The neural correlates of consciousness in sleep:

A no-task, within-state paradigm

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Summary

What are the neural correlates of consciousness? Studies that have addressed this question in the past either compared neural activity during tasks in which subjects report perceiving a stimulus or not, or have contrasted conscious wakefulness with unconscious sleep or anesthesia. However, such contrasts may include correlates of stimulus processing, response preparation or of changes in behavioral state, rather than of consciousness per se. To overcome these limitations, we developed a no-task, within-state paradigm in which sleeping subjects recorded with high density-EEG reported retrospectively whether they had been conscious or not. We identified specific frontal and parieto-occipital regions showing EEG changes several seconds preceding awakenings that distinguished between reports of consciousness and unconsciousness. While decreased parieto-occipital low-frequency activity was associated with highly perceptual experiences, increased frontal high-frequency activity was associated with highly thought-like experiences. Finally, we identified localized, content-specific activations for faces, spatial setting, movement and speech experienced in dreams.

Introduction

What are the neural correlates of consciousness (NCC) - 'the minimal neuronal mechanisms jointly sufficient for any one specific conscious percept' (Crick and Koch, 2003)? Over the past 25 years, this question has triggered a large number of studies that have employed two main approaches. In the *task-based, content-specific approach*, subjects perform a task in which they report whether they experienced a particular stimulus or not, and brain activity is contrasted between the two conditions. Many of these studies, performed using paradigms such as binocular rivalry, backward masking, and inattentional blindness, have shown a widespread activation of fronto-parietal networks when subjects report experiencing the stimulus (Dehaene et al., 2001; Lumer et al., 1998). However, it has become clear that at least part of this activation may reflect processes that precede or follow the experience of the stimulus, rather than the experience itself, including attention (de Graaf et al., 2012), expectation (Melloni et al., 2011), self-monitoring (Frassle et al., 2014), unconscious stimulus processing (Aru et al., 2012a; Pitts et al., 2012) and performance (Aru et al., 2012b; de Graaf et al., 2012). Moreover, subjects remain conscious throughout the task, meaning that while content-specific contrasts highlight the neural mechanisms that make a particular experience different from another (seeing a stimulus rather than a blank), they may miss many of the mechanisms that are necessary and sufficient for actually *having* the experience, that is, for consciousness itself. On the other hand, the *state-based, level of consciousness approach* to the NCC aims at uncovering the neural mechanisms that are necessary and sufficient for having consciousness, irrespective of its particular content. One does so by contrasting brain activity between conditions in which consciousness is present, typically wakefulness in healthy subjects not performing any task, with conditions in which consciousness is globally diminished or abolished, such as dreamless sleep, general anesthesia, or coma. However, this contrast has its own problems, because it cannot easily distinguish between differences in

brain activity that are due to the loss of consciousness as such and unrelated differences due to gross changes in behavioral state, drug effects, or brain lesions. Because of these methodological difficulties, developing new experimental paradigms that dissociate the NCC from various confounding factors is a priority for consciousness research (Aru et al., 2012a; Aru et al., 2012b; de Graaf et al., 2012; Hohwy, 2009; Miller, 2007; Pitts et al., 2012).

With this in mind, we employed a *no-task, within-state paradigm* that takes advantage of the spontaneous fluctuations of consciousness within sleep. When awakened from sleep, subjects sometimes report that before awakening they were unconscious, while at other times they report having experienced thoughts devoid of perceptual content, or simple perceptual hallucinations, or long, vivid dreams. Crucially for our purposes, sleeping subjects are disconnected from the environment on both the input and output side, meaning that sensory stimuli generally do not influence the content of experience and *no task* is being performed. Moreover, consciousness and unconsciousness can be contrasted *within* the same behavioral state, either rapid eye movement (REM) sleep or Non-REM (NREM) sleep.

To systematically assess consciousness during sleep we used a serial awakening paradigm (Siclari et al., 2013) in which subjects reported retrospectively whether they had been conscious or not, and of what, just before the awakening. To ensure consistency, subjects were trained in the retrospective report protocol for two weeks prior to the actual experiment. Brain activity was recorded using high-density EEG (hd-EEG), a technique well suited to our aims because it provides a good spatio-temporal resolution and affords comfortable sleep in a bed. Seven healthy, right-handed individuals (3 males, age 31 ± 8.8 years, 21–47 [mean ± SD, range]) underwent altogether 51 overnight hd-EEG recordings with 256 electrodes. They were awakened at pseudorandom intervals with a computerized alarm sound and interviewed via

intercom using a structured questionnaire. First, they had to indicate whether they had had a conscious experience (CE) or not (NCE). If they reported a CE, they were asked to describe its most recent content ('the last thing going through your mind prior to the alarm sound') and to rate the CE on a scale ranging from exclusively thought-like (thinking or reasoning unrelated to any sensory experience) to exclusively perceptual (strongly related to sensory experience, without thinking or reasoning). Finally, they had to report whether the CE contained specific categories of content, including faces, spatial setting, movement, and speech, which were chosen because they are associated with localized brain activity during conscious wakefulness. Examples of reports are presented in Table 1, detailed methods at the end of the manuscript. Of the 815 awakenings performed across all stages, 586 were carried out in NREM and 170 in REM sleep. Subjects reported a CE in 33% of NREM awakenings (7 subjects) and a NCE in 29% (7 subjects). For REM sleep awakenings the percentages were CE 77% (7 subjects) and NCE 5% (4 subjects). Awakenings in which subjects reported a CE but could not recall any content were excluded from further analysis (38% in NREM sleep and 18% in REM sleep).

Results and Discussion

Consciousness vs Unconsciousness in NREM sleep

We first sought to determine whether and how brain activity changes between consciousness and unconsciousness during NREM sleep, because of the large and balanced number of CE and NCE reports. We computed power spectral density at the scalp level in 2s windows, and plotted the difference in whole brain power between the two conditions, averaged over successively longer time periods before the awakening (up to 2 min Fig. S1a). Compared to NCE, brain activity associated with CE had higher power in the high-frequency range (18-50 Hz), especially in the time period immediately before the awakening, and lower power in the

low-frequency range (1-12 Hz) (Fig. S1a). Source localization analysis (sLORETA) revealed that, compared to NCEs, CEs had reduced low-frequency power (1-12 Hz) in a parieto-occipital hotspot and increased high-frequency power (18-50 Hz) in a frontal hotspot (Fig.1a). EEG slow frequencies in the delta and theta band during sleep are associated with neuronal down-states and bistability (Steriade et al., 2001), which have been linked to the loss of consciousness (Purdon et al., 2013; Tononi and Massimini, 2008). Thus, low frequency fluctuations around the parieto-occipital hotspot may prevent those brain regions from contributing to experience. Conversely, increased high frequency power, usually associated with high neuronal firing (Steriade et al., 1996), may facilitate the contribution of the medial frontal hotspot.

Consciousness vs Unconsciousness in REM sleep

We then asked whether the same contrast would produce similar results during REM sleep – a behavioural state that differs from NREM sleep in multiple ways. Indeed, despite the small sample of NCE reports in this state, the results were remarkably similar (Fig. S1b and Fig. 1b). Again, brain activity associated with CE, as compared to NCE, had increased power in the high-frequency range (25-50 Hz) and reduced power in the low-frequency range (5-12 Hz), and differences in high-frequency power were maximal in the time period immediately before the awakening (Fig. S1b). Most notably, source localization analysis revealed again a parieto-occipital hotspot with reduced low-frequency activity (5-12 Hz); and a frontal hotspot with increased high-frequency activity (25-50 Hz) (Fig. 1b). Thus, the neural correlates of consciousness *without* a task and *within* the same behavioural state are similar *across* two very different behavioural states. NREM and REM sleep are substantially different in terms of EEG signatures (slow waves and spindles in NREM sleep, low-voltage fast activity in REM sleep (Aserinsky and Kleitman, 1953)), neural activity (widespread bistability between down-

and up-states in NREM sleep, (Steriade et al., 2001)), neuromodulation (high acetylcholine in REM sleep, low in NREM sleep (Jones, 2005)), and regional activations (Maquet, 2000)). Thus, the correspondence of the two hotspots identified in both behavioral states suggests that the NCC can be much more restricted than the widespread fronto-parietal network suggested by between-state contrasts (Laureys et al., 1999; Maquet, 2000) and by task-related activations (Dehaene et al., 2001; Lumer et al., 1998). Since the two hotspots were obtained by averaging across dreams and subjects, it is possible that individual dreams with unusual content, including lucid dreams (Dresler et al., 2012; Voss et al., 2009), may involve additional brain areas. Conversely, it is possible that the contrast between CEs and NCEs may include some brain regions that are involved in the generation of dreams (for example, their narrative structure), which could happen unconsciously. If that were the case, the NCC would be even more circumscribed.

Highly thought-like and highly perceptual experiences vs Unconsciousness

Next, we wondered whether the two hotspots emerging from the contrast between consciousness and unconsciousness were involved in different kinds of CEs. Since dreams differ greatly along the dimension 'perception vs. thought' (Foulkes, 1962; Goodenough et al., 1965), subjects had been asked to rate their CEs accordingly. For this analysis, we focused on REM sleep awakenings, because reports were more detailed, subjects felt more confident about their answers concerning specific contents, and the absence of slow waves and spindles makes source localization of hd-EEG signals more reliable. By separately comparing against NCEs those CEs that had been rated as maximally perceptual and maximally thought-like (Fig. 2a), we found that highly perceptual CEs were specifically associated with decreased low-frequency power in the parieto-occipital hotspot (Fig. 2b). Instead, highly thought-like CEs were exclusively associated with increased high-frequency activity in a region of the

frontal hotspot (Fig. 2c). Similar results were obtained for NREM sleep, although the dissociation was less clear-cut. These results suggest that the NCC during sleep may be restricted to a single hotspot and change in location depending on the nature of the subject's dream.

Percetpual categories in REM sleep

Finally, we asked whether hd-EEG activity patterns recorded prior to awakenings could also reveal which perceptual categories were experienced during full-fledged sleep. As shown in Fig. 3a, CEs containing faces were associated with increased high-frequency activity in a circumscribed temporo-occipital region compared to CE without faces, most markedly so in the 2s preceding the awakening. Further analysis showed that this region of increased activity matched the fusiform face area (Fig. 3b). A region of interest analysis confirmed that high-frequency activity in the fusiform face area on the right side was significantly higher for CEs containing faces compared to CE without faces ($p=0.04$, paired one-tailed t-test), consistent with the specialization of this area in the perception of faces during wakefulness.

Subjects were also asked to determine whether the setting of the most recent CE was indoors, outdoors, or could not be specified. When we contrasted CEs having an indoor or outdoor setting with the remaining CEs, we found that CEs with a definite spatial setting were associated with increased high-frequency activity in the right posterior parietal cortex (rPPC) (Fig. 4a), an area implicated in spatial perception and visuo-spatial attention (Malhotra et al., 2009).

Furthermore, subjects were asked if they had been moving during the most recent CE, and if so, which body part. CE in which the subjects reported body movements (involving the body and trunk or limbs bilaterally) were associated with increased high-frequency activity in a region surrounding the right superior temporal sulcus (Fig. 4b) compared to CE without body

movements. This area is important for the perception of biological motion (Grossman et al., 2000) and viewing body movements (Puce et al., 1998). We did not find significant differences in the (pre)motor and supplementary motor regions, which are normally activated during movements that are performed or imagined in the waking state, suggesting that dreams involve primarily the perception of movements, rather than their execution. Finally, subjects had to indicate whether during the most recent CE before awakening anyone was speaking, including themselves. As shown in Fig. 4c, CEs containing speech were specifically associated with increased high frequency activity over a left posterior temporal region, tentatively corresponding to Wernicke's area.

Altogether, these results suggest that specific contents of a subject's dreams – such as faces, the spatial setting, movement, and speech – are associated with increased high-frequency EEG activity in specific cortical areas, and that these areas closely match those engaged during waking perception of the same contents. This regional specificity shows that high-density EEG can precisely localize the neural sources of fleeting dream contents. In a recent fMRI study, a pattern classifier trained while subjects perceived natural images during wakefulness (Horikawa et al., 2013) successfully decoded specific content categories reported by subjects awakened at the transition between wakefulness and sleep. Our results with hd-EEG extend these findings beyond falling asleep to periods of consolidated sleep, suggesting that dream reports reflect conscious experience that occurs during sleep rather than confabulations that are produced upon awakening (Dennet, 1976; Malcolm, 1957).

Conclusion

In conclusion, we investigated the NCC by contrasting the presence and absence of consciousness by relying on retrospective reports obtained upon awakening from sleep, without requiring subjects to respond to stimuli or to execute tasks. Moreover, we contrasted

consciousness and unconsciousness within the same behavioral state, whether NREM or REM sleep. By using hd-EEG recordings, we were able to localize the neural correlates of both the level of consciousness and of specific perceptual categories experienced during sleep, such as faces, places, movements, and speech. The results demonstrate that the NCC during sleep does not involve the broad fronto-parietal network commonly put forth as the substrate of consciousness (Dehaene et al., 2001; Lumer et al., 1998), suggesting that widespread prefrontal activation may relate more closely to control and execution of cognitive tasks than to CE per se. This conclusion is supported by recent work in which attention and other confounding factors were carefully controlled (Frassle et al., 2014; Kamphuisen et al., 2008) and is consistent with the persistence of consciousness after widespread frontal lesions. Instead, our data show that during sleep the typical NCC localizes to two hotspots, one centered in parieto-occipital cortex and one around frontal cortex. Moreover highly perceptual CEs activate exclusively the parieto-occipital hotspot and highly thought-like CEs only a region of the frontal one. Thus, it is possible that the NCC during sleep may be restricted to a single hotspot and change in location depending on the nature of the subject's dream.

Experimental Procedures

Study participants

Seven healthy, right-handed, non-medicated subjects screened for neurological, psychiatric and sleep disorders by a medical interview participated in the study [3 males, age 31 ± 8.8 years, 21–47 (mean ± *SD*, range)]. All the participants scored within normal limits on the Pittsburgh Sleep Quality Index (< 5 points) and the Epworth Sleepiness Scale (<10 points). Frequent recall of dreams or a special interest in dreaming was not a prerequisite for the study. The study was performed as part of a larger research project that was approved by the

Institutional Review Board of the University of Wisconsin, Madison. Written informed consent was obtained from all study participants.

Procedure

The procedure used in this study has been described in detail in a previous publication (Siclari et al., 2013). In brief, subjects received comprehensive explanations regarding the questionnaire used in the experiment, and filled it in at home every morning upon awakening for two weeks before the first study night. Awakenings were performed at pseudorandom intervals, irrespective of sleep stage, using a computerized sound lasting 1.5 sec. Subjects were instructed to signal that they had heard the alarm sound and to lie quietly on their back. They then underwent a structured interview about their mental activity that lasted between 20 sec and 3.5 min, depending on whether the subject reported a conscious experience and had to answer additional questions related to the content. Between five and ten overnight recordings were performed for each participant, with a maximum of three consecutive nights. To increase the number of awakenings in REM sleep with respect to NREM sleep, two additional nights were scheduled for three of the subjects, in which awakenings were only performed in REM sleep. The total number of nights was distributed as follows among subjects: S1:10 nights, S2:8 nights, S3:6 nights, S4:5 nights, S5:8 nights, S6:6 nights, S7:8 nights. Overall, 5 awakenings had to be excluded because of technical problems with the amplifier, 16 awakenings because subjects were too somnolent upon awakening to answer questions reliably.

Sleep recordings

Recordings were performed using a 256-channel high-density EEG (hd-EEG) system (Electrical Geodesics, Inc., Eugene, Ore.). Four of the 256 electrodes placed at the outer

canthi of the eyes were used to monitor eye movements and submental electromyography was recorded using the Electrical Geodesics polygraph input box. The EEG signal was sampled at 500 Hz and filtered between 0.3 and 50 Hz. Sleep scoring was performed over 30s epochs according to standard criteria (Iber et al., 2007).

Preprocessing of data

For each awakening, the signal corresponding to the 2 mins preceding the awakening was extracted and considered for analysis. Bad channels were visually identified and replaced with data interpolated from nearby channels using spherical splines (NetStation, Electrical Geodesic Inc.). To remove ocular, muscular, and electrocardiograph artifacts we performed Independent Component Analysis (ICA) using EEGLAB routines (Delorme and Makeig, 2004). Only ICA components with specific activity patterns and component maps characteristic of artifactual activity were removed (Jung et al., 2000).

Signal analysis

Spectral analysis (scalp level)

To compute the spectrograms shown in Figure S1, the signal corresponding to the 2 min before the awakening was extracted. Power spectral density estimates were computed by Fast Fourier Transform (FFT) in 2s Hamming windows, resulting in a 0.5 Hz bin resolution. After excluding electrodes located on the neck/face region, the signal was averaged across the remaining 185 channels to obtain a whole brain power estimate. The frequency resolution was then lowered to 1 Hz per bin. For each subject and 2s time bin, we calculated the mean power for CE and NCE. Then, we computed the differences between CE and NCE for each subject and the natural logarithm was calculated on the resulting values for all frequency bins. The mean differences across subjects were plotted over time.

Source localization

The previously cleaned, filtered and average-referenced EEG signal corresponding to the 2 mins before the awakening was extracted and analyzed at the source level. Source modelling was performed using the GeoSource tool (NetStation, Electrical Geodesics, Inc., Eugene, Ore.). A 4-shell head model based on the Montreal Neurological Institute (MNI) atlas and a standard coregistered set of electrode positions were used to construct the forward model. The source space was restricted to 2447 dipoles that were distributed over 7 mm^3 cortical voxels. The inverse matrix was computed using the standardized low-resolution brain electromagnetic tomography (sLORETA) constraint. A Tikhonov regularization procedure ($\lambda=10^{-1}$) was applied to account for the variability in the signal-to-noise ratio (Pascual-Marqui, 2002). We computed spectral power density using the Welch's modified periodogram method (implemented with the pwelch function in Matlab (Matlab, The Math Works Inc, Natick, MA)) in 2s Hamming windows to decompose the source signals into the frequency bands of interest defined above.

Statistical analysis

Statistical analyses were carried out in Matlab. To compare brain activity between CE and NCE, the source-modeled signal was averaged within frequency bands (5-12 Hz, 25-50 Hz) and time periods of interest (12s for REM sleep, 20s for NREM sleep). We then averaged the signal associated with CEs and NCEs within each subject for both frequency bands and stages (REM and NREM sleep) separately. Group level analyses were performed using paired t-tests for each of the 2447 voxels. The group contrast maps show the resulting statistically significant voxels ($p<0.05$) whose value was set either to 1 when the mean across subjects CE-NCE difference was positive (CE>NCE), or to -1 when the same difference was negative (CE<NCE). The same procedure was performed for content-specific comparisons.

To enhance the power of the statistical tests and minimize potential false positive results related to multiple comparisons (type I error), we adopted a combination of probability- and cluster- based thresholding. Specifically, a cluster-threshold was determined using a Monte Carlo simulation approach including 5000 repetitions (Forman et al., 1995) . For each cycle, randomly selected CE-segments were assigned to two sub-groups (n=3) and voxel-wise averaged for all subjects. Resulting individual maps were used to compute group-level t-tests at each voxel's location, as described for the CEvsNCE comparison. A probability threshold equal to alpha=0.05 was applied to each contrast and the size of all surviving clusters was recorded in a frequency table, which was then used to determine the minimum cluster size yielding a corrected p-value of 0.05 (corresponding to the 95th percentile of the whole distribution).

Definition of highly thought-like and perceptual experiences

To select a subset of highly perceptive and highly thought-like experiences of comparable sizes for the contrast with NCE, we plotted the frequency distribution of all the scores obtained in the four subjects that had had at least one NCE. The maximal score (4) was found in 8.3% of these experiences and was selected to define highly perceptive experiences. The score corresponding to this percentile for the thinking dimension (smaller than -1, encompassing 8.2% of experiences) was selected to define ‘highly thought-like experiences’. The same procedure was applied for NREM sleep, in which the scores of 4 and smaller than -1 were associated with 16.1% and 19.2% of experiences respectively.

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Figures

Figure 1

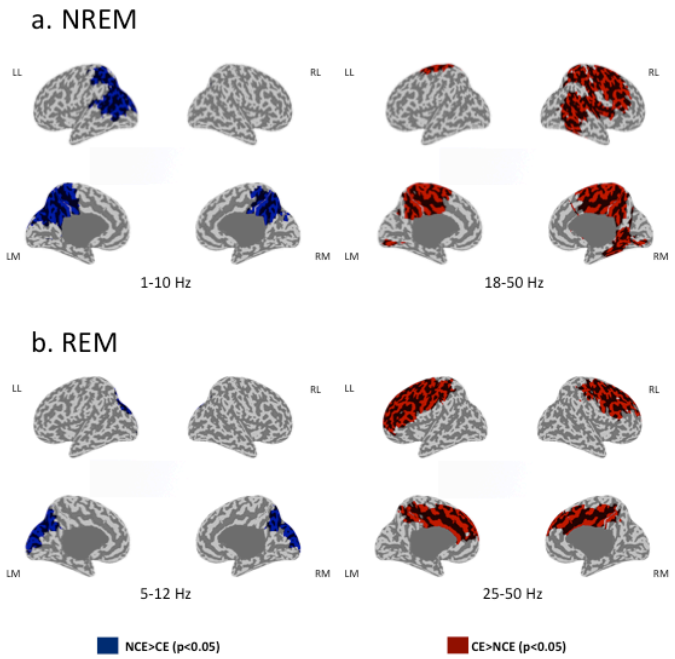

Figure. 1: Consciousness vs. Unconsciousness. **a.** Inflated cortical maps illustrating the topographical distribution of differences between CEs and NCEs at the source level for low (1-10 Hz, left) and high frequency power (18-50 Hz, right) in NREM sleep, averaged over the last 20 seconds before the awakening. Only significant differences at the $p<0.05$ level, obtained after correction for multiple comparisons are shown (two-tailed, paired t-tests, 7 subjects). Frequency bands and timeframes were selected as described in Supplementary Figure 1. **b.** Same as a. for REM sleep, for low frequency power (5-12 Hz, left) and high frequency power (25-50 Hz, right), 4 subjects. Differences are averaged over the last 12s before the awakening. LL=left lateral view. LM=left medial view. RL=right lateral view. RM=right medial view.

Figure 2

a.

Highly perceptual experiences	Highly thought-like experiences
A documentary about poor children somewhere in Eastern Europe	I was thinking about the possibility of having an erotic dream during this experiment, and that it would be very awkward.
I saw a TV commercial for a car.	I was thinking about the phrase: 'It pays to be wrong sometimes'.
I was watching a medieval play. A man and a woman were lying on the floor, pretending to be dead.	I was thinking about inviting someone to my house.

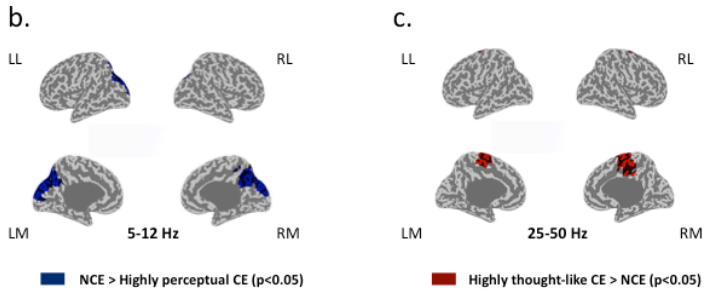

Figure. 2: Thinking and Perceiving vs. Unconsciousness. **a.** Representative examples of highly perceptual and highly thought-like most recent CEs in REM sleep. **b.** Inflated cortical maps illustrating voxels for which highly perceptual CEs significantly differed from NCEs in the low-frequency band (5-12 Hz) in REM sleep (4 subjects, two-tailed paired t-tests) at the $p<0.05$ level after correction for multiple comparisons. c. Same for a. for the contrast between highly thought-like CEs and NCEs in the high-frequency band (25-50 Hz) (3 subjects, two-tailed paired t-tests). LL=left lateral view. LM=left medial view. RL=right lateral view. RM=right medial view.

Figure 3

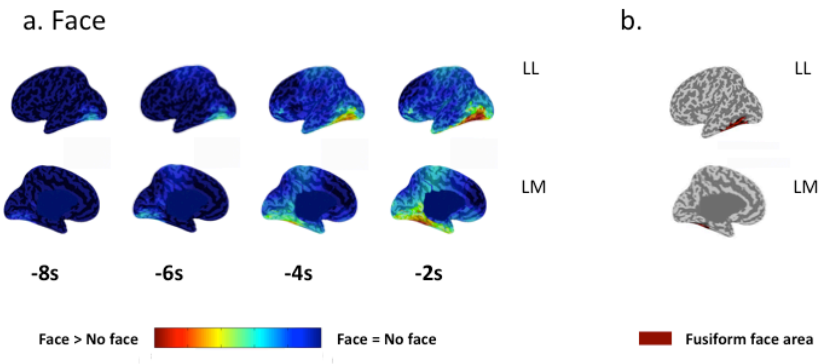

Figure 3: Face vs. No Face. **a.** Topographical differences in high-frequency brain activity (25-50 Hz) between CEs with and without a face (7 subjects) in REM sleep, averaged over different time periods before the awakening. **b.** Inflated cortical maps highlighting the location of the fusiform face area (as determined by (Rossion et al., 2003)). LL=left lateral view. LM=left medial view.

Figure 4

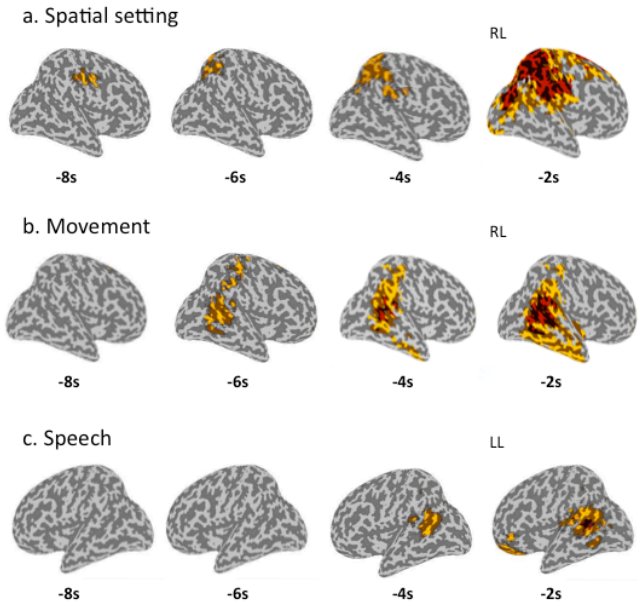

Figure 4: Other perceptual categories. **a.** Cortical inflated maps illustrating differences in high-frequency brain activity (25-50 Hz) between CEs containing a spatial setting and CEs without a spatial setting (6 subjects, two-tailed paired t-tests). Only voxels for which the difference was significant at the $p<0.05$ level (red) and the $p<0.1$ level (yellow) are shown for each timeframe before the awakening. **b**: same as **a**. for the contrast movement vs. no movement (7 subjects). **c**: same as **a.** and **b.** for the contrast speech vs. no speech (6 subjects). LL=left lateral view. RL=right lateral view.

Figure S1

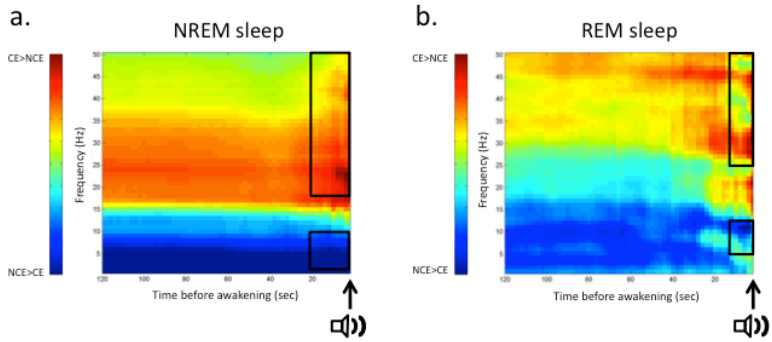

Figure S1: Consciousness vs. Unconsciousness. **a.** Spectrogram illustrating the difference in whole brain power at the scalp level between CEs and NCEs in NREM sleep, averaged over successively longer time periods before the awakening (the latter is indicated by a loudspeaker that represents the alarm sound). To represent all the frequencies on the same scale, the logarithm of the difference was plotted (7 subjects). The black boxes indicate the frequency bands and timeframes of maximal differences that were selected for further analysis. **b.** same as **a.** for REM sleep (4 subjects).

Table 1: Examples of reports of most recent conscious experiences.

Stage, time	Examples of reports of most recent conscious experiences
N2, 1:44 am	I was daydreaming. I was holding a musket, like a rifle, and I was skipping through images with it. Last image was a piece of pie, I am not sure but I think it was.
N2, 5:23 am	I was thinking about perfume and fragrance. The very last word was 'fragrance'.
N2, 5:55 am	The image of a Buddha belly, a bare belly.
N2, 6:51 am	I saw a person waiting in a car. Maybe it was me.
N3, 1:26 am	I was seeing geometric shapes that were moving very fast.
N3, 5:18 am	I was trying to tell the difference between a homemade and a store-bought basket or tray of pastry.
N3, 6:09 am	The last thing was raspberries, a pint of raspberries.
REM, 3:28 am	I was doing this experiment with another girl. I asked her what time it was and she said 7:07. No, she actually said 6:55. Her boyfriend was in the room, too. The last scene was just her face. It was quite a long dream before that.
REM, 3:59 am	I saw my brother eating hair on a plate.
REM, 6:36 am	In the last scene I was riding a bicycle in a street in B. Before that I was talking to someone in a court. Somebody taking care of the court. He gave lots of explanations about flowers.
REM, 6:05 am	It was the end of a movie. I was getting out on the street through a door. At that moment I heard the noise of the alarm sound and woke up.

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