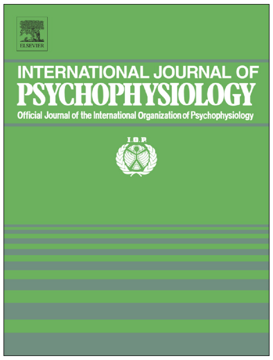

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Processing of Semantic Incongruency at the Onset of Sleep: An Auditory N400 Evoked Potential Study

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Abstract

The ability to organize self-generated thought into coherent, meaningful semantic representations is a central aspect of human cognition and undergoes regular alterations throughout the day. To investigate whether changes in semantic processing might explain the loss of coherence, logic, and voluntary control over thinking typically accompanying the transition to sleep, we recorded N400 evoked potentials from 44 healthy subjects. Auditory word pairs with varying semantic distance were presented while they were allowed to fall asleep. Using semantic distance and wakefulness level as regressors, we found that semantic distance reliably elicited an N400, and lower wakefulness levels were associated with increased frontal negativity within a similar time range. Additionally, and contrary to our initial hypothesis, the results showed an interaction of semantic distance and wakefulness that is best interpreted as an increased N400 effect with decreasing wakefulness. While these results do not rule out a possible role of semantic processes in the generation of diminished logic and thought control during the transition to sleep, we discuss the possibility of additional brain mechanisms that usually constrain the inner stream of consciousness during wakefulness.

Keywords: Transition to sleep, Event-related potentials, Semantic processing, N400, Formal thought disorder, Self-generated thought

1. Introduction

The transition to sleep, that is, the period between relaxed wakefulness and the onset of sleep (first occurrence of sleep stage 2) is a dynamic process, with a series of physiological, behavioral, and psychological changes accompanying this state (Goupil & Bekinschtein, 2012; Ogilvie, 2001; Yang et al., 2010). This was already recognized early on by Kleitman, who stated: “Whereas it is easy to distinguish between the conditions of alertness or being wide awake, and definite sleep, the passage from one to the other involves a succession of intermediate states, part wakefulness and part sleep in varying proportions - what is designated in Italian as dormiveglia, sleep-waking” (Kleitman, 1987, p. 71). Among the most prominent indicators of this state are various neurophysiological, cardiovascular, and respiratory changes, the appearance of slow eye movements and sleep-specific components of event-related potentials (ERPs) like the N350, N550, or P900 component, a decrease in muscle strength, and a loss of behavioral responsiveness (Ogilvie, 2001).

Besides the effects of decreased wakefulness on different physiological and behavioral parameters, changes can also be observed on a level of subjective experience, making the transition to sleep a unique state of mind (Vaitl et al., 2005). Changes in subjective experiences paralleling the physiological and behavioral alterations include the gradual loss of awareness of external stimuli, thought processes as well as sensory/perceptual experiences (e.g., hypnagogic imagery) (Siclari et al., 2013; Yang et al., 2010). In this context, especially the loss of coherence of thought, logic and voluntary control over thinking are most determinant for the correct identification of having fallen asleep (Yang et al., 2010), and at the same time, they suggest that changes in mental activity across the sleep onset process are related to changes in underlying neurophysiological activity (Fox & Girn, 2017). In support of this notion, the frequency of hypnagogic imagery has been shown to correlate with specific spectral EEG parameters (e.g., Foulkes & Vogel, 1965; Hayashi et al., 1999). To date, however, the processes mediating diminished thought control during the transition to sleep have not been investigated systematically.

As altered thought processes are considered a core feature of pathological conditions such as schizophrenia (Roche et al., 2015; Strik et al., 2017), one might assume that the loosening of associations characterizing the transition to sleep share some common features with the emergence of formal thought disorder in schizophrenia. Deficits in semantic processing have been proposed as a possible cause of bizarre associations and disorganized speech in formal thought disorder, as shown by studies investigating language-related evoked potentials (see e.g., Kumar & Debruille, 2004). Thus, the loosening of associations at the transition to sleep might imply that the brain mechanisms associated with semantic processing are modified during this state. However, unlike formal thought disorder in psychosis, the transition to sleep is a regular, reversible state, which therefore provides a unique opportunity to investigate the neurophysiological correlates of spontaneous variations in the evaluation of the coherence of thought.

In wakefulness, a classical index for the activity of brain mechanisms involved in semantic processing is the N400 of evoked potentials. The N400 effect is defined as a negative potential difference that is obtained by comparing ERPs elicited by stimuli that are semantically incompatible with the preceding context against ERPs elicited by stimuli that are compatible with such a context. The N400 effect is typically observed within a time range between around 200 to 600 ms, most prominent at centro-parietal electrode sites (Kutas & Hillyard, 1980).

Together with the altered logic and coherence of thinking during the transition to sleep, we, therefore hypothesized that the N400 effect systematically varies within the range of full wakefulness to the onset of sleep.

Other studies investigating ERPs during the transition to sleep and sleep in general indicate that the neurophysiological response to specific stimuli persists with the progression towards sleep but also shows increasing modifications (for review see Atienza et al., 2001; Ibáñez et al., 2009). For example, the amplitudes of the N100 and P300 components have been shown to be decreased in slow-wave sleep compared with wakefulness or rapid eye movement (REM) sleep, suggesting that the information received by the cortex is less processed during non-REM sleep than during REM sleep (e.g., Bastuji et al., 1995; de Lugt et al., 1996). Similar to this, the mismatch negativity (MMN) could be elicited during all sleep stages but showed a diminished amplitude during sleep compared with wakefulness (Atienza et al., 2000). In contrast, the amplitude of other components like the N2 and P2, and later components, that have been associated with the occurrence of K-complexes, showed consistent increases with sleep progression (e.g., de Lugt et al., 1996; Harsh et al., 1994).

Of particular relevance for the present study, previous investigations showed that the N400 could be elicited during non-REM and REM sleep, indicating an at least partially preserved detection of semantic incongruency during these states (e.g., Brualla et al., 1998; Ibáñez et al., 2006; Perrin et al., 2002). However, none of these studies directly compared the size of the N400 effect between different levels of wakefulness or sleep stages. The current study aimed to fill this gap and focused on the transition to sleep, where variability in the coherence of thinking is particularly prominent.

Regarding the directionality and causing mechanisms underlying the N400 effect, several theories have been put forward, the two most influential of which are the theory of semantic integration and the theory of facilitated lexical access. In the semantic integration view, the N400 reflects the integration of a target word within the longstanding semantic network and recently activated sentential context (Lau et al., 2008), which is based on previous inputs, world knowledge, and thus evolving expectations (Kutas & Federmeier, 2011). According to this view, the N400 is defined as an active, effortful, post-lexical process (Brown & Hagoort, 1993). The increased N400 peak after semantically incongruent stimuli is then explained by the effort needed to properly integrate an implausible or mismatching stimulus into an existing sentential context(Lau et al., 2008). Kutas and Federmeier (2011) highlighted the strength of this view as its capacity to account for the multi- and cross-modal nature of the N400. This is based on the assumption that all modes of access to a particular semantic information (auditory, visual, pictorial, lexical) converge to similar conceptual representations (Kutas & Federmeier, 2011). Moreover, the N400 has been argued to occur too late to only represent facilitated lexical access (Hauk et al., 2006).

In contrast, the theory of facilitated lexical access defines the process represented by the N400 as automatic and prelexical activation of brain regions associated with the target word in long-term memory (Brown & Hagoort, 1993). The increased N400 after semantically incongruent stimuli is then explained by the additional effort necessary to access the meaning of a word that has not been primed. Therefore, all conditions that ease the access to the representation of the target word, including prior congruent prime words, result in a reduced amplitude of the N400. This is argued to be based on the pre-activation of certain parts of the semantic network by the prime, facilitating the retrieval of the target word. In line with this notion, Lau et al. (2008) provided support for this view by demonstrating connections between brain regions associated with lexical access and evoked N400 potentials (Lau et al., 2008). While this data rules out a purely integrative, i.e., post-lexical role of the N400, integration can still play an important role in facilitating lexical access. More evidence that the N400 cannot fully be explained by post-lexical processes was presented by Hoeks et al. (2004). They found that sentence endings, that were semantically related to the previous word, but made the sentence meaningless, elicited no N400 but a later occurring component called the P600, and concluded that the N400 corresponds with the lexical retrieval of a word, while the P600 represents its integration into a broader semantic context (Brouwer et al., 2012; Hoeks et al., 2004).

Despite conceptual differences, the aforementioned theories predict that the N400 effect will be reduced when subjects process word pairs with varying semantic associations while falling asleep. More specifically, based on the semantic integration theory, one needs to make assumptions about the effect of sleep onset on semantic integration. The most likely prediction is that integration is less demanding, as conceptual representations are less constrained during this state. As a consequence, the effort made for the integration of incongruent stimuli is expected to be smaller, thus leading to a reduced N400. This hypothesis is supported by the fact the N400 is proportionally reduced to the degree of loosened associations in formal thought disorder or the recovery status of psychosis (Jackson et al., 2014; Kostova et al., 2005; Kumar & Debruille, 2004; Wang et al., 2011). On the other side, when N400 changes during sleep onset are predicted in terms of the theory of facilitated access, one has to make assumptions about the effect of sleep onset on semantic priming. As the processing of incoming information is generally reduced during sleep onset, it is likely that pre-activation by prime words is systematically diminished with decreasing wakefulness. Therefore, the assumed priming effect is reduced, yielding an increased N400 for congruent target words and consequently a reduced N400 effect.

By directly studying the N400 potential during the transition to sleep, we tried to answer whether changes in the processes associated with the N400 may also be useful to explain phenomena such as the loss of coherence, logic, and voluntary control over thinking that are typically characterizing this state. While subjects were allowed to fall asleep during the recording, we presented them with auditory word pairs with varying degrees of semantic associations. Because of the effect of different word characteristics on the neurophysiological processing of auditory stimuli (O’Rourke & Holcomb, 2002), the N400 evoked potentials were analyzed in reference to the recognition point, that is, the time elapsed after the onset of an auditory presented stimulus that is sufficient for correct identification of the semantic content of the stimulus. On a confirmatory basis, we expected to find a consistent effect of semantic distance that is characterized by a parietal negativity associated with increasing semantic distance, and the appearance of sleep-specific ERP components such as a frontocentral negativity around 300-500 ms (Atienza et al., 2001). Moreover, we expected the N400 effect to be systematically modified with decreasing wakefulness.

2. Methods

2.1. Subjects

Forty-four healthy, native German-speaking subjects were recruited from undergraduate University students and personal acquaintances. Nine of them had to be excluded from the data analysis because of the absence of a detectable alpha rhythm with eyes closed, which was required for reliable classification of wakefulness levels (see section 2.6.2). One additional subject was excluded because of technical problems with the EEG, leaving a final sample of 34 subjects (5 males, mean age 23.50 ± 3.34 years, range 19-33 years).

Subjects were screened for exclusion of neurological, psychiatric and sleep disorders before the experiment using a semi-structured interview. Further, subjects presenting with severe uncorrected hearing problems, psychoactive or hypnotic substance use, shift work, or incompatible wake-sleep rhythm due to other reasons were excluded from the study. There were no complaints of excessive daytime sleepiness as assessed by the Epworth Sleepiness Scale (ESS; Johns, 1991; scores ≤10), insomnia assessed by the Regensburg Insomnia Scale (RIS; Crönlein et al., 2013; scores ≤12), or sleep disturbances determined by the Pittsburgh Sleep Quality Index (PSQI; Buysse et al., 1988 scores ≤5). Participants were instructed to follow a regular sleep schedule and to refrain from the use of alcohol the day before the experiment. We decided against any sleep restriction on the night before the experiment to avoid effects of sleep deprivation on behavior, particularly falling asleep too quickly. To minimize potential factors that prevent subjects from being able to fall asleep, they were additionally instructed to avoid daytime napping and to refrain from caffeine and nicotine approximately four hours before the experiment. The study was conducted in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the University of Bern (approval no. 2019-04-00003). Written informed consent was obtained and undergraduate students received course credits for their participation.

2.2. Procedure

Participants were invited for the screening of exclusion criteria several days prior to the experiment. They further filled out a set of questionnaires to assess sleeping habits and potential sleeping problems respectively (see section 2.1). All questionnaires were presented via the browser-based survey platform Qualtrics XM (Qualtrics, 2019).

During the experiment, participants were lying in a dark, sound-attenuated room on a comfortable reclining chair. While being presented with the auditory semantic association task, they were informed that they were allowed to fall asleep. The only task was to keep the eyes closed and follow the natural course of one's mind. As the recording was part of a larger study, an interval of approximately 1.5 h of resting-state EEG preceded the actual recording (Diezig et al., 2022). The presentation of the task lasted for about 35 min. The timing of the stimulus presentation was chosen to maximize the time for participants to adapt to the setting and to be able to relax irrespective of the auditory stimulation. Moreover, the experiment took place in the early evening to increase the probability that participants were able to fall asleep.

2.3. Stimulus Material

The stimuli consisted of a pre-existing list of 180 pairs of semantically associated German nouns with a length of 4-5 letters, which were rated regarding their semantic distance and matched for visual, orthographic and phonological similarity (Dimigen et al., 2012). A female native speaker of German unknown to the participants spoke the words with neutral intonation and constant voice intensity. The duration of the spoken stimuli ranged from 405-918 ms (mean 628 ms). The recording and processing of the stimuli were performed using Audacity 2.2.2 (http://www.audacityteam.org/).

As subjects were allowed to sleep during the stimulus presentation, we implemented the measurements of the N400 potentials in a passive listening condition. Each trial started with the presentation of a prime word, followed by an inter-stimulus interval of 1000 ms and the presentation of a target word with varying degrees of semantic distance. The interval between two trials was set to 1500 ms. After this interval, the next trial started without any further intervention of the subject. The order of the word pairs was pseudo-randomized to prevent randomly generated semantic associations between the trials. Each word was presented twice (one time as a prime and one time as a target), resulting in a total of 360 trials. The stimulus pairs were presented via loudspeakers at a constant volume of 50 dB at the loudspeaker level using PsychoPy2 Version 1.90.2 (Peirce et al., 2019). The loudspeakers were placed on the right and left side behind the subject, at a distance of 65 cm from the subject's head. The onset of the prime and target words was marked in the EEG.

2.4. EEG Recordings

Multichannel EEG was recorded throughout the experiment using a 64-channel actiCAP snap electrode system (Brain Products GmbH, Gilching, Germany) placed according to the extended 10-20 system (Jasper, 1958) and referenced against FCz. Active electrodes were chosen because of their improved signal quality and lowered preparation time compared to passive electrode systems. The signals were sampled at 500 Hz and stored for offline analysis using BrainVision Recorder software and BrainAmp DC amplifiers (BrainProducts GmbH, Gilching, Germany). Impedances were improved until ≤10 kΩ. A 4-min resting state EEG with alternating opening and closing of the eyes was conducted before the start of the experiment to be able to identify eye movements for artifact rejection. No additional EOG or EMG channels were recorded.

2.5. Estimation of word Recognition points

To correct the effect of different word characteristics on the timing of the processing of auditory stimuli (O'Rourke & Holcomb, 2002), recognition points were determined for all the stimuli in an additional experiment using a gated word recognition task (Grosjean, 1980). To this end, each word was presented in fragments, starting with the first 40% of the individual word duration and continuing with the addition of 50 ms for each subsequent presentation. The stimuli were presented to the participants through headphones using PsychoPy2 Version 1.90.2 (Peirce et al., 2019). Participants (N = 14, different from the sample that underwent the N400 measurement) had to verbally identify or guess the meaning of the presented word. The trial terminated after three consecutive rounds with correct identification of the word, or when the word ended before the participant reached the required number of correct responses. Recognition points for each word were defined as the mean duration of gates across all participants required for the first correct identification of the word, followed by two additional correct responses. Based on this definition, the stimulus onset of each target word was replaced by its individual recognition point offline in the EEG. On average, the recognition point across all stimuli was 363.59 ms (SD = 79 ms).

2.6. EEG Data Processing

2.6.1. Preprocessing

EEG data preprocessing was performed using BrainVision Analyzer 2.2 (BrainProducts GmbH, Gilching, Germany) and MATLAB R2020b (Mathworks Inc. Natick, MA, USA). An independent component analysis (ICA) was applied to the resting state EEG and components typical for EOG and ECG signals were removed from the data. Remaining segments presenting physiological or technical artifacts were marked manually. Channels containing excessive artifacts were interpolated by use of spherical splines interpolation and the EEG was recomputed to average reference. In a further step, wakefulness levels were estimated (see section 2.6.2).

Finally, as the N400 is a relatively slow cognitive component, the signals were filtered between 0.3-7 Hz to improve the signal-to-noise ratio and to suppress unwanted variance in the alpha band.

2.6.2. Classification of Wakefulness levels (VIGALL)

Wakefulness levels were estimated offline by use of the Vigilance Algorithm Leipzig (VIGALL 2.1 plugin for BrainVision Analyzer, Hegerl et al., 2014). The algorithm assigns one out of seven wakefulness levels (0 = ‘alert’, A1/A2/A3 = ‘relaxed’, B1/B23 = ‘drowsy’, C = K-complexes or sleep spindles) at consecutive 1-s intervals based on the power and cortical distribution of the spectral EEG and the occurrence of sleep grapho-elements (i.e. K-complexes and sleep spindles). The required processing steps include a manual scoring of K-complexes and sleep spindles and a reduction of the data to a predefined montage. We generally followed the recommended procedure (Hegerl et al., 2016) except for some minor deviations. The horizontal eye movements (HEOG) were reconstructed based on a bipolar derivation of the prefrontal channels F7-F8 and the threshold for detection of slow eye movements (SEM) was set to 100 µV. Additionally, we removed all segments indicating open eyes during the trials by visual inspection. The main reason for this was to improve the accuracy of the classification algorithm. The data was reduced to 25 channels, bandpass filtered between 0.5-70 Hz with an additional notch filter at 50 Hz and down-sampled to 200 Hz prior to the classification. The obtained VIGALL markers were then imported into the data with all recorded channels (see section 2.6.1).

2.7. Statistical Analysis

The present study aimed at testing whether the auditory N400 effect varied, in a trial-by-trial way, as a function of momentary wakefulness levels. For this purpose, the EEG data were segmented into trials from 100 ms before to 1000 ms after the target stimulus according to the recognition point markers. Trials containing EEG periods marked as artifacts were excluded. Each trial was then assigned to the wakefulness level of the nearest VIGALL marker.

Because of large inter-individual differences in the distribution of wakefulness levels across trials, a classical comparison of averaged evoked potentials between different wakefulness levels was not available in reasonably large subsamples of our data. Instead, we used a regression approach where the different wakefulness levels (as quantified by the VIGALL algorithm) and the semantic distance between prime and target words served as rank-scaled linear predictors of ERP variance across trials. As we were mainly interested in the interaction of wakefulness level and semantic distance, a third predictor was constructed by multiplying the previous two predictors, yielding a set of three predictor values for each trial per subject (wakefulness, semantic distance, and semantic distance x wakefulness).

To obtain the scalp field data that can be explained by the variance of these three predictors, so-called covariance maps were computed (Koenig et al., 2008), which can be considered as channel- and time-wise beta values obtained by regressing the trial-by-trial ERP data against the predictors. Since the predictors were barely correlated (all $r < 0.02$), we applied single instead of multiple regression (Krzywinski & Altman, 2015). As a result, for each predictor and subject, a channel-by-time matrix of beta values was obtained that was labeled individual covariance maps of semantic distance, wakefulness level, and their interaction.

To establish whether and when in the analysis window the obtained individual covariance map series generalize across the sample of subjects, we applied a Topographic Consistency Test (TCT). This procedure assesses the probability of the presence of a constant scalp field across individual observations by comparing the global field power of the averaged scalp field across subjects to the global field power of the averaged scalp field after randomly shuffling the electrode order in each data set (Koenig & Melie-García, 2010). The TCT was computed with 5’000 randomization runs and a p-threshold of 0.05. To control for effects of multiple testing, additional testing based on the duration of continuous periods of significance observed in the data was performed (Koenig & Melie-García, 2010). Moreover, to test whether the interaction effect of semantic distance x wakefulness level matches the effect of semantic distance in terms of spatial similarity, spatial correlation between the covariance maps was assessed. Topographic analysis of variance (TANOVA) of the covariance maps obtained for semantic distance alone against the semantic distance x wakefulness level were computed to confirm the similarity of the maps on a level of significance testing. Finally, the ERP data were split according to high/low semantic distance and high/low wakefulness in the 33rd percentile to show ERP waveforms of the different conditions. The result of this additional analysis is presented in the supplementary material. All data were analyzed using the software RAGU (Koenig et al., 2011) and MATLAB R2020b (Mathworks Inc. Natick, MA, USA).

3. Results

3.1. Evolution of Wakefulness

In general, the data showed an overall variability of wakefulness levels and a noticeable decrease on average across session time (see Fig. 1).

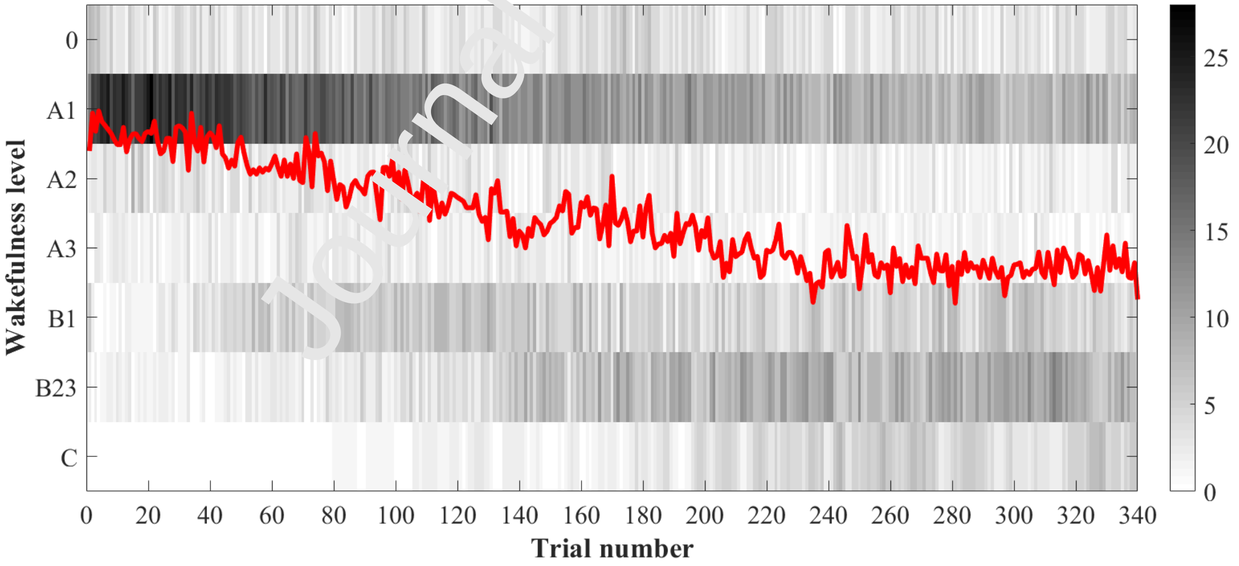

Fig. 1 Individual and mean course of wakefulness across trials. Grey values indicate the number of subjects assigned to a particular wakefulness level as quantified by the VIGALL algorithm (0 = ‘alert’, A1/A2/A3 = ‘relaxed’, B1/B23 = ‘drowsy’, C = K-complexes or sleep spindles) for each trial. The red line shows wakefulness averaged across subjects over time.

3.2. ERP Analysis

The first aim of the ERP analysis was to establish whether and when in the analysis window the three predictors (wakefulness, semantic distance, and semantic distance x wakefulness) yielded covariance maps that generalize across the sample of subjects. The TCT showed significant consistent activation from 194 to 432 ms for the effect of semantic distance (see Fig. 2a), which sustained the duration threshold test. Additionally, time windows with consistent topographies that did not comply with the duration criterion (min duration required for significant effect = 116 ms) were found from 34 to 96 ms and from 564 to 676 ms. For the wakefulness effect depicted in Fig. 2b, topographies were significantly consistent between 262 and 556 ms. Further consistencies were found from 32 to 86 ms and from 150 to 210 ms. However, these two shorter effects were not significant when correcting for multiple testing (min duration required for significant effect = 140 ms). The effect of both predictors (semantic distance x wakefulness) combined is illustrated in Fig. 2c. The TCT showed a period of consistency from 362 to 420 ms, which nearly reached significance in the duration threshold test (*p* = 0.077).

On the confirmatory side of the analysis, the observed effect of semantic distance from 194 to 432 ms showed a left-lateralized centro-parietal negativity, confirming the existence of a classical N400 effect in the present data. Because we analyzed the data with respect to the word recognition points and not the word onset, the latency of the N400 effect was shifted forward. Moreover, the effect of wakefulness observed from 262 to 556 ms showed an increased frontal negativity with decreasing wakefulness, which is well in line with the pre-existing literature on sleep-specific ERP components.

Finally, when testing whether the interaction effect of semantic distance x wakefulness level matches the effect of semantic distance in terms of spatial similarity, we found that the topographic pattern of the interaction effect showed a considerable spatial similarity (*r* = 0.70) and temporal overlap with the effect described by semantic distance, indicating an increase of the N400 effect with decreasing wakefulness. The TANOVA of the covariance maps obtained for semantic distance alone against the semantic distance x wakefulness level covariance in the identified time window revealed no significant difference between the two covariance maps (*p* = 0.171). Thus, while the analysis of the interaction of semantic distance and wakefulness per se did not yield fully sufficient evidence for a systematic effect, taking also into account the topographic and temporal similarity of the effect with the main effect of semantic distance made us conclude that wakefulness level has a systematic effect on the N400. However, this finding needs further validation and should be interpreted accordingly.

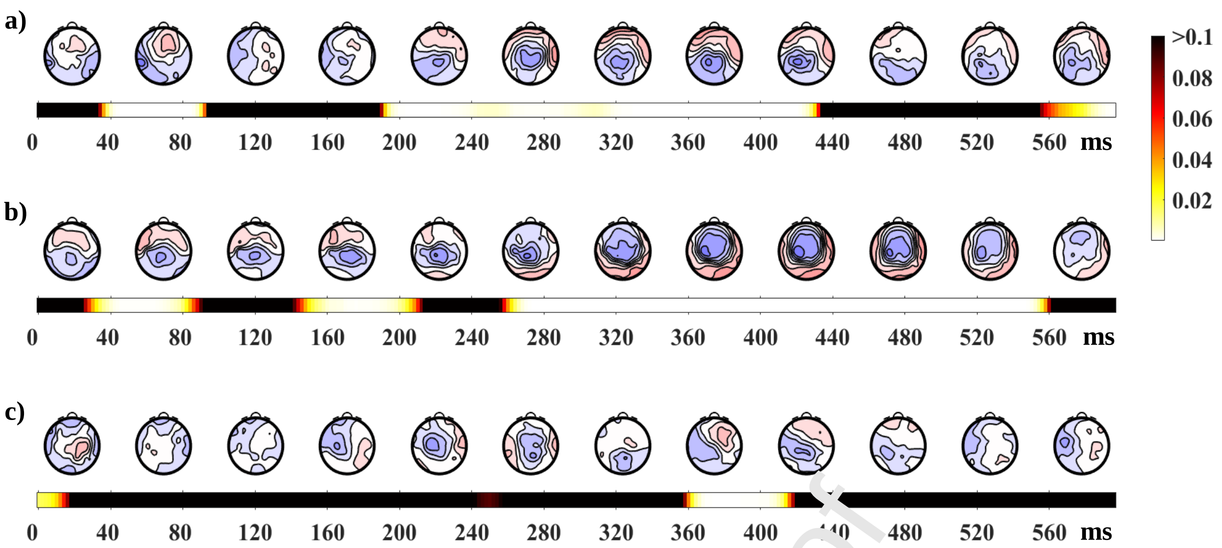

Fig. 2 Group averaged topographic map series (contour lines displayed in steps of 1 µV; red positive and blue negative electric potential) and p-values (color bar at right; p-values uncorrected) of the topographic consistency test (TCT) at every time point (depicted by color scales) for each of the three conditions *semantic distance* (a), *wakefulness* (b) and *wakefulness x semantic distance* (c). Covariance maps are displayed every 50 ms between 0 and 600 ms after the target stimulus recognition point.

4. Discussion

The present study examined the effect of decreasing wakefulness on the expression of the N400 component. Given that coherence, logic and voluntary control over thinking are frequently lost during the transition to sleep, and considering the most prominent current explanatory approaches of the N400 component, we expected the N400 effect (increasing negative deflection at centro-parietal electrodes with increasing incongruency) to be systematically reduced with decreasing wakefulness. By using a passive auditory semantic association task and correcting the onset of the evoked potentials of each trial for its word recognition point, we were able to elicit an N400 potential characterized by a centro-parietal negativity associated with increasing semantic distance between 194 and 432 ms after the target recognition point while subjects were falling asleep. Moreover, there was a significant main effect of wakefulness, confirming the existence of additional sleep-specific ERP components in the data (Atienza et al., 2001). The association of decreased wakefulness with a late frontal negativity has repeatedly been linked to the presence of K-complexes (Colrain, 2005). Since some but not all of our subjects reached VIGALL state C (which by definition contains K-complexes) during the recording, this seems quite likely but not conclusive. On the contrary, the hypothesis of a decrease in the N400 effect when falling asleep could not be confirmed. Instead, we found an increase in N400 with decreasing wakefulness, which overlapped with the main effect of semantic distance in time and spatial configuration. Importantly, this effect cannot be explained by the mere repetition of word pairs. As word repetition is known to attenuate the N400 (Hohlfeld, Ullsperger, & Sommer, 2008), and repetitions accumulate over time, one would expect a decreased N400 over time. However, the observation that the N400 increased with lower wakefulness, and that wakefulness was lower towards the end of the experiment (Fig. 1) implies that the N400 rather increased over time, contradicting an explanation of the effect by word repetition. Thus, unlike other conditions where a reduction of the N400 effect has been reported to be associated with impaired thought processes like formal thought disorder or delusions (Kiang & Gerritsen, 2019; Kostova et al., 2005), we could not extend these findings to the condition of falling asleep - a state with similar phenomenological characteristics (Goupil & Bekinschtein, 2012). Therefore, these findings offer novel and interesting insights into the neuro- and psychophysiology of falling asleep.

As the N400 potential is thought to represent an index of semantic processing, this raises the question of the possible mechanisms that contribute to the observation of an enhanced N400 effect during a state, which rather implicates deficient thought processes. At the neural level, the processing of semantic information (McKiernan et al., 2006; Seghier & Price, 2012; Wirth et al., 2011; Zhang et al., 2022) but also the generation of spontaneous, task-unrelated thoughts (Binder et al., 1999, 2009; Smallwood et al., 2012) have been shown to critically depend on the activity of several large-scale networks, including the so-called default mode network (DMN). Regarding the N400 component, the involvement of these networks has been found to depend on whether retrieval is usefully constrained or miscued by the surrounding context (Jacob et al., 2019; Lanzoni et al., 2020). Whereas a ‘semantic control network’ (including the inferior frontal and posterior middle temporal gyrus) is recruited for the processing of incongruent stimuli, DMN activity has been specifically related to the processing of congruent stimuli. This suggests a facilitatory role of the DMN for priming (Jackson, 2021; Lanzoni et al., 2020; Lau et al., 2008). Moreover, DMN activity inversely correlated with unusual thoughts/thought disorder in schizophrenia, which led to the assumption that the DMN may support the combination of concepts into meaningful representations (Hare et al., 2019; Jacob et al., 2019). At the same time, spontaneous, stimulus-independent thoughts, like the ones that might characterize mental activity during the transition to sleep, have been supposed to be essentially semantic because they depend on the activation and manipulation of acquired knowledge about the world (Binder et al., 1999, 2009).

In line with this notion, activation and functional connectivity in the DMN (Horovitz et al., 2008; Picchioni et al., 2008) but not the posterior cingulate cortex (PCC) (Kinreich et al., 2014) were found to increase during light sleep (but see Larson-Prior et al., 2011 for loss of DMN connectivity). Together with the fact that DMN activity is involved in semantic priming, this might explain why the N400 effect, contrary to our initial expectation, did not decrease but rather increased when subjects were falling asleep. According to the lexical retrieval account of the N400, pre-activation or priming by congruent prime words might not be systematically diminished during the transition to sleep but rather increased as a result of predominant DMN activity, yielding a decreased N400 for congruent target words and therefore an increased N400 effect. However, whereas DMN activity might also drive the occurrence of spontaneous thoughts during the transition to sleep in general, it does not provide an explanation for the loss of control and coherence over thinking characterizing this state.

On the other side, DMN activity has also been proposed to be involved in the post-lexical integration of semantic stimuli. Based on the theory of semantic integration, the smaller N400 effect often reported in schizophrenia is usually thought to result from a smaller N400 amplitude for incongruent targets, facilitating semantic integration of inappropriate content (Besche-Richard et al., 2014; Mohammad & de Lisi, 2013). In contrast, the increase of the N400 effect observed in our study might therefore suggest that the effort made for the integration of incongruent stimuli rather becomes larger during the associatively loosened state of falling asleep, thus leading to an increased N400 effect. However, since DMN activity has been shown to be stronger when multiple congruent primes were presented in a semantic priming task compared with a single prime (Lanzoni et al., 2020; Vatansever et al., 2015), the increased N400 effect might also be the result of facilitated integration of congruent targets, while processing of incongruent targets remains unaffected. As we used the semantic distance between prime and target words as a linear predictor for ERP variance between trials and it is not possible to control for an equal distribution of congruent and incongruent trials across wakefulness levels, we are not able to test which of the above options is accurate. The supplementary analysis of ERP waveforms split by high/low semantic distance and high/low wakefulness (see supplementary figures S3) revealed a more negative potential for incongruent targets as well as a more positive potential for congruent targets.

In schizophrenia, both, deficient early automatic semantic activation and late post-lexical processes have been put forward to explain deficits in semantic processing. Whereas it has been argued that these views are rather complementary than in conflict (Wang et al., 2011), they may also be partly dependent on differences in experimental task properties such as stimulus onset asynchrony (SOA) or the type of paradigm used to measure the N400 response to semantic processing (Kiang & Gerritsen, 2019; Kreher et al., 2009; Mohammad & de Lisi, 2013). In turn, these factors either might favor the predominance of early or late processes (Kuperberg et al., 2007). Longer SOAs for instance, that is, the time passed between the onset of the prime and the onset of the target stimulus, have been associated with a more negative N400, whereas priming paradigms using a short SOA produced reduced N400 (Mohammad & de Lisi, 2013). Similarly, in explicit tasks, patients showed reduced direct and indirect semantic priming in comparison with healthy controls whereas in implicit tasks, they showed normal or, in positively thought-disordered patients, increased direct and indirect N400 priming effects compared with healthy controls (Kreher et al., 2009).

As we used a task with a long SOA, one might argue that processes involving semantic integration dominated in the present study. However, the conclusion that the integration of incongruent stimuli either recruits more resources when falling asleep or alternatively, facilitated integration of congruent targets leads to an increased N400 effect both contradict the specific phenomenological characteristics observed during this state. Moreover, activity of the DMN has been suggested to be critical for organizing thoughts into coherent, meaningful utterances (Hare et al., 2019). However, this does not apply to the transition to sleep, as DMN activity is increased, but logic and coherence of thinking decrease during that time. Therefore, it is likely that DMN activity cannot account for this effect alone but additional brain mechanisms that possibly mediate the generation of the N400 effect might be enhanced or disinhibited during the transition to sleep, providing some further explanatory value. For example, the semantic control network has been shown to be activated when retrieval is miscued by the surrounding context (Lanzoni et al., 2020), and is thought to be involved in the selection of relevant aspects of knowledge while irrelevant information is suppressed (Jackson, 2021), but its interaction with wakefulness has not been systematically investigated so far. Moreover, the presence of a specific EEG microstate (reflecting whole-brain network dynamics) with sources in frontoparietal brain regions was associated with subjective experiences such as diminished thought control during the transition to sleep (Diezig et al., 2022) but it remains unclear whether and how this network is involved in the processing of semantic information.

5. Conclusion

The present study investigated brain mechanisms underlying the loss of logic, coherence and voluntary control over thinking observed during the transition to sleep. Based on the hypothesis that semantic processing might be important in this context, we expected the N400 effect of the auditory event-related potentials to be reduced when falling asleep. However, the results showed an enhanced N400 effect with decreasing wakefulness. Default mode network activity is involved in semantic processing, it increases when falling asleep, and it might partly explain these results but cannot account for the phenomenological experiences characterizing this state. While our findings do not exclude that semantic processing has a part in deficient thought processes, they stress the involvement of additional brain mechanisms that usually constrain the inner stream of consciousness.

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Author contributions

Sarah Diezig: methodology, conceptualization, software, stimulus material, investigation, data curation, software, formal analysis, visualization, and writing – original draft. **Melissa Spaar:** writing N400 literature – original draft, formal analysis. **Simone Denzer:** conceptualization, stimulus material, writing – review and editing. **Peter Achermann:** supervision, writing – review and editing. **Fred W Mast:** funding acquisition, conceptualization, resources, writing – review and editing. **Thomas Koenig:** conceptualization, methodology, formal analysis, writing – review and editing, resources and supervision.

Declarations

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Declarations of interest

None.

Ethics approval

This study was conducted in accordance with the principles of the Declaration of Helsinki. This study was approved by the Ethics Committee of the University of Bern (approval no. 2019-04-00003).

Consent to participate

Informed consent was obtained from all individual participants included in the study.

Data availability

The datasets generated in this study are available from the corresponding author upon reasonable request.

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Highlights

- Logic and control over thoughts are frequently lost at the onset of sleep
- Auditory N400 evoked potentials were investigated during the transition to sleep
- The N400 effect increased with decreasing wakefulness
- The results contradict N400 findings in diminished thought control in psychosis