Research paper

Pre-stimulus EEG oscillations correlate with perceptual alternation of speech forms

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HIGHLIGHTS

- Pre-stimulus brain dynamics influence the perceptual organization of speech.
- Reduced ongoing alpha activity precedes subsequent change of verbal form.
- Induced beta oscillations supports fast stabilization of the new verbal form.
- Right frontal positivity and posterior negativity evoked by change of verbal form.

ARTICLE INFO

ABSTRACT

Speech perception is often seen as a passive process guided by physical stimulus properties. However, ongoing brain dynamics could influence the subsequent perceptual organization of the speech, to an as yet unknown extent. To elucidate this issue, we analyzed EEG oscillatory activity before and immediately after the repetitive auditory presentation of words inducing the so-called verbal transformation effect (VTE), or spontaneous alternation of meanings due to its rapid repetition. Subjects indicated whether the meaning of the bistable word changed or not. For the Reversal more than for the Stable condition, results show a pre-stimulus local alpha desynchronization (300–50 ms), followed by an early post-stimulus increase of local beta synchrony (0–80 ms), and then a late increase and decrease of local alpha (200–340 ms) and beta (360–440 ms) synchrony respectively. Additionally, the ERPs showed that reversal positivity (RP) and reversal negativity components (RN), along with a late positivity complex (LPC) correlate with switching between verbal forms. Our results show how the ongoing dynamics brain is actively involved in the perceptual organization of the speech, destabilizing verbal perceptual states, and facilitating the perceptual regrouping of the elements composing the linguistic auditory stimulus.

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1. Introduction

Traditionally, speech perception has been seen as a passive process involving transformation of sensorial speech signals onto language forms [1]. According with this notion the speech perception would be determined by physical stimulus properties. However, it has been proposed [2] that the brain does not seem to be a passive processor of information, but rather a complex self-organizing dynamic system, from which emerges the conscious perception in a creative way [3]. Regarding this last point, there is evidence showing how ongoing brain activity may influence the manner in which the incoming simple sensory stimulus will be processed [4]. Nevertheless, whether complex processes as the perceptual organization of speech can be modulated by ongoing brain activity, is still unknown.

Studies exploring how conscious speech perception is organized, often analyze the brain activity during the so-called verbal transformation effect (VTE). VTE is a phenomenon occurring when words are repeated over and over again without pause, causing an abrupt change in verbal organization manifested through transitions between meanings within the same word [5]. For instance, rapid repetitions of the word 'life' result in bistable alternation between the perceived words 'life' and 'fly'. Because different meanings of the same word alternate spontaneously, VTE pro-

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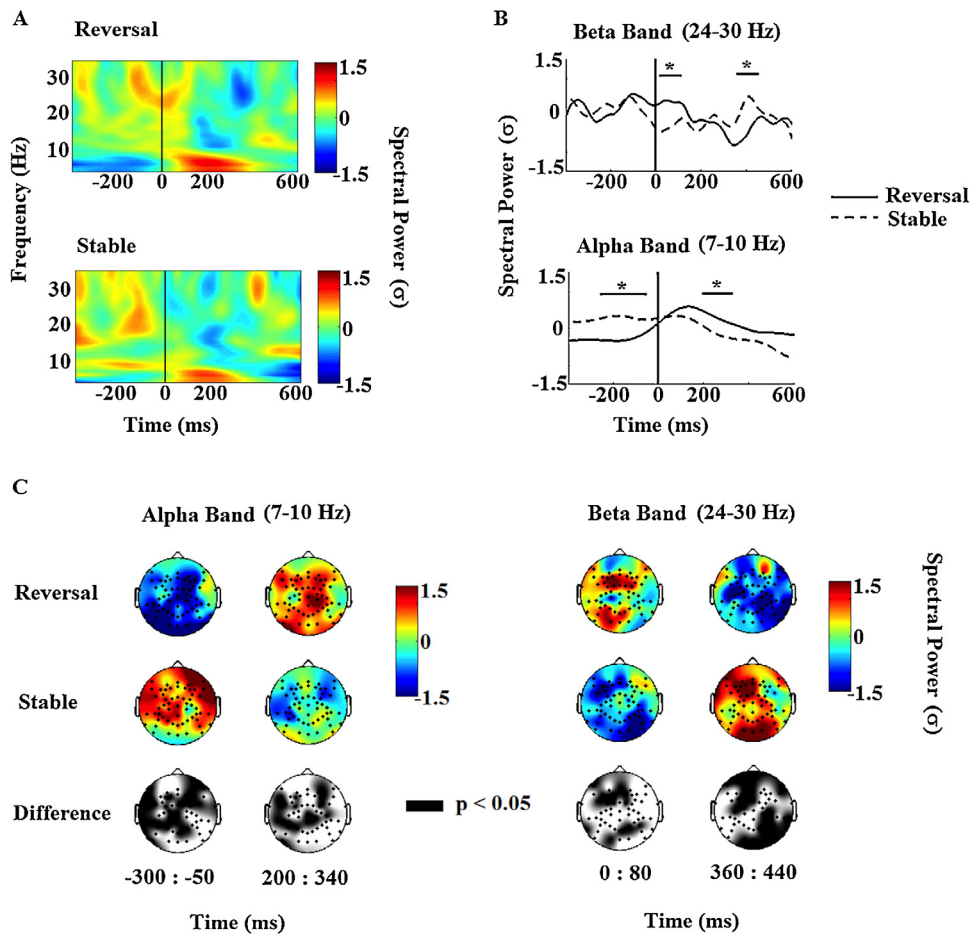[1] These authors contributed equally to this work.

Fig. 1. Spectral power charts, contrast between conditions, and its topographic distribution. (A) The time-frequency plot shows the grand average of all electrodes. Frequency range and time are respectively indicated in the y and x-axis of the maps. Color bars at the right side of the maps show amplitude values (in standard deviation units). Black vertical lines indicate the bistable word onset. Reversal and Stable conditions are indicated at the top of the each map. (B) Contrasts between conditions in alpha and beta bands. Solid lines and segmented lines represent the Reversal and Stable conditions, respectively. Mean phase-locking value (in standard deviation units) between all electrodes pairs and time are respectively indicated in the y and x axes of the graphs. Black vertical lines indicate the bistable word onset. The asterisks delimit time windows showing significant differences between conditions (p < 0.05 FDR corrected). (C) Topographic distribution of the alpha and beta spectral power. Top and middle rows represent the Reversal and Stable conditions, respectively. Color bars at the right side of the heads show amplitude values (in standard deviation units). Bottom row represent the statistical difference between conditions. Black regions over the heads displaying significant difference of local alpha and beta activity (*p* < 0.05, FDR corrected) averaged in the time windows identified in B.

vides an interesting way to study the neural processes underlying endogenously driven conscious speech perception. A recent neuroimaging study [6] showed that dorsal anterior cingulate cortex and inferior frontal regions play an important role in the organization of verbal forms during VTE. In addition, an intra-cortical EEG study [7] shown an increase of high frequency activity in the gamma band range (>40 Hz) within the left inferior frontal and left supramarginal gyrus, from 300 ms to 800 ms prior to the report of a change in perceived linguistic form.

Although these results provide detailed information about the brain regions and electrophysiological activity linked with the moment when a subject experiences the reversal of a linguistic form, both are not very informative about whether ongoing oscillatory activity before the onset of the bistable word influences the subsequent perceptual organization of the speech. To elucidate this issue, we analyze the local brain synchrony [8], or amplitude variations in EEG oscillatory activity before and immediately after the onset of a bistable word.

Based on previous reports suggesting that ongoing alpha [9] and beta spectral power [10] play an active role in the construction of simple and multimodal percepts respectively, and considering that oscillatory beta activity also has been linked with several linguistic process [11,12], we hypothesized that speech perception is

modulated by the pre and post-stimulus EEG activity in these frequencies bands. Specifically, we expect a decrease of pre-stimulus alpha oscillatory activity, and an early increase of beta local synchrony after the stimulus onset, only in those trials where a change in speech form would be reported. To test this hypothesis, we recorded EEG signals in subjects engaged in a verbal bistable task. In order to explore whether ongoing oscillatory EEG activity can anticipate the perceptual organization of speech, we used a paradigm similar to the one introduced by Kornmeier and Bach [13] where bistable stimuli are presented intermittently and the subjects were asked to indicate perceptual reversals by means of a button press after the stimulus. As an indicator of ongoing local brain synchrony, we computed spectral power [8]. Additionally, we analyze ERPs for comparison with previous results [14,15].

2. Methods

2.1. Subjects

Twenty-two subjects participated in an EEG experiment. Seven subjects were excluded from further analysis because more than 95 percent of their responses indicated only one of the two perceptual states (Reversal or Stable), or presented less than 20%

of artifact-free EEG trials per condition (total trials = 150; mean artifact-free trials: Reversal = 61.87, Stable = 69.40). The data from the other fifteen subjects (8 male, age range: 19–48 years, mean age = 26.40 years) were analyzed. All were native Spanish speakers, right-handed, with normal hearing and normal or corrected to normal vision and no history of neurological and/or psychiatric illness. All participants gave written informed consent as approved by the Ethical Committee of the Psychology School of the Pontifical Catholic University of Chile.

2.2. Stimuli

We used three Spanish bistable words for inducing the VTE. The words used were "carro" (car), "sapo" (frog) and "mago" (magician). When are presented repeatedly they can also be perceived as "roca" (stone), "poza" (pond) and "goma" (rubber) respectively. The meanings of bistable words were matched in several lexical variables (see Supplementary Table S1 for mean values of relevant lexical variables) using EsPal corpus [16]. To obtain a more reliable reference time for averaging EEG trials where perceptual reversal is observed, the bistable words was presented in different experimental blocks in an intermittent manner (see Ref. [13] for other advantages of the intermittent paradigm). We use three bistable words in different blocks to reduce the monotony of the task and thus maintain the subject's attention. Based on previous studies [6,7] showing that the time of stability from one verbal transformation to the next ranges from 3.74 s (±3.54) s to 8.37 s (±5.22), we repeated the bistable words for 5 s in a single trial (i.e.,/. . .carrocarrocarro. . ./), so that only one verbal transformation can be expected during each trial. Each experimental block had 50 trials, giving a total of 150 trials per experiment. Blocks presentation order was counterbalanced between subjects. The average duration of words was 374,6 ms with a 100 ms silent period inserted between words. All bistable words were uttered by a male native speaker of Spanish, recorded with Audacity 2.0.5, digitized (32 bit resolution) and sampled at 44.1-kHz sampling rate.

2.3. Procedure

Prior to the experiment, participants read the instructions for the VTE task. Each trial began with the presentation of a fixation cross in the center of the screen (random duration: 1500–2400 ms), followed by the repeated auditory presentation of a bistable word (duration: 5000 ms), and ending by a question mark that appeared on the screen as a cue for subjects to respond. In this period, subjects indicated whether they had perceived or not perceptual transitions among verbal forms by depressing one of two possible response buttons. The question mark remained until the subject response (see Supplementary Fig. S2 for experimental paradigm).

EEG was recorded inside a Faraday cage. The VTE task was programmed with the software E-Prime version 2.0. The auditory stimuli were presented binaurally via loudspeakers Divoom Iris-02 facing the subject; behavioral responses were collected with a response pad EGI 200.

2.4. Data analysis

EEG activity was recorded with 64-sensor HydroCel GSN nets referenced to vertex (Electrical geodesics, Eugene, OR, USA). The EEG was filtered online from 0.01 to 100 Hz in order to eliminate DC fluctuations, and digitized at 1000 Hz. Electrode impedances were below 40 kΩ, the optimal level for this system [17]. Finally, the signal was stored for offline analysis.

2.4.1. Spectral power

The raw EEG signal was first segmented into a series of epochs lasting 4000 ms including 2000 ms preceding the onset of the bistable word, and then re-referenced off-line to average reference. Electrodes placed near the eyes and face were excluded from analysis. Thus, we estimated phase synchrony for 59 out of 64 channels. Trials containing voltage fluctuations that exceeded ±200 μV or transients exceeding ±100 μV were excluded from analysis.

The artifact-free signal was convolved with a complex Morlet's wavelet 7 cycles, through trials and subjects for each condition. By this process we obtained amplitude values for frequencies between 1 and 48 Hz with 1 Hz frequency resolution. Amplitude information was used to compute the spectral power, which is obtained by averaging the time-frequency energy across single trials (see [8] for details). Spectral power across the duration of the trial, for each frequency bin, was normalized to a time window from 400 ms prior to 600 ms after onset of the bistable word. The normalized signal (S_N) was obtained by subtracting the average activity of the time window selected (μ) from the filtered signal (S) and then dividing by the standard deviation of the time window (σ), for each frequency band: $S_N = (S - \mu)/\sigma$. We performed the analysis of spectral power with Matlab 7.0.4 (Mathworks, Inc.).

2.4.2. ERP

The continuous EEG signal was filtered off-line with a band-pass filter (0.5–25 Hz) type FIR Kaiser, which has a linear phase response. Then, the filtered signal was segmented into a series of 1000-ms-long epochs. Each epoch started 400 ms before the onset of a bistable word and ended 600 ms later. All epochs were corrected for eye blinks and eye movements [18,19]. Afterwards, trials containing voltage fluctuations that exceeded ±200 μV or transients exceeding ±100 μV were rejected. Artifact-free epochs were averaged in relation to the onset of the bistable word, re-referenced off-line to average reference [14] and baseline-corrected over a 400 ms window before the onset of the bistable word. The EEGLAB Matlab toolbox was used for visualization [20].

2.5. Statistical analysis

2.5.1. Spectral power

Our statistical analyses pool together all electrodes to produce a global index of spectral power across a large frequency range. The statistical analyses of the spectral power distributions were thus performed on time-frequency charts resulting from averaging the electrophysiological responses of all sensors during the entire segment (−2000 to 2000 ms after bistable word onset). This resulted in a grand average time-frequency chart per experimental condition (Reversal and Stable) per subject. Then, those charts were grouped by condition and analyzed, first by visual inspection, and then by means of paired t-test (p < 0.05) in search of statistically significant differences. False Discovery Rate (q < 0.05) was used to correct for multiple comparisons in each one of the entry matrix of p-values [21]. Subsequently, the significant time-frequency windows were analyzed with a within-subject ANOVA. The α level was set at 0.05 for all tests. We applied Greenhouse-Geisser correction when necessary.

Topographical analysis was restricted to the time-frequency window previously selected. We averaged the time-frequency window of interest over all electrodes. This resulted in arrays of electrodes per subject, for each experimental condition. Then, those arrays were analyzed by means of paired t-test (p < 0.05) contrasting Reversal versus Stable perception conditions. False Discovery Rate (q < 0.05) was used to correct for multiple comparisons in each one of the entry matrix of p-values [21].
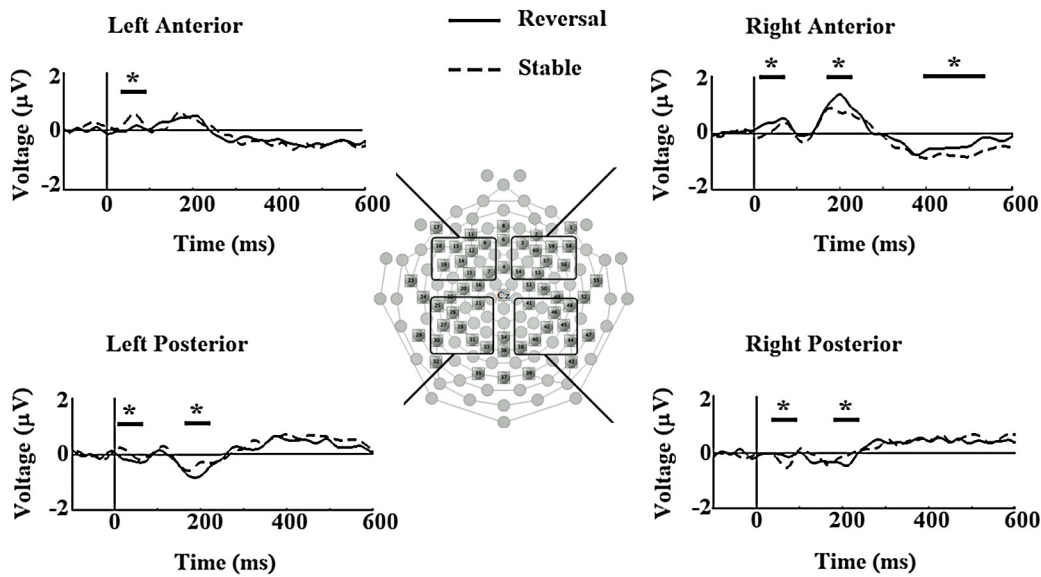
Fig. 2. ERPs elicited for Reversal and Stable conditions. Each graph shows the waveforms for Reversal (solid line) and Stable conditions (segment line), for each one of the four ROIs (left anterior, left posterior, right anterior, and right posterior). Voltage (in microvolts) and time are respectively indicated in the y and x axes of the graphs. Vertical lines indicate the onset of the bistable word. The asterisk indicates the ROI and time window that showed significant differences between conditions (p < 0.05 FDR corrected).

2.5.2. ERP

In order to improve statistical power [22], electrodes were combined into four region of interest (left anterior: F1-F3-F5-F7-FT7-FC1-FC3-FC5; right anterior: F2-F4-F6-F8-FT8-FC2-FC4-FC6; left posterior: CP1-CP5-TP7-P1-P3-P5-P7-P9; right posterior: CP2-CP6-TP8-P2-P4-P6-P8-P10). Grand average ERPs grouped by condition were analyzed by means of paired *t*-test (p < 0.05) in search of statistically significant differences between conditions. False Discovery Rate (q < 0.05) was used to correct for multiple comparisons [21]. Subsequently, differences in mean amplitudes of the four region of interest between the two conditions were tested by repeated-measurement ANOVAs. The α level was set at 0.05 for all tests and, when necessary, we applied Greenhouse-Geisser correction.

3. Results

3.1. Behavioral

The mean duration of the reversal intervals were 14.11 s, with a standard deviation of 22.773 s. A Kolmogorov-Smirnov test revealed that the intervals do not follow a normal distribution ($D = 0.345$, $p < 0.001$). We found that the percept durations are skewed toward longer durations (skewness = 5.05, SE = 0.125; kurtosis = 32.03, SE = 0.249), which fit with gamma ($\alpha = 1.2153$; $\beta = 11.6101$) and lognormal distributions ($\mu = 2.1821$; $\sigma = 0.797$) (see Supplementary Fig. S3 for statistical properties of the reversal intervals). These results are consistent with previous studies on auditory and visual bistability [23].

3.2. Pre- and post-stimulus spectral power

Results are shown in Fig. 1. We found that the mean alpha activity (7–10 Hz) over all electrodes was significantly lower for the Reversal than for the Stable condition from −300 ms to −50 ms ($F(1,14) = 11.757$, $p = 0.004$, $\eta^2 = 0.456$) before the onset of the bistable word, with a spatial distribution over left temporal, central and right frontal sites. After the onset of the bistable word, we found that the mean beta activity (24–30 Hz) was significantly higher for the Reversal than for the Stable condition from 0 ms

to 80 ms ($F(1,14) = 10.166$, $p = 0.007$, $\eta^2 = 0.421$), over left frontal-central and posterior sites, followed by an increase of mean alpha activity (7–10 Hz), from 200 ms to 340 ms ($F(1,14) = 5.908$, $p = 0.029$, $\eta^2 = 0.297$), over left temporal-parietal, central and bilateral frontal regions, and finally a late decrease of beta activity (24–30 Hz), from 360 ms to 440 ms ($F(1,14) = 9.337$, $p = 0.009$, $\eta^2 = 0.400$), over left frontal-central and right posterior regions.

3.3. ERP

Results are shown in Fig. 2. We found positive deflections of the ERP activity over right anterior regions that were significantly larger for the Reversal than for the Stable condition. Specifically, we observed a very early positivity (0–50 ms; $F(1,14) = 9.082$, $p = 0.009$, $\eta^2 = 0.393$; 0.323 μV difference), followed by a P2 (190–220 ms; $F(1,14) = 9.335$, $p = 0.009$, $\eta^2 = 0.400$; 0.528 μV difference), and a late positivity (400–550 ms; $F(1,14) = 9.527$, $p = 0.008$, $\eta^2 = 0.405$; 0.327 μV difference). Also, we found a bilateral N2 over posterior regions (Left posterior: 190–220 ms; $F(1,14) = 4.753$, $p = 0.047$, $\eta^2 = 0.253$; −0.374 μV difference; Right posterior: 190–220 ms; $F(1,14) = 4.670$, $p = 0.049$, $\eta^2 = 0.250$; −0.295 μV difference).

Additionally, we found very early positive deflections over left anterior-posterior regions that were significantly higher for the Stable than for the Reversal condition (Anterior: 45–70 ms; $F(1,14) = 5.677$, $p = 0.032$, $\eta^2 = 0.288$; 0.387 μV difference; Posterior: 0–30 ms; $F(1,14) = 7.404$, $p = 0.017$, $\eta^2 = 0.346$; 0.292 μV difference), along with a very early negativity over right posterior sites (66–72 ms; $F(1,14) = 4.830$, $p = 0.045$, $\eta^2 = 0.257$; −0.396 μV difference;).

4. Discussion

The main goal of this study was to investigate the role played by ongoing brain dynamics on the subsequent perceptual organization of the speech. We found that both the pre- and post-stimulus oscillatory fluctuations of EEG correlate with the endogenous formation of a new verbal form. In what follows, we discuss these findings and their implications in detail.

Regarding to pre-stimulus spectral power in the Reversal condition, we observed a strong local alpha desynchronization over

left temporal, central and right frontal sites. Previous studies have shown that ongoing alpha fluctuations influence the perceptual response to simple sensory stimuli [24,25], with the decrease of pre-stimulus alpha band power improving perception via regulation of the flow of incoming sensorial information [26]. Recently, this view has been challenged suggesting that reduced ongoing alpha band power does not always predict improved perceptual processing, but rather enhanced excitability of sensory cortex making it more susceptible to input [27]. As for its role in the perceptual organization of the speech, we suggest that the pre-stimulus alpha desynchronization would be related to an increase of criticality of the neural system, destabilizing brain dynamics maintaining the previous verbal form, and thus preparing the system for the organization of a new verbal form.

After stimulus onset, we observed an early increase of local beta synchrony over left frontal-central and posterior sites. Previous studies have related beta activity with fusion of multimodal information [10], readiness to integration of temporal information [28], and with a mechanism of spontaneous fluctuations in cortical networks biasing attentional competition during subsequent sensory processing [29]. Concerning its role in perceptual organization of the speech, we propose that the early increase of beta activity following the onset of stimulus presentation would facilitate the perceptual integration of the elements composing the word, leading to the constructions of a new verbal form.

Subsequently, we observed an increase of local alpha synchrony over left temporal-parietal, central and bilateral frontal regions, and a late local beta desynchronization over left frontal-central and right posterior sites. Numerous reports associate the increase of induced alpha spectral power with a mechanism of inhibitory control [30], and the decrease of beta oscillations with endogenous processing of Gestalt perception [31]. As for its role in the organization of the speech, we suggest that enhancement of the post-stimulus local alpha synchrony induces a decrease of criticality thus stabilizing the new verbal form. Finally, the late local beta desynchronization would signal the emergence of new verbal form as a meaningful global perception, whereupon the transient organization of speech is completed.

Importantly, this dynamic of deactivation/activation of local neural assemblies oscillating at alpha and beta frequencies, during the perceptual organization of speech, would be in agreement with the integrative theory proposed by Kornmeier and Bach [32], which states that spontaneous perceptual reversals are governed by two independent processes: first, a phase of destabilization of the stable perceptual interpretation, and then a very fast (40–60 ms after the point to maximal instability) phase of restabilization/disambiguation leading to the formation of a new percept. Regarding the perceptual organization of the speech, we suggest that the phase of destabilization would be represented by the ongoing local alpha desynchronization, whereas the phase of restabilization/disambiguation would be a complex process involving dynamic changes in the coordination of local alpha and beta networks after the onset of the bistable word.

In addition to the study of oscillatory EEG activity, the ERP analysis revealed that the Reversal condition evoked a very early positivity (∼30 ms), P2 (∼200 ms) and late positivity (∼450 ms) over right anterior regions, and bilateral N2 (∼200 ms) over posterior sites. We also note that Stable condition evoked very early positivity over left anterior (∼55 ms) and posterior (∼20 ms) regions, along with a very early negativity (∼70 ms) over right posterior sites. Concerning the P2, N2 and the late positivity elicited during Reversal condition, these results are in agreement with previous studies reporting three components associated with perceptual transitions, the reversal positivity (RP ∼120 ms) [33], reversal negativity (RN, ∼200 ms) and the late positive complex (LPC, ∼400 ms) respectively [15]. The RP would indicate a fast

process of perceptual disambiguation [33], the RN the transition between the two perceptual representations [15], and LPC reflects the outcome of the perceptual change [15]. Concerning the very early ERP activity, they could be related with endogenous processes that start just before that the bottom-up signals from the bistable word have reached the primary auditory cortex [33]. Nevertheless, future experiments should directly address this issue.

Taken together, these results challenge the traditional view that assumes that speech perception is the result of a passive brain processing. In contrast, our data show how the brain state prior to stimulation influence the subsequent emergence of a new verbal form, revealing the active and dynamic nature of the perceptual organization of speech.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.neulet.2016.04.038.

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