‘Honey, shall I change the baby? - Well done, choose another one’: ERP and Time-Frequency correlates of humor processing

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Abstract

We studied the electrophysiological correlates of verbal humor comprehension by comparing Event Related Potentials (ERPs) and Time-Frequency Representations recorded while 50 participants read humorous and non-humorous passages. Using linear mixed models on single trials we showed that humorous target words elicited a larger Left Anterior Negativity (LAN), sustained in time and followed by a positive shift involving P600 and Late Positive Complex (LPC) components. In the Time-Frequency domain, humor was associated with a power decrease in the beta-band of the EEG. Furthermore, participants' Autism-spectrum Quotient correlated with the size of the LAN, suggesting that social skills could affect humor comprehension during the early processing phase. Our results describe a sequence of events where incongruity-detection (associated with the LAN) precedes a composite set of mechanisms serving resolution and acting in parallel: the sustained LAN might reflect the search for an alternative script, while the P600 might index inferential processes arriving at the resolution and the updating of the discourse model. The processing differences associated with the LPC and the changes in beta power may reflect a later stage of more elaborative and reflective processing (where the receiver reflects upon the joke's solution) and the abandonment of the current discourse model.

Keywords: ERP; time-frequency; experimental pragmatics; neuropragmatics; humor and jokes

1. Introduction

Previous research in the neuroscience on humor, mostly carried out with fMRI methods, showed that the brain network processing humor involves two different components: one is a cognitive component, related to the mechanisms of incongruity detection and resolution – encompassing language, semantic knowledge, error monitoring, and Theory of Mind brain areas; the other is an emotional component, related to the feeling of mirth or amusement typically associated with a humorous experience – encompassing mesocorticolimbic dopaminergic areas, including the amygdala (for review see Rodden, 2018b; Vrticka, Black, & Reiss, 2013). The present study focuses on the electrical correlates of the cognitive component of the humorous experience, i.e., on the electrical correlates of those mechanisms that allow us to get a joke.

The most widespread account of humor comprehension is the incongruity-resolution theory, developed in modern cognitive psychology by Suls (1972), following early views of humor as arising from message incongruity (e.g., Schiller, 1938; for a review see Keith-Spiegel, 1972). According to the incongruity-resolution theory, getting a joke is a two-steps process. First, the receiver finds an incongruity between the message and his/her expectations; then, such incongruity must be solved by looking for a rule that makes the inconsistent information follow from the context, in a funny and surprising way. The resolution of the incongruity re-establishes the discourse coherence with a funny interpretation, leading to the feeling of mirth or amusement, and, eventually, laugh (e.g., Ramachandran, 1998). Mechanisms of incongruity detection and resolution are acknowledged as fundamental to humor processing in most of the more recent psychological accounts of humor (see Ruch & Hehl, 1998; Ventis, 2015; Wyer & Collins, 1992). However, these accounts differ with respect to the final stage of processing, arguing for a further phase that involves reflexive thought (Ventis, 2015) or the start of "meta-level analysis" (Ruch & Hehl, 1998) or prologued inferences in an "elaboration" stage (Wyer & Collins, 1992). In addition to such variety of mechanisms, humor is an extremely multifaceted phenomenon in which the range of variables involved in processing is wide, from psychological characteristics of the individuals to linguistic characteristics of the materials. Consequently, the study of humor lies at the crossroad of many disciplines, including linguistics and pragmatics (e.g., Attardo, 1994; Dynel, 2017; Yus, 2016), psychology (e.g., Goldstein & McGhee, 1972; Martin & Ford, 2018), and cognitive neuroscience (e.g., Goel & Dolan, 2001; Vrticka et al., 2013).

Arguably, one of the most appropriate methodologies to investigate the time course of cognitive mechanisms of humor is the Electroencephalogram (EEG), as it allows for tracking down the electrical activity of the brain as it unfolds over time, with millisecond precision. Yet, after almost twenty years of research on EEG and humor (since Coulson & Kutas, 2001), several gaps remain in the literature concerning the EEG reflection of incongruity detection and resolution mechanisms, as it will be reviewed in section 1.2. For instance, the literature debates about the manifestation of incongruity detection, linked by some to an increased response over left anterior electrodes, which is nevertheless deemed as "ephemeral" (Kutas, Van Petten & Kluender, 2006), and by others to the amplitude of the N400 component (e.g., Du et al., 2013). Moreover, the study of individual factors in affecting humor comprehension is by far more developed in the behavioral literature than in the ERP tradition, meaning that much is known about the factors affecting the outcome of the process, and less about the factors involved in processing. In this study, we exploited the knowledge achieved in the literature about the electrical correlates of general language comprehension mechanisms to study humor comprehension, leaving aside the emotional component of humor, and focusing on verbal humor, which, compared to the more condensed structure of cartoons (Tsakona, 2009), allows for a more precise identification of *when* (the word at which) incongruity occurs.

More specifically, we aimed (i) to provide additional evidence on the EEG correlates of incongruity detection and resolution and to test how "ephemeral" these effects are, and (ii) to investigate the variability in the EEG response by evaluating the effect of a set of individual-based and material-based predictors and by adopting appropriate and up-to-date statistical tools. To achieve the first aim, we used both the Event Related Potentials (ERP), in order to draw upon the existing literature, and the Time Frequency Representations (TFR) of the EEG, in order to offer novel and complementary evidence on the undergoing brain mechanisms. To meet the second aim, we analyzed single trials ERPs using linear mixed models, which allow for jointly modeling sources of variance pertaining to stimuli and to participants' characteristics.

1.1 Variability factors in humor processing

Humor is far from being a unitary phenomenon. Even restricting our investigation to the processing of verbal jokes (as opposed to visual), there are many distinctions such as conversational humor vs. canned jokes, one-liners vs. longer texts, etc. (Dynel, 2009). Beyond linguistic structure, a humorous experience greatly depends on how funny a joke is perceived, and much of the recent literature has investigated the role of jokes' funniness and surprise (e.g., Chang, Ku, & Chen, 2018; Feng, Chan, & Chen, 2014; Ku, Feng, Chan, Wu, & Chen, 2017), or the differences between controlled and voluntary grinning, and the genuine emotional responses to humor (Wild et al., 2006). Another crucial factor differentiating among types of jokes is how they differently involve incongruity detection and resolution mechanisms. For instance, in puns, where the incongruity may consist in morphological or phonological "reversals" (e.g., *You've had tee much martoonis*, Milner, 1972), both steps are normally involved, whereas in nonsense humor (e.g., *Why did the elephant paint its fingernails red? So it could hide in a cherry tree,* Cray & Herzog, 1967) a full resolution of absurdity cannot be achieved (for studies on nonsense humor see for instance, Ruch, 1992; Samson, Hempelmann, Huber, & Zysset, 2009).

In addition to the characteristics of the humorous materials, a large bulk of research has shown that many individual factors affect the way in which people perceive or understand humorous materials. In the clinical literature (for review see Rodden, 2018a), individuals affected with different syndromes show poor appreciation or comprehension of humor compared to non-humor, as in the case of major depression (e.g., Uekermann et al., 2008), schizophrenia (e.g., Corcoran, Cahill, & Frith, 1997; Marjoram et al., 2005), Agenesis of Corpus Callosum (Brown, Paul, Symington, & Dietrich, 2005), right frontal lobe damage (Shammi & Stuss, 1999), Autism Spectrum Disorder (ASD; e.g., Emerich, Creaghead, Grether, Murray, & Grasha, 2003; Samson & Hegenloh, 2010; Samson, Huber, & Ruch, 2013). For instance, in Emerich et al. (2003) ASD adolescents were presented with joke fragments and were asked to choose the correct funny ending, within a set of alternatives (straightforward ending, humorous non sequitur endings, neutral non sequitur endings): compared with the control peers, ASD participants made more errors, often choosing the straightforward endings. Similar comprehension difficulties were reported also for young adults with ASD using different tasks (yes/no comprehension and explanations) (Samson & Hegenloh, 2010).

A different literature has focused on the impact of a wide range of individual differences on humor comprehension and appreciation in the non pathological population: humor comprehension decreases and humor appreciation changes with physiological aging (Shammi & Stuss, 2003; Uekermann, Channon, & Daum, 2006); gender differences in processing or in the appreciation of different humorous materials have been often reported (e.g., Chang et al., 2018; Ferstl et al., 2017; Forabosco & Ruch, 1994; Kohn, Kellermann, Gur, Schneider, & Habel, 2011); experience seeking seems to be a personality trait that affects humor processing, with increased appreciation of nonsense humor, and decreased appreciation for incongruity-resolution humor (e.g., Forabosco & Ruch, 1994; Samson et al., 2009); furthermore, increased intolerance of ambiguity (and conservatism) has been linked to increased funniness for incongruity-resolution jokes and decreased appreciation for nonsense humor (e.g., Ruch & Hehl, 1983; Ruch, McGhee & Hehl, 1990).

The interplay of these many factors testifies the complex nature of humor processing and suggests that aiming at capturing the effect of multiple factors involved in humor comprehension is a fruitful approach to disentangle processing differences in joke understanding. In the present investigation we will consider the role of several factors affecting processing, both at the level of the materials and at the level of the participants, but restricting the investigation to only one kind of jokes, namely verbal jokes. In pursuing our first aim (i.e., investigating the EEG correlates of humor comprehension processes), we will focus on incongruity-resolution jokes based on semantic mismatches, and we will compare them to straightforward texts (see Table 2). In other words, we will not evaluate the processing differences between humorous types (as done for instance in Samson et al., 2009), but rather we will concentrate on the comparison between a dialogue containing a humorous semantic mismatch (deriving from the violation of expectations from verbal semantics or world knowledge) and a paired straightforward dialogue. In pursuing our second aim (i.e., filling in the gap on how individual factors affect the EEG correlates of humor comprehension), we will account for the effect on processing of two individual characteristics, namely working memory and social skills, and two jokes characteristics, namely funniness and surprise. Working memory is expected to be linked with ERP effects on left anterior electrodes, given previous literature (King & Kutas, 1995); social skills are expected to affect humor processing on the basis of the ASD literature. Jokes' funniness and surprise are also expected to affect processing, in line with the most recent ERP literature on the topic (Chang et al., 2018; Feng et al., 2014; Feng et al., 2017).

1.2 Electrophysiological investigations of humor processing

A number of studies investigated verbal humor processing using EEG measures such as the Event Related Potentials (ERPs) (Chang et al., 2018; Coulson & Kutas, 2001; Coulson & Lovett, 2004; Coulson & Williams, 2005; Du et al., 2013; Feng et al., 2014; Ku et al., 2017; Marinkovic et al., 2011; Mayerhofer & Schacht, 2015; Shibata et al., 2017). Because differences in the conditions under comparison are important to understand the relevance of the results in the literature, we summarize here the main distinctions in the manipulation and tasks within the set of selected papers: seven of these studies (Chang et al., 2018; Coulson & Kutas, 2001; Coulson & Lovett, 2004; Coulson & Williams, 2005; Du et al., 2013; Ku et al., 2017; Shibata et al., 2017) compared jokes to non-jokes (contextually coherent target words), whereas the other ones (Feng et al., 2014; Marinkovic et al., 2011; Mayerhofer & Schacht, 2015) compared jokes as well as non-jokes to a third, semantically incoherent, condition. Some studies used single line jokes (Coulson & Kutas, 2001; Coulson & Lovett, 2004; Coulson & Williams, 2005), while other used question/answer-type jokes (Chang et al., 2018; Feng et al., 2014; Ku et al., 2017; Marinkovic et al., 2011) or jokes involving short dialogues (Du et al., 2013; Mayerhofer & Schacht, 2015; Shibata et al., 2017). Studies asked participants for explicit judgments of funniness (Chang et al., 2018; Du et al., 2013; Feng et al., 2014; Ku et al., 2017; Marinkovic et al., 2011; Shibata et al., 2017), or used (humor unrelated) tasks, such as comprehension questions (Coulson & Kutas, 2001; Coulson & Lovett, 2004; Coulson & Williams, 2005; Mayerhofer & Schacht, 2015). Across studies, the differences between humorous and non-humorous materials have been related to four ERP components: the N400, the Left-Anterior Negativity (LAN), the P600, and the Late Positive Component (LPC).

Overall, the results are indicative of different phases in humor processing, yet the precise association between processing phases and ERP components is still debated, as it will be detailed below by distinguishing the incongruity detection and the resolution phases.

In addition to ERP, another measure that can be extracted from the EEG is the Time-Frequency Representations (TFR). The ERP technique consists in averaging together a number of EEG epochs, time-locked to the onset of the critical events (Luck, 2014). Averaging increases the ratio between the signal of interest and the underlying EEG noise, by reducing the contribution of EEG activity that is random or not time-locked to stimulus presentation. One of the drawbacks of the ERP technique is that the use of averaging obscures changes in frequency power that are not phase-locked to stimulus presentation (e.g., Herrmann, Grigutsch, & Busch, 2005), even when such oscillatory changes occur, are related to stimulus processing, and have a functional meaning (e.g., Bastiaansen et al., 2012). The time-frequency domain of the EEG can thus provide evidence – complementary to the ERP measures– on the cognitive processes involved in humor or, more generally, in language comprehension. Although this research field is flourishing, there are very few attempts to provide a comprehensive framework where oscillatory changes in different frequency bands are linked to specific functional mechanisms (for reviews of oscillatory changes in language processing see Meyer, 2018; Weiss & Mueller, 2012). So far, much of the research on TFR of language processing mechanisms has been devoted to speech processing (for a review see Ding & Simon, 2014), while less empirical evidence is available in the realm of written language comprehension, and none in verbal humor processing.

1.2.1 ERPs and the first step of humor processing: incongruity detection

Compared with non-humorous materials, the earliest ERP difference elicited by humorous stimuli has a negative polarity and is often interpreted as affecting the N400 component (Chang et al., 2018; high constraint jokes in Coulson & Kutas, 2001; Feng et al., 2014; Du et al., 2013; Ku et al., 2017). The N400 is a negative deflection of the ERPs that is maximally distributed over central parietal electrodes and peaks around 400 ms after stimulus onset. In the language processing literature, the N400 has been found to be sensitive to several factors, among which predictability and semantic congruence are the most relevant, but this component, rather than reflecting incongruity detection *per se*, seems to be modulated by how much a word matches contextual expectations (e.g., Kutas & Federmeier, 2011; Lau, Phillips, & Poeppel, 2008; Van Petten & Luka, 2012).

Other ERP studies of humor processing found negative effects over left-anterior electrodes associated with the LAN. Most often these LAN effects are late (i.e., after 500 ms), and long lasting (Coulson & Kutas, 2001; Coulson & Lovett, 2004; Coulson & Williams, 2005). Coulson and Kutas

(2001) argued that these negativities resembled the sustained LAN effects typically associated with the processing of sentences that increase working memory demands (King & Kutas, 1995) and that the LAN observed in humor comprehension was linked to frame-shifting operations. Notably, LAN effects (occurring in left anterior scalp locations, in a short time interval between 300 and 450 ms) have been consistently related to anomaly detection in syntactic processing. These LAN effects are typically observed for grammatical agreement violations (Molinaro, Barber, & Carreiras, 2011), and have been sometimes reported during the processing of anomalies concerning highly structured information, such as incorrect metric sentences (Schmidt-Kassow & Kotz, 2009), violations of non-linguistic sequences (Hoen & Dominey, 2000), and with (some kinds of) arithmetical errors (Núñez-Peña & Honrubia-Serrano, 2004). The functional characterization of the focal LAN as being related to anomaly detection seems not incompatible with a role of this component as an index of incongruity detection in humor.

Some recent studies on jokes' processing accounted for negative ERP differences in N400 terms, even when the topographical and temporal characteristics of the differences did not correspond to the canonical distribution of the N400. Specifically, the ERP effects were associated with the N400 even when described as: a) distributed in anterior electrodes (anterior and left electrodes in Chang et al., 2018; Du et al., 2013; Feng et al., 2014); b) long lasting (Experiment 2 in Mayerhofer & Schacht, 2015); c) anterior and long lasting (Ku et al., 2017); d) anterior left but short lasting (Experiment 3 in Mayerhofer & Schacht, 2015). A concern with some of these studies is that they did not test hemispheric asymmetries in the ERP effect: Feng et al. (2014) and Ku et al. (2017) analyzed a very small subset of midline electrodes; Chang et al. (2018) did not show the scalp topography of the effect; Marinkovic et al (2011) designed a combined MEG-EEG and, of necessity, used only three electrodes on the midline. We argue that whether the stage of incongruity detection is reflected by N400 or LAN effects is today still at stake.

1.2.2 ERPs and second step of humor processing: incongruity resolution

Compared with non-humorous materials, jokes often elicit ERP differences after 500 ms, and specifically more positive ERPs, which are deemed to affect the P600 or the LPC components (see good comprehenders in Coulson & Kutas, 2001; Coulson & Lovett, 2004; Coulson & Williams, 2005; Marinkovic et al., 2011; Shibata et al., 2017). The P600 component has been traditionally linked to global structural revision or repair of syntactically complex or ungrammatical sentences (Kaan & Swaab, 2003), and more recently to inferential interpretative processes (Bambini, Bertini, Schaeken, Stella, & Di Russo, 2016; Burkhardt, 2007; Domaneschi, Canal, Masia, Vallauri, & Bambini, 2018; Regel, Meyer, & Gunter, 2014). In humor, P600 effects have been specifically linked to the effort spent for re-establishing coherence after the detection of anomaly (Marinkovic et al., 2011; Shibata et al., 2017), or to the surprise component of humor (Coulson & Kutas, 2001). More recent studies, instead, have proposed that long lasting positive effects could be related to the LPC component and have argued for a role of this component in a third stage of humor processing, linked to more elaborative interpretation processes leading to the appreciation of humor (Chang et al., 2018; Ku et al., 2017).

We also need to point out that some authors observed positive effects alongside negative effects, i.e., in the same time window, and took this pattern as evidence against a serial processing. Specifically, the three studies that reported sustained LAN effects for at least some sub-groups of the experimental sample (Coulson & Kutas, 2001; Coulson & Lovett, 2004; Coulson & Williams, 2005) used the evidence of a temporal overlap between the sustained LAN and the positive effects to suggest that it is "unlikely that joke processing can be accounted for in terms of a simple two-stage model with surprise and coherence engaged in sequence" (Coulson & Kutas, 2001, p.74).

1.2.3 The Time-Frequency domain of non-literal language

The time-frequency domain of the EEG during humor processing has been investigated only once, and it was done using visual stimuli (Wang, Kuo, & Chuang, 2017): Authors reported that differences in frequency power were predominantly found in the theta-band, but were also present in delta, alpha, and beta ranges. These findings cannot be used to draw experimental predictions for the present study, because the condensed structure of visual jokes (Tsakona, 2009) can hardly be compared with the verbal jokes used here.

The evidence coming from the investigation of the comprehension of other instances of non-literal language is also very scant. For ironic sentences, where the intended meaning of an utterance corresponds to the opposite of the literal meaning, Regel et al. (2014) showed a stronger de-synchronization in the alpha range compared with literal sentences, while Spotorno et al. (Spotorno, Cheylus, Van Der Henst, & Noveck, 2013) observed a synchronization in the (lower) gamma-band. In the comprehension of idiomatic expressions (e.g., *break the ice*), as compared with literal sentences, two studies (Canal, Pesciarelli, Vespignani, Molinaro, & Cacciari, 2017; Rommers, Dijkstra, & Bastiaansen, 2013) reported similar effects of power decrease in the (higher) gamma frequency range: such changes were related to the more shallow combinatorial processes that idiomatic sentences may undergo due to their prefabricated nature. Jokes – however – represent a different phenomenon, where the humorous triggers are surprising, rather than extremely predictable.

If we look at the broader literature on more general language processing mechanisms, a recent view about predictive coding in language comprehension (Lewis & Bastiaansen, 2015; Lewis, Schoffelen, Schriefers, & Bastiaansen, 2016) proposed that the active maintenance of the current discourse representation leads to increased power in the beta range of the EEG (see also Engel & Fries, 2010; Weiss & Mueller, 2012), whereas encountering incongruent information, including syntactic violations (e.g., Segaert, Mazaheri, & Hagoort, 2018) or semantically incoherent words (e.g., Luo, Zhang, Feng, & Zhou, 2010) produces a drop in beta power. Activity in the gamma band has been related to semantic processing and meaning accommodation (e.g., Meyer, 2018), since, when encountering a semantic violation, gamma suppression is likely to occur (e.g., Bastiaansen, Magyari, & Hagoort, 2010).

1.3 Rationale of the study

The first aim of the study is to further inform a debate opened more than a decade ago, starting with Kutas et al. (2006), who described the main questions in ERP research on humor processing as follows: *"Whether the ephemeral sustained negativity over left frontal sites also will prove to distinguish jokes from non-jokes remains to be seen. A similar uncertainty colors the specificity of the late positivities (frontal and/or parietal) that occasionally characterize the ERPs to jokes"* (p.687). To date, the temporal and topographic discrepancies across the literature reviewed above suggest that the empirical landscape has not greatly changed. The extent to which incongruity-resolution theory is supported by ERP results is still uncertain, since the incongruity detection step of humor processing has been ambiguously linked to N400 or LAN effects, and the resolution step has not always been linked to the P600 component. Still, the temporal precision of the EEG technique arguably makes it the ideal approach to investigate the cognitive component of humor comprehension. Our first aim in this study is to use the EEG technique to track down the unfolding of humor comprehension in its cognitive mechanisms, and especially to solve the uncertainties related to the brain correlates of the processing steps hypothesized in the incongruity-resolution model. Results from the Time-Frequency domain of the EEG may further reveal the undergoing mechanisms.

The second aim of the study shares the same urge of Vrticka et al.'s (2013), who argued for the need of investigating how humor is modulated "by various factors such as culture, personality, sex, age and intelligence quotient (IQ)" (p.866). We will explore the role of a set of by-item and by-participant factors in shaping the electrophysiological response, since material-based and individual-based variability may partly explain the confusion in the pattern of ERP results available in the literature. Although individual differences were examined since the first ERP studies on humor (Coulson & Kutas, 2001), the approach was to use median split analyses, even though this may lead to spurious results (MacCallum, Zhang, Preacher, & Rucker, 2002). Furthermore, the role of social skills has been neglected till now, even though the link between inferential processes of pragmatic type – like those expected to be at play in humor (Attardo, Hempelmann, & Di Maio, 2002; Yus, 2017) – and social skills, especially Theory of Mind, has been highlighted throughout the literature on processing, development and decay (Bosco & Gabbatore, 2017; Cummings 2017; Lecce et al., 2018; Matthews et al. 2018; Pexman & Glenwright, 2007). We evaluated the impact of individual differences by administering two tests. One was the Autism-spectrum Quotient, originally designed to assess the degree to which an individual may have autistic traits (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) and previously used to investigate how individual differences related to social skills affect processing in various pragmatic domains, such as irony (Spotorno & Noveck, 2014) and scalar implicatures (Nieuwland, Ditman, & Kuperberg, 2010). We used AQ scores as a proxy of participants' social skills, as AQ can be related to autistic traits in the non-pathological population and mind-reading abilities, expecting that, consistently with the literature on ASD (Emerich et al., 2003; Samson & Hegenloh, 2010), participants with more autistic-like traits would be less effective in comprehending humor. We also used a sentence span test (Lewandowsky, Oberauer, Yang, & Ecker, 2010) to evaluate participants' working memory, and more specifically to investigate whether the relationship between the amplitude of LAN component and individual working memory capacity could be confirmed (Coulson & Kutas, 2001; King & Kutas, 1995). Furthermore, after the selection of the experimental materials, we assessed a set of relevant characteristics of the stimuli through a rating study: specifically, we collected scores for surprise and funniness, as two fundamental characteristics of the jokes (Chang et al., 2018; Feng et al., 2014; Ku et al., 2017), while ratings of difficulty, good continuation, and cloze probability were collected as control variables.

In general, we expected to find support for two-steps processing theories, confirming the involvement of –earlier– incongruity detection mechanisms and –later– resolution mechanisms. More specifically, this study should clarify whether the first stage is related to the N400 or to the LAN component and whether the second stage is linked to the P600, while predictors should provide information on which factors (either individual-based or material-based) modulate humor processing, and precisely at which stage. We expected to observe a sequence of ERP effects, where the ERP reflection of the mechanism of incongruity detection, associated either to the N400 or to the LAN components, should precede the resolution stage possibly reflected in P600 and LPC effects. We also expected to find a role for social skills in the comprehension of humor, with more socially inclined participants being more efficient in humor understanding, and to replicate the finding of a relation between working memory capacity and the amplitude of sustained LAN effects. Concerning the measures collected on our materials, we expected surprise to be associated with difficulties in drawing the inferences needed to re-establish coherence, while for funniness we expected an association with the size of the LPC. Finally, the investigation of the time-frequency domain of the EEG was carried out to offer novel and complementary evidence on the cognitive mechanisms underlying humor comprehension.

2. Method

2.1 Participants

52 participants (31 F) were involved in the EEG experiment. Age ranged from 18 to 34 years old (23.7 on average). They were right-handed (above 85% in the handedness questionnaire – Oldfield, 1971) native speakers of Italian, with normal or corrected to normal vision. No subjects reported to have any neurological or psychiatric disorders, and no subjects were under medication at the time of the experiment. Participants received monetary compensation for carrying out the EEG experiment. The experimental protocol was approved by the local Ethics Committee (Comitato Etico Area Vasta Nord Ovest, Azienda Ospedaliero-Universitaria Pisana). A different pool of 220 young adults (161 F, mean age = 22.76 years old, SD = 3.86) was involved in the different stages of the rating study (as detailed in section 2.3).

2.2 Cognitive assessment

For each participant to the ERP study we collected measures of verbal working memory and social skills (Table 1). Verbal working memory was assessed through a *Sentence Span* (SS) task (Lewandowsky et al., 2010): participants were presented with series of 3-to-8 statements and had to perform a speeded verification judgment at the end of each statement; after each response, a letter was presented, and at the end of each series participants were asked to type all the letters they could remember. Social skills were assessed through the *Autism-spectrum Quotient* (AQ) (Baron-Cohen et al., 2001; Italian version: Ruta, Mazzone, Mazzone, Wheelwright, & Baron-Cohen, 2012), a self-administered questionnaire where participants judged how strongly they agreed (on a four points scale) with a list of 50 statements. Scoring was carried out following Baron-Cohen et al. (2001) guidelines. Higher scores indicate stronger autistic traits, with scores higher than 32 possibly indicating clinical levels of autistic traits.

---Table1---

2.3 Materials

Seventy jokes were selected and adapted from classic Italian jokes books (Melegari, 1975; Bramieri, 1977) and from the Internet, excluding those about common taboos (Table 2). All jokes were three-line texts (two context-lines followed by the punchline), representing a dialogue between two characters. Jokes were selected for having a single word eliciting the humorous effect. Jokes could be coarsely defined as semantic, i.e., based on an incongruity generated either by lexical-semantic knowledge or world-knowledge (Vrticka et al., 2013). The word in which incongruity lied was identified by the experimenters and was defined as the target word (never occurring in sentence final position, to avoid wrap up effects). For each joke, a paired straightforward text was created by replacing the target word in the ending sentence with another word that would fit in the context but that was not humorous.

---Table 2---

Target words in the two conditions were matched for sentence position, number of letters, and (logarithmic) word frequency based on the CoLFIS database (Bertinetto et al., 2005; Bambini & Trevisan, 2012).

We conducted an extensive rating study on the materials using on-line questionnaires and recruiting a total of 220 participants. Cloze probability measures (Taylor, 1953) of the target words were collected from 72 participants (49 F, mean age = 24.29 years old, SD = 3.75) who completed fragments of the dialogues (truncated at the word preceding the target) with the first word that came to their mind. Funniness (*how funny was the dialogue?*) was evaluated by 64 participants (45 F, mean age = 24.36 years old, SD = 2.99), with a 7-points Likert-type scale; Good Continuation (*how is the last sentence in the dialogue a good continuation of the dialogue?*) was evaluated by 44 participants (33 F, mean age = 20.39 years old, SD = 2.05), with a 7-points Likert-type scale; finally, Surprise (*how unexpected is the final sentence in the dialogue?*) and Difficulty (*how difficult is it to understand the last sentence in the dialogue?*) were evaluated by 40 participants (34 F, mean age = 22.76 years old, SD = 3.86) using a 7-points Likert-type scale.

The ratings (Table 3) revealed that passages in the Humorous Condition (HUC) and Straightforward Condition (STC) differed for Funniness and Surprise, with HUC obtaining higher scores than STC. The two conditions did not differ in terms of Difficulty and both were rated high in Good Continuation, with HUC (4.27) being slightly less good compared with STC (4.66). Finally, although the ending was more surprising in HUC than STC, individual target words were actually more predictable in HUC compared with STC.

---Table 3---

---Figure 1---

2.4 Procedure

Participants sat in a comfortable chair approximately 80 cm from the display, in a dimly lit room. Each of the two context lines preceding the ending was presented as a whole in the centre of the computer screen, while the ending was presented word-by-word for 400 ms with a 200 ms inter-stimulus interval. Participants moved from the context to the ending by pressing a button. They were instructed to limit head movements and to relax muscle tension. They were aware that they would read dialogues that could be either funny or not and they were instructed to read them carefully. At the end of the EEG experiment, participants completed the SS and AQ tests.

2.5 Data acquisition and processing

The electroencephalogram (EEG) was acquired at 512Hz sampling rate in AC current with a hardware low cut-off filter (10 s time constant) using a Brainamp® 64 channel system (Brain Products® GmbH, Gilching, Germany). Fifty-eight electrodes were placed on the EEG cap according to the 10-20 International System: Fp1, Fpz, Fp2, AF7, AF3, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, Cpz, CP2, CP4, CP6, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, Poz, PO4, PO8, O1, Oz. AFz electrode was used as the online reference electrode, two electrodes were placed on the mastoids and three additional electrodes (below the left eye at the lateral canthi) monitored eye movements. Pre-processing was carried out in Matlab® (The MathWorks, Natick, US) with EEGLAB (Delorme & Makeig, 2004) and FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) toolboxes. Offline, the EEG was high-pass filtered (0.1Hz) and re-referenced to the average activity of the two mastoids. ICA decomposition was used to identify and remove eye-related activity only. The EEG was segmented into epochs around the presentation of the target words (from -800 to 1300 ms). Rejection of artifacts was carried out using an amplitude threshold of ±80 μV. Two participants were excluded on the basis of a rejection rate exceeding 40%, leaving a sample of 50 participants. The resulting average rejection rate was 9.75%, and an average of 31.70 and 31.47 epochs per participant were retained for HUC and STC conditions, respectively. ERPs were derived by further applying a 40Hz low-pass filter and a 300 ms pre-stimulus baseline correction. The power spectra from 4 to 40 Hz (with 1 Hz steps) of Time-Frequency Representations (TFR) were obtained from Fast Fourier Transformation using a frequency dependent width (6 cycles) Hanning window, sliding within each EEG epoch (from -800 to 1300 ms) every 10 ms. Power changes are reported as percentage change with respect to a pre-stimulus interval from -700 to -200 ms.

2.6 Data analysis

We used Linear mixed models (Pinheiro & Bates, 2000) on ERP single trials, in R (R Core Team) with lme4 package (Bates et al., 2014). This statistical tool has become extremely popular in behavioral research on language comprehension (e.g., Baayen, Davidson, & Bates, 2008) and has been advocated (Boisgontier & Cheval, 2016; Tibon & Levy, 2015) and applied also in the context of EEG research (e.g., Canal, Garnham, & Oakhill, 2015; Payne, Lee, & Federmeier, 2015), as it offers the advantage of simultaneously accounting for by-item and by-subject random variances and allows to test the effect of by-item predictors prior to averaging. The dependent variable was the mean voltage amplitude registered on each trial-participant-channel triplet, during the three time-windows that in the literature are associated with the components expected to be modulated by the experimental manipulation on humor: an early time-window (300-500 ms) to assess N400 or LAN effects; an intermediate time-window (500-700 ms) to assess P600 or sustained LAN effects; a late time-window (700-1100 ms) to asses LPC effects.

The statistical analysis of the ERP data was done in two steps. First, the Omnibus analysis (on a subset of 38 electrodes, excluding midline electrodes) aimed at characterizing the spatial distribution of the ERP effects, as it is usual in the traditional data analysis approach with ANOVAs: specifically, we investigated the interaction between Condition (HUC vs. STC), Anteriority [14 Frontal electrodes; 12 Central electrodes; 12 Parietal electrodes] and Hemisphere (Left vs. Right).

Following the results of the Omnibus analysis, we focused on the Region of Interest (ROI) analysis, which was carried out on two subsets of electrodes (Left Anterior: F7, F5, F3, FT7, FC5, FC3; Posterior: CP1, Cpz, CP2, P3, P1, Pz, P2, P4, PO1, POz, PO2) and investigated how Condition was modulated by four variables pertaining to the stimuli (Funniness, Surprise, Difficulty, Naturalness) and by four variables pertaining to the participants (Gender, Years of Education, Verbal Working Memory, and Autism-spectrum Quotient). In all analyses, Trial order was included to partial out effects of fatigue or training.

We assessed the contribution of each factor to the model's fit performing likelihood ratio tests (χ^2 statistic and associated p value are reported) between nested models (e.g., Zuur, Ieno, Walker, Saveliev, & Smith, 2009). This procedure allows to avoid over-fitting (Kliegl, Wei, Dambacher, Yan, & Zhou, 2011) and to compare models with the same random structure (we used by-item and by-participant random intercepts, and random slopes for Condition). The actual estimates of the models, describing the effects in the response measure (μV or β change), are reported. As widely discussed in the literature, the careful modeling of the random structure is crucial to avoid type I errors, and significant interactions in the fixed effect structure should appear in the random effects structure as well (Baayen & Milin, 2010; Barr, Levy, Scheepers, & Tily, 2013). Therefore, when significant interactions emerged in the ROI analysis, they were included in the random structure of the final models.

Results in the Time-Frequency domain were tested with a non-parametric cluster permutation test (Maris & Oostenveld, 2007) as implemented in FieldTrip. This approach has "considerable and growing appeal" in EEG research (Keil et al., 2014), especially when dealing with the three dimensional space (frequency bin, time, channel) of TFR. The input data consisted of a matrix of 650 time-points (from 0 to 1.3 seconds), 58 channels, and 35 frequency bins (from 5 to 40 Hz). For each significant cluster, we reported the value of t (maxsum) and the associated p value. Once we identified the range of frequency that was sensitive to the manipulation, data were aggregated across frequency bins and analyzed with the same procedure of the ROI analysis of ERPs described above.

ERP and TFR data from the time-windows under consideration, as well as the scripts used in the statistical analysis, are available in the Open Science Framework repository at https://osf.io/9ag4h.

3. Results

From the visual inspection of the ERP grand averages (Figure 1), the brainwaves have the typical shape of ERPs in response to visually presented words. The N1-P2 complex occurs soon after 0 ms and after 600 ms (the visual onsets of the target and of the following word) and is followed by the N400 deflection, reaching the maximum amplitude around 400 ms. Differences between conditions (see scalp-maps) suggest that, compared with STC, HUC is associated with more negative ERPs over left anterior electrodes and with more positive brainwaves over parietal electrodes.

---Figure 2---

3.1 Omnibus analysis

In the early time-window, we expected to observe effects either on the N400 or on the LAN. In particular, a LAN effect for humorous materials would be associated with a three-ways interaction (Condition by Hemisphere by Anteriority), whereas an effect on the N400 component should be associated to a main effect of Condition or a two-ways interaction Anteriority by Condition, being it not lateralized. The analysis revealed a significant interaction between Condition, Hemisphere and Anteriority (χ^2=34.75, p<0.001). Condition was significant over Frontal electrodes (-0.61μV, t=-2.52, p=0.013, CI=-1.09: -0.14), but not over Central (+0.02μV, t<1, CI=-0.46:0.51) nor Parietal ones (+0.27μV, t<1, CI=-0.23:0.77). Over Frontal electrodes, the effect was more negative over the Left hemisphere (L=-0.80μV; R=-0.43μV; L*vs*R=-0.37μV, t=-3.42, p<0.001, CI=-0.59:-0.16). The ERP difference due to Condition was thus focused on Frontal electrodes and on the Left hemisphere, indicative of the presence of the LAN. The lack of effect of Condition in Central electrodes suggests no involvement of the N400 component.

During the intermediate time-window, which usually captures P600 or sustained LAN effects, we expected a Condition by Anteriority interaction for "pure" P600 effects and a significant three ways interaction (Condition by Hemisphere by Anteriority) if the effect still involved the LAN. Analyses showed that a significant interaction between Condition, Hemisphere and Anteriority emerged (χ^2=82.70, p<0.001): the effect Condition was robust (and negative) in Frontal (-0.95µV, t=-3.73, p<0.001, CI=-1.45:-0.45) and (positive) in Parietal (+0.60µV, t=2.42, p<0.015, CI=+0.11:+1.09), but not over Central (+0.14µV, t<1, CI=-0.38:+0.67) electrodes. Concerning the three ways interaction, the effect was lateralized especially over Frontal electrodes, where the effect was more negative over the Left hemisphere (L=-1.38µV; R=-0.53µV; L*vs*R =-0.85µV, t=-7.22, p<0.001, CI=-1.08:-0.62) suggesting the engagement of the sustained LAN. Considering Parietal electrodes, the effect was more positive and right lateralized (L=+0.41µV; R=+0.86µV; L*vs*R =-0.44µV, t=-3.44, p<0.001, CI=-0.69:-0.19). The significant positive difference in Parietal electrodes suggests the engagement of the P600.

During the late time-window, we expected long lasting LPC effects (e.g., Feng et al., 2014). The topographical characterization of the effect should involve a Condition by Anteriority interaction, as the effect should not show strong hemispheric differences (unless sustained LAN effects carry over to this time window). Analyses showed a significant three ways interaction (χ^2=84.08, p<0.001: Condition was significant in Central (+0.92µV, t=3.17, p=0.002, CI=+0.33:+1.38) and Parietal (+0.85µV, t=3.92, p<0.001, CI=+0.46:+1.38), but not in Frontal (-0.14µV, t<1, CI=-0.65:+0.37) electrodes. Over Frontal electrodes, a significant interaction between Condition and Hemisphere emerged (L=-0.57µV; R=+0.29µV; L*vs*R =-0.86µV, t=-7.46, p<0.001, CI= -1.09 -0.63), suggesting that the negativity over Left anterior electrodes is still present (-0.57µV, t=-2.13, p=0.033) even though numerically reduced, if compared to the previous time window. Over Central electrodes, instead, the effect was positive and Right lateralized (L=+0.13µV; R=+0.86µV; L*vs*R =-0.74µV, t=-5.61, p<0.001, CI=-0.99:-0.48), with a similar pattern occurring over Parietal electrodes (L=+0.64µV; R=+1.04µV; L*vs*R =-0.40µV, t=-3.11, p<0.01, CI=-0.66:-0.15), suggesting the engagement of the LPC.

To sum up, the differences associated with HUC and STC occurred in all three time-intervals: In the first window a left anterior effect (LAN) emerged, in the second window the response is biphasic (LAN + P600), and in the third window the response is mainly positive (LPC). Once we identified the engagement of these components, we focused on the two scalp regions where the effects were more pronounced: one cluster of six left-anterior electrodes and one cluster of eleven parietal electrodes (see Figure 1).

3.2 ROI analysis

In order to test the effect of the set of the by-item and by-subject predictors on the ERP correlates we constrained further analyses to the two clusters of Left-Anterior (where LAN and Sustained LAN effects were found) and Posterior (where P600 and LPC effects were found) electrodes.

LAN (300-500 ms, left-anterior electrodes): Deviance analysis revealed significant effects of Condition (χ^2=10.48, p=0.001), the significant interaction between Condition and Funniness (χ^2=4.39, p=0.036), and the interaction between Condition and AQ scores (χ^2=6.29, p=0.012). When including by-subject random slopes adjustments for the interaction of Funniness and Condition, the effect failed to reach significance (t=-1.71, p=0.089), whereas the interaction with AQ survived when by-item slope adjustments were included. The effect of Condition was robust (-0.89μV, t=-3.28, p=0.001, CI=-1.43:-0.34) and modulated by AQ scores (Δβ=-0.51, t=-2.10, p=0.039, CI=-0.97:-0.03): An increase in AQ scores was associated with more negative LAN for HUC compared with STC (Figure 2). No effects of participants' Gender, Education, and Working Memory or materials' Funniness, Surprise, Difficulty, and Naturalness emerged.

---Figure 3---

Sustained LAN (500-700 ms left-anterior electrodes): In the sustained LAN spatio-temporal window, a robust effect of Condition (χ^2=21.52, p<0.001) emerged. HUC elicited more negative ERPs than STC (-1.43μV, t=4.90, p<0.001, CI=-2.00:-0.86). No effects of participants' or materials' variables emerged.

P600 (500-700 ms posterior electrodes): Deviance analysis on the P600 spatio-temporal window revealed significant effects of Condition (χ^2=5.72, p=0.017), a significant interaction between Condition and Surprise (χ^2=5.74, p=0.017), and no other interaction. When including by-subject random slopes adjustments for the interaction of Surprise and Condition, the effect was very close to be reliable (Δβ=+0.94, t=+1.97, p=0.051, CI=+0.00:+1.88): overall, HUC elicited slightly more positive ERPs than STC (+0.77μV, t=+1.71, p=0.091, CI=-0.11:+1.66), and items that were rated as more surprising were associated with larger differences between HUC and STC. No effects of participants' Gender, Education, Working Memory, and Autism Quotient or materials' Funniness, Difficulty, and Naturalness emerged.

LPC (700-1100 ms posterior electrodes): Deviance analysis on the LPC spatio-temporal window revealed a significant effect of Condition (χ^2=14.14, p<0.001), which was not modulated by any other variable. During this time-window HUC was more positive than STC (+1.29μV, t=+3.89, p<0.001, CI=+0.64:+1.94). No effects of participants' or materials' variables emerged.

3.3 Time-Frequency Representations analysis

The cluster permutation test on TFR revealed robust differences between HUC and STC, concerning one single cluster of data. HUC was associated with a decrease in power [t(maxsum)=-24204, p=0.012] compared with STC, which affected the data in a time-interval ranging from 700 to 900 ms, in a frequency range spanning from 14 to 21 Hz. The distribution of the difference was focused over Frontal electrodes. The frequency bin closely corresponds to the beta range (Figure 3). Single trial analysis was carried out on TFR data in the beta range, from six Frontal electrodes in one time-window (700-900 ms). Mixed models confirmed that the differences between conditions were significant (χ^2=4.37, p=0.037): power in the beta range decreased for HUC compared with STC (-10.55%, t=-2.11, p=0.037, CI=-20%:-1%). No effects of participants' or materials' variables emerged.

---Figure 4---

4. Discussion

We investigated the temporal development of humor processing mechanisms using the millisecond resolution of EEG-based measures and assessed the role of a set of individuals' and materials' characteristics in modulating the neural response. The first aim of the study was to clarify the EEG correlates of humor comprehension. The results revealed a pattern that is consistent with models describing a first stage of incongruity detection followed by a (more complex) stage of resolution. In the first time window the difference between conditions emerged over left anterior electrodes, while in the second time window the differences between conditions concerned both a negative effect in left anterior electrodes and a positive effect in posterior electrodes; during the last time window the ERP effect continued to be positive over posterior electrodes. Furthermore, in the analysis of the time-frequency domain of the EEG, we observed a power decrease in the beta-band of the EEG associated with humorous compared with straightforward dialogues. Concerning our second aim, related to the effect of by-item and by-subject variables, two predictors were found to modulate the ERP response: participants' AQ scores correlated with the size of the LAN in the first time window, whereas jokes' surprise ratings correlated with the P600 amplitude in the second time window. Furthermore, in the analysis of the time-frequency domain of the EEG, we observed a power decrease in the beta-band of the EEG associated with humorous compared with straightforward dialogues.

To start with the discussion of the findings for aim 1, our results describe a sequence of ERP differences in humor processing that is in line with the incongruity-resolution theory (Suls, 1972) claiming that humor comprehension involves a first processing step of incongruity detection and a subsequent step in which incongruity is resolved. However, the results also indicate that humor comprehension processes occur in parallel, and they may be long lasting, as schematically illustrated in Figure 5. Below, we argue that at least two different parallel mechanisms follow the detection of incongruity. They may both serve resolution, but one, the sustained LAN, may involve the search of relevant information to interpret the sentence, while the other, the P600, may reflect the inference making process. LPC and power changes in the beta-band may instead be indicative of a later stage of humor processing, as proposed by several psychological accounts of humor.

---Figure 5---

The earliest difference between conditions consisted in more negative ERPs (from 300 to 500 ms) to humorous materials. We interpret this finding as a modulation of the LAN component, because the possibility that the difference between humorous and straightforward target words modulated the N400, typically affecting the ERP during the same time-interval over central and parietal electrodes (Kutas & Federmeier, 2011), is ruled out by the left anterior scalp distribution of the effect. This finding is fairly consistent with some of the available evidence that showed the involvement of the LAN component (good comprehenders in Coulson & Kutas, 2001; Coulson & Lovett, 2004; Coulson & Williams, 2005), and it is less compatible with the studies that associated the incongruity detection stage to the N400 component (e.g., Du et al., 2013; Feng et al., 2014; Ku et al., 2017). A lack of N400 modulation (in absence of LAN) also occurred in other studies (right-handers did not show N400 effects in Coulson & Lovett, 2004; Marinkovic et al., 2011; Shibata et al., 2017) and was sometimes interpreted as due to the characteristics of the jokes (e.g., Coulson & Kutas, 2001). Drawing on the evidence of LAN for grammatical agreement violations (Molinaro et al., 2011), the involvement of the LAN in the present study supports a more general role of this component in incongruity detection (not only related to syntactic anomalies), and suggests that the humorous triggers were perceived as outright violations. Furthermore, this early effect was modulated by Autism-spectrum Quotient scores, indicating that participants with more autistic-like personality traits exhibited larger LAN effects and thus possibly perceived the incongruity as even more outright, compared with individuals with lower AQ scores. It has been argued elsewhere that individuals within the Autism spectrum are "humorless" (Samson et al., 2013) or less sensitive to (some kinds of) humor (Emerich et al., 2003). Our results are in line with this evidence and further specify when (i.e., at which stage) such difficulties for individuals with higher AQ may arise: participants with less developed social skills paid more effort in the incongruity detection step, thus very early on in the process of humor understanding. This may reflect a stronger sensitivity to incongruity, possibly due to a failure in processing contextual clues, and more specifically those clues that characterize humorous materials. More socially inclined participants, on the other hand, displayed reduced LAN effects, as if they better recognize the humorous context of the joke and thus are more prone to accommodate the incongruity.

During the intermediate time-interval (500-700 ms), part of the differences between conditions is still focused over Left Anterior locations. This is compatible with the pattern shown by participants with good comprehension skills in Coulson and Kutas (2001): Authors argued that sustained LAN effects in humor could reflect “frame-shifting needed to re-establish coherence” (p.74), and that these operations were linked to working memory. In line with this interpretation, and the literature reporting Anterior Negativities for processes related to the continued search of information for finding discourse referents (Canal et al. 2015) or for interpreting literary metaphors (Bambini, Canal, Resta, & Grimaldi, 2019), we take the sustained LAN as indexing the search for an alternative funny script to solve the joke. As for working memory, we observed no interaction between Sentence Span scores and the ERP effects in any of the two time-windows where LAN effects were tested.

Moreover, it is during this time-window that P600 effects surface over centro-parietal electrodes, possibly indicating the initiation of the resolution step. The P600 component has been linked to inferential mechanisms in other studies on the comprehension of humor (Marinkovic et al., 2011; Shibata et al., 2017), but also in studies targeting other pragmatic domains such as irony (Regel et al., 2014; Spotorno et al., 2013), metaphor (Bambini et al., 2016), and presuppositions (Burkhardt, 2007; Domaneschi et al., 2018). In keeping with this literature, our results suggest that, as soon as after 500 ms from the presentation of the humorous trigger, participants engage in the resolution of the incongruity through inferential operations. During resolution, receivers are supposed to “backtrack and realize that a different interpretation (i.e., an alternative script) was possible” (Martin & Ford, 2018; p.153). Inferential processes building on background information (local sentence context, cultural stereotypes, the situation described in the dialogue) are used to arrive at the alternative script and to update the discourse model, as described in different pragmatics-oriented accounts of humor (Yus, 2017; Attardo et al., 2002). We believe that the ERP reflection of the resolution stage consists in both sustained LAN and P600 activities, where the former takes the task of searching for and the latter of inferentially arriving at the alternative script and updating the discourse representation. Interestingly, jokes with higher Surprise ratings were associated with larger P600 effects, possibly because, for more surprising jokes, the link between the situation described and the alternative script is less direct, making the access to the script more demanding. To illustrate the process with an example and considering the joke in the title (*Honey, shall I change the baby? - Well done, choose another one*), the humorous effect arises from a) the detection of incongruity – when reading *choose* one realizes that *change* does not refer to the expected script of *changing the baby's clothes*–, and b) searching and finding the alternative script – *change the baby with a calmer one*.

In the last time-window (700-1100 ms), positive ERP differences in parietal electrodes are still ongoing. This finding is compatible with different explanations. One possibility is that the inferential processes started during the P600 last for several hundreds milliseconds up to the LPC time window, evolving into a cognitive elaboration stage of humor (Wyer & Collins, 1992), defined as "the conscious generation of inferences about features that are not captured by [...] initial encodings and are not necessary for comprehension, as well as other thoughts that might be stimulated by the encodings" (p.670). This idea was supported by a number of empirical studies (Chang et al., 2018; Chan, Chou, Chen, & Liang, 2012). However, the distinction between inferences in comprehension and inferences in elaboration is admittedly difficult, for Wyer and Collins themselves: "(i)t might, of course, be argued that these latter inferences are also made in the service of understanding the implications of the information and, therefore, are also part of comprehension".

Along the same lines, the LPC might be seen in light of the proposals that the humorous experience involves a late stage of processing, in which reflexive thought (e.g., Ventis, 2015) and meta-level analysis (Ruch & Hehl, 1998) are called upon. Ventis (2015), for instance, adopting Kahneman's framework (Kahneman, 2011), argues that the detection of incongruity is responsible for a switch from an intuitive, fast, and heuristics-based form of thought into a slow and reflexive mode, based on logic and rational thought, which is needed to find the proper (funny) solution for the incongruity arisen. In Ruch and Hehl (1998) a meta-level analysis represents the third stage of comprehension following resolution, where the receiver further engages in speculating upon the resolution. The receiver is aware that the fit of the solution is an "as if"-fit (p.142), and that she or he does not need to update her or his knowledge of the world, but rather plays with the ambivalence between sense and non-sense. To continue with the example, after solving the joke (*change the baby with a calmer one* instead of *changing the baby's clothes*), the reader plays with the ambivalence between scripts (*change clothes* vs. *change baby*), with no need of updating her or his knowledge of the world (the belief that *parents change the clothes of their crying babies* does not need to be changed). It may be this final, meta-analytic stage of processing that induces the sustained LPC effects.

A different view could be that the LPC reflects the emotional response to humor, i.e., the amusement phase, as proposed in some recent EEG works that also reported late effects (e.g., Ku et al., 2017). However, whether the ERP differences in this time window relate to amusement is difficult to say with the present results, as we did not measure any specific emotional response. In order to unambiguously link this processing time window with amusement, future research should complement the investigation by taking other measures, such as electromyographic, cardiovascular (Lackner et al., 2013), skin-conductance, or pupillometric measurements. For instance, the pupil diameter analysis in Mayerhofer and Schacht (2015) suggests that humor appreciation and amusement may indeed start after 800 ms from the presentation of the humorous target.

Overall, the ERP correlates of humor comprehension seem to be associated with a LAN effect preceding later effects. The involvement of the LAN perfectly fits with the hypothesis that the first processing step of humor comprehension consists in the detection of incongruity, given that the LAN has been related to anomaly detection in other linguistic domains (e.g., Molinaro et al., 2011). Moving to the next phase, the temporal overlap between the sustained LAN and the P600 effect following 500 ms does not support a strictly serial sequence of mechanisms and suggests instead that the resolution step may be associated with a set of ERP correlates (the sustained LAN and the P600), indicative of a different undergoing mechanisms with different functions in solving the joke. In this phase, the search for an alternative discourse representation reflected in the sustained LAN might go hand in hand with inferential activities indexed in the P600. The effects in the later time-window (beta power change and LPC) may be associated with a final, more elaborative and reflexive, step of processing.

This pattern of results points to an open (psychophysiological) question, as to whether the early and the late portions of the negative effects (LAN and sustained LAN) and of the positive effects (P600 and LPC) reflect the involvement of the same brain mechanisms. The tight similarity in the scalp distribution of the effects in contiguous time-windows supports continuity in the underlying processing mechanisms. There are nevertheless reasons to maintain a distinction between the early and the late portions of the components, and between the related mechanisms. Specifically, LAN and sustained LAN effects have been linked to different mental operations: the LAN is often taken to reflect anomaly detection (Molinaro et al., 2011; Núñez-Peña & Honrubia-Serrano, 2004), whereas sustained (anterior) negative effects have been associated with the search for information in the larger context in order to fully determine the meaning of an utterance, and have been observed for the processing of filler-gap dependencies (King & Kutas, 1995; Kluender & Kutas, 1993), anaphor resolution (Canal et al., 2015; Nieuwland, 2014), the recomputation of discourse representations (e.g., Baggio, Lambalgen & Hagoort, 2008), and the processing of the multiple meanings associated with literary metaphors (e.g., Bambini et al., 2019, although less clearly left lateralized). The differences between P600 and LPC components is less clear across the literature because these two components refer to distinct traditions (language-related P600 and memory-related LPC), but some authors proposed that earlier and later positive effects in humor processing map onto different mechanisms, i.e., resolution and amusement, respectively (Ku et al., 2017). Possibly some further evidence in favor of a distinction between the early and the late portions of the components comes from the item-based and participant-based analysis. Our findings of a relation between AQ scores and the LAN (but not sustained LAN), and between the measure of Surprise and the P600 (but not the LPC) seem to suggest that the cognitive processes underlying early and late time-intervals do not overlap. Moreover, theoretical views of humor assuming that the resolution stage should be followed by a later stage where different processes are taken upon (e.g., Ruch & Hehl, 1998; Wyer & Collins, 1992) may support a functional distinction between the P600 and the LPC.

The results of the analysis of TFR may help in further clarifying the nature of the processes underlying humor comprehension: the power change in the beta-band of the EEG may be associated with the last stage of processing of the joke, as it occurs during the late time window, between 700 and 900 ms. One influential view on the functional meaning of beta oscillations posits that they are "related to the maintenance of the current sensorimotor or cognitive state" (Engel & Fries, 2010). When a change in the status quo is needed, beta-band activity is reduced, and this is observed in the language processing literature as well (Weiss & Mueller, 2012). Specifically, beta power increases word after word during sentence reading, but, when materials lack of syntactic structure or contain violations, no increase occurs (Bastiaansen et al., 2010). The beta desynchronization reported for humor may reflect the abandonment of the status quo, i.e., a phase in which the discourse representation initially supported by the joke context is discarded after the reader has arrived at the alternative script through inferential mechanisms (e.g., Attardo et al., 2002; Yus, 2017). We must acknowledge that power changes in the beta-band were never reported in literature on the oscillatory dynamics of non-literal language processing, but the number of studies is very limited and with mixed findings (Canal et al., 2017; Rommers et al., 2013; Regel et al., 2014; Spotorno et al., 2013). The possibility that beta power decrease follows resolution deserves further research, but is nonetheless intriguing, and may fit in the predictive coding account (Lewis & Bastiaansen, 2015), which hypothesizes that activity in the beta-band is related to top-down predictions that increase when the confidence about incoming words increases, and decrease when predictions are not confirmed (see also Meyer, 2018).

Shifting to the discussion of the findings for the second aim of the study, we found evidence for the effect of two factors related to individuals and stimuli characteristics. The effect of AQ scores on the LAN response deserves special attention, not only because it confirms that individual differences can be used instrumentally to better describe the neural correlates of cognitive mechanisms (Kanai & Rees, 2011), but also because it supports the idea that language processing, especially in its pragmatic aspects, is affected by extra-sentential factors (Van Berkum, 2009), encompassing personality traits and social skills (e.g., Van den Brink et al., 2010). Previous research using the AQ to investigate the processing of classical phenomena in pragmatics found that individuals with higher social skills exhibited higher sensitivity to under-informativeness (Nieuwland et al., 2010) and could better use implicit cues to anticipate ironic utterances (Spotorno & Noveck, 2014). Here we found that social abilities, rather than working memory, gender, and education, are related to how people process humor, and that more socially inclined participants seem able to readily recognize the humorous contexts in which jokes appear, allowing for a less disruptive effect of incongruity in the electrophysiological response. Although we acknowledge that AQ is indicative of autistic traits rather than Theory of Mind skills, autism traits are associated with a decrement in Theory of Mind performance (Gillespie, Mitchell, & Abu-Akel, 2017). Thus, the correlation between AQ scores and the EEG response may also point to the relation between humor processing and Theory of Mind. The available fMRI and clinical literature has shown that brain areas associated with Theory of Mind are actively involved in processing humorous materials (e.g., Campbell et al., 2015), and that patients with syndromes that disrupt social cognition show impaired comprehension or appreciation of jokes (e.g., Corcoran et al., 1997; Samson, 2012). Our results suggest that the link between humor and Theory of Mind might be profitably explored also at the processing level in typical populations. This would be a highly relevant research line for future studies, considering that the link between the way in which we derive the speaker's intended meaning and social cognition – especially Theory of Mind – is a largely debated topic, at the theoretical level (Sperber & Wilson, 2002) as well as in clinical (Martin & McDonald, 2003) and experimental literature (Bosco, Tirassa, & Gabbatore, 2018; Catani & Bambini, 2014; Hagoort & Levinson, 2014; Spotorno, Koun, Prado, Van Der Henst, & Noveck, 2012).

Clearly our study has also a number of limitations. First, even though we investigated the effect of some intrinsic features of jokes (funniness and surprise), we did not venture further into the exploration of jokes diversity. Comparing the EEG response to different types of jokes might reveal processing differences between qualitatively distinct kinds of inferences (e.g., inferences driven by linguistic mismatches in puns vs. inferences more strongly hinging on Theory of Mind skills), similarly to what has been done in fMRI research (e.g., Samson et al., 2009). Second, a different set of individual predictors may be chosen, possibly using tests that – compared to the AQ used here – more closely measure mentalizing abilities and personality features. Third, the study was not designed to investigate the last stages of humor processing, which might reflect the emotional component of humor: electrodermal and electromyographic indexes (e.g., Thompson, Mackenzie, Leuthold & Filik, 2016), cardiovascular responses (Lackner et al., 2013), or pupil diameter data (Mayerhofer & Schacht, 2015), possibly co-registered during EEG, may help in linking emotional processes to the neural response.

5. Conclusion

Our study started from the need of facing the uncertainty about the EEG correlates of humor comprehension (Kutas et al., 2006) and whether it was possible to distinguish the two steps proposed by Suls (1972) during verbal humor comprehension. Our results support a relatively sequential model of humor comprehension in which the LAN, related to incongruity detection, and the P600, related to the inferential mechanisms of resolution, interact one after the other. However, the temporal overlap between the sustained LAN and the P600, as well as the subsequent beta power changes and the LPC effect, suggest a more complicated pattern, in which resolution capitalizes on a set of mechanisms acting in parallel, responsible not only for inferring a solution but also for searching for alternative scripts and, possibly, further elaborating on the joke's solution. By following the electrical correlates of humor comprehension millisecond by millisecond, we were able to describe the complex interplay of processes related to anomaly detection and resolution, subject to individual-based and material-based variations. The present study indicates that future research on the EEG correlates of humor processing should take into account the role of the whole set of ERP components (LAN or late LAN, P600 and LPC), in an individual differences perspective. This might become even more fruitful when research expand to other aspects of humor which we did not consider here, such as the differences between humor types and the link between the cognitive and the emotional components.

Author Contribution

VB and PC ideated and designed the research. PC, SDP, and LB constructed the materials and collected the data. CB and IR technically supported data collection. PC and LB analyzed the data. PC and VB interpreted the data and wrote the first draft of the manuscript. All authors contributed to this article, both substantially and formally, and approved the final version of the manuscript.

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Table 1. Characteristics of the sample of participants that took part in the EEG experiment

Sample Characteristics	Mean (SD, range)
Age	23.86 (SD=4.27; range=18:34)
Years of Education	15.48 (SD=3.66; range=8:23)
Gender	31 Female
Working memory (Sentence Span)	65.43% (SD=22%; range=4%:96%)
Autism-spectrum Quotient	18.90 (SD=4.74; range=10:28; maximum score=50)

Table 2. Two examples of the experimental materials (literal English translation from original Italian). The table shows the first two context-lines, which were the same for both conditions, and the ending, differing across condition. The target word to which ERPs were time-locked is italicized.

Item	Part	Humor Condition (HUC)	Straightforward Condition (STC)
1	Context 1	A newlywed young couple wakes up in the middle of the night because the firstborn is crying.	
	Context 2	She says: 'Dear, I get up. The baby never stops, perhaps it is time I change him?'. And he says:	
	Ending	'Well done, *choose* another one.'	'Well done, *calm* him down.'
2	Context 1	The shopkeeper speaks with a client: 'The umbrella costs 30 euro.'	
	Context 2	And the client asks: 'And what can I get for less than that?' And the shopkeeper:	
	Ending	'You can get the *rain* if you wish.'	'You can get the *raincoat* if you wish.'

Table 3. Characteristics of the sample of materials that were used in the EEG experiment as result of the rating study.

	Humor Condition (HUC) Mean rating (range)	Straightforward Condition (STC) Mean rating (range)	Difference
Surprise	4.5 (2.75:6.2)	3.05 (1.3:5.3)	t(69)=6.72, p<0.001
Funniness	3.97 (2.53:5.22)	2.07 (1.34:4.03)	t(69)=18.95, p<0.001
Difficulty	2.86 (1.25:5.05)	2.60 (1.15:4.55)	t<1
Good Continuation	4.27 (2.55:5.95)	4.66 (2.09:6.73)	t(69)=-2.35, p=0.022
Cloze Probability	30.6% (0%:92%)	9.7% (0%:81%)	t(69)=5.1, p<0.001
Length of ending sentence	8.46 (2:15)	8.64 (2:15)	t<1
Target position	6.28 (1:13)	6.3 (1:13)	t<1
Target word length	7.65 (3:13)	7.41 (2:13)	t<1
Target word frequency (log)	2.36 (0:3.41)	2.27 (0:3.48)	t<1

Figure Captions

Figure 1. Table of correlation between stimuli characteristics. Pearson product-momentum coefficients are reported for each test between two measures. Colored squares represent significant correlations ($p<0.01$). Funniness and Surprise are positively related (red colored), while Difficulty is negatively related (blue colored) to both Funniness and Surprise.

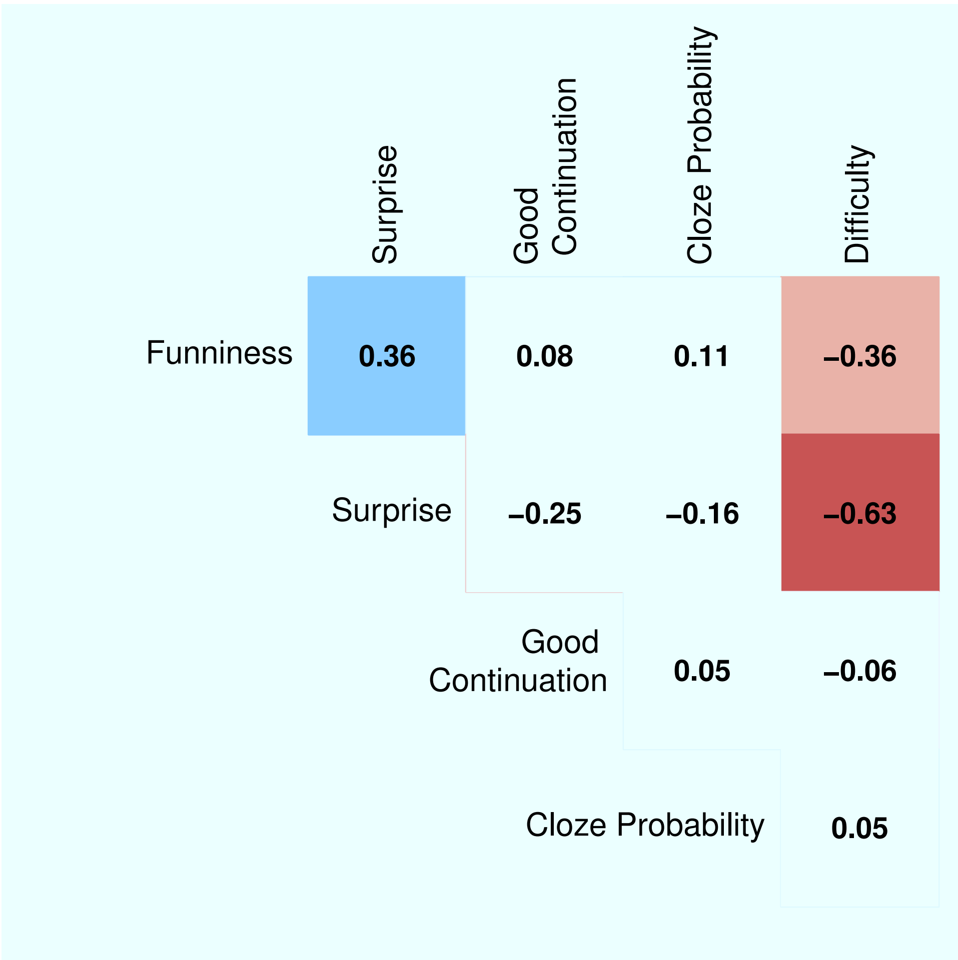
Figure 2. Grand Average Event Related Potentials. ERPs from a set of 19 representative electrodes plus horizontal and vertical ocular channels. ERPs associated with STC are depicted in light blue and those associated with HUC are depicted in orange. Negativity is plotted up. At the bottom of the figure, the scalp maps of the differences between conditions (HUC minus STC) in the three time-windows of interest (early, intermediate, and late) are shown.

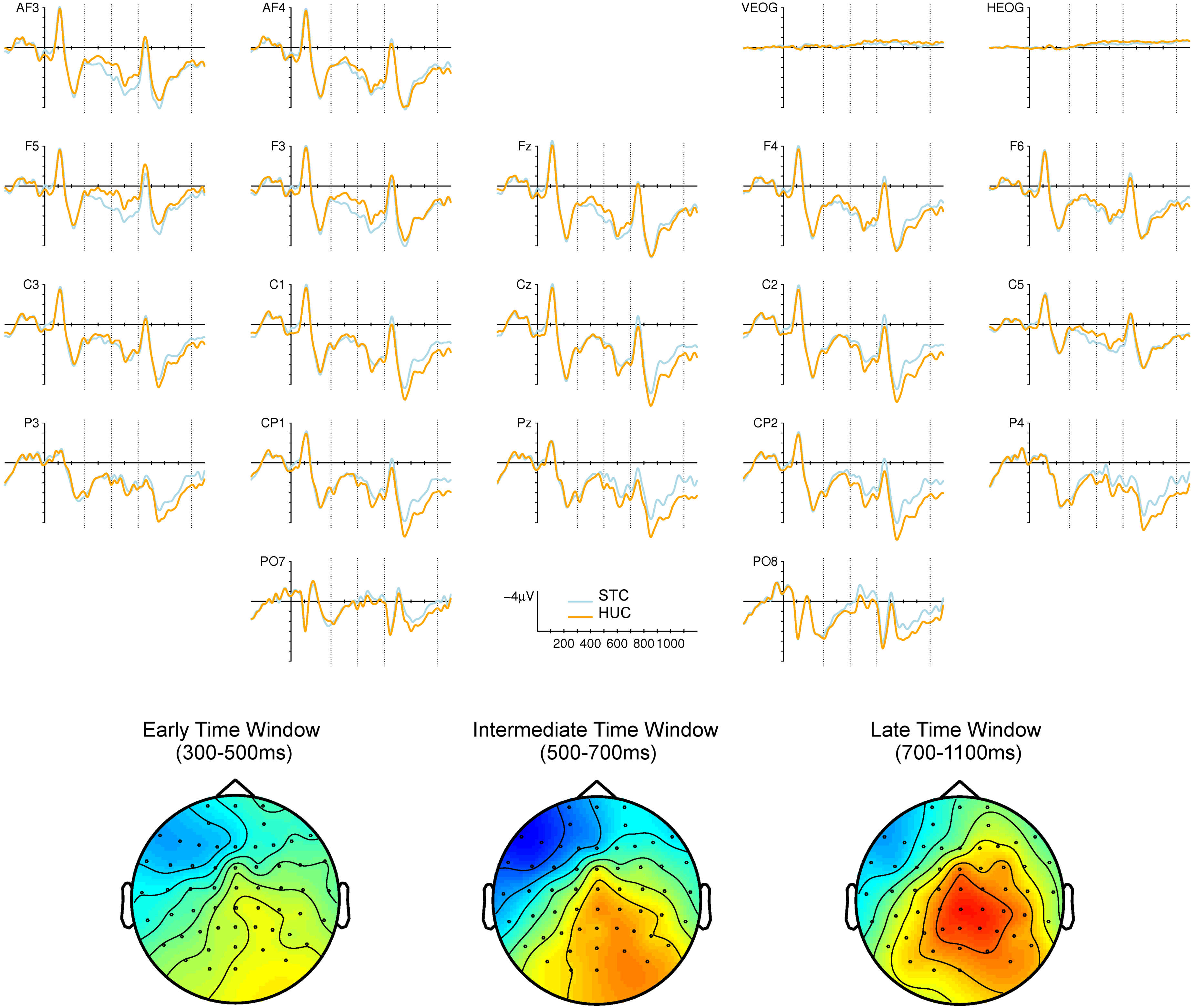
Figure 3. ROI analysis. Results from two different clusters of data are represented from six Left Anterior electrodes (F7, F5, F3, FT7, FC5, FC3) and eleven Posterior electrodes (CPZ, CP1, CP2, P3, P1, PZ, P2, P4, PO3, POZ, PO4), on left and right panels, respectively. The top panels show the temporal development of the difference between HUC and STC, during the whole ERP epoch, from the two clusters of electrodes. The average difference across time-points is shown in orange, while the gray lines represent the fifty ERP averages of each participant. Vertical lines mark the time-intervals associated to the three time-windows of interest: Early (300-500 ms), intermediate (500-700 ms), and late (700-1100 ms). The bottom panels depict the estimates of the two models on the LAN (on the left) and the P600 (on the right) response, showing the relationship between voltage amplitude and Autism-Spectrum Quotient scores (on the left), and Surprise ratings (on the right). Single dots represent Best Linear Unbiased Predictors of the effect of humor for each single participant (one the left) or item (on the right), around the estimate of the effect of Humor. Negativity is plotted down.

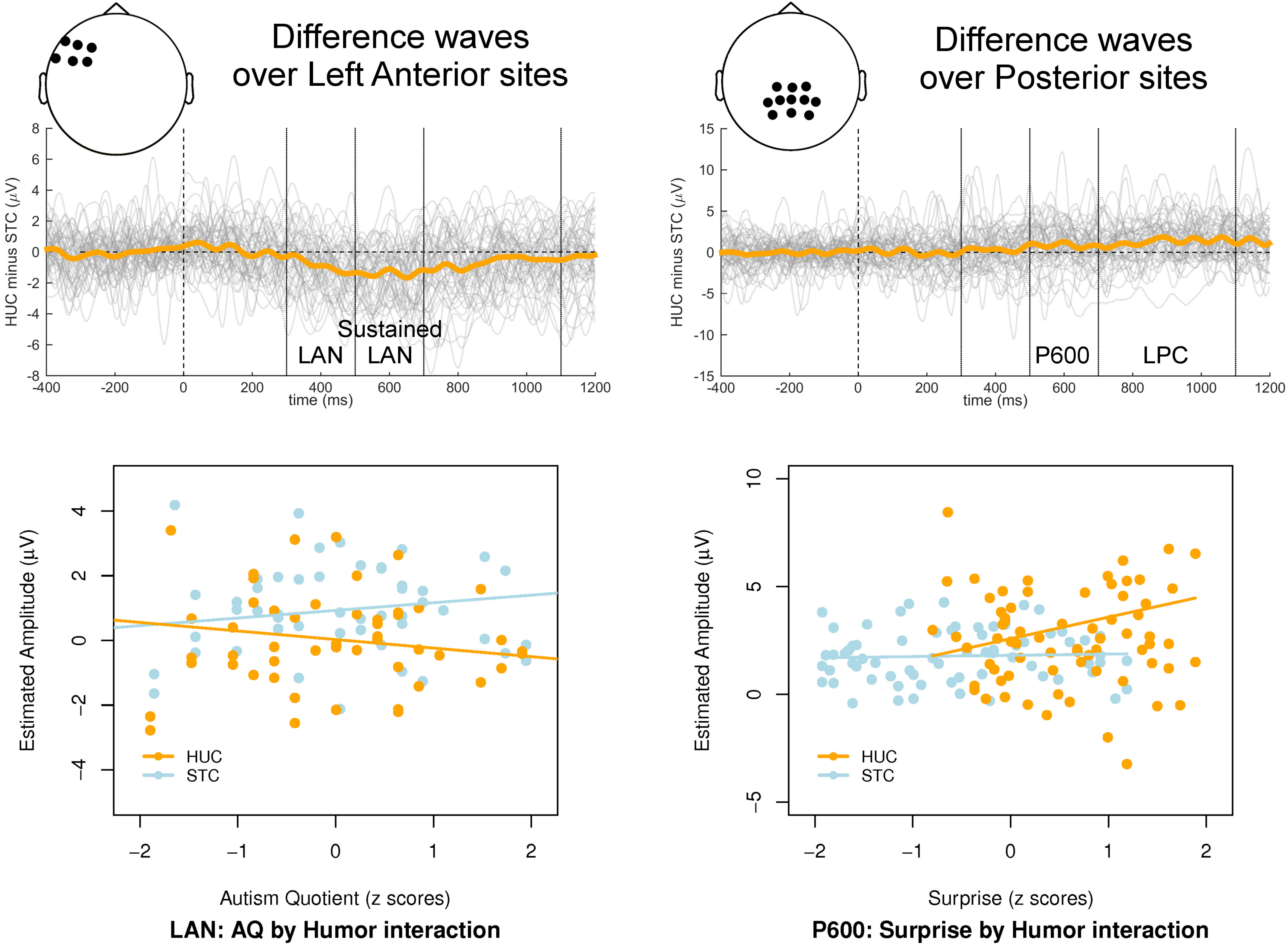
Figure 4. Time-Frequency Representations analysis. The left column shows power of different frequencies of the EEG (from 4 to 40Hz) around the presentation of the target word. Power is represented percentage change with respect to the (-700 to -200 ms) pre-stimulus interval. The white rectangle delimits the data space where the cluster permutation test was carried out. The second column of panels represents the area in the TFR space that was considered for statistical testing, with the upper panel showing the power difference (HUC-STC) between conditions, ranging from 4 to 35Hz, and 0 to 1000 ms. The bottom panel shows the significant cluster of adjacent data that was identified by the permutation test. The scalp map represents the spatial

distribution of the difference between conditions, affecting the 14 to 21 Hz frequency range and the 700 to 900 ms time range.

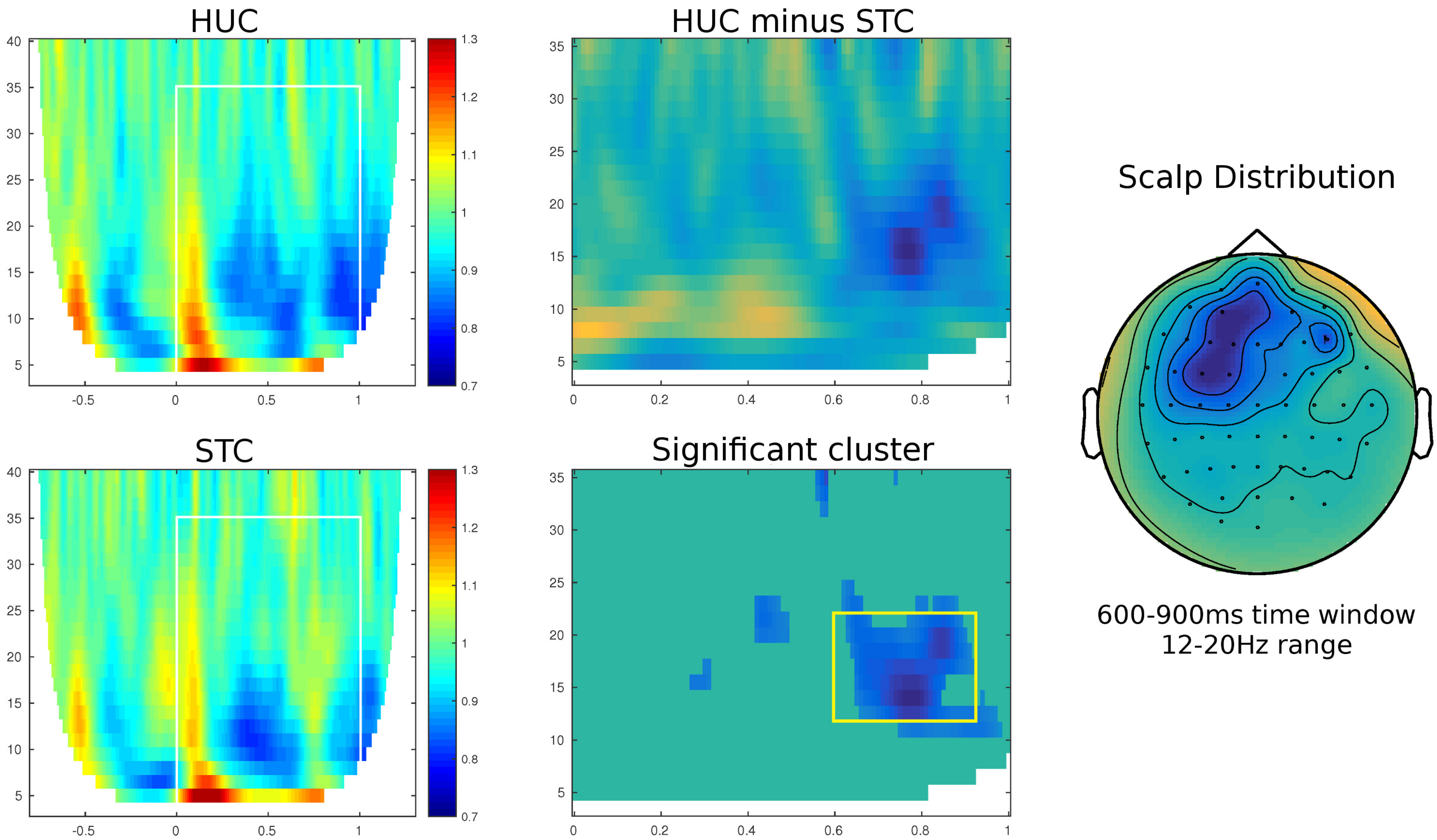
Figure 5. Schematic representation of the EEG correlates of humor comprehension mechanisms. The figure exemplifies the study findings on the temporal development of the EEG response to humor processing, illustrating the complex set of mechanisms at play. The first two lines from the top of the figure display the ERP averages over Left Anterior electrodes (top most line) and Posterior electrodes (second line), while the third line represents the beta power change over Frontal electrodes. The rectangles indicate the three stages involved in humor comprehension, and their relation on the time line (bottom line from 0 to 1100 ms around the presentation of the target word) with the EEG response. The first step of incongruity detection intersects only Left Anterior electrodes in the early time window (see LAN effect of humor). Incongruity resolution, occurring immediately after the first step, intersects the sustained LAN and the P600. The later processes, linked to different cognitive mechanisms depending on the theoretical frame (e.g., elaboration, meta-level analysis, reflexive thought), are reflected in the ERPs in Posterior electrodes and the beta power change. On the bottom line, the time period in which by-participant and by-item predictors affect the ERP response is depicted.

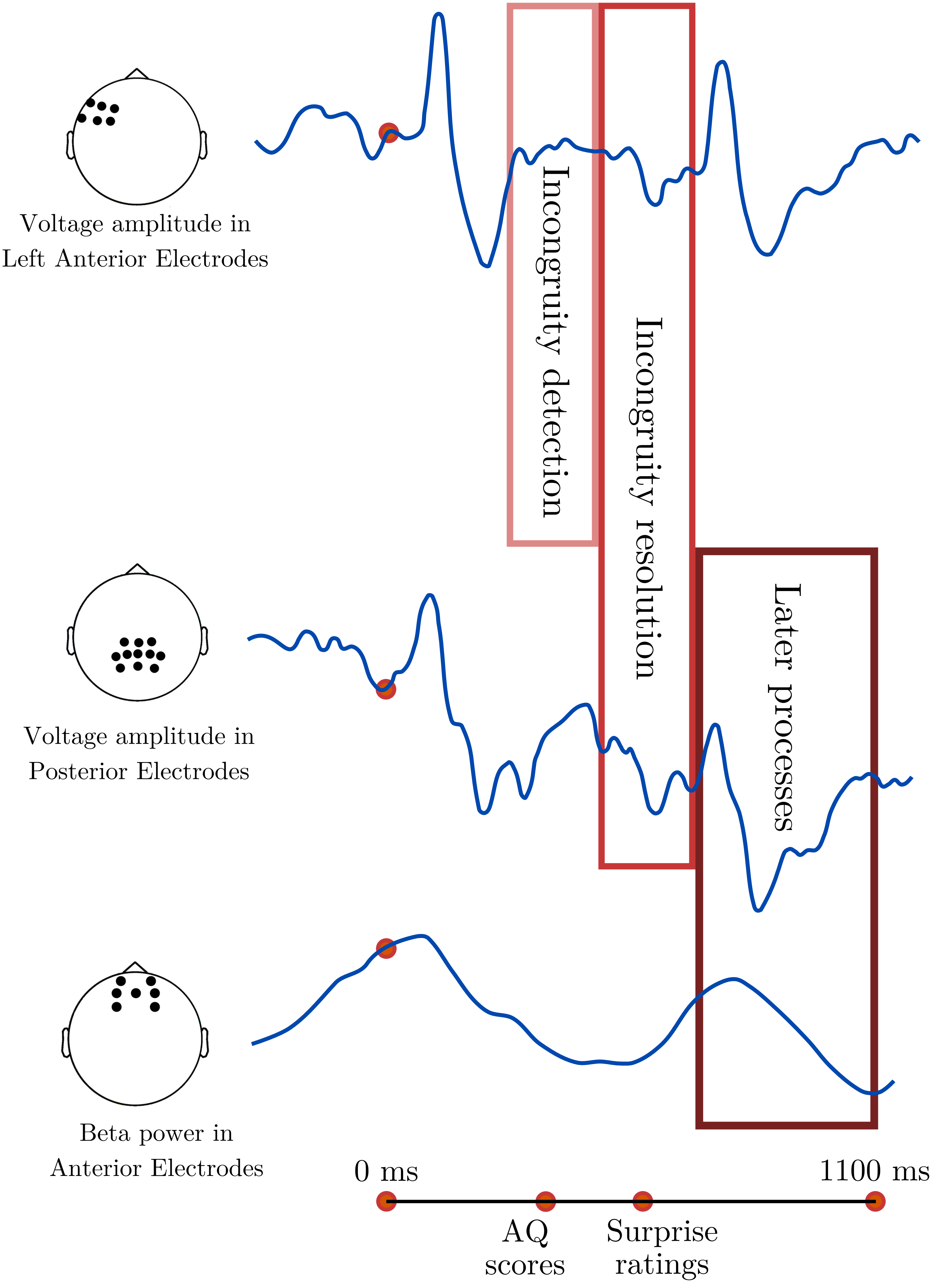

Surprise
Good Continuation
Cloze Probability
Difficulty
Funniness
0.36
0.08
0.11
−0.36
Surprise
−0.25
−0.16
−0.63
Good Continuation
0.05
−0.06
Cloze Probability
0.05


AF3
AF4
VEOG
HEOG
F5
F3
Fz
F4
F6
C3
C1
Cz
C2
C5
P3
CP1
Pz
CP2
P4
PO7
PO8
−4μV
STC
HUC
200 400 600 800 1000
Early Time Window
(300-500ms)
Intermediate Time Window
(500-700ms)
Late Time Window
(700-1100ms)



Difference waves
over Left Anterior sites
HUC minus STC (μV)
time (ms)
LAN
Sustained
LAN
Difference waves
over Posterior sites
P600
LPC
Estimated Amplitude (μV)
HUC
STC
Autism Quotient (z scores)
LAN: AQ by Humor interaction
Surprise (z scores)
P600: Surprise by Humor interaction


HUC
STC
HUC minus STC
Significant cluster
Scalp Distribution
600-900ms time window
12-20Hz range



Voltage amplitude in
Left Anterior Electrodes
Incongruity detection
Incongruity resolution
Later processes
Voltage amplitude in
Posterior Electrodes
Beta power in
Anterior Electrodes
0 ms
1100 ms
AQ
scores
Surprise
ratings