Contents lists available at ScienceDirect

Consciousness and Cognition

While you were sleeping: Evidence for high-level executive processing of an auditory narrative during sleep

Stuart Fogel [a,b,c,d], Laura Ray [a], Zhuo Fang [a,b,c], Max Silverbrook [d], Lorina Naci [e], Adrian M. Owen [d,f,*]

[a] School of Psychology, University of Ottawa, Ottawa, Canada
[b] Sleep Unit, University of Ottawa Institute of Mental Health Research at The Royal, Ottawa, Canada
[c] University of Ottawa Brain & Mind Research Institute, Ottawa, Canada
[d] The Brain & Mind Institute, Western University, London, Canada
[e] School of Psychology, Trinity College, Dublin, Ireland
[f] Department of Physiology and Pharmacology and Department of Psychology, Western University, London, Canada

A B S T R A C T

During sleep we lack conscious awareness of the external environment. Yet, our internal mental state suggests that high-level cognitive processes persist. The nature and extent to which the external environment is processed during sleep remain largely unexplored. Here, we used an fMRI synchronization-based approach to examine responses to a narrative during wakefulness and sleep. The stimulus elicited the auditory network and a frontoparietal pattern of activity, consistent with high-level narrative plot-following. During REM sleep, the same frontoparietal pattern was observed in one of three participants, and partially in one other, confirming that it is possible to track and follow the moment-to-moment complexities of a narrative during REM sleep. Auditory network recruitment was observed in both non-REM and REM sleep, demonstrating preservation of low-level auditory processing, even in deep sleep. This novel approach investigating cognitive processing at different levels of awareness demonstrates that the brain can meaningfully process the external environment during REM sleep.

1. Introduction

The importance of processing external information while preserving sleep, has generated many questions about how external information is gated, and the extent to which meaningful processing occurs during sleep. It is well known that sensory information can be processed to varying degrees during sleep (Dang-Vu, McKinney, Buxton, Solet, & Ellenbogen, 2010; De Koninck & Koulack, 1975; Tavakoli, Varma, & Campbell, 2018), and the use of simple auditory stimuli and binary decision tasks have proved fruitful in informing us about the presence, and depth of information processing during the complete or partial loss of conscious awareness.

Previous studies have shown that the presentation of simple auditory stimuli results in low-level sensory processing during sleep (Dang-Vu et al., 2011; Portas et al., 2000; Schabus et al., 2012). For example, one study examined the pattern of brain activation elicited by a simple tone during sleep. Bilateral activation of the auditory cortex, thalamus, and caudate nucleus were observed in awake participants and during NREM sleep (Portas et al., 2000). This suggests that basic auditory processing remains intact in NREM

(Portas et al., 2000). However, a reduction in activity in frontal and parietal regions was identified in NREM, compared to wakefulness (Portas et al., 2000). Since these regions are known to support executive functioning (Barbey et al., 2012; Hampshire & Owen, 2006; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005), it was suggested that sensory processing in the sleeping brain may occur in the absence of conscious awareness (Portas et al., 2000).

More recently, Dang-Vu et al. (2011) demonstrated greater auditory-cortex activation following simple auditory tone presentation (compared to silence) during NREM2 sleep, except in the presence of sleep spindles when incoming sensory information appeared to be attenuated. This suggests that spindles may serve to isolate the cortex from the environment during sleep (Dang-Vu et al., 2011). Schabus et al. (2012) showed that the presence of high slow wave activity (SWA) did not alter auditory cortex activation to simple tones presented during SWS; rather, the oscillations modulated responses in higher-order cortical areas. Taken together, these findings highlight the importance of the presence of spontaneous sleep-specific cortical activity for the processing of simple auditory stimuli and support the notion that events such as NREM spindles and slow waves determine its level of downstream processing.

Most recently, when presented with novel words during NREM2, a lateralized readiness potential (LRP), similar to that seen during wakefulness, persisted, but was absent during SWS and REM sleep (Andrillon et al., 2016). However, a preserved LRP response was found for previously trained words presented in REM (Andrillon et al., 2016), suggesting that semantic processing is also preserved during REM sleep.

Naturalistic paradigms that use more complex stimuli, *i.e.*, "real-life" stimuli unconstrained by any task-specific behavioural output (De Koninck & Koulack, 1975; Zaki & Ochsner, 2009), are particularly useful when applied to neuroimaging studies as they provide a window into how the brain processes continuous information in real time. As individuals experience the events of a story, brain activity across individuals is highly correlated (i.e., many brain responses become "synchronized" reflected by high inter-subject correlation (ISC)) (Hasson, Malach, & Heeger, 2010). In other words, our brains process low and high-level meaningful information in a consistent way from one individual to the next. Moreover, Naci and colleagues (Naci, Cusack, Anello, & Owen, 2014; Naci, Graham, Owen, & Weijer, 2017; Naci, Sinai, & Owen, 2017) showed that synchronous activity between individuals in extra-modal high-level brain regions in the frontal and parietal cortices reflects the collective recruitment of those executive processes that lead to understanding of a narrative plot. Thus, naturalistic paradigms evoke similar brain activity across different healthy individuals, and importantly, this can provide a unique and reliable and robust neural signature of high-level cognition at the single-subject level (Naci et al., 2014; Naci, Graham, et al., 2017; Naci, Sinai, et al., 2017). Higher-order brain responses such as speech comprehension, and executive functions such as working memory, long-term memory retrieval, theory of mind and prospective memory, are necessary to follow and comprehend the narrative of a plot. These are all highly complex cognitive operations that recruit areas of frontal and parietal cortices, and typically co-occur with 'lower level' sensory processes, which correspondingly recruit the respective brain areas that support them (e.g., auditory cortex). If the same 'naturalistic' approach is adopted using an auditory-only narrative, then neither eye-opening nor any behavioural response is required, making the technique highly suitable for use in sleep research to assess both sensory processing, and to detect the presence of higher-order executive functions at the single-subject level in states of consciousness that are otherwise inaccessible.

Here, we conducted two studies that build upon a paradigm that we have used previously (Naci et al., 2014) involving participants attending (with eyes closed) to a rich auditory narrative that unfolds over several minutes. Because the paradigm requires no responses from the participant, it is ideal for examining the spatial and temporal neural correlates of information processing across variations of consciousness, such as sleep-wake states.

These two studies combined the synchronization-based analytical approach from our previous work (Naci et al., 2014; Naci, Graham, et al., 2017; Naci, Sinai, et al., 2017) employing fMRI during wakefulness (**Study 1**), and then, using simultaneous EEG-fMRI, to investigate the extent to which complex, "real-world" information is processed and understood in different sleep states (**Study 2**). Akin to our work in patients with disorders of consciousness, given the challenges inherent in obtaining naturally occurring sleep recordings in an MRI environment while simultaneously recording EEG, we have employed analysis techniques that are appropriate, robust and specifically designed to identify the presence of cognitive processes and consciousness at the single-subject level. We hypothesized that: (**1**) to understand the narrative of a complex auditory stimulus, executive processes will be consistently recruited, leading to synchronous activity across frontoparietal networks. Also, as we have shown previously, (**2**) we expected this higher-order, cross-individual synchronization to be driven by the unfolding narrative of the story, as modelled by subjective ratings (Naci, Sinai, et al., 2017). Further, during sleep (**3**), the inherent organization of functional networks would differ as a function of sleep stage, (**4**) given previous evidence that low-level auditory processing varies during sleep, we also expected to find altered stimulus-specific responses in the auditory cortex during sleep, and (**5**), if wakefulness-like frontoparietal information processing during sleep were identified, this would vary depending on sleep stage, but would be most likely to be present during REM sleep, and least likely during SWS.

2. Methods

2.1. Methodology common to study 1 and study 2

2.1.1. Ethics statement

All participants provided informed consent and were financially compensated. This research was approved by the Western University Health Science REB.

2.1.2. Auditory stimulus

The stimulus was a 5 min, 12 s auditory clip from the movie, "*Taken*" (Besson & Morel, 2008) played from a laboratory computer, digitally time-locked to the MR-scanner through custom-built hardware and software. The excerpt has a suspenseful and clear narrative of a conversation between a father and daughter that climaxes with the girl's abduction. The father then delivers a threatening speech to the kidnappers. The stimulus has previously been shown to elicit synchronous activity in the frontoparietal network (Naci et al., 2014; Naci, Sinai, et al., 2017) during wakefulness, reflecting similar executive functioning across participants as each individual absorbs the narrative.

2.1.3. MRI imaging acquisition and preprocessing

2.1.3.1. MRI recording parameters. Functional magnetic resonance imaging was performed at a 3.0 T Prisma MRI (Siemens, Germany) using a 12-channel head coil. A T1-weighted 3D MPRAGE sequence was used for anatomical scans [voxel size = $1 \times 1 \times 1$ mm^3, TR = 2300 ms, TE = 2.98 ms, matrix size = $256 \times 256 \times 176$, FA = 90°]. Functional images during resting state (220 scans) and "*Taken*" (150 scans) were acquired by a T2*-weighted EPI sequence [40 slices, voxel size = $3.44 \times 3.44 \times 3$ mm^3, TR = 2160 ms, TE = 30 ms, inter-slice gap = 10%, matrix size = $64 \times 64 \times 40$, FA = 90°]. The same recording parameters were used in Study 2, except that a 64-channel head coil was used.

2.1.3.2. MRI image preprocessing. Functional images were preprocessed and analyzed using SPM8 (Welcome Department of Imaging Neuroscience, United Kingdom) and Automatic Analysis software (Cusack et al., 2015). To minimize T1-saturation effects and allow participants to acclimatize to scanner noise, the first five volumes per scanning run were discarded. Data preprocessing included: fMRI motion correction, slice-timing correction, coregistration with structural, normalization to Montreal Neurological Institute (MNI) space, and smoothing using a Gaussian smoothing kernel of 10 mm full width at half maximum. Spatial normalization was performed using SPM8′s segment-and-normalize procedure, whereby, the T1 structural scan was segmented into grey and white matter and normalized to the segmented MNI-152 template and then applied to all EPIs. To remove low-frequency noise, a temporal high-pass filter was then applied at each voxel (1/128 Hz cut-off). The same image preprocessing steps were used for Study 2.

2.2. Study 1 methods: Awake study

2.2.1. Participants

Sixteen healthy adults participated in this study. All participants were right-handed and had no history of psychiatric or neurological disorders. One participant was excluded due to a headphone malfunction. Therefore, 15 participants (8 female; M(SD) = 24.9 (7.4) years) were included in the final analyses.

2.2.2. Experimental procedure

Participants who met inclusion criteria underwent a daytime fMRI session to establish baseline BOLD responses to the auditory stimulus. Brain images were recorded while participants listened to the auditory stimulus in the scanner via in-ear pneumatic headphones. An unrelated audio clip was used to set the volume to a comfortable level. After structural imaging, a resting-state scan and a scan that involved 'free listening' to the auditory stimulus were acquired. For the resting-state scan, participants were asked to lie awake for 8 min with their eyes closed. For the free listening session, participants were asked to listen to the auditory stimulus and follow the story with their eyes closed. The order of the two functional scanning conditions was counterbalanced across participants.

2.2.3. Suspense ratings

In order to explicitly connect the synchronized processing between individuals to engagement with the plot of the "*Taken*" audio track, an independent group of participants (N = 20, 12 female, M(SD) = 19.9(3.90) years) performed a behavioural experiment in which they rated how suspenseful they found the audio clip. Previous studies have shown that ratings of suspense provide a reasonable proxy of how engaging a movie is (Naci et al., 2014). Specifically, participants were presented the audio clip via over-ear headphones in a sound-isolated room. They were instructed to provide ratings on a 9-point scale from 1-least suspenseful to 9-most suspenseful. Every 2.16 s (time-matched to the TR of the MRI), the audio was paused and participants were given 3 s to respond using a key-press. In a leave-one-out set of Pearson correlation analyses, each participant's ratings were compared to those of the rest of the group (n-1). To get an average correlation value, each correlation coefficient was normalized (Fisher's r-to-z transformation), then the average of these values was computed and back-transformed into a correlation coefficient.

2.2.4. MRI imaging analysis

2.2.4.1. fMRI Group ICA. Independent component analysis (ICA) was employed to separate the activity of distinct brain networks involved in the processing of the auditory stimulus. ICA is a data-driven approach for extracting functional networks from fMRI data (Huettel, Song, & McCarthy, 2014). ICA does not require any prior assumptions or modelling; instead, it identifies spatial sets of voxels that express similar temporal activations and are maximally distinct to other components. These independent components (ICs), can be visually inspected and classified into known functional networks. Neuronal components were identified as their respective functional network through visual inspection. Noise components were classified as non-neuronal based on the distribution of power across the

frequency spectrum (e.g., high frequency signals which cannot correspond to the BOLD signal) and spatial location (signals originating outside the head). As all participants heard the exact same stimulus, the group ICA method, tensor-ICA was performed (Beckmann & Smith, 2005). Tensor-ICA assumes the temporal BOLD response pattern to be the same across individuals and provides a single decomposition where each component is characterized by the BOLD signal variation across the temporal, spatial, and participant domains (Beckmann & Smith, 2005). This is the most appropriate group ICA method, because the spatial distribution of networks is known to be consistent across participants and task conditions (Damoiseaux et al., 2006). MELODIC software was used to perform the ICA, and a 20-component cut-off (Smith et al., 2009) was implemented for group data. Five canonical functional networks were identified, including visual, auditory, frontoparietal, motor and medial. These were previously found important for processing naturalistic stimulation (Naci, Cusack, Anello, & Owen, 2014; Naci, Graham, et al., 2017; Naci, Sinai, & Owen, 2017). Importantly, previous work has shown that auditory and frontoparietal networks are recruited during a narrative auditory stimulus in awake participants and reflect the collective recruitment of those executive processes that lead to understanding of a narrative plot. This approach can provide a unique and reliable and robust neural signature of high-level cognition at the single-subject level (Naci et al., 2014; Naci, Graham, et al., 2017; Naci, Sinai, et al., 2017).

2.2.4.2. fMRI regression analysis. The purpose of Study 1 was to confirm that this method could reliably predict network activity at the individual level in awake individuals, as shown by (Naci, Sinai, et al., 2017), with a different set of scanning parameters. A previous set of leave-one-out analyses using the tensor ICA method and the general linear model (GLM) in 15 individuals listening to *Taken* demonstrated reliable prediction of each participant's auditory and frontoparietal activity from the group (n-1) time-course (Naci, Sinai, et al., 2017). Accordingly, the auditory and frontoparietal time-courses obtained from the wake control group ICA were used as regressors in the GLM of data from each awake individual in Study 1.

To examine the neural correlates of high-order cognitive processes, which support 'plot-following' during the auditory stimulus, suspense ratings were used to estimate brain activity. The group-averaged suspense ratings were convolved with a canonical hemo-dynamic response function (HRF) and then used as a parametric regressor in the GLM of the awake group data. To determine if plot-following reliably predicted the activity observed in the group, the suspense regressor was used in the GLM for data from each awake individual.

Movement parameters in the three directions of motion and three degrees of rotation, and session mean BOLD signals were modelled as nuisance variables. Linear contrasts were used to obtain participant-specific estimates for each of the independent analyses investigating the involvement of the auditory/frontoparietal networks, and for the networks which may support the subjective experience of suspense. Linear contrast coefficients, derived for each participant, were entered into the second level random-effects analysis. Only clusters of voxels that reached significance ($p < 0.05$ threshold) and survived correction for multiple comparisons using family-wise error (FWE) correction were reported.

2.3. Study 2 methods: Sleep study

2.3.1. Participants

Thirty-five healthy adults participated in this study. All participants were right-handed, had no history of psychiatric or neuro-logical disorders, and had no signs of sleep disorders indicated by the Sleep Disorders Questionnaire (Douglass et al., 1994). To verify that participants maintained a regular sleep schedule, they were asked to wear an actigraph and to complete a sleep-wake log for one-week prior to the MRI session. Participants were excluded if actigraphy or sleep-wake logs suggested non-compliance with the study instructions. Five participants were excluded for non-compliance, 3 participants obtained < 5 min of consolidated NREM sleep in the scanner, and one participant had a large dental implant artifact. Therefore, 26 participants (15 female; M(SD) = 23.8(4.0) years) were included in the final analyses, sleeping for 44 min in the scanner, on average.

2.3.2. Experimental procedure

Participants who met inclusion criteria underwent an initial orientation session, where they were given the actigraph and sleep-wake log. One week later, participants underwent MRI scanning, during which time simultaneous EEG-fMRI was recorded while participants slept in the scanner. The scan procedure started at 21h00. The EEG equipment was installed and tested, in-ear pneumatic headphones were positioned, and an unrelated audio clip was used to set the volume. This was followed by localizer scans, a T1 MPRAGE structural scan, and an awake resting-state scan. For the resting-state scan, participants were asked to lie awake for 8 min with their eyes closed. The sleep recording started at 22h00. The average sleep onset latency was 8.16 ± 10.11 min. Participants were allowed to sleep for up to a maximum of 120 min in the MRI scanner. The auditory stimulus was presented immediately prior to the end of the scanning session while the participant was still asleep. Participants were required to have had a period of at least 5 min of uninterrupted stimulus-free NREM2/3 sleep and to have remained asleep throughout the duration of the auditory stimulus (5 min, 12 s) to be included in the subsequent analysis of the MRI data. To ensure headphone positioning remained intact during the sleep session, the participants were awoken and presented an unrelated audio clip at the end of the scanning session. At this time, participants were asked if they remembered hearing the auditory stimulus presentation. All participants that were asleep for the duration of the audio playback had no recollection of hearing the stimulus. Following the EEG-fMRI sleep session, participants slept for the remainder of the night in the sleep laboratory.

2.3.3. EEG acquisition and preprocessing

2.3.3.1. EEG recording parameters. Simultaneous polysomnography was comprised of 64-channel MR-compatible EEG cap which included one electrocardiogram (ECG) lead (Braincap MR, Easycap, Germany) and two MR-compatible 32-channel amplifiers (Brainamp MR plus, Brain Products, Germany). EEG recordings were referenced to FCz. To aid with the visualization of the R-peak of the QRS complex (for ballistocardiographic (BCG) correction), three additional bipolar ECG derivations were recorded, using an MR-compatible 16-channel bipolar amplifier (Brainamp ExG MR, Brain Products, Germany). As recommended by Mullinger, Yan, & Bowtell (2011), we repositioned participants in the scanner so that they were shifted away from the iso-center of the magnetic field by 40 mm. At this position, the MRI images are not impacted, but the BCG artifact is reduced by 40%. EEG data were transferred via fiber optic cables to a personal laptop where Brain Products Recorder software (Brain Products, Germany) was synchronized to the scanner clock. Data were digitized with a resolution of 500-nv/bit at 5 kHZ and were low pass filtered at 500 Hz and high pass filtered with a 10 s time constant corresponding to a high pass frequency of 0.0159 Hz.

2.3.3.2. EEG data processing. Electroencephalographic data were corrected for gradient-induced and cardioballistic artifacts in two separate steps. First, MRI gradient artifacts were removed using an adaptive average template subtraction method (Allen, Josephs, & Turner, 2000) implemented in Brain Products Analyzer, and down-sampled to 250 Hz. Secondly, the ECG R-peaks were semi-automatically detected, visually verified, and manually adjusted when necessary, to correct inaccurate R-peak detections. Then, adaptive template subtraction was used to remove BCG artifacts time-locked to the R-peak of the QRS complex of the cardiac rhythm. The quality of the data was visually verified and the amplitude of the residual artifacts time-locked to the R-peaks was inspected. An ICA-based approach (Srivastava, Crottaz-Herbette, Lau, Glover, & Menon, 2005) was applied to remove any remaining BCG residual artifact if the peak of the maximum amplitude of the residual artifact exceeded 3 μV during the QRS complex. A low-pass filter (35 Hz) and a high-pass was filter (0.3 Hz) was applied to the EEG data, which were then re-referenced to averaged mastoids. Consistent with standard practices for EEG-fMRI acquisitions, specialized EEG caps do not include free electrodes for EMG, which are contraindicated due to safety concerns. Accordingly, duplicate channels for FT9 and FT10, re-referenced to contralateral mastoids were used for the creation of electrooculogram (EOG) channels, and were band-pass filtered from 0.5 to 10 Hz to visualize horizontal eye movements. Similarly, a new bipolar channel was created from re-referencing F7 to F8 and was band-pass filtered from 10 to 50 Hz to visualize electromyogram (EMG) activity from the underlying temporalis muscles (**Supplementary** Fig. 1). It is important to note this is a deviation from the standard AASM electrode placements, which in turn, may pose a limitation. Following the artifact correction, sleep stages were manually scored in accordance with AASM standard criteria (Iber, Ancoli-Israel, Chesson, & Quan, 2007) using the "VisEd Marks" eeglab (Delorme & Makeig, 2004) toolbox.
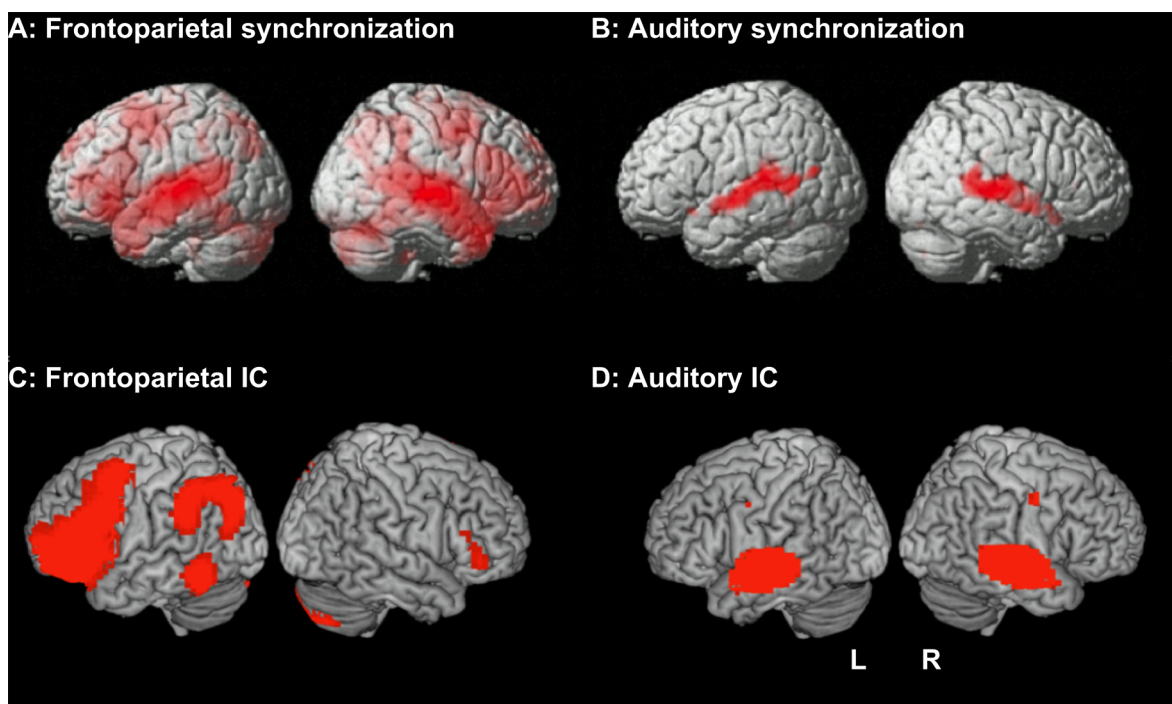

Fig. 1. Synchronization of brain activity during auditory stimulus and group ICA results. A: Whole brain inter-subject correlation for "*Taken*" audio track (p < 0.0001, FWE corrected). B: Correlated activity estimated by the auditory envelope for "*Taken*" audio track (p < 0.05, FWE corrected). Group ICA results. C: Frontoparietal network. D: Auditory network.

2.3.4. MRI imaging analysis

2.3.4.1. Auditory stimulus sleep data. The sleep-scored EEG data were analyzed over the duration of the auditory stimulus. As expected, the percentage of sleep during stimulus presentation varied by individual. Through the duration of the auditory stimulus, 5 participants remained 100% asleep, 9 had mixed wake and 8%-76% sleep, and 12 were awake. Of the 5 sleepers, 3 were in REM, 1 in NREM2, and 1 in SWS and NREM2 (87% SWS).

2.3.4.2. fMRI regression analysis. Previously developed measures of brain activity and subjective experience (Naci, Graham, et al., 2017; Naci et al., 2018) elicited by "*Taken*" were used to assess any potential stimulus-driven and higher-order brain activity in sleep. Time-courses for the auditory and frontoparietal networks' response to the narrative were derived from group-ICA in the awake control group (see *Study 1 – "Wake Study"*). These time-courses were used as regressors in the GLM for each sleeping participant (N = 14) to investigate auditory and frontoparietal network activity in sleeping individuals that was similar to that of awake individuals. The group-averaged suspense ratings from Naci et al. (2018) were convolved with the HRF to generate the regressor that estimated how engaged each participant was throughout the story. This regressor was then used in GLMs of the data of each sleeper to investigate how engaging their "*Taken*"-related experience was. The following nuisance variables were also included in the GLM: movement parameters in the three directions of motion and three degrees of rotation and the session mean BOLD signal. Linear contrasts were used to obtain participant-specific estimates for each of the independent aforementioned analyses investigating the involvement of the auditory and frontoparietal networks, or the networks supporting the subjective experience of suspense. Linear contrast coefficients, derived for each participant, were entered into the second level random-effects analysis. Only clusters of voxels that survived comparison ($p < 0.05$ threshold), corrected for multiple comparisons using family-wise error (FWE) correction, were reported.
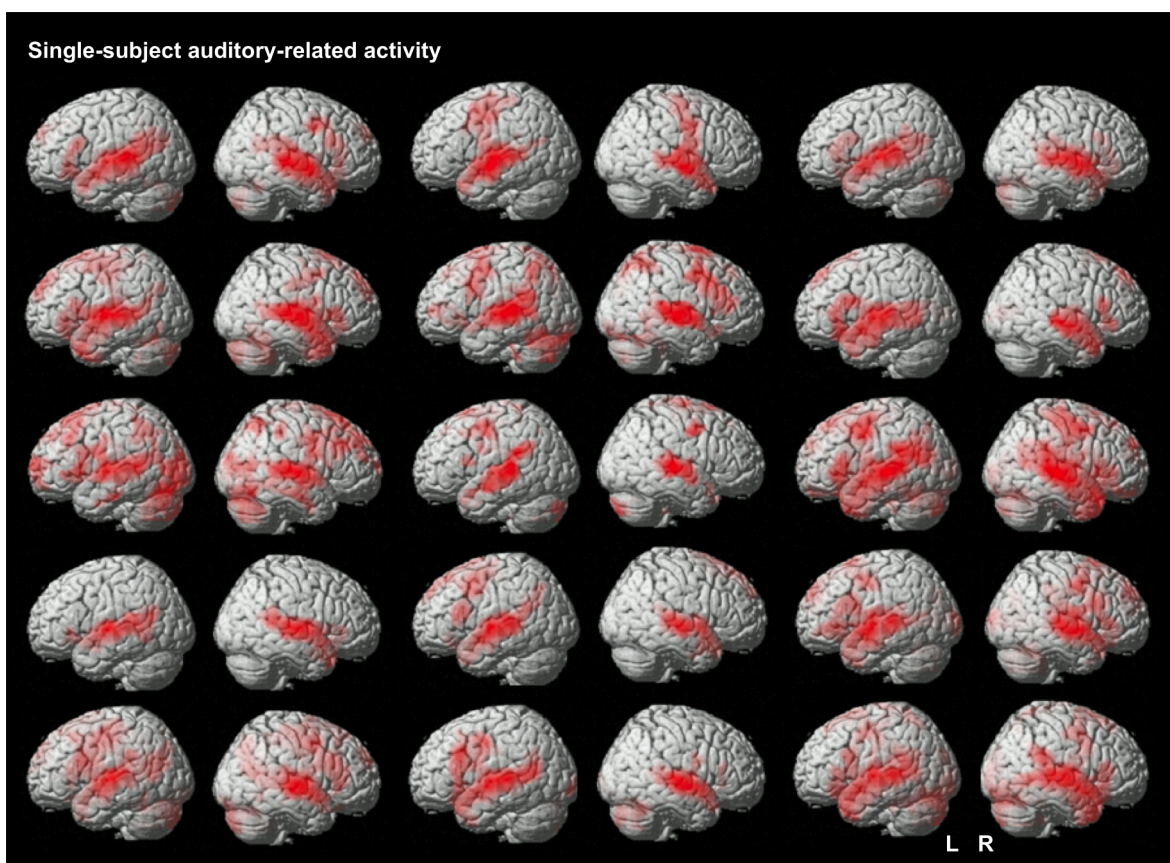
Fig. 2. Single-subject auditory-related activity. Significant ($p < 0.05$, FWE corrected) activity estimated by the time-course of the auditory IC derived from the wake group auditory stimulus in individual participants. The observed significant activity demonstrates that processing in the auditory regions at the single-subject level can be predicted from the group in 100% of participants (15/15).

3. Results

3.1. Study 1 results: Awake study

3.1.1. Synchronization of brain activity across participants during the auditory stimulus

The extent of brain activity similarity evoked by the audio track across awake participants was examined. Whole-brain analysis revealed inter-subject correlation of neural activity ($p < 0.0001$, FWE corrected) in the frontoparietal network (Fig. 1**A**), known to support executive function (Barbey et al., 2012; Hampshire & Owen, 2006; Naci et al., 2014; Sauseng et al., 2005). To show that this synchronous activity was not merely the result of the exposure to the same low-level auditory stimulation across different individuals, a regression analysis was run using the auditory envelope from the audio track. This auditory envelope varied in volume and intensity with the audio track, which contained no language. The analysis revealed inter-subject correlated activity in the region of the auditory cortex only (Fig. 1**B**). Together, these findings replicated those of Naci, Graham, et al. (2017) and demonstrated that the "*Taken*" audio track reliably elicited significantly similar brain activity across participants in dissociable sensory-driven and higher-order fronto-parietal brain regions.

To extract network-specific activity, a 20-component tensor ICA was performed. For each network, the IC that best-fitted the expected spatial extent in the auditory and frontoparietal networks was selected as the representative IC for the subsequent analyses (Fig. 1**C & 1D**). For the frontoparietal network, the spatial map of the fronto-parital IC showed dominant left distribution in the superior, middle, and inferior frontal gyri, and in the right inferior parietal lobule and inferior temporal gyrus (Fig. 1**C**). The auditory IC showed bilateral distribution in the superior temporal gyrus and superior temporal sulci (Fig. 1**D**).

The ICA-derived time-course for the auditory component was then used as a regressor in the GLM analysis. This regressor successfully estimated activity in the auditory network in all 15 awake participants ($p < 0.05$, FWE corrected), suggesting similar perceptual processing across awake individuals (Fig. 2). Next, the time-course of the frontoparietal component in the GLM analyses of individual participants was used. Significant activity was estimated ($p < 0.05$, FWE corrected), and the expected frontoparietal
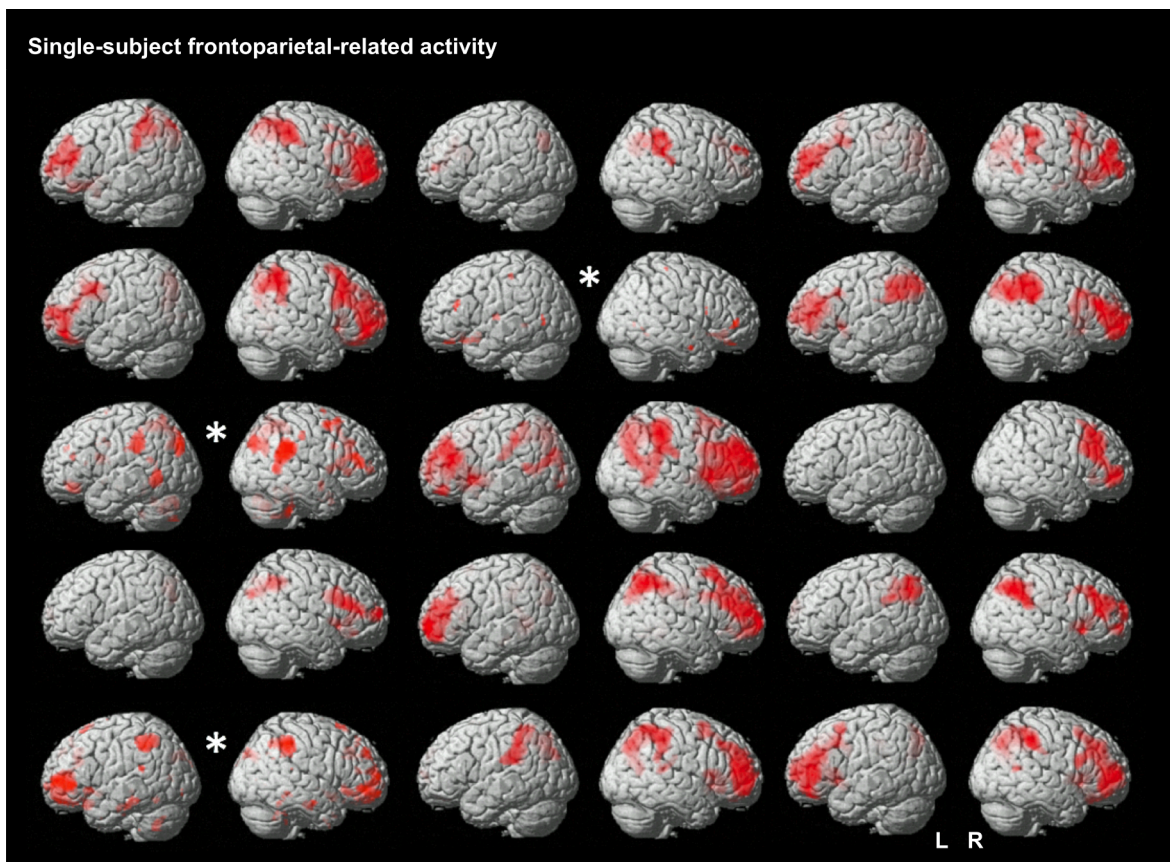
Fig. 3. Single-subject frontoparietal-related activity. Significant activity estimated by the time-course of the frontoparietal IC of the awake group "*Taken*" data ($p < 0.05$, FWE corrected) in individual participants. The observed significant activity demonstrates that processing in the frontal and parietal regions at the single-subject level can be predicted from the group in the majority (80%) of participants (12/15). Of the remaining 3 participants, 2 (13%) showed appropriate, but weak (sub-threshold) activity in the frontoparietal regions, which may be expected for single-subject datasets. "*" denotes results prior to FWE correction; these clusters do not meet significance once corrected.

network distribution was observed in 12 of 15 individuals (Fig. 3). Two additional participants showed activity in the frontoparietal network that did not meet statistical significance (noted by '*' in Figure). This result is consistent with previous research, which showed higher inter-individual variability (lower ISC) in regions supporting higher-order cognition compared to sensory-driven brain areas (Hasson, Nir, Levy, & Fuhrmann, 2004).

3.1.2. Shared experience during the auditory stimulus

Fig. 4**B** shows each individual's ratings of suspense over the duration of the stimulus and the group-averaged rating. In a leave-one-out analysis, each individual's sequential suspense ratings were compared to the group-averaged ratings of all other participants which showed highly similar suspense ratings across different participants [$r = 0.89$, $t(18) = 8.28$, $p < 0.001$]. These results suggested that different participants experienced suspense in a highly similar manner on a moment-by-moment basis.

Given that the experience of suspense was highly consistent and predictable, the subjective measure of suspense was included as a regressor in the GLM for the fMRI data, in order to investigate the brain regions that supported the shared experience. This model significantly estimated activity ($p < 0.05$, FWE corrected) in a set of regions including the left middle frontal gyrus, inferior frontal gyrus, right superior temporal gyrus, calcarine sulcus, bilateral lingual gyrus, and left supramarginal gyrus (Table 1). These regions comprise the left frontoparietal functional network and a set of auditory and speech-related brain regions (Fig. 4**A**).

These results demonstrate that suspense ratings for the "*Taken*" narrative predicted activity in a network of regions known to support the subjective experience of plot-following, including the frontoparietal network. To determine the suitability of this measure for the assessment of the potential experience of suspense in individual sleepers (**Study 2**), we then tested whether the group-level activity could be reliably observed in each individual during wakefulness.

For each participant who heard the audio track in the scanner, the group-averaged suspense rating in the GLM of their individual
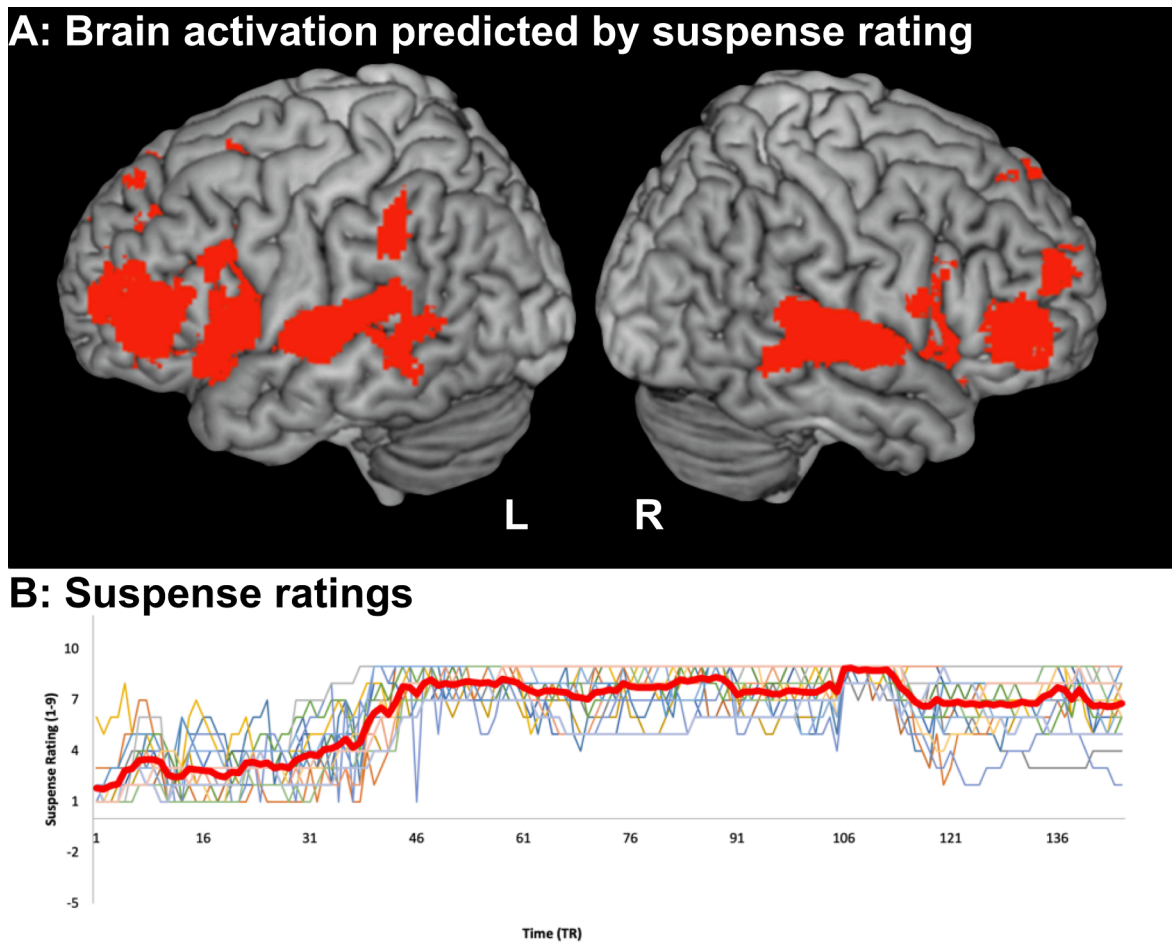
Fig. 4. Brain activation predicted by suspense ratings. A: The ratings of suspense predicted brain activity in frontoparietal and auditory regions of the participants who heard the auditory stimulus inside the scanner. ($p < 0.05$, FWE corrected). B: Suspense ratings over the duration of the "*Taken*" audio-narrative ($N = 20$). Suspense was rated on a scale from 1 (least suspenseful) to 9 (most suspenseful). Ratings were collected every 2.16 s to correspond with the repetition time (TR) used in the fMRI study. Each line displays a participant's suspense ratings over time. The bold red line represents the group-average suspense rating.

Table 1
Group activation predicted by suspense rating.

Brain area	Hemisphere	MNI coordinate of cluster peaks			Z	p value (FWE)
		x	y	z		
Middle frontal gyrus	Left	−26	38	−4	5.52	0.003
Superior temporal gyrus	Left	−46	−22	2	5.07	0.029
Inferior frontal gyrus	Left	−40	40	−2	4.95	0.046
Superior temporal gyrus	Right	62	−24	8	5.05	0.031
Cuneus	Left	−2	−86	4	4.92	<0.001*
Lingual gyrus	Bilateral	−8	−78	4	4.50	<0.001*
Supramarginal gyrus	Left	−52	−42	38	4.03	0.010*

Significant whole-brain results for the group data modeled by the group-averaged suspense ratings at p < 0.05 FWE corrected at the peak level and at the cluster level (*).

data were used. These single-subject models demonstrated that significant brain activity in the frontal, parietal and temporal regions could be estimated by the independent behavioural measure (p < 0.05, FWE corrected) for the majority (80%, 12 of 15) of awake participants (Fig. 5). These findings open the possibility that similar results could be obtained in the absence of reports, as well and for investigating the experience of listening to the movie plot unfold in the absence of generating a subjective report in individual participants. Therefore, the group-averaged suspense ratings provide a suitable measure for testing the potential experience of following the plot in individual sleepers who are unable to provide subjective reports.
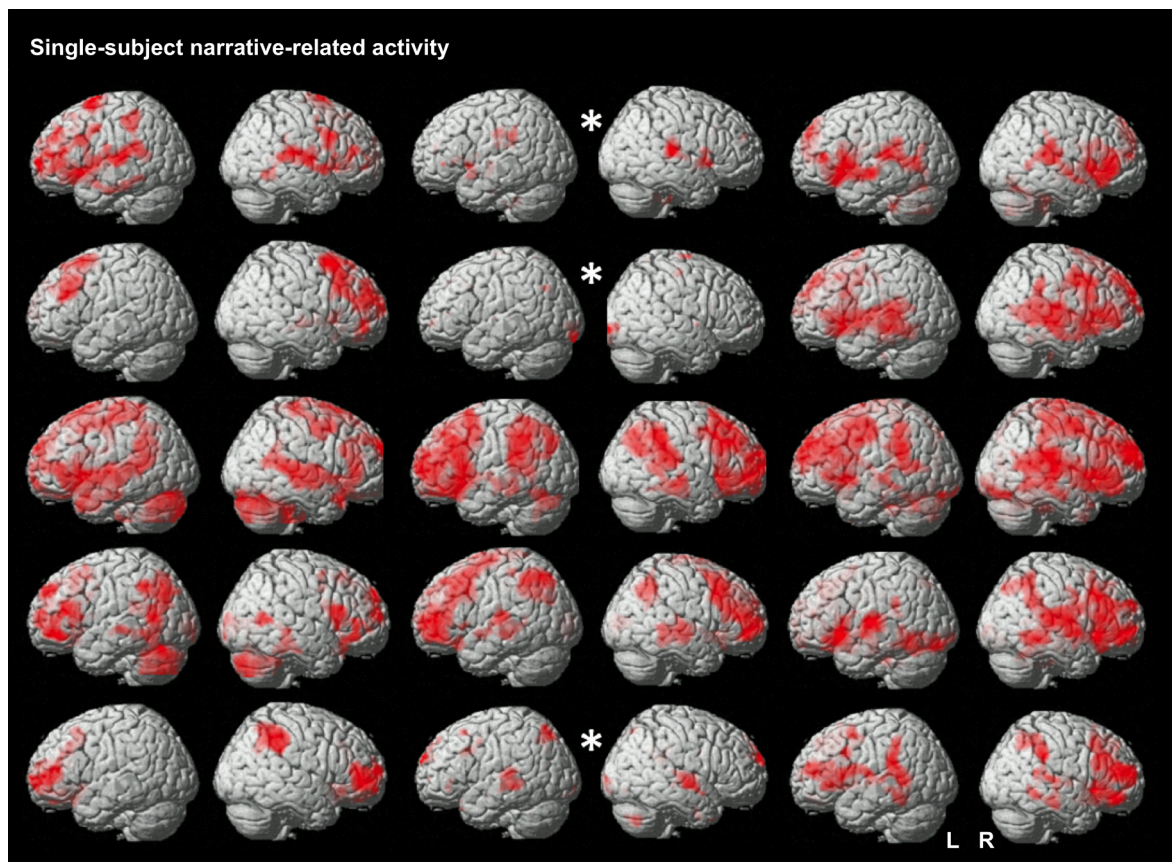
Fig. 5. Single-subject narrative-related activity. Significant brain activity estimated in awake single individuals, who listened to "*Taken*" inside the scanner, by the average suspense ratings collected from a separate group of participants tested outside the scanner (p < 0.05, FWE corrected). The auditory and frontoparietal regions in the majority (80%) of individuals (12/15) responded significantly to how engaging the narrative was as indexed by ratings of suspense. In 13% (2/15) of participants only auditory regions were predicted by suspense ratings, but these exhibited weak and sub-threshold activity that did not meet the significance criterion. Results prior to FWE correction are denoted with '*'; these clusters do not meet significance once corrected.

3.2. Study 2 results: Sleep study

3.2.1. Stimulus-specific brain activity during sleep

To investigate the extent of stimulus processing and the capacity to follow a narrative during sleep, the brain activity of each sleeper was compared to the processing templates derived from the awake control group. Only data from participants who slept through the entirety of the "*Taken*" stimulus (N = 5) were included in the analyses (Table 2). First, to assess each individual's ability to process the low-level auditory features, the ICA-derived auditory time-course from the awake group was used as a regressor in a GLM analysis of each sleeper's data. Sensory-driven processing in the auditory network was observed unilaterally (right-hemisphere) in two of three individuals in REM (P01, P05), bilaterally in one sleeper in REM (P06) and in the participant with NREM2/3 (P14; 87% SWS) ($p < 0.05$, FWE corr.), but not for the participant who experienced NREM2 sleep only (P09) (Fig. 6A).

Next, the frontoparietal time-course was used to estimate brain activity related to stimulus understanding in individual sleepers. The frontoparietal time-course estimated significant brain activity ($p < 0.05$, FWE corrected) in one sleeper (P05-REM) (Fig. 6B). Prior to family-wise error correction, one additional sleeper (P06-REM) showed processing in the same frontoparietal network; this activity, albeit sub-threshold, suggested that this sleeper might have tracked external information during the auditory stimulus. This activity was not observed during NREM2 or NREM2/3.

Finally, evidence that any sleeping participant may be comprehending the story was investigated by using a more direct measure of plot engagement, namely, the subjective perception of suspense, obtained in the behavioural experiment. The group-averaged suspense ratings were previously shown to reliably estimate activity within the frontoparietal distribution in awake individuals. Similar to participants who were awake, large significant clusters of activity in the frontal, parietal, and temporal regions were observed in P06 (REM). Sleeper P05 (REM), showed part of this pattern in the frontopolar cortex and PFC. This activity was not observed during NREM2 or NREM2/3 in two additional participants (Fig. 7).

4. Discussion

The current study examined the extent to which complex, ecologically valid information can be processed during wakefulness and sleep at the single-subject level, using a compelling movie narrative in order to assess high-level processing. Similar to previous findings from Naci, Graham, et al. (2017), this complex auditory stimulus was found to elicit widespread ISC across the brains of awake listeners (Hasson et al., 2004; Naci et al., 2014). As expected, continuous tracking of specific plot details across individuals was reflected by consistent recruitment of auditory and frontoparietal networks. Reliable estimates of the activity of these networks in response to the "*Taken*" stimulus were generated in each awake individual, suggesting that the use of this paradigm for the identification of the presence of stimulus-specific processing in sleeping individuals was possible at the single-subject level.

Consistent with previous studies, no activity reflective of the auditory stimulus processing was observed in the auditory and frontoparietal networks during NREM2 sleep. Sleep spindles are known to restrict processing in the auditory cortex (Dang-Vu et al., 2011), to prevent signs of arousal from sleep (Cote, Epps, & Campbell, 2000). In addition, the brain's capacity to respond to rhythmic auditory stimuli is disrupted during spindle events and slow waves (Lustenberger et al., 2018). As the "*Taken*" stimulus was continuously unfolding, even brief interruptions of auditory processing resulting from spindles and slow waves may be enough to diminish similarity of processing in auditory and frontoparietal networks and give rise to idiosyncratic processing patterns across different individuals. The lack of ISC suggests that NREM2 does not provide a reliable condition for processing continuous auditory information. As low-level processing is required for upstream processing, it follows that narrative-related activity in higher-order networks was not observed in NREM2 either. However, the possibility that sleep spindles and slow waves are specifically involved in blocking incoming

Table 2
Percentage of time in each sleep stage during the auditory stimulus per participant.

Participant	Sleep Stage				
	Wake	NREM1	NREM2	NREM3	REM
P01*	0	0	0	0	100
P02	62	25	13	0	0
P03	30	13	58	0	0
P04	45	0	19	4	32
P05*	0	0	0	0	100
P06*	0	0	0	0	100
P07	46	13	41	0	0
P08	92	8	0	0	0
P09*	0	0	100	0	0
P10	24	0	45	31	0
P11	13	26	62	0	0
P12	50	0	32	18	0
P13	92	6	2	0	0
P14*	0	0	13	87	0
Mean	0.0	0.0	22.6	17.4	60.0
SD	0.0	0.0	39.0	34.8	49.0

Note. Percentages are out of the total stimulus duration (5 min 12 sec). * Indicates included in sleep analyses.
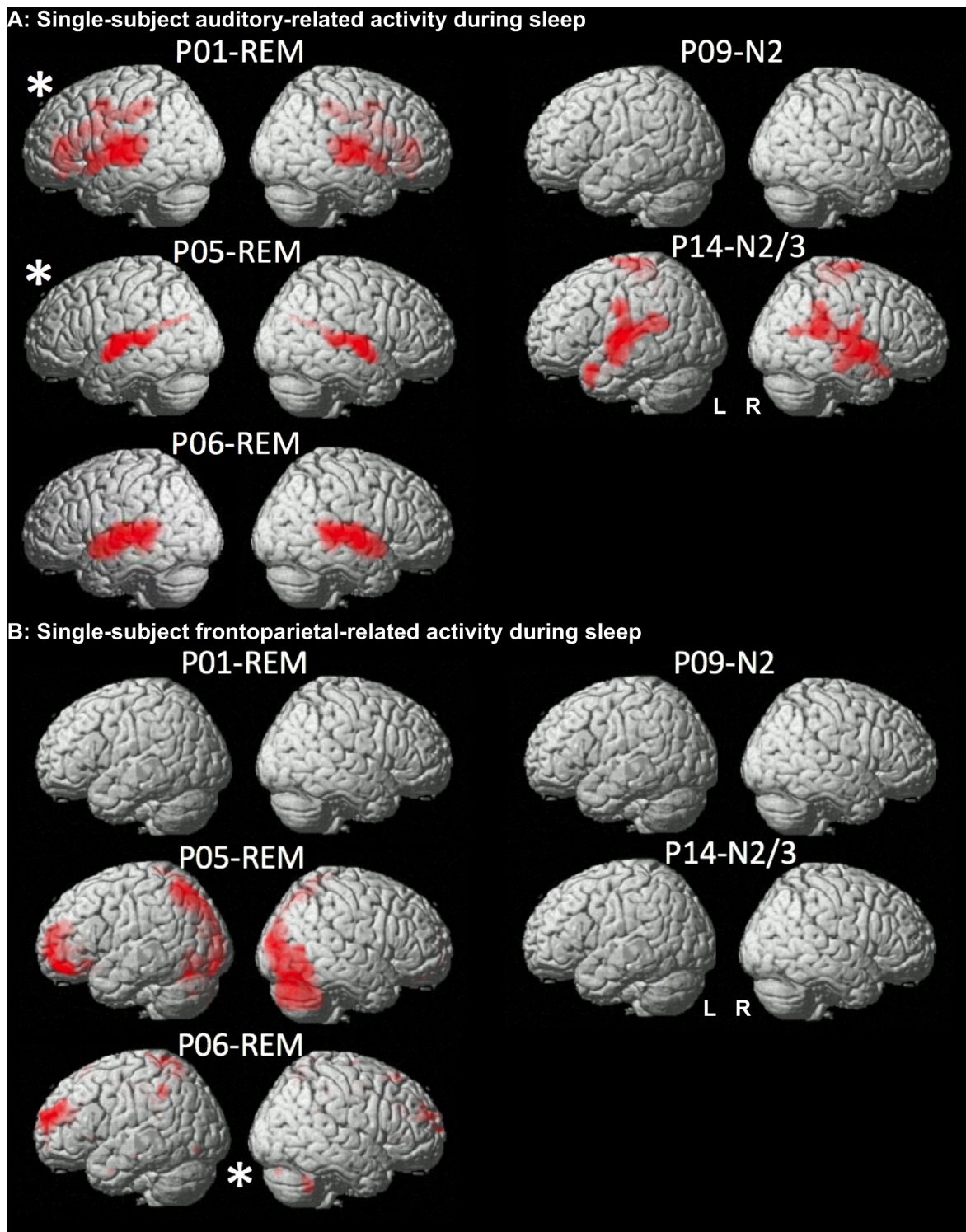
Fig. 6. Single-subject auditory-related and frontoparietal-related activity during sleep. A: Significant (p < 0.05, FWE corrected) activity of sleeping participants in response to the "*Taken*" stimulus, as estimated by the time-course of the auditory IC from the wake group. Sensory processing is preserved bilaterally in one participant in REM and one participant with mixed NREM2 and 3 stages. P01 and P05 was observable, but did not survive FWE correction for multiple comparisons (*). B: Significant activity (p < 0.05, FWE corrected) of sleeping participants estimated by the time-course of the frontoparietal IC of the wake "*Taken*" data. One participant in REM (P06) showed the expected, but weak (sub-threshold) activity in the frontal and parietal regions (*). The significant activity of one REM sleeper (P05) did not show the expected frontal and parietal distribution.
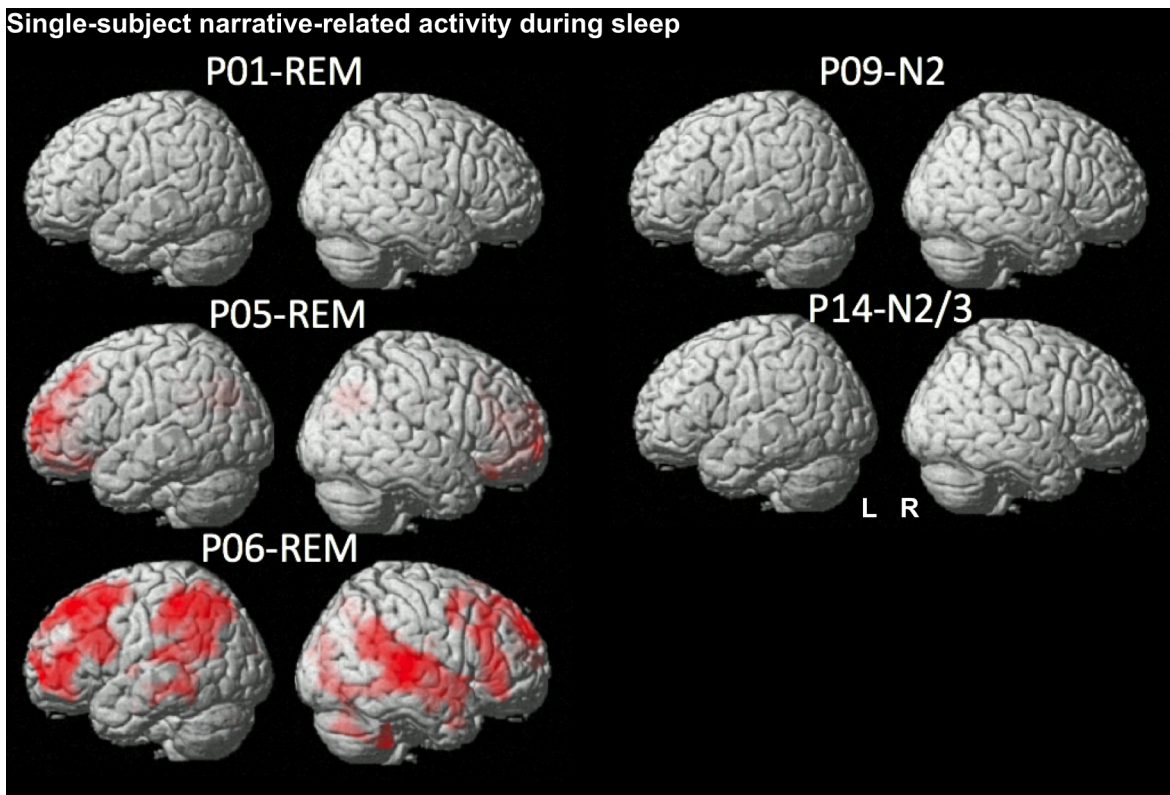
Fig. 7. Single-subject narrative-related activity during sleep. Significant brain activity (p < 0.05, FWE corrected) estimated in sleeping participants, who were presented the "*Taken*" stimulus in the scanner, by the set of average suspense ratings from the awake group. The auditory and fronto-parietal regions in one participant in REM (P06) and partially in another (P05) responded significantly to suspense throughout the narrative.

in this particular case is speculative and remains to be directly investigated using more in naturalistic auditory processing paradigms.

The ISC activity in the auditory network of the individual in SWS demonstrates preservation of the ability to process low-level auditory features. Wake-like auditory network responsivity has been previously demonstrated in SWS (Schabus et al., 2012); however, the propagation to higher order association regions was shown to depend on the phase of SWA. The current findings may be explained by this phase-dependent modulation, given that during SWS there was preserved auditory processing in the auditory cortex, but no activity reflective of higher order processing.

Our results tentatively suggest that brain activity during REM may allow for the meaningful processing of auditory information. Low-level processing of the auditory features of the stimulus was observed in all individuals in REM sleep. Strikingly, one participant that showed significant bilateral auditory stimulus-specific activity in the auditory network, also showed brain activity indicative of higher-level information-processing. This suggests that bilateral processing may be necessary for further higher-level processing to be possible. In addition, for this participant in REM (and partially in another), the behavioural measure of suspense from the wake group significantly modeled frontal and parietal activity, similar to that of the awake group. To our knowledge, this is the first time that fMRI activity indicative of higher-level cognition has been observed during REM sleep. Although this was only convincingly demonstrated in one individual, and partially in one other, obtaining fMRI data during REM is notoriously difficult. That said, these methods were born out of procedures from our work in patients with disorders of consciousness that are appropriate, robust and specifically designed to identify the presence of cognitive processes and consciousness at the single-subject level. Future studies could boost REM sleep propensity using sleep deprivation techniques to more extensively study REM sleep using this approach. Despite progress in simultaneous EEG-fMRI research, this remains a significant methodological hurdle to overcome; required to obtain robust sample sizes necessary to make inferences to larger populations.

REM sleep is associated with wakefulness-like cortical activity, suggesting that information processing consistent with wakefulness occurs within REM sleep. Interruptions in otherwise continuous noise can elicit allocation of attentional resources during REM (Muller-Gass & Campbell, 2014), and there appears to be an inverse relationship between the level of conscious awareness and the degree of connectedness to the environment in NREM and REM. This has been demonstrated in one study (Andrillon et al., 2016) in which words previously presented during wakefulness, disrupted REM sleep by an increase in higher frequency brain activity (>12 Hz). Other brain oscillations that reflect the conscious recognition of a sound, are present in wakefulness and REM, but not SWS (Kállai, Harsh, & Voss, 2003; Llinas & Ribary, 1993). Finally, variability in the extent of sensory processing within REM may explain the differences seen across REM sleepers in this study. For example, the presence of phasic bursting of the intensity of rapid eye movements themselves has

been shown to reduce responsiveness to the external environment (Ermis, Krakow, & Voss, 2010). However, this is not the case during periods of tonic REM. Given the sparsity of the available data, this possibility remains to be directly investigated.

Dreams during REM have a wake-like narrative property (Siclari, Bassetti, & Tononi, 2012), suggesting a preserved ability to continuously integrate information. Siclari, LaRocque, Postle, & Tononi (2013), awakened participants through the night and collected subjective reports to investigate the phenomenal conscious features of their dream experience. The richness and duration of conscious experience was reported to be highest in REM. However, dreams in REM have been found to lack analytical thought (Hobson & Pace-Schott, 2002), suggesting that if the auditory stimulus were to enter mental content during sleep it may not be meaningfully understood. Thus, dream consciousness is thought to be mostly disconnected from the sleeper's physical environment. Consistent with this notion, external stimuli are rarely incorporated into dream content (Dement & Wolpert, 1958; Nir & Tononi, 2010), and when they are, can have an impact on emotional processing (De Koninck & Koulack, 1975), however, wake-like sensory awareness is rarely achieved (Burton, Harsh, & Badia, 1988). It should be noted that very salient environmental information (Berger, 1994) or a physical stimulus (Dement & Wolpert, 1958) have a greater likelihood of being incorporated into dreams. In the "*Taken*" narrative, the majority of the information is not salient, thus, it is remarkable to find that the continuous information from the auditory stimulus elicits a wake-like response in sleeping individuals. However, without a dream report, no claims regarding the incorporation of the auditory stimulus into dream mentation can be made from the current study.

4.1. Conclusions

The narrative-following-related brain activity observed during REM in one participant, and partly in one other suggests that it is possible to track and incorporate the moment-to-moment complexities of the narrative from the auditory stimulus into coherent thought and have an associated conscious experience. However, two sleepers lacked this BOLD signal stimulus response, which suggests that only some individuals, or for only some of the time, in REM can track and integrate information from their environment. This novel finding highlights that sleep may be even more complex than the literature suggests, and much work remains to be done to understand the information processing capacities across sleep-wake states. This study provides a novel approach for future investigations and provides unique insight into the capacity of the brain to process the meaning of information from the external environment across natural variations in states of consciousness.

CRediT authorship contribution statement

Stuart Fogel: Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration. **Laura Ray:** Data curation, Writing – review & editing. **Zhuo Fang:** Investigation, Data curation, Supervision. **Max Silverbrook:** Investigation, Formal analysis, Visualization, Writing – original draft. **Lorina Naci:** Conceptualization, Methodology, Software, Formal analysis, Visualization, Writing – review & editing, Supervision, Project administration. **Adrian Owen:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.concog.2022.103306.

References

Allen, P. J., Josephs, O., & Turner, R. (2000). A method for removing imaging artifact from continuous EEG recorded during functional MRI. *Neuroimage, 12*(2), 230–239. https://doi.org/10.1006/nimg.2000.0599

Andrillon, T., Poulsen, A. T., Hansen, L. K., L É Ger, D., Kouider, S., Léger, D., & Kouider, S. (2016). Neural Markers of Responsiveness to the Environment in Human Sleep. *The Journal of Neuroscience, 36*(24), 6583–6596. https://doi.org/10.1523/JNEUROSCI.0902-16.2016

Barbey, A. K., Colom, R., Solomon, J., Krueger, F., Forbes, C., & Grafman, J. (2012). An integrative architecture for general intelligence and executive function revealed by lesion mapping. *Brain, 135*(4), 1154–1164. https://doi.org/10.1093/brain/aws021

Beckmann, C. F., & Smith, S. M. (2005). Tensorial extensions of independent component analysis for multisubject FMRI analysis. *NeuroImage, 25*(1), 294–311. https://doi.org/10.1016/j.neuroimage.2004.10.043

Berger, M. (1994). Dreaming and REM Sleep-Commentary. *World Federation of Sleep Research Societies Newsletter, 3,* 13.

Besson, L., & Morel, P. (2008). *Taken*. United States: 20th Century Fox.

Burton, S. A., Harsh, J. R., & Badia, P. (1988). Cognitive activity in sleep and responsiveness to external stimuli. *Sleep: Journal of Sleep Research & Sleep Medicine, 11,* 61–68. US: American Academy of Sleep Medicine.

Cote, K. A., Epps, T. M., & Campbell, K. B. (2000). The role of the spindle in human information processing of high-intensity stimuli during sleep. *Journal of Sleep Research, 9*(1), 19–26. https://doi.org/10.1046/j.1365-2869.2000.00188.x

Cusack, R., Vicente-Grabovetsky, A., Mitchell, D. J., Wild, C. J., Auer, T., Linke, A. C., & Peelle, J. E. (2015). Automatic analysis (aa): Efficient neuroimaging workflows and parallel processing using Matlab and XML. *Frontiers in Neuroinformatics, 8,* 90. https://doi.org/10.3389/fninf.2014.00090

Damoiseaux, J. S., Rombouts, S. A. R. B., Barkhof, F., Scheltens, P., Stam, C. J., Smith, S. M., & Beckmann, C. F. (2006). Consistent resting-state networks across healthy subjects. *Proceedings of the National Academy of Sciences of the United States of America, 103*(37), 13848–13853.

Dang-Vu, T. T., Bonjean, M., Schabus, M., Boly, M., Darsaud, A., Desseilles, M., … Maquet, P. (2011). Interplay between spontaneous and induced brain activity during human non-rapid eye movement sleep. *Proceedings of the National Academy of Sciences of the United States of America, 108*(37), 15438–15443. https://doi.org/10.1073/pnas.1112503108

Dang-Vu, T. T., McKinney, S. M., Buxton, O. M., Solet, J. M., & Ellenbogen, J. M. (2010). Spontaneous brain rhythms predict sleep stability in the face of noise. *Current Biology, 20*(15), R626–R627. https://doi.org/10.1016/j.cub.2010.06.032

De Koninck, J, & Koulack, D (1975). Dream content and adaptation to a stressful situation. *Journal of Abnormal Psychology, 84*(3), 250–260.

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Dement, W., & Wolpert, E. A. (1958). The relation of eye movements, body motility, and external stimuli to dream content. *Journal of Experimental Psychology, 55*(6), 543–553. https://doi.org/10.1037/h0040031

Douglass, A. B., Bornstein, R. F., Nino-Murcia, G., Keenan, S., Miles, L., Zarcone, V. P., … Dement, W. C. (1994). The Sleep Disorders Questionnaire. I: Creation and multivariate structure of SDQ. *Sleep, 17*(2), 160. https://doi.org/10.1093/sleep/17.2.160

Ermis, U., Krakow, K., & Voss, U. (2010). Arousal thresholds during human tonic and phasic REM sleep: Phasic and tonic REM sleep. *Journal of Sleep Research, 19*(3), 400–406. https://doi.org/10.1111/j.1365-2869.2010.00831.x

Hampshire, A., & Owen, A. M. (2006). Fractionating attentional control using event-related fMRI. *Cerebral Cortex, 16*(12), 1679–1689. https://doi.org/10.1093/cercor/bhj116

Hasson, U., Malach, R., & Heeger, D. J. (2010). Reliability of cortical activity during natural stimulation. *Trends in Cognitive Sciences, 14*(1), 40–48. https://doi.org/10.1016/j.tics.2009.10.011

Hasson, U., Nir, Y., Levy, I., & Fuhrmann, G. (2004). Natural Vision. *Science, 303*, 1634–1640.

Hobson, J. A., & Pace-Schott, E. F. (2002). The cognitive neuroscience of sleep: Neuronal systems, consciousness and learning. *Nature Reviews Neuroscience, 3*(9), 679–693. https://doi.org/10.1038/nrn915

Huettel, S., Song, A., & McCarthy, G. (2014). Statistical Analysis II: Advanced Approaches. *Functional Magnetic Resonance Imaging* (3rd). Oxford, United Kingdom: Oxford University Press.

Iber, C., Ancoli-Israel, S., Chesson, A. L., & Quan, S. F. (2007). *The AASM manual for the scoring of sleep and associated events: Rules, terminology and technical specifications* (1st ed.). Westchester, IL: American Academy of Sleep Medicine.

Kállai, I., Harsh, J., & Voss, U. (2003). Attention to external stimuli during wakefulness and sleep: Evoked 40-Hz response and N350. *Psychophysiology, 40*(6), 955–966. https://doi.org/10.1111/1469-8986.00114

Llinas, R., & Ribary, U. (1993). Coherent 40-Hz oscillation characterizes dream state in humans. *Proceedings of the National Academy of Sciences of the United States of America, 90*(5), 2078–2081. https://doi.org/10.1073/pnas.90.5.2078

Lustenberger, C., Patel, Y. A., Alagapan, S., Page, J. M., Price, B., Boyle, M. R., & Fröhlich, F. (2018). High-density EEG characterization of brain responses to auditory rhythmic stimuli during wakefulness and NREM sleep. *NeuroImage, 169*(December 2017), 57–68. https://doi.org/10.1016/j.neuroimage.2017.12.007

Muller-Gass, A., & Campbell, K. (2014). Event-related potential measures of gap detection threshold during natural sleep. *Clinical Neurophysiology, 125*(8), 1647–1652. https://doi.org/10.1016/j.clinph.2013.11.043

Mullinger, K. J., Yan, W. X., & Bowtell, R. (2011). Reducing the gradient artefact in simultaneous EEG-fMRI by adjusting the subject's axial position. *NeuroImage, 54*(3), 1942–1950. https://doi.org/10.1016/j.neuroimage.2010.09.079

Naci, L., Cusack, R., Anello, M., & Owen, A. M. (2014). A common neural code for similar conscious experiences in different individuals. *Proceedings of the National Academy of Sciences of the United States of America, 111*(39), 14277–14282. https://doi.org/10.1073/pnas.1407007111

Naci, L., Graham, M., Owen, A. M., & Weijer, C. (2017). Covert narrative capacity: Mental life in patients thought to lack consciousness. *Annals of Clinical and Translational Neurology, 4*(1), 61–70. https://doi.org/10.1002/acn3.376

Naci, L., Haugg, A., MacDonald, A., Anello, M., Houldin, E., Naqshbandi, S., … Owen, A. M. (2018). Functional diversity of brain networks supports consciousness and verbal intelligence. *Scientific Reports, 8*(1), 13259. https://doi.org/10.1038/s41598-018-31525-z

Naci, L., Sinai, L., & Owen, A. M. (2017). Detecting and interpreting conscious experiences in behaviorally non-responsive patients. *NeuroImage, 145*(Pt B), 304–313. https://doi.org/10.1016/j.neuroimage.2015.11.059

Nir, Y., & Tononi, G. (2010). Dreaming and the brain: From phenomenology to neurophysiology. *Trends in Cognitive Sciences, 14*(2), 88–100. https://doi.org/10.1016/j.tics.2009.12.001

Portas, C. M., Krakow, K., Allen, P. J., Josephs, O., Armony, J. L., & Frith, C. D. (2000). Auditory processing across the sleep-wake cycle: Simultaneous EEG and fMRI monitoring in humans. *Neuron, 28*(3), 991–999. https://doi.org/10.1016/S0896-6273(00)00169-0

Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *International Journal of Psychophysiology, 57*(2), 97–103. https://doi.org/10.1016/j.ijpsycho.2005.03.018

Schabus, M., Dang-Vu, T. T., Heib, D. P. J., Boly, M., Desseilles, M., Vandewalle, G., … Maquet, P. (2012). The Fate of Incoming Stimuli during NREM Sleep is Determined by Spindles and the Phase of the Slow Oscillation. *Frontiers in Neurology, 3*, 40. https://doi.org/10.3389/fneur.2012.00040

Siclari, F., Bassetti, C., & Tononi, G. (2012). Conscious experience in sleep and wakefulness. *Schweizer Archiv Für Neurologie Und Psychiatrie, 163*, 273–278. Tononi, Giulio: Department of Psychiatry, University of Wisconsin – Madison, 6000 Research Park Blvd, Madison, WI, US, 53519, gtononi@wisc.edu: Schwabe & Co.

Siclari, F., LaRocque, J. J., Postle, B. R., & Tononi, G. (2013). Assessing sleep consciousness within subjects using a serial awakening paradigm. *Frontiers in Psychology, 4*(AUG), 1–9. https://doi.org/10.3389/fpsyg.2013.00542

Smith, S. M., Fox, P. T., Miller, K. L., Glahn, D. C., Fox, P. M., Mackay, C. E., … Beckmann, C. F. (2009). Correspondence of the brain's functional architecture during activation and rest. *Proceedings of the National Academy of Sciences of the United States of America, 106*(31), 13040–13045. https://doi.org/10.1073/pnas.0905267106

Srivastava, G., Crottaz-Herbette, S., Lau, K. M., Glover, G. H., & Menon, V. (2005). ICA-based procedures for removing ballistocardiogram artifacts from EEG data acquired in the MRI scanner. *NeuroImage, 24*(1), 50–60. https://doi.org/10.1016/j.neuroimage.2004.09.041

Tavakoli, P., Varma, S., & Campbell, K. (2018). Highly relevant stimuli may passively elicit processes associated with consciousness during the sleep onset period. *Consciousness and Cognition, 58*, 60–74. https://doi.org/10.1016/j.concog.2017.10.012

Zaki, J., & Ochsner, K. (2009). The Need for a Cognitive Neuroscience of Naturalistic Social Cognition. *Annals of the New York Academy of Sciences, 1167*, 16–30. https://doi.org/10.1111/j.1749-6632.2009.04601.x.The