

Contents lists available at ScienceDirect

Journal of Neurolinguistics

journal homepage: www.elsevier.com/locate/ jneuroling



Specialization of neural mechanisms underlying the three-stage model in humor processing: An ERP study



Yen-Ju Feng ^a, Yu-Chen Chan ^b, Hsueh-Chih Chen ^{a,*}

ARTICLE INFO

Article history:
Received 7 July 2014
Received in revised form 29 August 2014
Accepted 29 August 2014
Available online xxx

Keywords: Event-related potentials (ERPs) Humor N400 P600 Late-positive potential (LPP)

ABSTRACT

Most studies of the neural correlates of humor processing have used functional magnetic resonance imaging, but few studies have examined the temporal dynamics of humor processing. The current study examined the temporal dynamics of cortical activation that underlies incongruity detection, resolution and elaboration of humor. Event-related potentials were measured while 31 participants read jokes, non-jokes and nonsensical sentences. The results showed that nonsensical sentences elicited the most negative ERP deflection (N400) between 350 and 500 ms, which possibly reflects incongruity detection in humor. Jokes and non-jokes elicited a more positive deflection (P600) than nonsensical sentences between 500 and 700 ms. which possibly reflects a reanalysis process during incongruity resolution.

Moreover, jokes elicited the most positive slow-wave activity between 800 and 1500 ms, which may be related to emotional processing during elaboration. These results support that N400, P600 and Late Positive Potential (LPP) index the cognitive functions involved in humor processing.

© 2014 Elsevier Ltd. All rights reserved.

^a Department of Educational Psychology and Counseling, National Taiwan Normal University, Taiwan

^b Institute of Learning Sciences, National Tsing Hua University, Taiwan

^{*} Corresponding author. Tel.: +886 223413865. E-mail address: chcjyh@gmail.com (H.-C. Chen).

1. Introduction

Humor plays a critical role in our daily lives because it is a significant component of what makes human lives unique. Cognitive theories of humor are not a new development. The incongruity resolution theory (Suls, 1972), based on false expectation, is one of the most influential theories that attempts to elucidate the basis of humor. Suls' theory suggests that readers make a prediction while reading a text; if there is no conflict with the prediction, the reader will keep reading without any feelings of surprise or enjoyment. However, the reader will feel puzzlement or humor if there is a conflict with the prediction, depending on whether they inferred information that provides a link between the initial body of the joke, cartoon or situation and its ending within the text.

Wyer and Collins (1992) later developed the comprehension and elaboration theory to explain humor processing. According to these authors, comprehension refers to the stage of incongruity detection and resolution of humor, whereas elaboration refers to the subsequent enjoyment that follows humor comprehension. This elaboration involves conscious inferences of features that are not made explicit during comprehension and further thought that is stimulated by the newly understood situation, and this process induces conscious or unconscious feelings of amusement. These elaborations involve effective appraisals of the stimulus event for humorous content.

Currently, most investigations of the neural processes associated with humor have been guided by Suls' incongruity resolution theory (Suls, 1972) or Wyer and Collins' comprehension and elaboration theory (Wyer & Collins, 1992).

Our previous study (Chan, Chou, Chen, & Liang, 2012) successfully differentiated the respective brain areas that correspond to comprehension and elaboration by comparing funny, unfunny, and garden path sentences. Stimuli in the funny condition involved the processes of incongruity detection, incongruity resolution and subsequent elaboration. Stimuli in the garden path condition required the processes of incongruity detection and incongruity resolution but not elicited elaboration. Stimuli in the unfunny condition involved neither humor comprehension (including incongruity detection and resolution) nor elaboration. Consequently, the stage of elaboration can be isolated by subtracting the neural activities elicited by garden paths from activities elicited by funny items. The stage of comprehension can be segregated by subtracting neuronal activities elicited by unfunny items from activities elicited by garden paths.

In addition, Chan et al. (2013) further dissociated the neural circuits underlying incongruity detection and resolution in humor in cooperation with three conditions, including funny, unfunny and nonsensical sentences. Stimuli in the funny condition involved the process of incongruity detection and resolution. Stimuli in the nonsensical condition involved the process of incongruity detection but no resolution because of the irresolvable punch lines. Stimuli in the unfunny conditions contained none of the sub-phrases in humor comprehension. Under a similar rational, the sub-stages within humor comprehension can be differentiated from each other by contrasting these three stimulus types. Our previous functional magnetic imaging (fMRI) studies integrated the previous two-stage models into a three-stage model.

These studies provided important information on the neural circuitry underlying sub-stages of humor processing, but they failed to investigate neural circuitry directly because most of the studies tended to subtract the activity elicited by funny materials from non-funny or other types of material. Additionally, studies utilizing fMRI in the investigation of humor using a three-stage model provide scarce dynamic information due to the limited temporal resolution inherent to fMRI.

Coulson and Kutas's (2001) report is one of the few (event-related potential) ERP studies that investigated humor processing from the perspective of temporal resolution. These authors investigated neural mechanisms underlying the stages of incongruity detection and resolution utilizing one-line jokes, non-jokes and true/false questions that assessed humor comprehension, particularly whether participants understood the jokes. The results of this study demonstrated that individuals who were good at comprehending jokes exhibited significant effects at 350–500 ms (N400) and 500–900 ms compared to the poor comprehension group. A study by Du et al. (2013) also demonstrated that jokes elicited more negative ERP deflections over frontocentral scalp regions than non-jokes at 350–450 ms and 600–800 ms. Additionally, jokes induced more positive deflections over anterior and posterior regions.

Both of these ERP studies significantly contributed to the field of humor processing. However, the other sub-stages of humor, aside from the stage of incongruity detection, are practically indistinguishable from one another. One possible reason may be inadequate control stimuli. Both of the studies mentioned above merely utilized unfunny items as control stimuli when investigating humor processing. Additionally, both studies manipulated experimental material by changing sentence endings (punch lines), which resulted in experimental sentences in joke and non-joke conditions that were identical until the final word of the sentence (e.g., "A man who has lost ninety percent of his brain is called a widower/zombie"; Coulson & Williams, 2005). However, this manipulation makes it difficult to disregard the possibility that the observed differences in neuronal activity could be attributed to the final word of the sentence itself.

Electroencephalography (EEG) was utilized in present study to validate the three-stage model from the perspective of temporal resolution. There were several discrepancies between the current ERP study and previous fMRI studies (Chan et al., 2012, 2013). First, we produced question/answer type statements instead of traditional jokes that were composed of concise punch lines and used them as experimental stimuli in the current work. The major reason for this use is that more concise punch lines allowed fora more accurate time lock of the occurrence of humor. Second, garden path sentences were excluded from the current work because question/answer-type statement punch lines were too short to manipulate into the garden path form.

Punch lines for jokes were matched to their corresponding setups in a surprising but witty way to involve the processes of incongruity detection, incongruity resolution and subsequent elaboration. Punch lines for non-jokes were logically matched to the corresponding setups, and the punch lines for nonsensical sentences were senseless in relation to their corresponding setups. Consequently, non-jokes did not involve either humor comprehension (incongruity detection and resolution) or elaboration. Only the process of incongruity detection was involved in nonsensical sentences. Comparisons of jokes, non-jokes and nonsensical sentences allowed the neural mechanisms underlying incongruity detection, incongruity resolution and the subsequent amusement to be disentangled from one another.

We also hypothesized that the stage of incongruity detection would be reflected in the amplitude of the N400, which is a broadly distributed negativity with an amplitude that is sensitive to semantic violations or an unexpected effect (Coulson & Kutas, 2001; Du et al., 2013). We hypothesized that the amplitude of the N400 elicited by nonsensical sentences would be the strongest during this time interval due to their excessive illogical contexts, followed by jokes, which were accompanied with mild and resolvable incongruity. Non-jokes would elicit the smallest response because these stimuli were composed of extremely logical punch lines.

Furthermore, we expected that the stage of incongruity resolution could be reflected by the P600 measurement because the amplitude represents the process of classification. This component might represent an effort to form an association between setup sentences and punch lines and integrate the violation of expectations that were established by the previous statement and the final outcome in the case of successful resolution. We hypothesized that the P600 amplitudes that were induced by nonsensical sentences during this interval would be weaker than the amplitudes of jokes and non-jokes due to their irresolvable context. Further, no differences between jokes and non-jokes would be observed because both stimuli were comprehensible to some degree.

Finally, we predicted that the amplitude of the Late Positive Activity (LPP), which has been linked to underlying activity in reward-related structures, would reflect the stage of elaboration (Liu, Huang, McGinnis-Deweese, Keil, & Ding, 2012; Sabatinelli, Keil, Frank, & Lang, 2013). We anticipated that the amplitude of the LPP induced by jokes during this time interval would be the strongest due to their distinctive affective components.

2. Methods

2.1. Participants

A total of 31 healthy, right-handed Chinese adults (15 males) between the ages of 20-30 years (mean \pm SD: 21.5 ± 1.7 years) participated in this study. The comprehensibility of jokes exceeded 80%. Participants were recruited by an announcement at a university, and the subjects were paid for their

participation. All participants were free of hearing impairments and neurological and psychiatric diseases, naïve to the experimental procedures, and had normal or corrected-to-normal vision. All participants were required to provide informed consent, received verbal and written instructions of all details of the experiment and were allowed to withdraw at any time. The participants did not expect to obtain any benefit from being in this research study other than the treatment benefit and free investigations/tests. However, each participant received a sum of NT. 500 as compensation for their inconvenience and commute. The local ethical committee approved this research (National Taiwan University, Taipei, Taiwan).

2.2. Experimental design

The present study used a two-factor, within-subject design. Manipulation of stimulus type (jokes, non-jokes, and nonsensical sentences) and electrode positions (Fz, Cz, Pz) served as the independent variables, and the ERP measurement served as the dependent variable.

2.3. Material

Presentation of the setup sentences was performed by a question followed by a corresponding concise answer that served as a punch line to avoid eye movement and precisely time-lock neural activity. First, 90 funny question/answer-type statements were collected to use as jokes in the current study. We manipulated the setup sentences rather than the punch lines to ensure that the neuronal activity we observed was not due to differences in the punch lines. We subsequently produced coherent and non-coherent setups for each joke's punch line to serve as non-jokes or nonsensical sentences in our set of experimental stimuli. Therefore, three types of stimuli were included within one set that shared the same punch line. In addition, we randomly divided the 90 sets of experimental stimuli into three blocks. Each participant observed only one block within each stimulus type, and the same punch line was never observed twice. Therefore, the presentation of experimental stimuli was counterbalanced between subjects. We minimized the influence of semantic associations as much as possible across the three conditions to eliminate the possibility of priming effects. Nevertheless, most of the non-jokes were related to semantic memory.

It is impossible to diminish the level of semantic association for non-jokes to the level of jokes and nonsensical sentences, but we attempted to keep it low. Therefore, the generally low level of semantic association was unlikely to result in lexical priming effects.

Below is an example set of our materials, including each of the three types of stimuli, which serves as a demonstration of the characteristics of each type of stimulus.

Setup sentence for joke:

添義家沒有電話,請猜一句成語?

(Tian yi's household does not have a cable phone; guess the idiom.)

Setup sentence for non-joke:

比喻事情完美無懈可及的成語為?

(Which metaphor describes something that is impeccable?)

Setup sentence for nonsensical sentence:

國際換日線位於哪一個洋之中呢?

(In which ocean is the International Date Line located?)

All of the setup sentences within each set of materials shared the same punch line. The specific punch line for this example was "天衣無縫" (pronunciation: tian yi wufeng; meaning: "without a trace"). For the joke, the punch line is surprising, but it fits in a clever and unexpected way. Participants

found this joke funny because 添義 (Tian yi, a person's name) is pronounced the same as 天衣 (tian yi, celestial clothes impeccable) in Mandarin. Additionally, "沒有" (does not have) in the setup sentences of the joke can be translated into "無" (pronunciation: wu; meaning: "does not have"), and "電話" can be translated into "phone" in English. Therefore, "does not have a cable phone" in the setup sentence of the joke can be abbreviated and translated into "無" phone, which sounds the same as 無縫 (wu feng, "without trace"). For this example set of stimuli, if the participant read the joke ("Tian yi's household does not have a cable phone; guess the idiom."), then he/she would never see the corresponding non-joke ("Which metaphor describes something that is impeccable?") or nonsensical sentence ("In which ocean is the international date line located?").

In total, 90 sets of experimental stimuli were included in the present study, with each set consisting of three types of stimuli: jokes, non-jokes and nonsensical sentences. Therefore, there were 90 pairs of sentences for each stimulus type and a total of 270 pairs of experimental sentences (Table 1).

All of the experimental sentences were rated by a separate group of participants prior to the formal ERP experiment using nine-point Likert scales (Fig. 1). The presentation of experimental stimuli was counterbalanced, and no participant ever observed a punch line more than once. The lengths of the setup sentences were comparable across the three conditions and were constrained to be within 11–14 Chinese characters. Punch lines were also limited to 2–4 Chinese characters. Experimental stimuli were counterbalanced across the subjects, and the order of presentation of each sentence type was randomized.

2.4. Procedure

E-Prime software (Schneider, Eshman, & Zuccolotto, 2012)was used to control the stimulus presentation and timing. The participants were seated approximately 110 cm from the screen during the formal experiment. They were instructed to read experimental sentences and to rate the following factors on a 4-point Likert scale following each sentence: (a) surprise: whether the punch line surprised them after reading the setup sentence (not surprised at all/not surprised/surprised/extremely surprised); (b) comprehensibility: how well they understood the meaning of the punch line in relation to the corresponding setup (did not comprehend at all/did not comprehend/comprehended extremely well); and (c) funniness: their thoughts on the funniness of the punch line (not at all funny/not funny/funny/extremely funny; Fig. 2). Each experimental trial began with the presentation of a central fixation mark (duration = 1000 ms) to orient the participant to the center of the screen. Next, a setup sentence was presented (duration = 4000 ms), followed by a punch line (duration = 2000 ms). A fixation mark (duration = 4000 ms) also appeared between the setup and the punch line to avoid eye movement artifacts elicited by reading. All stimuli were presented centrally and subtended a horizontal visual angle varied between 1.8 and 3.1°.

2.5. EEG acquisition

Electroencephalogram (EEG) data were continuously recorded from 32 scalp electrodes that were mounted on an elastic cap in accordance with a modified 10-20 system with two additional mastoid electrodes. All electrodes were online referenced to the average of the left and right mastoids. Eye blinks and vertical eye movements were monitored using electrodes located above and below the left eye. Horizontal electro-oculogram (EOG) data were recorded from four electrodes placed above and below the right eye, 1.5 cm lateral to the external canthi. A ground electrode was placed on the fore-head. A continuous EEG signal was amplified with a bandpass from 0.05 to 70 Hz using a SynAmps2 (Neuroscan, Inc.) amplifier and digitized at a sampling rate of 500 Hz. The electrode/skin impedance was maintained <5 k Ω during recording.

2.6. Data analysis

EEG data were processed and analyzed offline using Scan 4.4 software (Compumedics Ltd., Australia). EEG data were corrected for blinks using the ocular artifact reduction algorithm (ARTCOR) implemented in Scan 4.4 (Compumedics Neuroscan, 2003). ERP waveforms were time-locked to the

Table 1The exemplar and relevant connotations of experimental stimuli.

	Setup sentences	Punch line	Connotation		
Joke	一個人全身塗成金色,猜一成語? (A person being painted in gold, guess an idiom?)	一鳴驚人 (amaze the world with a single brilliant feat)	一名金人 和一鳴「驚人」同音 「yi ming jing ren」 (amaze the world with a single brilliant feat), i		
Non-joke	指平凡的人突有傑出表現的成語? (Which idiom refers to an ordinary person suddenly having an outstanding performance?)		pronounced similar as 「yi ming jii ren」 (one gold person)		
Nonsensical	植樹節在紀念歷史上的哪位人物? (Who is being honored at Tree Planting Day?)				
Joke	一隻獅子中兩槍才會死,猜一詞? (A lion will only die when shot twice, guess an idiom?)	一屍兩命 (One corpse two life)	一屍兩命和一「獅」「兩命」(所以 需要中兩槍)同音 「yi shi liang ming」is pronounced similar as 「yi」(one)「shi」(lion」 「liang ming」(two lives), therefore needed to be shot twice.		
Non-joke	指孕婦死亡,胎兒連帶死亡的詞? (Which idiom refers to a fetus's death being associated with a pregnant woman's death?)				
Nonsensical	為什麼天上月亮會一直跟著我們? (Why is the moon following us?)				
Joke	移動建國中學的鋼琴,猜一成語? (Moving Municipal Jianguo High School's piano, guess an idiom?)	一見鍾情 (Love at first sight)	建國中學簡稱建中,「移」動「建 中」的「琴」和一見鍾情四字同音 Jianguo High School is also referre		
Non-joke	形容男女只見一面即相戀的成語? (Which idiom describes woman and man falling in love when met for first time?) 皮膚新陳代謝差的話容易長什麼?		as Jianzhong, 「yi」 (moving) 「Jianzhong」's 「qing」 (piano) pronounced similar as 「yi jian zhong qing」 (love at first sight).		
Nonsensical	皮膚新陳代謝差的話谷易長什麼? (What would easily appear when your metabolism is pretty low.)				
Joke	糟老頭子打哈欠,請猜一句成語? (Old man yawning, guess an idiom?)	一望無涯 (stretching beyond the horizon)	老人打哈欠,旁人 (看過去)一望無 牙;和一望無涯同音 As the old man yawns, no tooth ca		
Non-joke	用來比喻視野非常遼闊的成語為? (Which metaphoric idiom describes wide horizons?)		be seen 「yi wang wu ya」, is pronounced similar as 「yi wang wu ya」 (strethching beyond the		
Nonsensical	電視新聞中播報氣象的人被稱為? (The weather forecaster in the news is often described as?)		horizon).		
Joke	藍色的刀槍,猜一句成語? (Blue swords and spares, guess an idiom?)	刀槍不入 (neither swords nor spears can enter — impervious to swords and spears)	刀槍不入的「不入」和blue同音 「dao qiang bu ru (impervious to swords and spears) 」's 「bu ru」		
Non-joke	形容人武功高強的成語為? (Which idiom describes people with extensive material arts?)	. ,	sounds similar as blue.		
Nonsensical	遇到緊急事件發生時需要? (What is needed when emergency happens?)				

onset of the punch line. The averaged ERP epoch was 2000 ms and included a 100-ms pre-solution baseline. All epochs were band-pass filtered in the range of 0.1–30 Hz using digital, zero-phrase shift filtering. Trials with EOG artifacts (EOG voltage change exceeding $\pm 100~\mu V$) and trials contaminated with artifacts due to amplifier clipping, bursts of electromyography activity, or peak-to-peak deflection exceeding $\pm 100~\mu V$ were excluded from averaging.

Three time windows were statistically compared to dissociate stages of incongruity, resolution and emotional processing during humor processing: 350–500 ms (incongruity detection), 500–700 ms (incongruence resolution) and 800–1500 ms (affective processing). ERP effects were assessed for each time interval by performing repeated-measure analysis of variance (ANOVA) (Greenhouse & Geisser,

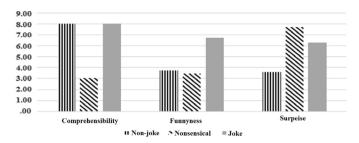


Fig. 1. In the rating of comprehensibility, nonsensical sentences scored the lowest. In the rating of funniness, jokes scored the highest. In the rating of surprise, nonsensical scored the highest then did jokes and non-jokes scored the lowest.

1959) on the three midline electrode sites (Fz, Cz and Pz). Stimulus type (jokes, non-jokes and nonsensical sentences) served as the within-subject factors, which resulted in a 3 (stimulus type) \times 3 (midline site) repeated-measures ANOVA. Pairwise post-hoc follow-up analyses with LSD corrections were applied to all ANOVAs to examine exact differences between stimulus types. Greenhouse—Geisser corrections were applied to ANOVAs as necessary. An alpha level of 0.05 was used for all statistical tests.

3. Results

3.1. Behavioral results

The mean response times (RTs) and rating scores (RESPs) are shown in Tables 2 and 3. Repeated-measures ANOVAs were performed on RTs and RESPs for the three types of stimuli (joke, non-joke and nonsensical).

Mean reaction times for different types of stimuli did not differ from one another (Table 2). However, rating scores showed significant differences for surprise $[F(2,90)=197.42,\ p<.01,\ \eta_p^2=0.72]$, comprehension $[F(2,90)=342.53,\ p<.01,\ \eta_p^2=0.93]$ and funniness $[F(2,90)=73.08,\ p<.01,\ \eta_p^2=0.76;$ Table 3]. Nonsensical sentences had the highest surprise scores among the three types of stimuli, followed by jokes and non-jokes, which is consistent with our expectations. Comprehension scores for the jokes and the non-jokes were comparable, and the nonsensical sentences scored the lowest. The jokes scored higher on funniness than the other two stimulus types, and scores for the non-jokes were not different from those for the nonsensical sentences.

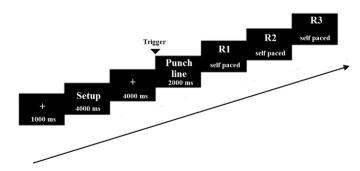


Fig. 2. Experimental procedure. ERP recording was time locked to the onset of punch lines. After each experimental trial, participants were instructed to rate on a 4-point Likert scale (R1) surprise: whether the punch line surprised them after reading the setup sentence (not surprised at all/not surprised/surprised/extremely surprised) (R2) comprehensibility: how well they understood the punch line's meaning in relation to the corresponding setup (did not comprehend at all/did not comprehend/comprehended/comprehended extremely well), and (R3) funniness: how funny they thought the punch line was (not at all funny/not funny/funny/extremely funny).

Table 2The mean and standard deviation of reaction-time (RT).

RT	Joke		Non-joke		Nonsensical		F-value
	Mean	SD	Mean	SD	Mean	SD	
Surprise	1242.16	252.20	1178.26	337.08	1330.04	330.59	0.16
Comprehensibility	1063.70	212.10	1051.86	240.48	1021.54	211.80	0.74
Funniness	1003.25	290.74	1016.17	258.98	932.37	217.92	0.39

3.2. ERP results

All stimuli elicited P1/N1/P2 and N400 components, which are typical of ERPs to visually presented words. ERPs during the latter part of the epochs were characterized by two positive-going waves (500–700 and 800–1500 ms post-stimulus). No effects were apparent on the P1/N1/P2 complex waveforms. Analysis results of ERPs that were measured in the interval of the N400 component (350–500 ms post-onset) and the interval of the late positivity components (500–700 and 800–1500 ms post-onset).

3.2.1. 350-500 ms

Analysis of this time window was intended to capture the N400 component, which is a broadly distributed negativity with an amplitude that is sensitive to the difficulty of lexical integration. Statistical analysis of the 350–500 ms time window revealed main effects of stimulus type [F(2, 60) = 18.07, p < .001, $\eta_p^2 = 0.38$] and midline site [F(2, 60) = 6.02, p = .004, $\eta_p^2 = 0.17$]. There was no interaction between these two variables [F(4, 120) = 2.21, p = .072, $\eta_p^2 = 0.07$]. In general, analysis of the 350–500 ms time window revealed that the nonsensical sentences (mean = 5.62; SD = 5.61) elicited a more negative deflection than the jokes (mean = 9.17; SD = 5.14) and the non-joke sentences (mean = 10.58; SD = 4.21; Fig. 4). Moreover, the jokes also elicited a stronger N400 amplitude than the non-jokes (p = .036). The observed N400 effects elicited at Fz (mean = 7.78; SD = 0.75) and Cz (mean = 8.21; SD = 0.66) for the main effect of midline site were larger than Pz (mean = 9.40; SD = 0.65).

3.2.2. 500-700 ms

Statistical analyses of the 500–700 ms time window revealed an interaction between stimulus type and midline site $[F(4, 120) = 5.50, p < .001, \eta_p^2 = 0.16]$. Additionally, there were main effects of stimulus type $[F(2, 60) = 12.38, p < .001, \eta_p^2 = 0.29]$ and midline site $[F(2, 60) = 16.39, p < .001, \eta_p^2 = 0.35]$. Follow-up simple main effects analyses revealed that the amplitudes of the P600 elicited by nonsensical sentences at both Fz and Cz (Fz: mean = 5.15; SD = 5.47; Cz: mean = 6.32; SD = 5.85) were smaller than amplitudes elicited by jokes (Fz: mean = 9.62; SD = 5.08; Cz: mean = 11.05; SD = 5.19) and non-jokes (Fz: mean = 8.55; SD = 3.81; Cz: mean = 10.96; SD = 4.23) (Fig. 3).

3.2.3. 800-1500 ms

Statistical analyses of the late time window between 800 and 1500 ms revealed main effects of stimulus type $[F(2, 60) = 5.17, p = .009, \eta_p^2 = 0.15]$ and midline site $[F(2, 60) = 6.70, p = .002, \eta_p^2 = 0.18]$. There was no interaction between these two factors $[F(4,120) = 2.01, p = .098, \eta_p^2 = 0.06]$. Generally, the

Table 3The mean, standard deviation and relevant statistical results of rating score.

Rating score	Joke		Non-joke		Nonsensical		F-value	Post-hoc	
	Mean	SD	Mean	SD	Mean	SD			
Surprise	2.58	0.37	1.73	0.24	3.41	0.38	197.42	Nonsensical > joke > non-joke	
Comprehensibility	3.27	0.39	3.43	0.32	1.48	0.32	342.53	Joke, non-joke > nonsensical	
Funniness	2.58	0.34	1.79	0.34	1.66	0.29	73.08	Joke > non-joke, nonsensical	

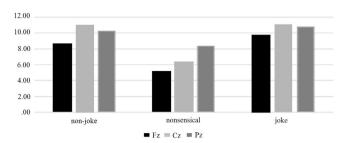


Fig. 3. Follow-up analysis revealed that the amplitudes of P600 elicited by nonsensical sentences were smaller than jokes and non-jokes did significantly over Fz, Cz and Pz. Voltage scale from 0 to $+12 \mu V$.

800-1500 ms waveform elicited by the jokes (mean = 6.34; SD = 3.92) had a higher amplitude than the waveform elicited by the non-jokes (mean = 4.47; SD = 3.96; p = .001) and the nonsensical sentences (mean = 4.36; SD = 4.24; p = .008). The observed LPP effects elicited at Cz (mean = 5.53; SD = 0.62) and Pz (mean = 5.29; SD = 0.51) for the main effect of midline site were larger than the amplitude elicited at Fz (mean = 4.35; SD = 0.56).

4. Discussion

Our previous studies utilized event-related fMRI to elucidate the neural basis of humor processing and identified different brain regions that are associated with the stages of incongruity detection, resolution and elaboration, which resulted in a proposed three-stage model of humor processing (Chan et al., 2012, 2013). In contrast, the current study used EEG to probe the temporal dynamics of substages of humor processing (i.e., incongruity and resolution, and the feeling of enjoyment following the comprehension of humor) in a design that incorporated three conditions (jokes, non-jokes, and nonsensical sentences).

4.1. Incongruity detection — the role of N400

The nonsensical sentences generally produced the strongest activity at the early time window ranging from 350 to 500 ms in the present study. Moreover, the jokes also elicited more extensive neural activity than the non-jokes during this time window. These results are consistent with our hypothesis and may reflect the N400 component, which is an endogenous event-related brain potential that is sensitive to semantic processing during language comprehension.

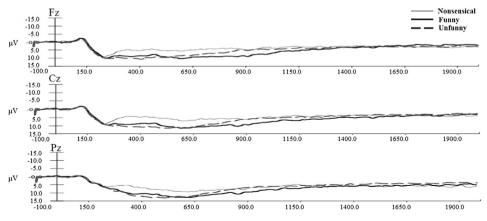


Fig. 4. Representative of Fz, Cz and Pz. Voltage scale from -15.0 to +15.0 μ V. Time scales in milliseconds. In comparison with non-jokes, jokes elicited stronger N400 and LPP effects in the 350-500 ms and 800-1500 ms time window respectively.

We examined the associative semantic closeness between sentence stems and punch lines across funny and unfunny conditions to assess priming influences on the N400 attenuation observed here. In the funny category, 53.3% of the punch lines contained either a synonym (e.g., 世上哪種水果的視力最差?芒果。 "What fruit has the worst eyesight? Mango.") or direct repetition (e.g., 死刑犯坐在椅上等槍決,猜成語?坐以待斃。"A death row prisoner sits on a chair awaiting execution by gunfire. Guess a phrase. To sit and wait for death."), and 51.1% of the punch lines in the unfunny category contained these relationships (e.g., 製成芒果冰沙的主要成份?芒果。 "The main ingratiate for making Mango slushy is? Mango."). Therefore, both the funny and unfunny conditions contained roughly equal numbers of endings with close semantic association: 53.3% in the funny sentences and 51.1% in unfunny sentences. Therefore, the neuronal attenuation of N400 that we observed between the funny and unfunny sentences did not result of the priming effect but the incongruity detection process.

Accordingly, we suggest that the N400 may play a pivotal role in the detection of incongruity from the perspective of an updated semantic expectation view, which suggests that the amplitude of the N400 reflects semantic integration and an updating of semantic expectations (as in associative relationships), which is used to improve future lexical access. An incongruent semantic context results in the need for greater updating and a larger N400 (Franklin, Diena, Neely, Huber, & Waterson, 2007). Also, Li, Shu, Liu, and Li (2006) suggested that the amplitudes of N400 can served as a function of how well the verb argument is congruent with the preceding verb. This explanation is consistent with the results of the current study. Suls (1972) argued that humor perception critically depends on resolving incongruities between punch lines and expectations that are shaped by the setup sentences. Therefore, the process of incongruity detection might interact with semantic expectations. Du et al. (2013) reported that funny items elicited a more negative deflection between 350 and 400 ms than non-funny items. These authors suggested that the N400 amplitude might reflect the registration of surprise, which is a fundamental element in the detection of incongruity. Consistent with this previous study, jokes also evoked a larger brain response than non-jokes in the current study.

4.2. Resolution of the incongruity — the role of P600

Neural activity subsequent to the N400 attracted attention related to cognitive mechanisms. Our results demonstrated that jokes and non-jokes elicited a more positive ERP deflection than nonsensical sentences between 500 and 700 ms at Cz and Pz. We postulated that this positivity was potentially analogous to the P600. P600, which is sometimes called LPC, was associated with task classification (Palmer, Nasman, & Wilson, 1994). Tu et al. (2014) contrasted humorous, non-humorous and unrelated cartoon pictures in cooperation with ERPs and demonstrated that both humorous and non-humorous items elicited a more positive ERP deflection than unrelated items between 800 and 1000 ms at central and anterior electrode sites. They suggested that this positivity might reflect a classification process of preliminary evaluation to establish whether there are attainable cues in the pictures to form possible associations between contexts and pictures (association evaluation) before comprehending the relationship in detail.

Therefore, the present study also suggested that this positivity might act as a function of classification when participants tried to obtain any attainable cues in setup sentences to form a possible resolution to the punch lines. It was too difficult for the participants to obtain any cues in nonsensical sentences to form associations between setup sentences and the corresponding punch lines. Therefore, participants had to pay more attention to affirm whether there were any possibilities to form associations. In addition, previous studies (Kok, 1997; Polich, 2007) showed that the smaller amplitude for nonsensical sentences might reflect that greater attention resources were employed. Therefore, it is not surprising that the nonsensical sentences with absolutely illogical and incorrect contexts elicited the weakest P600 effects, as we had predicted. Also, the P600 that was elicited by the jokes did not differ from the P600 elicited by the non-jokes, which is consistent with our expectations.

4.3. Amusement − *the role of LPP*

A broad positive potential elicited by the jokes peaked over centroparietal brain areas later in the processing stream (after approximately 800 ms). We speculate that this peak may reflect the LPP,

which is modulated by emotional relevance (Liu et al., 2012; Sabatinelli et al., 2013). A more positive ERP wave in humor studies was elicited by funny items than unfunny items within broad latency windows (Du et al., 2013; Gierych, Milner, & Michalski, 2005; Tu et al., 2014), which was correlated with emotional arousal. Consequently, it is reasonable to postulate that the significant difference between the jokes and the non-jokes/nonsensical sentences from 800 to 1500 ms might reflect the feeling of amusement in humorous appreciation.

In summary, the jokes elicited a more negative deflection between 350 and 500 ms (N400) at Fz and Cz compared to the non-jokes, and this deflection may be involved in the detection of incongruence during humor comprehension. The jokes and the non-jokes sentences elicited larger positive deflections than nonsensical sentences at Fz and Cz between 500 and 700 ms. There were no significant differences between the jokes and the non-jokes, consistent with our expectation because the jokes and the non-jokes were comprehensible to some degree. Finally, the jokes evoked a stronger LPP (800–1500 ms) than the other two types of sentences at Cz and Pz, which may reflect the affective processing of humor appreciation.

Our findings support the sequential humor model, and affirmed how the three sub-stages of humor process are differentiated from each other in cooperation with the additional nonsensical sentences. Although Du et al.'s (2013) research suggested the existence of the three-stage model by revealing several ERPs differences between jokes and non-jokes, it failed to establish the rational link between each component and each specific cognitive function in humor. One possible reason may be inadequate control stimuli. Therefore, we adopted our experimental stimuli by producing additional nonsensical sentences. Additionally, the punch lines in the current study were much shorter than those in previous research. Consequently, we time-locked the occurrence of humor more precisely. Finally, the present study was the first work to utilize paired experimental sentences to investigate the humor process.

However, there are several limitations and suspicions that should be considered before definitive conclusions are drawn. First, the current work is not able to elucidate the source of each specific ERP component. Our previous results (Chan et al., 2012, 2013) precisely labeled the relevant brain areas in humor processing, but we still need other methodologies to localize the sources of each component during humor processing. Additionally, we ensured that at least 80% of our jokes were comprehensible to all the participants, but we cannot negate the possibility of individual differences in joke processing. One reasonable resolution might be a division of the data into two extreme sets (e.g., point 1 vs. point 4) to examine how the ERPs may be varied accordingly. However, most of our participants tended to answer conservatively and seldom participants exhibited extreme responses. Regardless of the rating criteria used (e.g., surprise, comprehension, funniness), it is hard to split the data into two sets and examine the ERP effect in the current work. Therefore, we may broaden our experimental material and refine our experimental paradigm to eliminate the relevant suspicions in investigations of humor. In future studies, methodological refinement, careful experimental design and the creation of peculiar humorous stimuli are required to further unravel the meaning of the biomarker of humor processing.

Acknowledgments

We wish to thank the Ministry of Science and Technology for funding this project via the following grants: Specialization of Neural Mechanisms Underlying the Three-stage model in Humor Processing: An ERP study (MOST 103-2420-H-003 -005 -MY3). The work was also supported by the Ministry of Education, Taiwan, under the Aiming for the Top University Plan at National Taiwan Normal University. Finally, we would like to thank the International Research Intensive Center of Excellence of National Taiwan Normal University and the National Science Council, Taiwan, R.O.C. for their support (NSC102-2911-I-003-301).

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jneuroling. 2014.08.007.

References

- Chan, Y. C., Chou, T. L., Chen, H. C., & Liang, K. C. (2012). Segregating the comprehension and elaboration processing of verbal jokes: an fMRI study. *Neuroimage*, 61(4), 899–906. http://dx.doi.org/10.1016/j.neuroimage.2012.03.052.
- Chan, Y. C., Chou, T. L., Chen, H. C., Yeh, Y. C., Lavallee, J. P., Liang, K. C., et al. (2013). Towards a neural circuit model of verbal humor processing: an fMRI study of the neural substrates of incongruity detection and resolution. *NeuroImage*, 66, 169–176. http://dx.doi.org/10.1016/j.neuroimage.2012.10.019.
- Compumedics Neuroscan. (2003). Offline analysis of acquired data (SCAN 4.3—Vol. II, EDIT 4.3) [Software manual]. El Paso, TX. Coulson, S., & Kutas, M. (2001). Getting it: human event-related brain response to jokes in good and poor comprehenders. Neuroscience Letters, 316(2), 71–74. http://dx.doi.org/10.1016/S0304-3940(01)02387-4.
- Coulson, S., & Williams, R. F. (2005). Hemispheric asymmetries and joke comprehension. *Neuropsychologia*, 43, 128–141. http://dx.doi.org/10.1016/j.neuropsychologia.2004.03.015.
- Du, X., Qin, Y., Tu, S., Yin, H., Wang, T., Yu, C., et al. (2013). Differentiation of stages in joke comprehension: evidence from an ERP study. *International Journal of Psychology*, 48(2), 149–157. http://dx.doi.org/10.1080/00207594.2012.665162.
- Franklin, M. S., Diena, J., Neely, J. H., Huber, E., & Waterson, L. D. (2007). Semantic priming modulates the N400, N300, and N400RP. Clinical Neurophysiology, 118(5), 1053–1068. http://dx.doi.org/10.1016/j.clinph.2007.01.012.
- Gierych, E., Milner, R., & Michalski, A. (2005). ERP responses to smile-provoking pictures. *Journal of Psychophysiology*, 19(2), 77–90. http://dx.doi.org/10.1027/0269-8803.19.2.77.
- Greenhouse, S. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, 24, 95–112. http://dx.doi.org/10.1007/BF02289823.
- Kok, A. (1997). Event-related-potential (ERP) reflections of mental resources: a review and synthesis. *Biological Psychology*, 45(1), 19–56. http://dx.doi.org/10.1016/S0301-0511(96)05221-0.
- Li, X., Shu, H., Liu, Y. Y., & Li, P. (2006). Mental representation of verb meanings: behavioral and electrophysiological evidence. *Journal of Cognitive Neuroscience*, 18, 1774–1787. 10.1162/jocn.2006.18.10.1774.
- Liu, Y. L., Huang, H. Q., McGinnis-Deweese, M., Keil, A., & Ding, M. Z. (2012). Neural substrate of the late positive potential in emotional processing. *The Journal of Neuroscience*, 32(42), 14563–14572. http://dx.doi.org/10.1523/JNEUROSCI.3109-12. 2012.
- Palmer, B., Nasman, V. T., & Wilson, G. F. (1994). Task decision difficulty: effects on ERPs in a same-different letter classification task. *Biological Psychology*, 38(2), 199–214. http://dx.doi.org/10.1016/0301-0511(94)90039-6.
- Polich, J. (2007). Updating P300: an integrative theory of P3a and P3b. Clinical Neurophysiology, 118(10), 2128–2148. http://dx.doi.org/10.1016/j.clinph.2007.04.019.
- Sabatinelli, D., Keil, A., Frank, D. W., & Lang, P. J. (2013). Emotional perception: correspondence of early and late event-related potentials with cortical and subcortical functional MRI. *Biological Psychology*, 92(3), 513–519. http://dx.doi.org/10.1016/j.biopsycho.2012.04.005.
- Schneider, W., Eshman, A., & Zuccolotto, A. (2012). E-Prime: a reference guide. Retrieved from http://psy.swan.ac.uk/staff/lucignoli/E-Prime/ReferenceGuideV2_2012.pdf.
- Suls, J. M. (1972). A two-stage model for the appreciation of jokes and cartoons. In P. E. Goldstein, & J. H. McGhee (Eds.), The psychology of humour. Theoretical perspectives and empirical issues (pp. 81–100). New York: Academic Press.
- Tu, S., Cao, X. J., Yun, X. J., Wang, K. C., Zhao, G., & Qiu, J. (2014). A new association evaluation stage in cartoon apprehension: evidence from an ERP study. *Journal of Behavioral and Brain Science*, 4, 75–83. http://dx.doi.org/10.4236/jbbs.2014.42010. Wyer, R. S., Jr., & Collins, J. E., 2nd (1992). A theory of humor elicitation. *Psychological Review*, 99(4), 663–688. http://dx.doi.org/10.1037/0033-295X.99.4.663.