trial, otherwise, it was considered a 'no recall' trial. **(b)** Representative examples of vertex waves, cortical spindles, and K complexes. **(c)** Image Residue was estimated using semantic similarity. Consider 2 consecutive trials (inset). Note that trial 4 corresponds to the 'shark' image shown in (a).

beep, produce 30 s reports with a random balanced assignment of the target stage, to obtain 12 reports from WK, 12 reports from N1, and 12 reports from N2. Each trial began with the 15 s display on a computer monitor of an affective image sampled from a validated database of affective images (Lang et al., 2008), or publicly available images matched to those but with better resolution. The images were the same across participants, and the image order was randomized for every participant. The images were sorted according to affect, with 1/3 of the images (n = 12 images) being positive (e.g. children laughing, puppies), 1/3 of the images (n = 12 images) negative (e.g. shark attack, person beheaded) and 1/3 of the images (n = 12 images) neutral (e.g. a truck, an umbrella). Next, the experimenter (NBM) requested the participant to orally report on the image for 30 s. The participant was asked to report in response to the question "*what did you see*?", and to rate from 1 to 10 the affective valence of the image (1 for extremely negative, 10 for extremely positive). After this initial image report (x), the participant was instructed to close the eyes, go to sleep, and pay attention to visual imagery during the following period. Trials were randomly preassigned to WK, N1, and N2, and the resulting sequence of target states was implemented by online sleep-staging during the recording session. The criteria were as follows: for WK, robust alpha oscillations in occipital channels; for N1, marked decrease in those oscillations; for N2, presence of cortical spindles and/or K complexes (Fig. 1b). When the criterion was reached for each target stage, the experimenter triggered a beep to interrupt mentation and induce the participant to open the eyes. We aimed to capture the initial moments of each sleep stage. The median time with eyes closed before being startled by the beep that ended each trial was 128.5 s, with a minimum of 1.7 s and a maximum of 1768.5 s. The participant was asked again "*what did you see?*" to generate the imagery report (y) and rated its affective valence from 1 to 9. The individuals were also asked to report "*what did you think?*" immediately after reporting "*what did you see?*"; the analysis of data related to this second question will be reported elsewhere. Oral reports were recorded in MP4 format. When the participant was able to recall any visual imagery, the trial was considered an 'Imagery Recall' trial otherwise it was considered a 'No Recall' trial (Suppl. Table S2). Thus, for the calculation of imagery recall we only took into consideration whether the participant reported anything in response to the question "what did you see?", irrespective of the similarity between image report and imagery report. The participants were previously instructed to describe their visual experiences, and the question they answered upon being woken up (what did you see?") explicitly referred to a visual experience. There were no instances of reports occurring within non-visual sensory modalities. Since the participants were deprived of sleep during the second half of the night that preceded the experiment, they typically experienced very intrusive visual imagery upon closing their eyes. EMG and EOG signals were used for online sleep staging, which was then re-assessed offline to confirm stage identification (see below).

Measurement of image residue and affect residue

To quantitatively measure semantic similarity between oral reports (x) and (y), word embedding techniques were used. Word embedding is based on the *distributional hypothesis,* which states that semantically similar words tend to appear in similar contexts (Harris, 1954). These techniques exploit statistical regularities within large text corpora to embed words in a vector space. In this vector space, words with similar meanings tend to be located close to each other, providing a natural framework to compute semantic similarities among words. The properties of word embedding (Turney and Pantel, 2010) have applications in a wide variety of fields, including education (Foltz et al., 1999), literature (Diuk et al., 2012), dream theory (Altszyler et al., 2017) and cognitive science (Landauer and Dumais, 1997). Given that the reports were in Portuguese, we used the *Fasttext* pre-trained multilingual word embedding (Grave et al., 2018; Joulin et al., 2018). The model was built using a sliding window of predefined length that moves along a Portuguese Wikipedia corpus. At each step, a neural network was trained to predict the central word from the context, that is, from the other words in the window. Once the neural network was trained, a vector representation for each word in the corpus was extracted from the input and output layers of the model, which was used as the word embedding. To measure the semantic similarity between two oral reports, the reports were transcribed by professional personnel blind to the experiment (http://www.audiotext.com.br/), transformed to lowercase, word-tokenized and cleared from non-alphabetic tokens and stop-words using the nltk Portuguese stop-word list (Bird et al., 2009). Then, for each transcript, an average word embedding was computed. Finally, the Image Residue (IR) was calculated as the cosine similarity of the average word embedding ($\boldsymbol{v_1}$,$\boldsymbol{v_2}$)

$$IR = \cos\left(v_1, v_2\right) = \frac{v_1 . v_2}{|v_1| . |v_2|}$$

where $|\mathbf{v_i}|$ refers to the Euclidean norm of the vector $\mathbf{v_i}$.

Image and imagery reports were compared using this method (Fig. 1c).

Affect Residue (AR; Suppl. Table S2) was defined as:

$$AR = \frac{\max\left(Valence\right) - |Valence(x) - Valence(y)|}{\max\left(Valence\right)}$$

Estimation of random levels of image or affect residue

Random levels of Image and Affect Residue (Fig. 2a) were estimated for each trial and for each participant as follows: i) for each opened-eye image report we calculated the average IR and AR relative to all the closed-eyes imagery from all other participants on the same trial; ii) for each closed-eyes imagery report we calculated the average IR and AR relative to all the opened-eye image reports from all other participants on the same trial; iii) these two average values were then averaged to compose a grand-average random level for each trial per participant (Fig. 2b). Please note that the imagery reports were not systematically affected by previous trials, since there are no monotonic increases or decreases of correlations after a specific trial, but rather general high correlations across all image reports. Since all the words of each report were taken into consideration, these effects reflect the overall high degree of similarity of the words used in the consecutive imagery reports, as well as the non-predictability of the imagery reports from one trial to the next. A similar across-trial effect also occurs for low correlations (blue columns).

Offline sleep staging

Sleep staging was manually performed by a sleep scoring expert, following the standard criteria of the American Association for Sleep Medicine (Berry et al., 2015). Artifacts (eye blinks, slow eye movements, muscle artifacts and bad channels) were visually identified and excluded from subsequent analyses, using Brain Analyzer (Brain Vision Analyzer, Brain Products GmbH, Gilching, Germany). A specific EEG display montage was also used for the detection of sleep graphoelements, including F3, Fz, F4, C3, Cz, C4, O1, Oz, O2, to be compliant with AASM relative to backup electrodes in case the first recommended derivation was detected as a bad channel. Following the AASM manual recommendations, the sleep graphoelements were visually identified on the corresponding channel (e.g., K-complexes were scored over frontal derivations where they usually reach their maximal amplitude, while vertex waves over central derivations).

EEG analysis

The data were down-sampled to 100 Hz, filtered from 0.5 – 30 Hz and sleep-staged by an expert blind to the experimental procedure. A total of 1,008 trials were collected. Trials with movement artifacts were excluded, and missing channels were interpolated. Artifacts due to eye

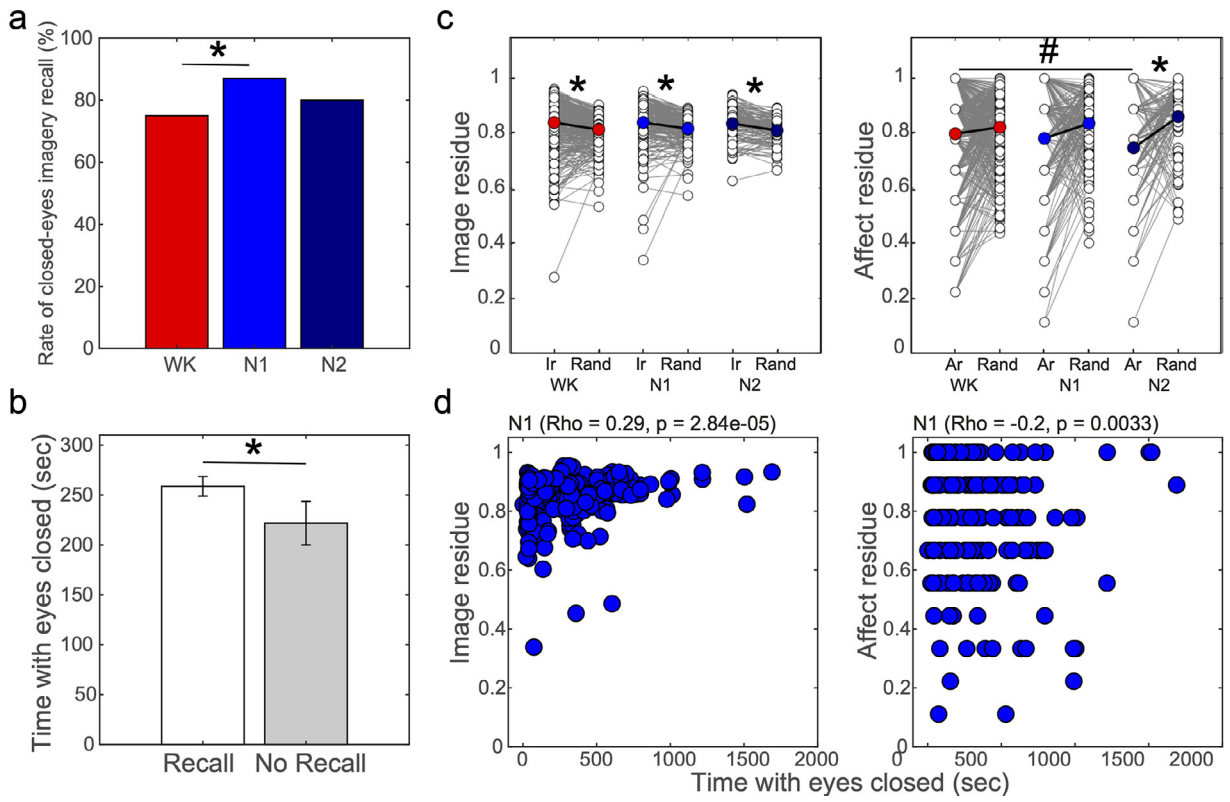

Fig. 2. Sleep onset increased imagery recall but decreased Affect Residue. (a) The Recall Rate of closed-eyes imagery was significantly higher at N1. * indicates significant differences using the Chi-square test (Bonferroni correction for 3 comparisons, $\alpha = 0.0167$) **(b)** Trials with imagery recall were longer than trials with no imagery recall (Bonferroni corrected for 4 comparisons, $\alpha = <0.0125$). **(c)** Image and Affect Residues compared to random values for WK, N1, and N2. Wilcoxon Ranksum test with Bonferroni correction, * for differences between Image or Affect Residues compared to random values and, # for difference between WK and N2 (correction for 6 comparisons, $\alpha = 0.0083$). **(d)** Image or Affect Residues versus time with eyes closed during N1 trials. Spearman's correlation Rho and p values indicated on top (Bonferroni correction for 12 comparisons, $\alpha = 0.0042$). Note that the distribution of Image Residues is strongly concentrated within large values (> 0.6), while the span of Affect residues is much wider, including small values (< 0.4). Since the confidence interval of the Spearman correlation between time with eyes closed and Image Residue (Rho: 0.1539 to 0.4101) does not overlap with the corresponding confidence interval for Affect Residue (Rho: -0.3324 to -0.0689), the difference between them is significant. There is, therefore, substantially more decay over time in Affect Residue than in Image Residue, which seems to increase over time during N1.

movements and heart beats were automatically removed using independent component analysis (ICA). The four steps performed for artifact removal are described below. First, the ICA method was applied to decompose the EEG data into independent components (ICs). For this, the EEGLAB´s function 'runica' was used. Second, the computed ICs were processed by the ICLabel EEGLAB´s plug-in (Pion-Tonachini et al., 2019) generating a multi-label classification vector for each IC (IC-Class vectors). The IC-Class vectors indicate the probability that each IC belongs to seven different classes: 'Brain', 'Muscle', 'Eye', 'Heart', 'Line Noise', 'Channel Noise' and 'Other'. As a result of this step a classification matrix was obtained, where each row represents an IC-Class vector. Then, each IC-Class vector was converted to binary values 'Brain' or 'non-Brain'. The IC-Class vectors that exceeded a predefined threshold (Pion-Tonachini et al., 2019) for the classes 'Eye' or 'Heart' but did not exceed a threshold for 'Brain' were labeled as 'non-Brain' components. In contrast, those IC-Class vectors that surpassed a threshold for 'Brain' and did not surpass the specified value for the other classes were labeled as 'Brain' components. The following threshold values were used to determine the category that excels the respective value: 'Brain' = 0.44; 'Muscle' = 0.18; 'Eye' = 0.13; 'Heart' = 0.33; 'Line 'Noise' = 0.04; 'Channel Noise' = 0.13; 'Other' = 0.15. With the aim to classify all ICs, a Support Vector Machine (SVM) classifier was trained by using the previously labeled IC-Class vectors as the training set. Presentation of the classification matrix to the SVM classifier allowed for an estimation of the class ('Brain' or 'non-Brain') for each IC. Finally, the ICs classified as 'Brain' were back projected, which resulted in clean EEG data.

A total of 930 artifact-clean trials were used for subsequent analyses (534 trials in Waking, 238 trials in N1 and 158 trials in N2). The data were analyzed using Matlab and the EEGLAB toolbox. The EEG record was segmented into trials of 20 s, starting 20 s before an awakening. For each segment, vertex sharp waves, sleep spindles and K complexes were marked by the expert (Fig. 1b). In addition, Power spectral density (PSD) using the Welch method was computed for each segment (Welch, 1967). In total, 14 frequency bands were analyzed from 0.5 Hz to 28.5 Hz, with a frequency bandwidth of 2 Hz. For each channel in the EEG dataset, the Power Spectral Density (PSD) was computed with the pwelch Matlab function using 4 s of Hamming window length, 80 % overlap, 512 frequency points, 'oneside' option. For each channel, trial and participant index the relative power in selected frequency bands (Pow_Band_i) was computed as follows (for simplicity the indexes for a channel, trial, and participant were omitted in the equation):

$$Pow_{Band\,i\,i} = \frac{\sum_{f\,Low_i}^{f\,High_i} PSD}{\sum PSD} \quad i = 1, 2, \ \ldots, 14$$

where *High* and *Low* refer to the upper and lower boundaries of each frequency band.

Spearman correlations between Image and Affect Residue and EEG power were calculated (Fig. 4).

Statistical analysis

Kolmogorov-Smirnov and Levene tests showed that the Image Residue and Affect Residue data are not normally distributed but had homogeneous variance. Kruskal-Wallis tests were used to verify differences related to wake-sleep stages (Suppl. Table S3). Other non-parametric statistical tests employed were the Chi-square, Wilcoxon Ranksum, Wilcoxon signed-rank test, and Spearman correlation. In Fig. 4, statistical significance at $\alpha = 0.05$ was estimated using the Bonferroni correction for multiple comparisons across the 64 EEG electrodes, 14 frequency bands and 3 wake-sleep stages considered, which corresponds to $\alpha = 0.0000186$.

In Fig. 3 the entropies of the valence distributions were calculated as

$$S = -\sum_{i=0}^{n} p * \log_2(p)$$

Data and code availability

The dataset and code generated in the current study are available from the corresponding author upon request.

Results

Imagery recall

A total of 28 adult participants were assessed (Suppl. Table S1). We first determined the degree of Imagery Recall (i.e., presence or absence of imagery) for the different sleep-wake stages. Although Imagery Recall was quite high across stages, a significant increase was detected as participants transited from WK to N1, as hypothesized (WK: 75.1 %; N1: 87.4 %, N2: 80.4 %, Chi-square p = 0.0001 for WK vs. N1, other comparisons were not significant, Fig. 2a). When all trials from WK, N1, and N2 were pooled, Imagery Recall was related to longer periods with eyes closed, in comparison with 'No Recall' trials (Wilcoxon Ranksum, p = 0.0067, Fig. 2b). In other words, the longer the participants processed the image with eyes closed, the more likely they were to produce an imagery report thereafter. This effect was not detected for any specific stage (WK p = 0.0862; N1 p = 0.6881; N2 p = 0.6583). No differences related to sleep oscillations were found between trials with and without Imagery Recall (Wilcoxon Ranksum p values: Vertex: N1 = 0.3086, N2 = 0.8876; Spindles: N2 = 0.4178; K Complexes: N2 = 0.6372).

Image and affect residue

To characterize the 'day residue' within each stage, Image Residue and Affect Residue were compared with their corresponding randomized values. Image Residue values were higher than random levels across stages (Wilcoxon Ranksum, p < 0.0001 for the three stages considered, Fig. 2c, Suppl. Table S3), while Affect Residue values were similar to random values for WK and N1, and lower than random levels at N2 (Wilcoxon Ranksum, p < 0.0001, Fig. 2c, Suppl. Table S3). Next, we evaluated whether the Image or Affect Residues differed significantly across stages. This occurred only for Affect Residue (Kruskal-Wallis p = 0.0051, Suppl. Table S2), which was higher in WK trials than in N2 trials (Fig. 2c, Wilcoxon Ranksum p = 0.0010, Suppl. Table S3). Image Residue showed no significant differences across stages (Fig. 2c, Suppl. Table S3). Although there were no Image Residue differences across stages, exclusively for N1 there was a significant and positive correlation with time spent with eyes closed (Spearman Rho = 0.29, p < 0.0001, Fig. 2d, Table 1). Interestingly, also for N1 only there was a significant negative correlation between Affect Residue and time with eyes closed (Spearman Rho = -0.20, p = 0.0033, Fig. 2d, Table 1). There were no significant correlations between sleep biomarkers and either Image or Affect Residues (Table 1). There were no word count differences between eyes open and eyes closed for stages N1 and N2, but there was a significant difference during WK (Suppl. Table S4). Furthermore, across the three stages of interest there were significant positive correlations between Image Residue and word count, with eyes open as well as closed (Suppl. Table S4). Thus, the more the participant talked about both image and imagery, the greater was the similarity between their imagetic contents. In contrast, there were no significant correlations between word count and Affect Residue (Suppl. Table S4).

Next, we sought to describe the dynamics of affective valences between Image and Imagery, and the relationship between their residues. We found a positive correlation between the affective valences of Image and Imagery in WK and N1 trials, with the strongest effect in WK trials (Spearman correlation, WK Rho = 0.39, p<0.0001; N1 Rho = 0.25, p = 0.0003; N2 Rho = 0.17, p = 0.0635; Fig. 3a). In addition to the rescaling (rank preservation as indicated by positive Spearman correlations) of the affective valences, we observed a neutralization of the affective valences for Imagery, in comparison with Image (Fig. 3b; Kolmogorov-Smirnov test for affective valence distributions for WK p<0.0001, N1 p = 0.0005, and N2 p<0.0001, with Bonferroni correction for 3 comparisons, $\alpha = 0.016$).

For the three states considered, the variance of the affect scores decreased from the image report (eyes open) to the imagery report (eyes closed), reflecting affect neutralization (mean ± variance: from 5.13 ± 2.49 to 5.57 ± 1.82 in WK; 5.11 ± 2.45 to 5.42 ± 1.62 in N1; 5.41 ± 2.65 to 5.18 ± 1.44 in N2). To further characterize this neutralization, we counted the amount of neutral affective valence grades and compared the frequency after the visualization of image (eyes open) or imagery (eyes closed). As shown in Fig. 3c, there was significant affective neutralization for imagery obtained within WK, N1 and N2. In addition, the entropies of the distributions dropped substantially from Image to Imagery, with the strongest effect within N2 (Fig. 3d). There was no significant correlation between Image and Affect Residue, nor between Image Residue and the affective valences of Image or Imagery, neither when considering all trials, nor when considering specific stages (Rho values ranging from -0.12 to 0.7, p > 0.05).

Power spectrum density versus Image or Affect Residue

In contrast with affective valences, the visual contents were far from neutralized in Imagery, which produced a semantically rich set of reports and a wide dynamic range of Image Residues (Fig. 1c, correlation matrix). To gain insight into the neural correlates of the Image Residue at sleep onset, we investigated how Image Residue related to EEG oscillations and power spectrum density within the 20s interval before each beep that terminated the WK, N1 and N2 trials.

First, we assessed the correlations of Image Residue with the abundance of vertex sharp-waves, cortical spindles, or K complexes. Contrary to our expectations for cortical spindles, no significant correlations were detected (Table 1). Similar results were observed for Affect Residues (Table 1).

Next, we assessed the correlations of Image and Affect Residues with EEG power within specific frequency bands. Well-established EEG spectral markers of the target stages were observed, such as the robust occipital alpha (8.5-10.5 Hz) power during WK, the surge of theta power (4.5-8.5 Hz) during N1, and the drop in EEG power for frequencies > 8.5 Hz during N2 (Suppl. Fig. S1). During WK there were significant negative correlations between Image Residue and power in both the theta (4.5 to 6.5 Hz) and low beta (14.5-16.5) bands, with significant positive correlations between Image Residue and power in the high beta band (24.5 to 28.5Hz) (Fig. 4a). During N1 there were significant negative correlations between Image Residue and power in the theta band (4.5 to 6.5Hz), as well as significant positive correlations between Image Residue and power in the high beta band (22.5 to 28.5Hz). No significant correlations were detected during N2. Although there was an overall similarity of WK and N1 regarding the correlations between Image Residue and

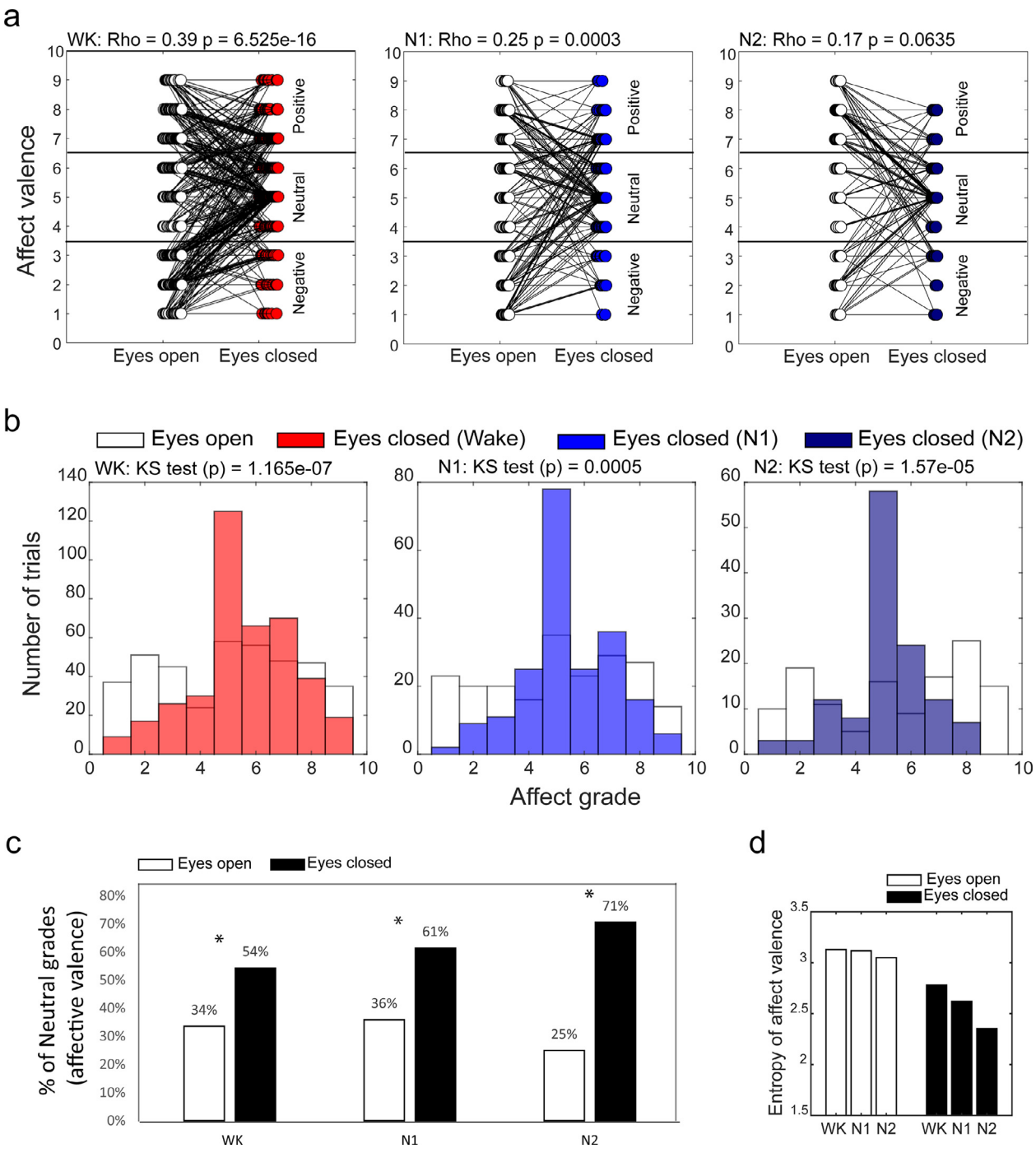

Fig. 3. Sleep onset neutralized affects. (a) Affective valences informed by the participants related to Image (eyes open) or Imagery (eyes closed). Most of the trials showed a neutralization of Imagery valences irrespective of Image valence. This neutralization corresponded to a valence rescaling since the valence ranks for WK and N1 trials were to some extent preserved (Spearman's Rho and p values indicated on top). **(b)** Although the distribution of affective valences was uniform for the Images (eyes open), for Imagery (eyes closed) there was a concentration of valences around neutral values. Kolmogorov-Smirnoff tests confirmed that the Image and Imagery distributions were quite different for the three stages considered (p values on top). Negative valences comprised [0-3], neutral valences comprised [4-6] and positive valences comprised [7-10]. **(c)** The amount of neutral affective valence grades increased from the visualization of images (eyes open) to the visualization of imagery (eyes closed), as shown by a chi-square test (* indicates $p < 0.0001$ for the three stages considered). **(d)** The entropies (in bits) of the valence distributions decayed from Image (eyes open) to Imagery (eyes closed), with the most reduction observed in N2 trials.

EEG power within specific frequency bands, the distribution of significant channels revealed interesting topographic difference across states. The right-hemisphere region of negative correlations with EEG power in the theta band was substantially larger in N1 than in WK, and the single negative correlation with the low beta band found in WK was absent from N1. Furthermore, the positive correlations between Image Residue and EEG power in the high beta band observed during WK in central frontal channels was clearly shifted to parietal and occipital channels over the right hemisphere during N1. The correlations between Affect Residue and EEG spectral bands were non-significant, with the excep-

Table 1
Image and Affect Residues correlated significantly with the time spent with eyes closed in N1, but not with the abundance of vertex sharp-waves, cortical spindles, or K complexes. The results correspond to Spearman Correlations between Image Residue and the variables of interest. For the significant cases, with Bonferroni correction for 12 comparisons ($\alpha = 0.0042$), Rho and p values are indicated in boldface.

Correlations	Vertex waves		Cortical spindles		K Complexes		Time with eyes closed	
Image Residue	Rho	p	Rho	p	Rho	p	Rho	p
WK	n/a	n/a	n/a	n/a	n/a	n/a	-0.04	0.3784
N1	0.14	0.0387	n/a	n/a	n/a	n/a	**0.29**	**2.84E-05**
N2	0.07	0.4564	-0.09	0.2890	0.00	0.9722	0.07	0.4095
Affect Residue	**Rho**	**p**	**Rho**	**p**	**Rho**	**p**	**Rho**	**p**
WK	n/a	n/a	n/a	n/a	n/a	n/a	-0.09	0.0633
N1	-0.17	0.0118	n/a	n/a	n/a	n/a	**-0.20**	**0.0033**
N2	-0.06	0.4937	0.00	0.9912	0.02	0.8073	-0.17	0.0620

tion during WK of two frontal right channels in the right hemisphere (Fig. 4b), which showed significant negative correlations with power in the beta band (18.5 to 20.5Hz).

Discussion

Here we used tools from natural language processing and a systematic comparison of image and imagery reports to provide the first quantitative description of how Image and Affect Residues change in the transition from waking to sleep. We took advantage of the hypnagogic imagery at sleep onset, which offers the chance to collect dozens of reports per recording session (Foulkes, 1962; Nielsen, 2000; Stickgold et al., 2000; Horikawa et al., 2013). As expected, mind wandering began soon after the eyes were closed, leading to visual hypnagogic imagery. As expected, the highest incidence of imagery recall occurred during N1 (Fig. 2).

Of note, the affective valences experienced before falling asleep were not preserved or intensified by it, but rather converged towards neutral emotional valences. Affects were strongly neutralized in Imagery reports across the three stages of interest (Fig. 3). These results are in accordance with the literature, as they add direct evidence for the role of sleep for affective regulation (Revonsuo, 2000; Valli et al., 2005; Nishida et al., 2009; Sterpenich et al., 2009; Gujar et al., 2011; van der Helm et al., 2011; Payne et al., 2012) (Groch et al., 2013; Menz et al., 2013; Payne et al., 2015; Werner et al., 2015; Alger and Payne, 2016; Hesameddin et al., 2016). The significant correlation between the affective valences of Image reports and their corresponding Imagery reports within WK and N1 trials (with stronger effects in WK) indicates that the neutralization of affects before sleep onset represents a partial rescaling, i.e., a semi-orderly compression of the dynamic range of affects (Sterpenich et al., 2009).

Image Residues did not differ across stages and remained significantly above random levels for the three stages, in contrast with Affect Residues, which collapsed below random levels in N2 trials. This indicates that the imagetic and affective aspects of the memory trace are differentially processed. While the sleeping participants tended to preserve the imagetic contents of recently acquired memory traces, the affective valence began to be neutralized just after closing the eyes, with strongest effects at sleep onset. The lack of any significant correlations between Image and Affect Residues, neither considering all trials nor each stage, further suggests that the imagetic and affective aspects of memory traces are decoupled by sleep, with the persistence of the former and the decay of the latter. The N1 stage seems to be especially important for this process. Not only did N1 show the most trials with imagery recall, but only during N1 was there a significant correlation between the time with eyes closed and either Image or Affect Residues (Table 1). While more time with eyes closed was related to higher similarity between Image and Imagery, it was also related to lower Affect Residue. Therefore, N1 indeed favors rich imagery (Blanco et al., 2015; Nielsen, 2000; Horikawa et al., 2013), while at the same time neutralizing affects within minutes of eyes closure. The lack of significant correlations between Affect Residue and either word count or EEG power within specific frequency bands is likely a direct result of this neutralization.

Across participants, Image and Affect Residues correlated with EEG power within specific frequency bands but not with the abundance of vertex waves, K complexes or cortical spindles. Image Residue was inversely correlated with power in the low-frequency theta band across multiple cortical regions, especially during N1, as expected (Siclari et al., 2017). Importantly, Image Residues did not fall below chance levels (Fig. 1c, Fig. 2c), which suggests the absence of active processes able to specifically inhibit the lingering imagery of the pre-sleep stimulus. The hypotheses regarding decreased or increased Image Residue following the respective occurrence of K complexes, vertex waves or cortical spindles were not corroborated, nor was the hypothesis regarding a temporal decay of recall within each stage.

During WK with eyes closed, participants experienced a drift from the image just seen, which persisted in mind in a faint yet measurable manner. Consider the following example. Image report: *I saw horrible black snakes with all-yellow body traces, and there were many of them as if it were a nest. They seemed to be quite alive.* Imagery report (WK): *I do not remember seeing anything. I think I've been reviewing the image. She was moving and she was very ugly. Ugly snakes with nails and they were quite black and had yellow dots*. In this example, after some hesitation, the image of black and yellow snakes is recovered in a similar (albeit more elaborate) manner minutes later.

At the onset of sleep, however, Imagery and Affect begin to diverge. The example shown in Fig. 1a,c depicts a WK trial in which the central aversive element of the Image, the menacing shark, is simply missing from the Imagery, although the surrounding context is well preserved. Another participant exposed to the same Image and then awoken during N1 reported seeing "a blue monster in the sea". While semantically close, the imagery still leaves out the main object in the stimulus, "shark". Indeed, in most cases the affective valences from N1 or N2 are statistically unpredictable from the stimuli employed.

Overall, the results show that Imagery was significantly driven by prior stimulation across the three stages but was also impacted by other competing memories. Except for trials with no recall, the hypnagogic imagery did not seem to fade against a void of mental content. While there was a lingering of visual contents across stages, the affect residue was neutralized with partial re-scaling, which points to the complex interplay of visual and affective memory residues soon after closing the eyes to sleep.

One limitation of our study was sampling imbalance. Since the experiment was designed to capture the initial 30 s of each target stage, several trials labeled online as N2 ended up being reclassified off-line as N1 (i.e., 'light' N2 became 'deep' N1). The smaller sample possibly led to the absence in N2 of statistical significance for the correlation between

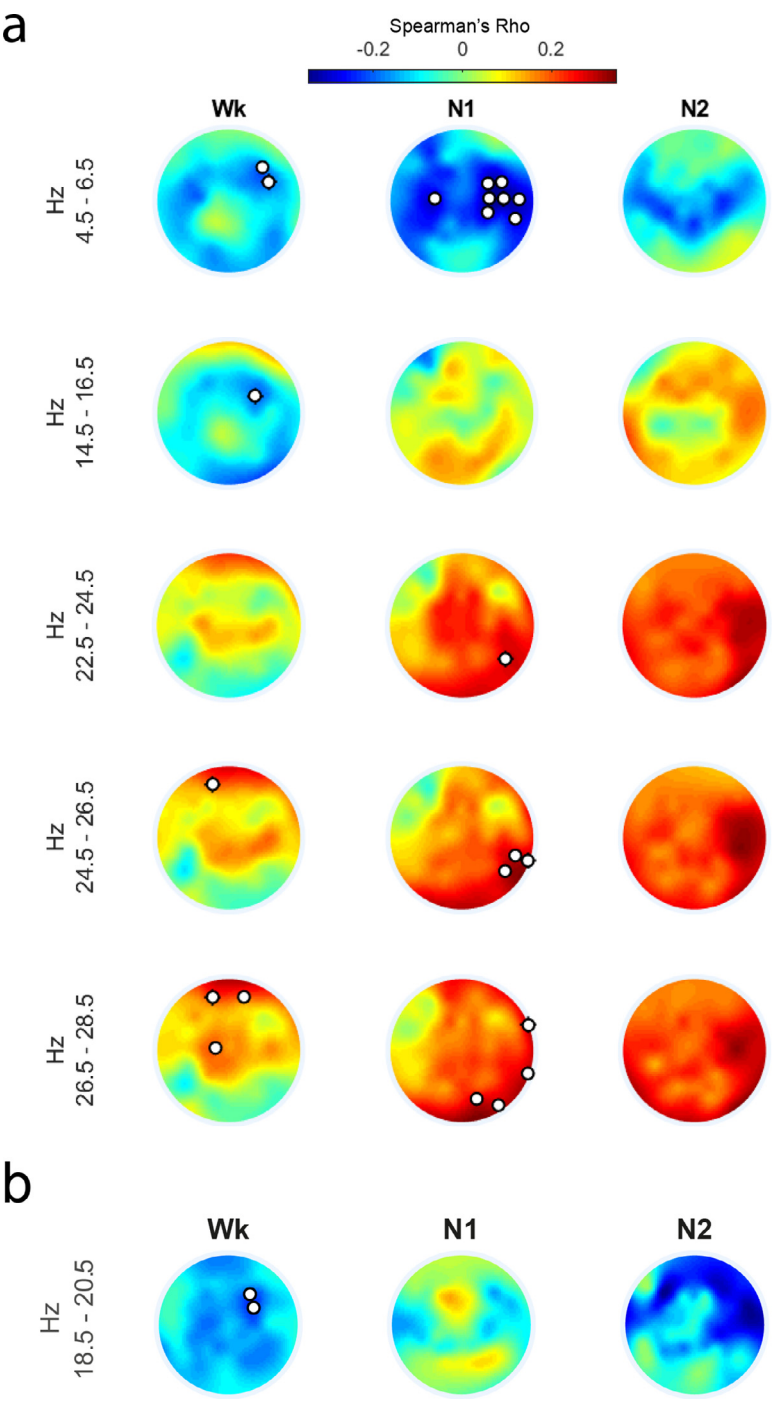

Fig. 4. Topographic plots of Spearman correlations between EEG power within various frequency bands and a) Image Residues or b) Affect residues. White dots indicate channels with significant correlations with $\alpha = 0.0000186$ after Bonferroni correction. Nasal oriented to the top.

Image Residue and EEG power spectrum in the theta band (Fig. 4a), but the overall topography of the correlation patterns detected point in the same direction as N1. Since the data were not perfectly balanced, we could not determine whether the lack of significant correlations in N2 is real, or rather reflects an underpowered assessment. One additional caveat is that the imagery recalled upon awakening from N2 may reflect mentation during the preceding N1 stage. Furthermore, here we focused on hypnagogic imagery at sleep onset, which is not fully representative of the "proper" dreams that can be sampled upon awakenings from consolidated N2, SWS or REM sleep. During the sessions the participants were asked about sleepiness and motivation, but we did not quantify these responses. Also, the significant positive correlations between Image residue and word count (Suppl. Fig. S4) indicate that inter-individual verbosity differences likely affected the measurement of Image Residue. Another caveat is that "time with eyes closed" comprised all the time elapsed between closing the eyes and waking up to a beep. This means that for N1 and N2, "Time with eyes closed" indeed conflated WK and sleep stages whose boundaries are not always well defined, as people doze off in idiosyncratic and not necessarily monotonic manners. Finally, we did not obtain other memory measures to assess image recall at a later stage, nor measured encoding success, and therefore the use of a single memory measure (i.e., the semantic similarity between visual stimulus and imagery report) should be considered another limitation of our study.

Imagery tends to decrease as sleep advances and EEG oscillations slow down, as indicated by recall rates around 50% after awakenings

from slow-wave sleep (Nielsen, 2000). In our experiment, the grounded design with reference stimulus and the computational approach for the quantification of Image Residue enabled the detection and measurement of latent similarities between reports, which are hard to measure without subjective bias when contents are rated by external judges. This methodological difference, or the discrepancy between N1 and REM mentation, may explain the very low levels of episodic replay of waking events previously found in overnight self-collected dream reports (Fosse et al., 2003). Future experiments using imagery grounded on visual stimuli should include longer episodes of N2, as well as episodes of slow-wave sleep and REM sleep.

Altogether the results show that after closing the eyes there is a spontaneous and progressive neutralization of the affective valences of the ongoing imagery. When the initial stages of sleep are reached, visual contents continue to reverberate while affective valences are neutralized. Most notably, theta power during sleep was associated with smaller Image Residue in N1 and neutralization of affective valence in N2. Increased theta power is therefore opposed to image reverberation, in agreement with the notion that increased cortical power in the theta band indicates cognitive interference (Nigbur et al., 2011). We speculate that the transition of waking into sleep abolishes the affective reverberation yet sustains the visual reverberation of the most recent images seen, against a torrent of spontaneously generated memories associated with theta oscillations generated in memory-related temporal circuits involving the hippocampus (Gu et al., 2017). This effect may be related to the recent evidence that sleep onset enhances creativity (Lacaux et al., 2021).

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Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2022.119690.

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