



## Pre-stimulus beta oscillations within left posterior sylvian regions impact auditory temporal order judgment accuracy

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### ABSTRACT

Both neural and behavioral responses to stimuli are influenced by the state of the brain immediately preceding their presentation, notably by pre-stimulus oscillatory activity. Using frequency analysis of high-density electroencephalogram coupled with source estimations, the present study investigated the role of pre-stimulus oscillatory activity in auditory spatial temporal order judgments (TOJ). Oscillations within the beta range (i.e. 18–23 Hz) were significantly stronger before accurate than inaccurate TOJ trials. Distributed source estimations identified bilateral posterior sylvian regions as the principal contributors to pre-stimulus beta oscillations. Activity within the left posterior sylvian region was significantly stronger before accurate than inaccurate TOJ trials. We discuss our results in terms of a modulation of sensory gating mechanisms mediated by beta activity.

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### 1. Introduction

The building up of a coherent representation of the auditory environment requires an accurate integration of the order of stimuli occurrence within rapidly varying auditory streams. Fast temporal processing abilities can be reliably assessed using temporal order judgment (TOJ) paradigms in which participants are required to report the order of occurrence between physical events presented in fast sequence (e.g. Bernasconi et al., 2010a).

Neuroimaging data indicate a prominent role for the left temporo-parietal region in the perception of temporal order in the sub-second time scale. Davis et al. (2009) demonstrated a selective involvement of the left temporal parietal junction (TPJ) in TOJ by contrasting fMRI response recorded during the completion of a visual TOJ vs. a shape discrimination task on physically identical stimuli. Recent electrophysiological studies from our group corroborated and extended this result by demonstrating that left posterior sylvian region (PSR) activity during early sensory integration stages and its interaction with right hemispheric homotopic areas determine auditory TOJ accuracy. Left PSR activity predicted TOJ performance and training-induced improvement in TOJ was supported by a lateralization of

brain response from initially bilateral networks towards left PSR. Moreover, we showed that a functional decoupling between left and right PSRs facilitated TOJs (Bernasconi et al., 2010a,b). We interpreted these results in terms of a temporal “stamping” of the first presented stimulus within left PSR, which in turn determines TOJ performance.

However, while the neural processes elicited by the stimuli obviously influence behavioral performance, mounting evidence indicates that brain states preceding the presentation of stimuli could also critically determine their processing and, by extension, performance. Previous literature indicates that pre-stimulus oscillatory activity can impact both quantitative (e.g. reaction time; Gonzalez Andino et al., 2005) and qualitative (e.g. perceptual awareness; Rihs et al., 2009) aspects of the processing of forthcoming stimuli. With regard to fast temporal processing, oscillatory activity has been advanced to play a role in determining the duration of the minimal temporal window within which presented stimuli are perceived as simultaneous (VanRullen and Koch, 2003 for review). As perceiving the two stimuli separately is necessary for extracting their order of occurrence, oscillations can be assumed to impact TOJ (e.g. Kristofferson, 1967).

Based on our previous finding that the sensory integration of the first stimulus of a pair critically impacts temporal order judgment and that pre-stimulus oscillatory activity influences early sensory integration stages (e.g. Romei et al., 2010), the present study aimed at determining the role of pre-stimulus oscillatory activity in the performance in a TOJ task. In order to assess whether pre-stimulus

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baseline electrophysiological oscillations will modulate as a function of subsequent TOJ accuracy, we contrasted frequency power recorded before accurately vs. inaccurately perceived TOJ as well as the underlying brain sources.

## 2. Methods

### 2.1. Participants

11 right-handed males (Oldfield, 1971), aged 20–28 years (mean  $\pm$  s.e.m:  $23.6 \pm 0.8$  years) participated in the study. This study is based on a reanalysis of the data by Bernasconi et al. (2010a;b). No participant had a history of neurological or psychiatric illness, and all reported normal hearing. Each participant provided written, informed consent to procedures approved by the Ethics Committee of the Faculty of Biology and Medicine of the Centre Hospitalier Universitaire Vaudois and the University of Lausanne.

### 2.2. Stimuli and task

Stimuli were pairs of 10 ms duration white noise bursts (1 ms rise/fall time; 44,100 Hz digitization, generated using Adobe Audition 2.0) presented via insert earphones (model ER-4P; Etymotic Research) at 86 dB SPL either to the left and then to the right ear (Left–Right or LR) or alternatively to the right and then to the left ear (Right–Left or RL). Within a pair, the sounds were separated by a constant stimulus onset asynchrony (SOA). The SOA was individually adjusted for each participant before the TOJ training, using an auto-adaptative one up–two down staircase procedure (starting with 60 ms SOA, steps of 5 ms, over 60 trials) to reach a near-threshold difficulty level corresponding to ca 70% correct responses. The SOA ranged from 15 to 80 ms across participants (mean SOA  $\pm$  s.e.m =  $27.7 \pm 5.9$  ms). In the EEG experiment, participants completed 6 blocks of trials. Each block was composed of 200 pairs of sounds, resulting in a total of 600 pairs for each side condition (LR or RL), the order of which was randomly determined. After each pair of sounds, participants were required to respond with their right hand within 2000 ms after trial offset by pressing the left response-box button when they perceived an LR pair and the right button when they perceived an RL pair, using two fingers of the same (right) hand for both responses. Visual feedback was given 1000 ms after responding, indicating whether the response was accurate (green square), inaccurate (red square), or no answer (yellow square). The feedback was displayed for 500 ms. The next trial was presented 1000 ms after the feedback offset. Participants were instructed to respond accurately rather than quickly. The experiment was conducted in an acoustically attenuated and electrically shielded booth. Participants fixated a central cross while listening to the stimuli. Stimulus/feedback delivery and participant's responses were controlled by Eprime 2.0 software (Psychology Software Tools, <http://www.pstnet.com/eprime>).

### 2.3. EEG acquisition and preprocessing

Continuous EEG was recorded at 1024 Hz through a 128-channel Biosemi ActiveTwo system referenced to the CMS-DRL ground, which functions as a feedback loop driving the average potential across the montage as close as possible to amplifier zero (Biosemi, Amsterdam, Netherlands). In order to lower the influence of the visual feedback presented after participants' response, our epoch of interest was limited to the 200 ms pre-stimulus period, i.e. starting 800 ms after the presentation of the feedback. The 200 ms epochs were extracted according to the accuracy of the subsequent response, yielding 2 experimental conditions: accurate and inaccurate TOJ trials. Because we focused on the pre-stimulus period and that the stimulus types (LR or RL) were randomly presented, the analyses were performed independent of stimulus type. In order to maintain equivalent signal-

to-noise ratios for AEPs leading to accurate and inaccurate performance, the same number of trials was included from each category for a given participant. This was achieved in the following manner. First, performance was evaluated across all 6 blocks completed by a given participant in order to identify the lowest performance rate within any of the blocks (i.e. either the lowest percent of correct responses or incorrect responses). This value was then used to determine the number of EEG epochs included in the AEP for both trial types from each of the 6 blocks. The average number of accepted EEG epochs per condition across the 6 blocks was:  $269 \pm 32$  (mean  $\pm$  s.e.m) for both accurate and inaccurate conditions. Importantly, this procedure allowed us to ensure that our effects were not due to simple learning or exposure, because accurate and inaccurate trials were equated throughout the experimental blocks. The average percentage of no responses for the condition LR is  $0.36\% \pm 0.09\%$  (mean  $\pm$  s.e.m) and for the RL condition:  $0.39\% \pm 0.14\%$ . The number of no responses didn't differ between conditions ( $p$ -val  $> 0.8$ ). Trials with no responses were not considered in the averaging. Prior to group-averaging, data at artifact-contaminated electrodes from each participant were interpolated using 3-D splines (Perrin et al., 1987). The average number of interpolated electrodes was (mean  $\pm$  s.e.m)  $12.1 \pm 1.3$  (min–max = 3–16). Data were then recalculated against the average reference and high-pass-filtered (0.16 Hz and DC removed).

Behavioral data were analyzed according to the signal detection theory (Macmillan and Creelman, 1991). Sensitivity ( $d'$ ) was calculated according to the following formula:  $d' = z(H) - z(FA)$ ; where  $z(H)$  and  $z(FA)$  represent the transformation of the hit (H) and false-alarm (FA) rates into z-scores (Green and Swets, 1966). Hits were the LR trials reported as LR and false alarms were RL trials reported as LR (as the same number of LR and RL pairs were presented, the  $d'$  is symmetric; Hit + Miss = False Alarms + Correct Rejection = 100%. Therefore, the  $d'$  would be identical if accurately perceived RL pairs were considered as Hits and LR trials reported RL as False Alarms). Consequently, the  $d'$  index takes into account the global behavioral performance, encompassing accuracy to both LR and RL pairs.

### 2.4. EEG analyses and source estimation

#### 2.4.1. FFT Approximation

The Fast Fourier Transform (FFT) Approximation approach (Lehmann and Michel, 1990), implemented in the Cartool software, was used for the frequency analyses of the 200 ms pre-stimulus period. As compared to classical FFT power representing squared potential values, the FFT Approximation (FFTA) calculates the FFT for each channel and then uses the complex values of all electrodes to calculate the first principal component (PC) for each frequency point. In contrast to the FFT power map, FFTA preserves the polarity information and is reference-independent, thereby allowing source estimation to be directly calculated in the frequency domain.

FFTA were applied to a frequency band ranging from 5 to 55 Hz with 5 Hz steps for each epoch of each condition and for each participant. The outputs of this analysis were averaged across conditions for each frequency band and participant, separately.

In order to assess modulations in frequency power, the Global Power Spectra (GPS) was calculated separately for each frequency band by averaging the absolute value of the frequency power at each electrode. GPS were then submitted to paired t-test between accurate and inaccurate conditions. These analyses served to determine the frequency band(s) showing significant modulation across conditions on which source estimations were in turn calculated. A control analysis in which GPS was contrasted as a function of the preceding feedback across frequency reveals that our effect cannot be accounted for by the previous feedback (all  $p$ -vals  $> 0.12$ ).

We estimated the sources underlying FFTA topographies using a distributed linear inverse solution applying the local autoregressive

average (LAURA) regularization approach (Grave de Peralta Menendez et al., 2001; Grave de Peralta et al., 2004). LAURA selects the source configuration that better mimics the biophysical behavior of electric fields (i.e. activity at one point depends on the activity at neighboring points according to electromagnetic laws). Homogeneous regression coefficients in all directions and within the whole solution space were used. The solution space is based on a realistic head model and included 4024 nodes selected from a 6×6×6 mm grid equally distributed within the gray matter of the Montreal Neurological Institute's average brain (courtesy of R. Grave de Peralta Menendez and S. Gonzalez Andino; <http://www.electricalneuroimaging.ch/>).

LAURA was applied on the 18–23 Hz frequency band for both conditions of each participants and subsequently averaged across participants. Sources calculated for the accurate and inaccurate conditions were then submitted to paired t-test with a spatial criterion of 11 contiguous solution points and a significance threshold of  $p < 0.02$  at the single node level.

**3. Results**

The group averaged  $d'$  was  $1.02 \pm 0.2$  (mean  $\pm$  s.e.m.) and percent correct  $68.5 \pm 3.37\%$ , indicative of an above threshold sensitivity. Reaction times were slower in the inaccurate than accurate condition ( $659.6 \pm 36.23$  ms and  $629.6 \pm 32.93$ , respectively;  $t(10) = 2.633$ ;  $p < 0.03$ ). Participants performed similarly ( $p\text{-val} > 0.4$ ) for the LR and RL stimuli ( $69.6\% \pm 3.7$  and  $67.4\% \pm 2.9$ , mean  $\pm$  s.e.m., respectively).

Analyses of pre-stimulus oscillatory activity revealed a significantly stronger global power spectra over the beta (18–23 Hz) frequency band in the accurate than inaccurate condition ( $t(10) = 8.663$ ;  $p < 0.02$ ;  $\eta^2 = 0.464$ ; Fig. 1). No other frequency band exhibited significant differences (Fig. 1b). LAURA source estimations calculated from FTA topographies for the 18–23 Hz frequency band revealed bilateral posterior sylvian generators in both accurate and inaccurate

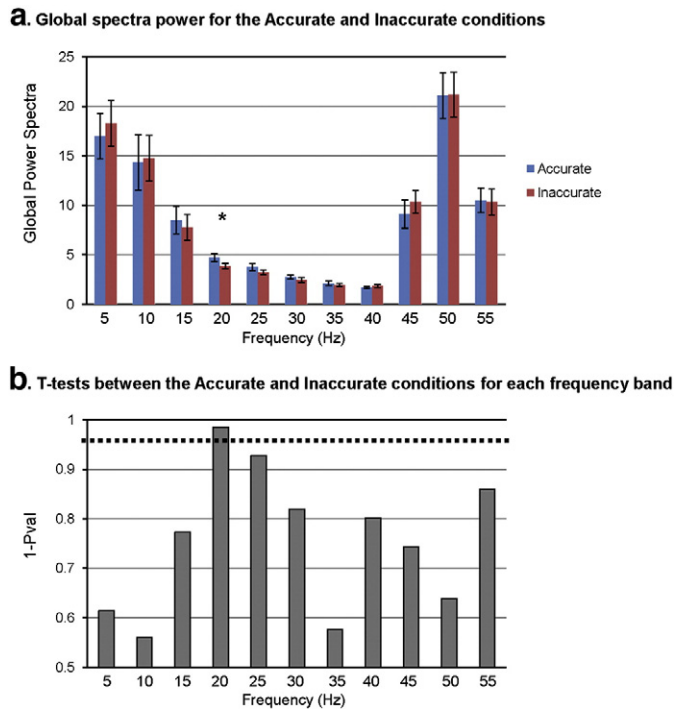
conditions, but with a pattern of activation more strongly lateralized to the left hemisphere in the accurate condition. Statistical analysis confirmed this finding by showing a significantly stronger beta generator for the accurate than inaccurate condition within the left posterior sylvian region (Fig. 2; maximal difference at  $[-57, -38, \text{and } 20 \text{ mm}]$  using the coordinate system of Talairach and Tournoux, 1988).

**4. Discussion**

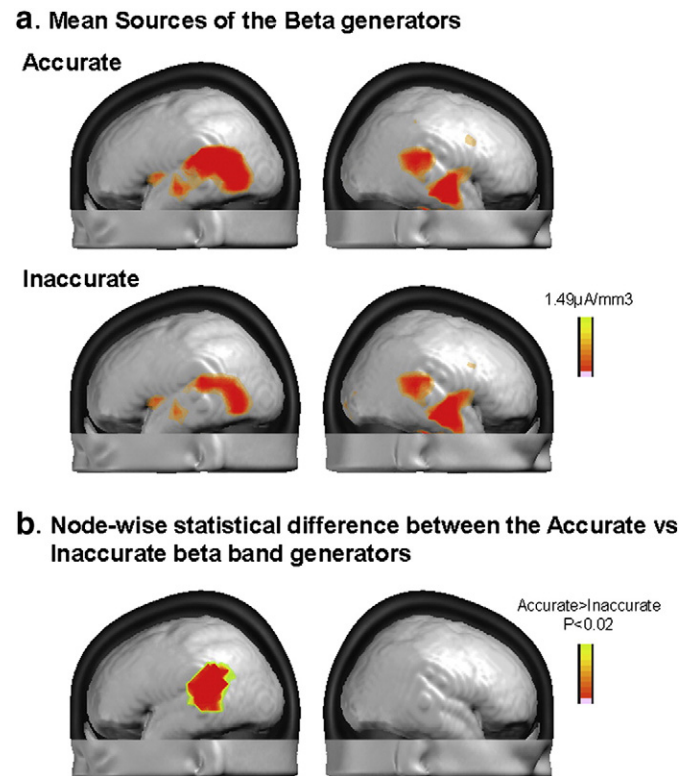
The analysis of oscillatory activity during the pre-stimulus period revealed significantly stronger beta power before accurate than inaccurate auditory spatial temporal order judgments. Source estimations revealed that this difference followed from stronger beta activity before accurate than inaccurate trials within left posterior sylvian regions (PSR).

Our results suggest that a high level of pre-stimulus beta activity promotes TOJ performance. Pre-stimulus beta activity could have influenced TOJ accuracy by acting over sensory gating mechanisms consisting in the reduction of brain responses to the second sound of pairs presented in fast sequence. By suppressing responses to repeated sounds, gating mechanisms would help prevent sensory overload (Adler et al., 1982; Kisley et al., 2004). Since accurate TOJs require unbiased perception of the first and/or second sound of the pair, they cannot be achieved if the processing of each of the two sounds interferes with each other. An efficient gating of the first sound would therefore facilitate TOJ by inhibiting the response to the second sound, thereby improving the perception of the first sound.

This hypothesis is supported by two lines of evidence. On the one hand, modulations in the amplitude of gating-related P50 evoked potential has been associated with shift in the point of subjective simultaneity (e.g. Eimer, 1998; Luck et al., 2000). On the other hand,



**Fig. 1.** a. Power–frequency analysis. Mean Global Power Spectra (GPS) for each frequency band and the accurate (blue) and inaccurate (red) conditions (s.e.m indicated). The asterisks indicate significant ( $p < 0.02$ ) differences between the two conditions. b. Result of the t-test between GPS of the accurate vs. inaccurate condition.



**Fig. 2.** a. Mean LAURA source estimation of beta generators for the accurate and inaccurate conditions. b. Node-wise statistical analyses of the difference in LAURA source estimations between brain generators of beta oscillations in the accurate vs. inaccurate condition. Beta generators were stronger in the accurate than inaccurate condition within left posterior sylvian regions.

Hong et al. (2008) demonstrated that beta activity modulates gating mechanisms. By extracting frequency components of electrophysiological responses to pairs of auditory stimuli recorded under passive listening conditions, the authors observed that an increase in the strength of the beta response to the first stimulus was associated with an increase in the suppression of the electrophysiological response to the second sound.

Recent evidence indicates that pre-stimulus spontaneous variability in oscillatory activity at baseline can account for the variability in early processing stages of incoming stimuli (Hanslmayr et al., 2007; van Dijk et al., 2008; Lakatos et al., 2005). Though the precise direction of these interactions remains unclear, induced beta activity measured immediately preceding stimulus presentation might thus possibly have influenced the oscillatory response to the first stimulus and in turn gating mechanisms and TOJ performance.

This hypothesis is further supported by the result of source estimations revealing stronger beta activity in the accurate than inaccurate conditions within left PSR. Our previous studies indicate that TOJ accuracy depends on left PSR activity during early sensory integration of the first stimulus (Bernasconi et al., 2010a;b). Compatible with the involvement of the peri-sylvian region in gating mechanisms (e.g. Grunwald et al., 2003; Weisser et al., 2001), pre-stimulus beta activity within PSR areas likely interacted with gating-related beta response to the first sound, subsequently enhancing inhibition of the second interfering sound.

Modulation in pre-stimulus beta power could have followed from spontaneous fluctuations or from endogenous top-down mechanisms. Linkenkaer-Hansen et al. (2001) demonstrated that baseline oscillatory power can vary spontaneously, randomly generating a more or less favorable TOJ processing context. Consistent with this hypothesis, Laufs et al. (2003) reported spontaneous beta frequency (17–23 Hz) oscillations within the temporo-parietal junction at rest.

Alternatively, recent evidence on the functional role of beta activity suggests that it could index the anticipation of forthcoming stimuli. Because the timing of stimulus presentation was predictable in our experimental setup, modulations in anticipatory top-down mechanisms, including attention, could have occurred. Such processes have been demonstrated in a study by Van Ede et al. (2010), showing that pre-stimulus beta power modulates depending on participants' preparation of the arrival of expected somatosensory stimuli, more beta power, however, decreasing performance. Baseline beta fluctuation might have followed from changes in alertness (Roux et al., 2006; Buschman and Miller, 2007, 2009), which in turn have been shown to modulate gating processes (Guterman and Josiassen, 1994; Guterman et al., 1992). This hypothesis is compatible with our result for slower RTs in the inaccurate than accurate condition.

Our result for a role of pre-stimulus beta activity in TOJ accuracy could also be accounted for in the framework of the “perceptual moment” theory, positing that perception is not continuous but rather composed of a succession of short, discrete temporal intervals of processing associated with constant percept (Stroud, 1956). According to this theory, the minimal SOA over which two successive stimulations are perceived as simultaneous depend on the size of the interval and on when stimuli are presented relative to the sequence of perceptual moments (e.g. Hirsh and Sherrick, 1961). Since the order of stimuli presented in the same discrete processing epoch cannot be discriminated, perceptual moments interact with TOJ accuracy (e.g. Kristofferson, 1967). Interestingly, the duration and the phase of perceptual moment have been advanced to be determined by brain oscillation (VanRullen and Koch, 2003 for review). While our analyses provide no information about the phases of oscillatory activity, beta oscillation would correspond to the duration of the mean SOA (40–50 ms) used in our experiment. Accordingly, it could be hypothesized that the role of pre-stimulus beta oscillation on TOJ accuracy was mediated by their matching with the SOA used in the TOJ task.

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