



Oscillatory brain activity differentially reflects false belief understanding and complementation syntax processing

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Abstract

False belief understanding (FBU) enables people to consider conflicting beliefs about the same situation. While language has been demonstrated to be a correlate of FBU, there is still controversy about the extent to which a specific aspect of language, complementation syntax, is a necessary condition for FBU. The present study tested an important notion from the debate proposing that complementation syntax task is redundant to FBU measures. Specifically, we examined electrophysiological correlates of false belief, false complementation, and their respective true conditions in adults using electroencephalography (EEG), focusing on indices of oscillatory brain activity and large-scale connectivity. The results showed strong modulation of parieto-occipital alpha (8–12 Hz) and beta (13–20 Hz) power by the experimental manipulations, with heightened sustained alpha power reflective of effortful internal processing observed in the false compared to the true conditions and reliable beta power reductions sensitive to mentalizing and/or syntactic demands in the belief versus the complementation conditions. In addition, higher coupling between parieto-occipital regions and widespread frontal sites in the beta band was found for the false-belief condition selectively. The result of divergence in beta oscillatory activity and in connectivity between false belief and false complementation does not support the redundancy hypothesis.

Keywords False belief understanding · Complementation syntax · EEG · Alpha · Beta

Introduction

Humans are social creatures—a central aspect of our behavior is to build and maintain relationships with other people. One process that facilitates social behavior is the ability to understand that different people can hold conflicting beliefs about the same situation, and that these beliefs are sometimes inconsistent with factual reality, often referred to as “false belief understanding (FBU)” (Wellman et al., 2001) or more broadly as “theory of mind” (Blakemore, 2006), or “mentalizing” (Amodio & Frith, 2006). For example, in the object-transfer scenario (Wimmer & Perner, 1983), a boy puts the chocolate in the blue cupboard and then leaves. During his absence, his mom moves the chocolate to the green cupboard. People with FBU will be able to represent that when the boy comes back and looks for the chocolate, he

will act on his false belief to look for the chocolate in the blue cupboard. FBU has been associated with a wide range of social and cognitive outcomes (Farrar et al., 2017), including communication skills (Achim et al., 2015), peer popularity (Slaughter et al., 2015), and academic achievement (Blair & Razza, 2007). Deficits in FBU contribute to social impairments in autism spectrum disorders (Baron-Cohen et al., 1985), frontal variant frontotemporal dementia (fvFTD; Gregory et al., 2002), and substance use disorder (Sanvicente-Vieira et al., 2017), etc.

A number of human neuroscience studies aim to identify the neurophysiological correlates of FBU tasks. For example, studies using functional brain imaging to examine hemodynamic changes during FBU tasks have characterized a network of brain regions showing increased blood flow in the FBU conditions, compared to the control conditions such as the parallel physical reasoning situations (e.g., false photograph task; Saxe & Kanwisher, 2003). These regions include two core areas, the medial prefrontal cortex (mPFC) and the bilateral temporoparietal junction (TPJ; van Overwalle, 2009; Schurz et al., 2014), and other regions (i.e., bilateral posterior superior temporal sulci, anterior cingulate cortex, precuneus, inferior frontal gyrus, bilateral temporal pole, and precentral gyrus;

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Molenberghs et al., 2016). Complementing hemodynamic studies, several authors have used electroencephalography (EEG) to examine electrophysiological brain dynamics during FBU tasks at high temporal resolution (e.g., Liu et al., 2004, 2009). These studies have typically extracted time-locked brain waves (event-related potentials; ERPs). Using this approach, a frontal late (around 800 ms post-stimulus) ERP wave has been identified to be more positive in false belief compared to control conditions, interpreted to reflect representations of the others' mental state (Liu et al., 2004, 2009; Sabbagh & Taylor, 2000). In addition, a late positive ERP complex (300–600 ms post-stimulus) with a broad central distribution in adults and posterior distribution in children was found and interpreted to be associated with distinguishing false belief from true belief (Meinhardt et al., 2011).

Given the fundamental role of FBU for human behavior and experience, and its importance in many extant models of atypical development, a substantial number of behavioral studies have examined the cognitive and linguistic factors that contribute to FBU. For example, it is well documented from the developmental literature that language facilitates FBU development (Milligan et al., 2007). Among all aspects of language capacity, understanding sentential complementation has been proposed to be a linguistic prerequisite to FBU (de Villiers & Pyers, 2002). Mental-state verbs such as *think* and communication verbs such as *say* in English take tensed complements. For example, the accuracy of the entire sentence, *Tom thinks it is raining outside (tensed complement) but it is really sunny*, is independent of the correctness of the embedded tensed complement. That is, the embedded complement can be wrong because it is actually sunny outside whereas the whole sentence can be correct because it reflects Tom's thought. In this way, the sentential complementation directly distinguishes the content of the mind from reality. According to the complementation hypothesis (de Villiers & de Villiers, 2000; de Villiers, 2005), this distinction between thinking and reality, which is made possible by complementation syntax, is the essence of FBU. In order to reason about people's mental states, mastery of the tensed complements of mental state verbs and communication verbs is required. Complementation syntax allows FBU by providing the linguistic structure necessary for separating a (mistaken) thought from reality. Children who are delayed in language development (e.g., children who are deaf, children with autism, or children with specific language impairment) are also delayed in FBU. In the standard complementation task (de Villiers & Pyers, 2002), mastery of complementation syntax is assessed by testing people's memory for the tensed complements following mental-state verbs or communication verbs. The scenario is as follows (de Villiers & Pyers, 2002): Clara *thought/said* Zach had flowers behind his back, but it was really leaves. The memory question to measure complementation understanding is then asked: what did Clara *think/say*? Performance in the standard complementation task often predicts performance in FBU (de Villiers & Pyers, 2002; de

Villiers, 2007; de Villiers & de Villiers, 2014). Alternatively, critics to de Villiers' complementation hypothesis (Ruffman et al., 2003; Slade & Ruffman, 2005; Farrar et al., 2013) argue that general language capacities such as vocabulary, semantics, syntax, and pragmatics are sufficient for FBU development and that complementation syntax alone is not required. One notion from the critics is that the false-complementation task involves false belief understanding because they both measure the internal processing of decoupling people's mistaken thoughts from reality (Cheung et al., 2004; Ng et al., 2010; Farrar et al., 2017). According to this argument, in the standard complementation task, to correctly answer the complementation memory question, participants need to not only *remember* what Clara thought/said, but also *understand* that what Clara thought/said may not necessarily be consistent with what Zach really had. In this sense, the complementation task requires participants to decouple people's mental states from reality, which is also measured in the FBU tasks. That is, the complementation syntax task is redundant with the FBU measure.

Of interest in the present study is to examine whether FBU and complementation syntax have divergent patterns of brain oscillations. Identifying such patterns can contribute to clarify whether the two measures are redundant. To our knowledge, only two studies with Chinese young adults have directly compared FBU and complementation syntax at the neural level using fMRI (Cheung et al., 2012) and ERPs (Chen et al., 2012). In both studies, non-verbal false-belief and false-complementation conditions were implemented using vignettes of pictures and sentences in Chinese respectively. Findings from both studies showed that FBU and false-complementation had shared as well as unique neural signatures. For example, a late slow ERP waveform was found in both conditions but was more anterior for FBU and more centro-frontal for false-complementation. The right TPJ was engaged in both conditions but the left TPJ and the right middle frontal gyrus (MFG) were uniquely related to FBU whereas the left inferior frontal gyrus (IFG) and right superior temporal gyrus (STG) were uniquely associated with false complementation.

These neurophysiological studies have identified the functional neuroanatomy of brain regions as well as the latency and gross topography of ERP components, differing between the false-belief and the false-complementation tasks. To contribute to this body of research, the current study examined the time-varying power and phase-locking of EEG oscillations in adults. EEG oscillatory activity reflects rhythmic fluctuations of neural population activity in different frequency bands in response to sensory stimulation or internal mental processing (Freeman, 1975). Over the past decades, conceptual and empirical work has highlighted the additional spatial and temporal brain processes reflected in oscillatory brain activity, beyond the information reflected in time locked event-related potentials (e.g., Engel et al., 2001; Fabi & Leuthold, 2016; Güntekin & Başar, 2014; Klimesch, 1999): Frequency-domain analyses can capture

phase-relationships in space or time, used in measures such as inter-site phase locking or coherency, which captures spatial dependencies across the scalp (Lachaux et al., 1999) and their modulation by specific cognitive or affective challenges (Bressler & Menon, 2010). These analyses also benefit from the fact that many oscillations are statistically stationary across a certain duration, i.e., the time epoch of near-periodic cycling at a given frequency, whereas ERPs tend to be not statistically stationary (Keil et al., 2014). Brain oscillations especially at lower frequencies (< 20 Hz) provide good signal-to-noise ratios even with few trials; they tend to be temporally sustained, a property that allows averaging of spectral power changes across participants, even when the latencies are highly variable as is often the case in clinical and developmental samples (Keil, 2013).

Despite the desirable properties described above, EEG oscillations have not yet been used in FBU research. By contrast, a rich body of research has considered oscillatory activity during language comprehension tasks (Bastiaansen et al., 2002; Haarmann & Cameron, 2005; Meyer et al., 2013, 2015; Weiss et al., 2005). Particularly, beta (13–30 Hz) activity has been suggested to be critical during higher-order linguistic functions (Weiss & Mueller, 2012). For example, beta band oscillatory power was found to be relatively heightened when exposed to syntactically correct, compared to incorrect language (Bastiaansen & Hagoort, 2006; Bastiaansen et al., 2010; Davidson & Indefrey, 2007; Schneider et al., 2016), and was also relatively heightened during top-down predictive processing (Lewis & Bastiaansen, 2015). In a similar vein, beta power has been reported to correlate with the amplitude of the N400 ERP during language completion, when semantically incongruent endings were presented, but not during congruent endings (Lewis et al., 2017; Wang et al., 2012). Reviewing the literature, Lewis and colleagues (2015) suggest that beta changes may index the amount and type of change in the cognitive processing set, including predictions from memory. In their model, the relative change in beta power after the typical initial stimulus-induced amplitude decrease is thought to reflect the active maintenance of cognitive set (prompting a beta power increase) or a change in the set (accompanied by a relative beta power decrease). If the neural language comprehension model by Lewis and colleagues (2015) applies to story-like sequences of vignettes as used in the present study, any changes in the set prompted by the critical vignette should be accompanied by a decrease in beta power.

In the present study, the first aim was to establish the brain oscillations correlated with false belief and false complementation by comparing the two with their respective true conditions. We utilized a standard false-belief task, the object-transfer scenario (Wimmer & Perner, 1983), implementing a false-belief condition. The same scenario was applied to the true-belief condition, except that the location of the object did not change. Thus, the protagonist had a true belief about the object's location. Similarly, a standard complementation task

(de Villers & Pyers, 2002) was adopted to create a parallel false-complementation condition to the false-belief condition. The same paradigm was implemented in the true complementation task, except that what the protagonist thought/said was consistent with reality (e.g., *Mina told her mom there was a squirrel by the tree, and it was really a squirrel. What did Mina tell her mom was by the tree?*).

We predicted that differences in working memory, inhibitory control, and internal versus sensory processing reliably distinguish the false versus true conditions in alpha oscillations in the 8–12 Hz range (Bartsch et al., 2015). The true conditions across tasks entail less internal mental processing because of the lack of “conflict” (e.g., the conflict between the protagonist's belief/statement with reality; Meinhardt et al., 2011; Sommer et al., 2007), leading to reduced requirements in working memory (e.g., it is not necessary to track the change of object location) and inhibitory control (e.g., not necessary to inhibit the true belief over false belief since there is no conflicting information). Behavioral evidence (Mayer & Träuble, 2015) also shows that children cross-culturally are more successful on true-belief than false-belief conditions. From a neurophysiological perspective, as a growing number of studies have observed, there is *increased* alpha power in tasks that involve internal (but not sensory/perceptual) cognitive activity (Klimesch et al., 1999, 2007; Hanslmayr et al., 2011; Herrmann et al., 2004). This activity tends to be most pronounced at posterior, especially parietal, locations, and has often been measured by averaging across a parietal cluster of sensors, typically centered around electrodes Pz or Poz (e.g., Bartsch et al., 2015; Bonnefond & Jensen, 2012). Alpha oscillations may be considered as an index of internal cognitive processes, potentially directly reflecting the large-scale spatio-temporal dynamics involved in these processes (Bartsch et al., 2015), or indexing the active suppression of distracting sensory information during internal processing (Bonnefond & Jensen, 2012; Foxe & Snyder, 2011). For example, alpha power in left parietal regions increased with the increased demands of inhibition and working memory during sentence processing (Meyer et al., 2013). We thus expected to see heightened parieto-occipital alpha power for the false, compared to the true conditions across tasks, reflecting the false conditions' additional, internal, cognitive processes.

In addition to examining the hypotheses outlined above, for the alpha and beta bands, we explored additional changes occurring in the range of frequencies between 4 and 20 Hz, not only in terms of their time-varying spectrum (power change), but also in terms of their phase-locking across scalp regions. To address the issue of multiple comparisons that accompanies such an explorative approach, these analyses were conducted using permutation-controlled statistical analyses as described in more detail in the methods section.

Our second aim was to compare brain oscillations specifically correlated with false-belief versus false-

complementation task to address our primary conceptual question of whether or not the two are redundant. To address this issue, we examined differences in indices of oscillatory brain activity and large-scale connectivity for the false-belief and false-complementation tasks. Identifying any such differences may contribute to clarifying the role of language in FBU.

Method

Participants

A total of 46 adult volunteers were recruited from a university participant pool for general psychology course credits. Of these 46 participants, two were excluded due to excessive artifacts (more than 50 % trials rejected). The remaining 44 participants ($M_{\text{age}} = 19.41$ years; $SD = 0.21$; 27 female; four left-handed; 28 White, eight Hispanic, six Asian, one African American, one Middle-Eastern) were included in the subsequent analyses.

Materials

There were 12 cartoon stories in each of the false-belief, true-belief, false-complementation, and true-complementation conditions (see Fig. 1), presented in one of two pseudo-random orders. The 48 stories together with two practice stories were presented using PsychToolbox (Brainard, 1997) in MATLAB. Each story contained five vignettes (picture-sound pairs) with the story narrative in the first three vignettes. An auditory question ($M = 3.09$ s, range = 1.48–4.23 s) was then asked at the onset of the fourth vignette for false-belief and true-belief conditions (e.g., *Where does Sally look for her book when she comes back?*) and the two types of complementation tasks (e.g., *What did Minnie tell Goofy she had?*). Two choices were shown in the fifth vignette. A 500-ms gray screen was embedded between each vignette within every story.

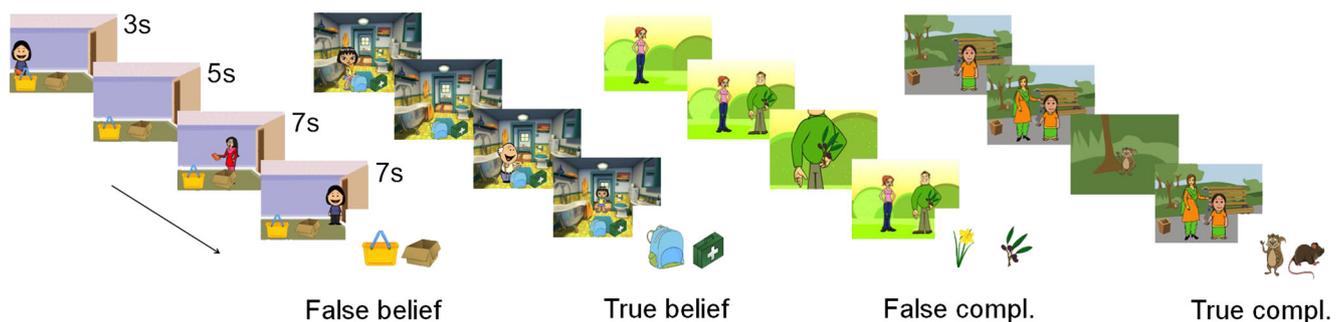


Fig. 1. Examples of cartoon stories. Durations of the first four vignettes were 3 s, 5 s, 7 s, and 7 s, respectively. After a story's complete vignette sequence (with the fifth vignette visible), participants responded verbally and then clicked the mouse button to proceed to the next story

Response recording

During the fifth vignette of each story, participants were asked to verbally answer the questions, including the question shown in the fourth vignette and the control questions asked by the experimenter. Their verbal responses were recorded by the experimenter on the recording sheet.

Procedure

Once providing informed consent, participants were seated in an electrically shielded room where the EEG sensor net was applied. They were instructed to watch a series of cartoon stories and answer questions at the end of each story. They were asked to avoid excessive movements including eye blinks and eye movements and limit any motor movement. Participants sat 1.2 m away from a 23-in. 3-D LED monitor (Samsung S23A750D) with a 120-Hz refresh rate, placed outside the shielded chamber, and viewed through a shielded window.

EEG data recording

EEG was recorded continuously using a 257-channel Electrical Geodesics sensor net and digitized at a rate of 250 Hz, with the vertex sensor (Cz) as the recording reference, and an online low-pass filter set at 50 Hz. Scalp impedance for each sensor was kept below 70 K Ω , which is recommended (Ferree et al., 2001) for this high-input impedance amplifier (200 M Ω input impedance). Further EEG data processing was implemented offline. The fourth vignette was the target event to which the EEG data were time-locked.

EEG data reduction and analyses

Offline EEG processing was conducted using EMEGS software (Peyk et al., 2011). EEG data were converted to the average reference, high-pass filtered at 1 Hz (second-order Butterworth filter, 1 dB point at 1 Hz), and low-pass filtered at 40 Hz (3 dB point at 40 Hz, 18th-order Butterworth filter),

and then segmented from 600 ms pre- to 4,000 ms post-onset relative to the fourth vignette for all conditions. The extracted segments were then submitted to an artifact detection procedure (Junghöfer et al., 2000). This procedure uses statistical indices of data quality (absolute voltage, variance of the voltage, maximum derivative of the voltage) to first identify bad channels, followed by identification of bad trials. Bad channels (first step) were interpolated by spherical spline interpolated data from the full channel set. Trials were retained if more than 90 % of the channels were artifact-free, and remaining channels interpolated on a trial-by-trial basis, with a goodness-of-fit criterion in place to avoid invalid interpolation of channels in the same area of the scalp (Peyk et al., 2011). After artifact correction, an average of 10.3 trials per condition (range: 4–12 trials) and no significant differences among conditions (all $F_s < 1$) were available for subsequent analyses. These trials were then converted to a current source density (CSD) representation of the data, to heighten the spatial specificity of the signal, using the algorithm described in Junghöfer et al. (1997; also see Vorwerk et al., 2014), which uses Green's spherical spline functions to estimate the interpolated scalp potential and assumes standard conductivities of 300, 900, 3.75, and 300 ($\text{Ohms} \cdot \text{cm}^{-1}$), for brain, cerebrospinal fluid, skull, and scalp, respectively.

Time-frequency analyses

Time-frequency analyses quantify the temporal dynamics of brain oscillations, allowing researchers to analyze the time varying changes in spectral power and phase of the signal at a specific frequency band. The present study examined large-amplitude oscillatory events below 20 Hz, with a specific focus on parieto-occipital alpha and beta oscillations. To this end, artifact-free EEG epochs (in CSD space) were convolved with a family of complex Morlet wavelets (e.g., Tallon-Baudry & Bertrand, 1999), using a wavelet coefficient $F/\sigma F = 7$. Thus, the ratio of each frequency F and its standard deviation in the frequency domain σF was held constant, leading to greater uncertainty in the frequency domain (but better time resolution) for higher frequencies, compared to lower frequencies (lower time resolution, less uncertainty about the frequency). For example, at 10 Hz, the uncertainty (measured as Full Width at Half Maximum of the wavelet) in the frequency domain was 1.42 Hz, and the uncertainty in the time domain was 112 ms. Wavelets were calculated for frequencies between 4.35 and 21.73 Hz, in steps of .87 Hz, and a baseline correction was implemented by dividing each time-frequency point by the mean amplitude of its frequency in the time range between -500 and -152 ms. This baseline choice ensured that no post-vignette brain activity in the frequency bands of interest entered the baseline segment through smearing in the time domain (Keil et al., 2014). The relative

change in time-varying amplitude after baseline division was expressed in percent and used for statistical analyses.

Connectivity analyses

To quantify systematic relations of oscillatory phase at a given frequency and time, we calculated the inter-site phase-locking (ISPL) value (Lachaux et al., 1999), which reflects the extent to which phase-differences between sensors remain constant across trials. To minimize sensitivity to spurious connectivity estimations reflective of volume conduction we normalized the complex phase and the complex inter-site phase differences to unit length prior to phase-averaging (see McTeague et al., 2015, and Wieser et al., 2016, for a full description of the algorithm). This is equivalent to the imaginary part of coherence algorithm proposed by Nolte et al. (2004). Given our focus on parieto-occipital alpha and beta oscillations, we calculated the ISPL between Pz and all remaining sensors across trials for each time point and frequency, resulting in a measure of inter-site phase synchrony between the parieto-occipital seed location and the remainder of the cortical surface.

Statistical analyses

Two complementary strategies were adopted for statistical analyses. First, in a strictly hypothesis driven approach, wavelet amplitude data were averaged for each participant and condition across 14 parieto-occipital electrodes (Pz, POz and all of their nearest neighbors) in a time between 1,000 and 3,500 ms, and for the wavelets with a central tuning frequency from 8.69–12.17 Hz (alpha band) and 13.04–19.99 Hz (beta band), thus capturing sustained alpha and beta modulation during the fourth vignette. Note that these frequencies do not represent a sharp cut-off, because of the wavelet's smearing in the frequency domain (e.g., 1.42 Hz at 10 Hz). The focus on these regions of interest was motivated by a word-prompted mental imagery study (Bartsch et al., 2015) and other studies of alpha power changes with predominantly visual stimulation (Nunez et al., 2001; Romei et al., 2010; Sheth et al., 2009; Tuladhar et al., 2007) and an interest in internal cognitive processing (Bonfond & Jensen, 2012; Foxe & Snyder, 2011; Hanslmayr et al., 2011; Herrmann et al., 2004; Klimesch et al., 1999, 2007). Throughout these studies, a preponderance of posterior sensors was found for alpha and beta band changes. In these studies, as in the present one, researchers took advantage of the symmetrical and broad distribution of the band power changes, to pool the scalp measurements from several electrode sites into fewer dependent variables used for statistical analysis. In the present study, a time window starting at 1,000 ms was chosen to accommodate any alpha-blocking effects due to the onset of the vignette, and avoid spurious effects of transient (vignette-onset) ERPs on the time-frequency representation. The resulting dependent variable represented the expected

topography of alpha oscillatory and maximum alpha amplitude typically observed in dense-array EEG studies of alpha power changes (e.g., Keil et al., 2006). A repeated-measures general linear model was calculated on this mean alpha amplitude variable using the within-subject factors of Task Type (Belief/Complementation) and Falsehood Type (False/True).

Time-frequency phenomena beyond the spatio-temporal ROIs in the alpha and low beta band were examined separately by the exploratory, permutation-controlled statistical approach described below. Specifically, there was no a-priori hypothesis regarding the timing and exact frequency of any task-related changes in connectivity, which led us to use a permutation-controlled, exploratory approach to examine these changes. In this second exploratory step, time-frequency plots (both for power changes and for inter-site phase locking relative to site Pz) were created for each sensor, participant and condition. Then, F -values, following an analysis of variance (ANOVA) design (Task type \times Falsehood), were calculated for each electrode, time, and frequency, reflecting differences among the experimental conditions. Significant main effects or interactions were followed up by permutation t -tests comparing individual conditions. Thresholds for statistical significance were determined using a F -max and t -max permutation technique as recommended by Blair and Karniski (1993; see also Keil et al., 2005). To this end, 8,000 F - or t -planes were generated based on data in which the condition was randomly shuffled. The maxima of these F - or t -value planes were used to create a distribution of F -max or t -max values for each time/frequency point. The top and bottom 2.5 % tails of the resulting distribution served as the critical

values for determining statistical significance of an empirical F -value or t -value at a given time-frequency point. For the present data, this procedure resulted in a critical F -value ($p < .05$) of 11.21 and a critical t -value of 3.76 for power. A critical F -value ($p < .05$) of 12.90 and a critical t -value of 3.55 were found for inter-site phase-locking. This analysis allows addressing questions regarding changes of spectral amplitude over time and effects in frequency bands other than the alpha band. Importantly, adopting a F -max/ t -max procedure allowed us to control for the possibility of Type I errors occurring as a result of performing comparisons at each sensor, electrode, and frequency.

Results

Data description Wavelet analyses showed strong modulation of parieto-occipital alpha (central tuning frequencies between 8.69 and 12.17 Hz) and low beta (between 13.04 and 19.99 Hz; Meyer et al., 2013; Shahin et al., 2009) power by the experimental manipulations (Fig. 2). Two major oscillatory changes were visible, both pronounced across posterior sensors: (1) Heightened sustained alpha power was observed throughout the duration of the vignette in the two false conditions (also see Fig. 3); and (2) The time-varying power in the beta range showed a pronounced decrease, after vignette onset, in a time window from 500–1,000 ms post-onset and sustained this pattern until the end of the vignette in the two belief conditions. These oscillatory changes were the focus of the subsequent statistical analyses.

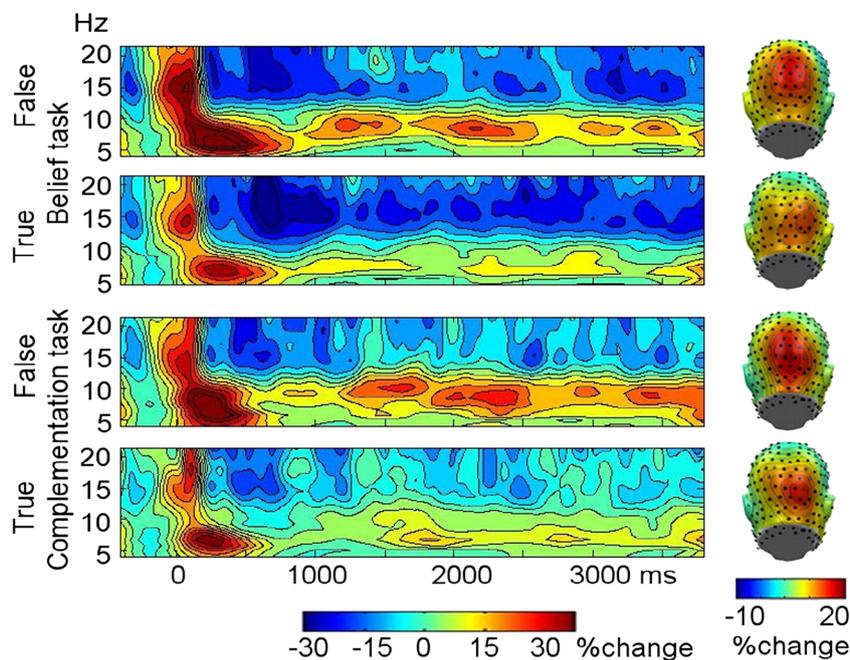


Fig. 2 Grand mean ($N = 44$) time-frequency planes showing power changes at parietal sensors relative to a pre-vignette baseline. Note the modulation of alpha and beta power by the experimental manipulations.

Topographical maps on the right show changes in alpha power for the time between 1,000 and 3,500 ms after vignette onset. This time range was also used for statistical analysis

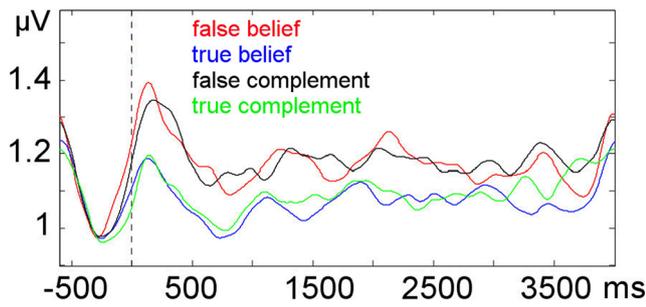


Fig. 3 Time course of parietal alpha for the four conditions

Analyses of variance A 2 Task Type (Belief/Complementation) × 2 Falsehood Type (False/ True) repeated measures analysis of variance (ANOVA) of the mean alpha power changes showed a main effect of falsehood. The false conditions were associated with heightened posterior sustained alpha power (from 1,000 to 3,500 ms after vignette onset) compared to the true conditions, $F(1,43) = 5.35, p = .026$, across belief and complementation tasks. Task type did not affect sustained posterior alpha power changes, $F(1,43) = 2.93, p = .094$, nor did task type interact with falsehood type, $F(1,43) = 0.004, p = .95$.

Given the strong and consistent power reductions seen in the beta band, these changes were also subject to the same ANOVA model, examining the mean beta power changes (13.7–19.8 Hz)—averaged across the same sensor group and a time range from 500–1,000 ms after vignette onset. This analysis showed a main effect of task type, in which the belief conditions were associated with decreased beta power compared to the complementation conditions, $F(1,43) = 7.25, p = .010$. By contrast, falsehood type did not affect beta power changes, $F(1,43) = 0.055, p = .82$, nor did falsehood type interact with task type,

$F(1,43) = 0.90, p = .35$. That is the belief tasks (across true and false) exhibited a beta power reduction compared to the complementation tasks (across true and false).

Permutation-controlled analyses: Time-varying power As shown in Fig. 4, F -values exceeded the critical value for extended periods of time, selectively in the alpha and beta bands. Notably, only main effects were observed, with task type affecting the beta band in the range between 15 and 20 Hz, and falsehood affecting the lower alpha band, with effects maximal between 8 and 10 Hz. The permutation-controlled significance threshold (11.21) was not met for any F -value reflecting the interaction term.

Follow-up t -tests were used to further examine the main effects, and are shown separately for each condition pair in Fig. 5 to illustrate the convergence of the time course and specific frequency range in which effects were observed, across two factor combinations representing the same main effect: In line with the F -test of the full model, time-varying changes exceeding the absolute critical t -value of 3.76 were observed within the alpha and beta band, at posterior locations. For the comparisons between the true and false versions of each task (Fig. 5, top two panels), a sustained enhancement selectively in the alpha band is visible, which crossed the critical value for more than 50 % of the duration of the viewing epoch at central parieto-occipital locations, showing peak t -values above 5 at the same posterior sensors. No anterior locations were found to show t -values above the critical value. Also, no frequencies outside the alpha range showed significant effects of falsehood. For the comparisons between task types (bottom two panels in Fig. 5), significant differences were restricted to the beta band, shown primarily at posterior locations and sustained throughout the vignette duration. Again, a

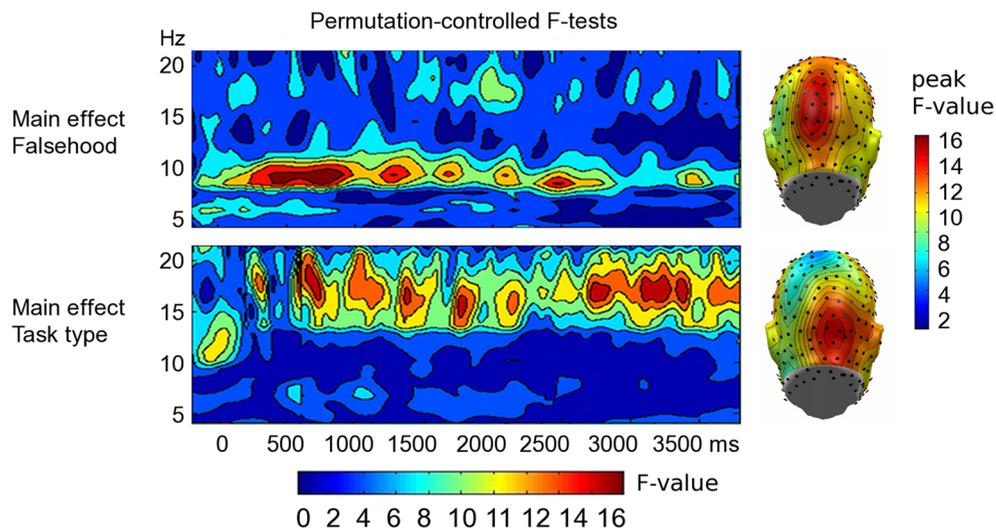


Fig. 4 Permutation-controlled F values comparing power changes for the main effect of falsehood (false vs. true conditions) and task type (belief vs. complementation syntax conditions) for each time–frequency point. Example time–frequency planes are shown for parieto-occipital sensor

Poz (left panels), together with topographical map of peak F -values in the respective frequency ranges of interest (right panels), with alpha-band changes displayed in the top panel, and beta changes in the bottom panel

substantial set of parieto-occipital sensors showed sustained significance (above the permutation-controlled threshold) for more than half of the duration of the vignette (shown as highlighted sensor locations in Fig. 5, bottom right panels), and these locations were overlapping with the location showing peak *t*-values.

Permutation-controlled analyses: Inter-site phase-locking relative to sensor Pz Only one time-frequency range exceeded the permutation-controlled *F*-threshold (i.e., 12.90), for the permutation-controlled ANOVA conducted for each time point, frequency, and sensor. In contrast to time-varying power this analysis indicated a robust interaction effect, during the first second of vignette processing in the beta range, across posterior sensors. This effect was followed by comparing the false-belief to the false-complementation condition and the false-belief versus true-belief condition. As shown in Fig. 6, higher ISPL values indicated

higher coupling between parieto-occipital regions and widespread frontal sites for the false-belief condition, compared to the false-complementation condition, selectively in the beta band (maximum around 13 to 15 Hz), in a time window extending from 600 ms to 1,100 ms after vignette onset. The comparison of “true” conditions did not result in any *t*-values exceeding the threshold.

To further examine the effect of the false-belief manipulation compared to the other conditions, we mapped the peak *t*-values obtained for the two possible comparisons that may underlie the interaction effect initially observed (false belief vs. true belief and false belief vs. false complementation; Fig. 7). This follow-up analysis showed that the false-belief task differed in connectivity from both the true-belief task and the false-complementation task in the beta band, with both maps showing converging regions of differing connectivity. There were no ISPL effects for any other time ranges or frequencies, including the alpha band.

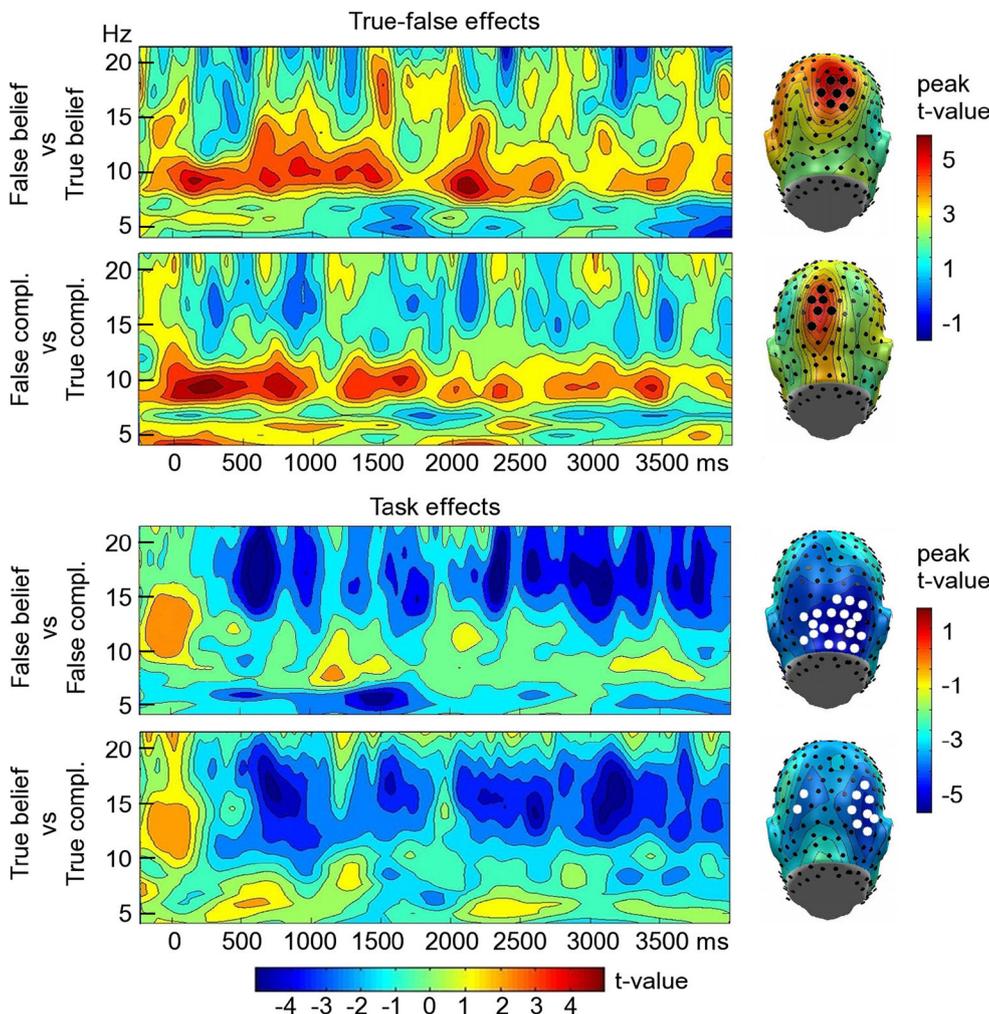


Fig. 5 Pairwise *t* values comparing power changes between the experimental conditions for each time-frequency point. Example time-frequency planes are shown for parieto-occipital sensor Pz (left panels), together with topographical distributions of peak *t*-values in the respective frequency ranges of interest (right panels), with alpha-band changes

illustrated in the top two panels, and beta changes highlighted in the bottom two panels. *Note:* The highlighted black and white electrodes on the topography cross the significance threshold for more than 50 % of the duration of the epoch

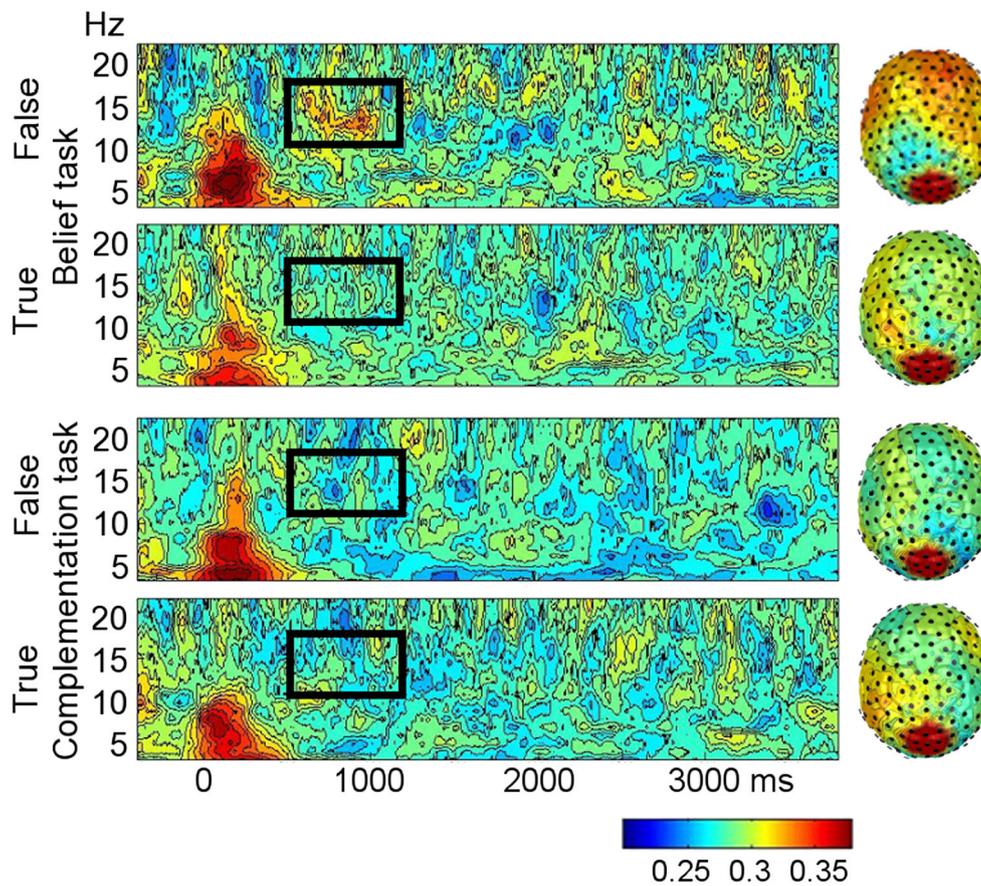


Fig. 6 Inter-site phase-locking (ISPL; relative to Pz) averaged cross the middle frontal sensors

Discussion

The current study investigated large-scale brain oscillatory activity correlated with false belief, false complementation, and their respective true conditions. The results suggest that sustained, induced, neural population activity in the alpha and

beta bands shows complementary sensitivity to the experimental manipulations, with alpha amplitude sensitive to falsehood versus truthfulness, and beta dynamics sensitive to belief versus complementation. In both cases, we focused on sustained oscillatory activity, present during the majority of the critical vignette’s duration. This focus maximized the

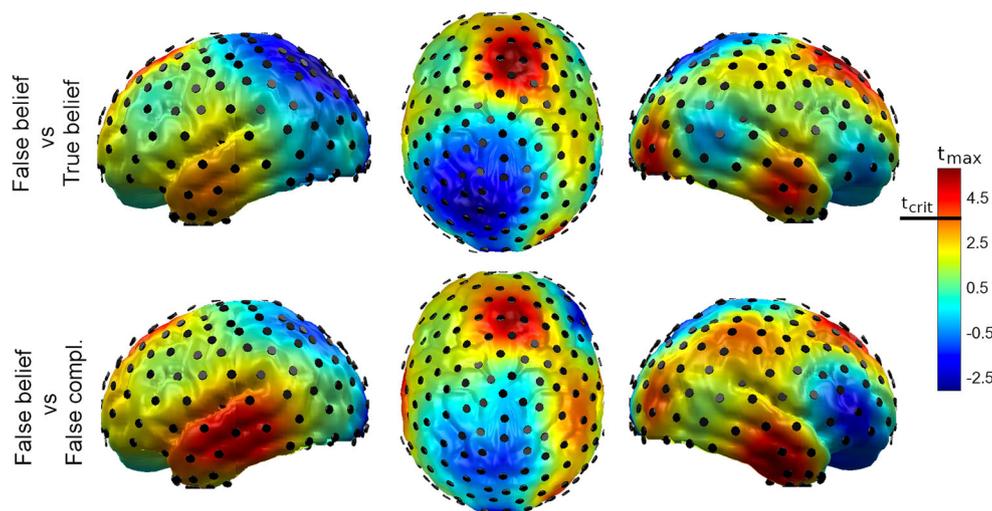


Fig. 7 Topographical mapping of pairwise *t* values comparing ISPL changes in the beta band between the false-belief and true-belief conditions and between the false-belief and false-complementation conditions

sensitivity of the analytic approach to sustained cognitive processes rather than reflecting initial sensory processing of vignette information.

Heightened alpha power was observed during the false-belief and false-complementation conditions, compared to the true conditions. The false conditions were designed to differ from the true conditions in only one aspect, which is the “conflict” between the protagonist’s belief/statement and reality. As such, the false conditions involve a number of additional, internal, cognitive processes (Meinhardt et al., 2011; Sommer et al., 2007) including identifying/recalling the protagonist’s mistaken thought/statement as such, and comparing it with one’s own memory. In contrast, the true conditions do not entail processing conflicting information, which may be taken to suggest that less mental effort is needed in the true conditions. The current results are in line with recent notions that consider alpha oscillations as an of index large-scale spatio-temporal dynamics involved in internal cognitive processing (Bartsch et al., 2015; Herrmann et al., 2004; Klimesch et al., 1999, 2007). In this perspective, the present differences in alpha-band oscillatory activity may represent a neural substrate of effortful internal processing (e.g., evaluating two conflicting views) associated with the false conditions compared to the true conditions.

Decreased beta power was observed in the false-belief and true-belief conditions compared to the complementation conditions. Such difference could result from the possibility that belief tasks require *mentalizing* (i.e., thinking about others’ psychological perspective; Amodio & Frith, 2006) whereas complementation tasks do not necessarily require mentalizing (Cheung et al., 2004; de Villiers, 2007; de Villiers & de Villiers, 2014). It is also possible that belief and complementation conditions differ in their syntactic processing demands, contributing to the difference in beta-band activity. Specifically, the complementation conditions potentially entailed higher syntactic binding demands than the belief conditions because the participant must directly connect the protagonist’s initial thoughts/statement (e.g., *Clara thought/said Zach had flowers behind his back*) with the observed and remembered facts (e.g., *but it was really leaves*) using the sentential complementation structure (de Villiers, 2007). Such syntactic difference possibility dovetails with the finding of beta activity modulation during language comprehension, as described in the introduction (Bastiaansen & Hagoort, 2006; Bastiaansen et al., 2010). Here, the fact that a relative decrease of beta power was seen during the critical vignette during belief trials compared to complementation trials is consistent with the hypothesis (Lewis and Bastiaansen, 2015) that updating, rather than maintaining a cognitive set of predictions and rules prompts beta power decreases. Heightened beta-band connectivity between fronto-temporal and parietal sites was observed specifically in the false-belief condition, which supports the notion that the false-belief tasks is

associated with heightened top-down signaling originating in frontal cortex (e.g., Gazzaley & Nobre, 2012). The false-belief condition combines falsehood processing with belief processing (mentalizing), and thus has been related conceptually to effortful higher-order cognitive processing (Kuhn, 2000). Future research may design studies to specifically address the generality of the hypothesis that false belief processing involves specific enhancement of prefrontal top-down modulation.

Taken together, the current results are consistent with previous studies (Chen et al., 2012; Cheung et al., 2012) in finding both shared (i.e., alpha oscillation) and unique neural signatures (i.e., divergence in beta oscillatory activity between tasks, and the interaction in connectivity) associated with false-belief and false-complementation tasks, suggesting the two tasks engage interactive but separate neural networks (van Ackeren et al., 2016). Such a finding does not support the notion that the neural correlates of complementation syntax task are redundant with the neural correlates of false belief processing.

Future studies are needed to explore whether the findings can be replicated in children and populations with brain lesions. Behavioral studies provide mixed support for the necessity of complementation syntax for false belief processing (de Villiers & de Villiers, 2014; Low, 2010; Slade & Ruffman, 2005). Aphasic adults with grammatical impairments, including complementation syntax, still pass false-belief tasks (Apperly et al., 2006; Siegal & Varley, 2006). Patients with stroke-induced aphasia were found to perform better in language comprehension when alpha and beta band (8–30 Hz) power decreases in frontal, temporal and parietal regions (Kielar et al., 2016). On the other hand, the importance of complementation syntax varies for different developmental populations (Farrar et al., 2017; Tager-Flusberg & Joseph, 2005). For typically developing children, complementation syntax is sometimes linked to FBU but just as often is not related (de Villiers & Pyers, 2002; Tardif et al., 2007). However, for children with autism spectrum disorders, specific language impairment, and deafness, complementation syntax appears to be more important to FBU (e.g., Farrar et al., 2017; Schick et al., 2007). Data shedding light on the neural dynamics of these processes would help to determine the importance of complementation syntax in FBU and the underlying mechanisms, for different populations. Such information would be useful for designing more efficient training and intervention programs for children with developing FBU and patients with FBU deficits.

Conclusions

The current study provides the first systematic investigation of neural oscillations in cortical networks associated with false

belief understanding and complementation syntax. We provide evidence showing that false-belief and false-complementation tasks prompt different neural responses, with false-belief tasks showing oscillatory activity consistent with greater connectivity and heightened internal processing. Such results against the redundancy hypothesis provide the foundation for subsequent studies that aim to explore the relation between these fundamental neurocognitive processes. Such results also provide neurophysiological data complementary to behavioral data for addressing the ongoing theoretical debate on the role of language in false belief understanding.

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