An Electrophysiological Study on Intra- and Inter-modal Duration Discrimination: Effects of Performance Level

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Abstract

Duration discrimination is severely impaired when the duration markers are delivered from different sensory modalities (inter-modal) instead of from the same modality (intra-modal). The present study examined the brain activity related to this impairment using event-related potentials. Durations were marked either by two auditory signals (AA) or by an auditory and a visual signal (AV), and there were two levels of discrimination difficulty (easy and difficult). A negative component (contingent negative variation) which appeared between the two markers at fronto-central sites and is said to be related to time perception, was larger for AA than for AV, and was not influenced by discrimination difficulty. A principal component analysis showed that the first and the third principal component captured differences in brain activity patterns between sensory modalities and difficulties, whereas the second principal component could reflect brain activity related to time perception in general, regardless of the modalities.

Keywords: Time perception; modality; event-related potentials; contingent negative variation; principal component analysis

Introduction

Many activities in our everyday life, for example, speaking, playing sports, and enjoying music, require precise perception of time. However, there is no sensory organ specialized for perceiving time, and the brain needs to process and integrate the temporal information delivered from multiple sensory modalities. How the brain processes temporal information from different sensory inputs and whether or not there is a central clock mechanism for time perception has been one of the fundamental questions in time perception studies (e.g., Grondin, 2010; Mauk & Buonomano, 2004).

When two brief signals are presented successively, they can mark an empty time interval in between. A time interval marked by signals of the same sensory modality is called an "intra-modal" interval whereas an interval marked by signals from different sensory modalities is called an “inter-modal” interval. Generally, sensitivity to time is better (which can be seen as lower discrimination threshold and/or less variability) for auditory than for visual signals (Grondin, 1993), and inter-modal intervals are much more difficult to discriminate than intra-modal intervals (Grondin & Rousseau, 1991).

Gontier et al. (2013) investigated the brain activity related to such modality differences in duration discrimination using electroencephalography. Auditory (A) and visual (V) signals were used to mark the beginning and the end of the time intervals, and there were four modality conditions: AA, VV (intra-modal conditions), AV, and VA (inter-modal conditions). They recorded the event-related potentials (ERPs) while the participants categorized the presented time intervals as either ‘short’ or ‘long’; they should respond short for the 450-ms interval and long for the 550-ms interval. One of the focuses in their ERP analyses was on a negative component, Contingent Negative Variation (CNV) (Walter et al., 1964), which had been studied in relation to time perception (e.g., Macar & Vidal, 2009). Results showed that the amplitude of the CNV that was recorded at fronto-central electrodes increased significantly from 250 ms until the end of the 550-ms interval in the AA conditions, while no significant change in the time course of this component was observed for the other three modality conditions.

One possibility for the increase in the CNV amplitude only for the AA interval was that this increase in the CNV reflected a processing in the brain that is specific to auditory time perception. However, there was another possibility that this increase was related to the difficulty of the task; the performance in the behavioral task was much better for the AA condition compared to the other three modality conditions, and better for intra-modal than for inter-modal conditions. It is possible that the increase in the CNV amplitude simply reflected the easiness to judge the duration in the AA condition.

In the present study, we tried to clarify this issue by examining how the difficulty to discriminate duration influences the time course of CNV. We focused on the AA and AV modalities, which showed highest and lowest performance, respectively, in the behavioral results of Gontier et al. (2013), and prepared an easy condition and a difficult condition for both modality conditions. If the increase in the CNV amplitude was due to the easiness to discriminate durations, this increase should be smaller for the difficult conditions than for the easy conditions, regardless of the modalities. Alternatively, if the CNV increase reflected activity specific to auditory intra-modal time perception, the increase in CNV amplitude should appear only for the AA conditions, regardless of the difficulty. Furthermore, we tried to analyze the activity recorded at all electrodes on the scalp and to look into whether there was a common activity for all modality and difficulty conditions by conducting a principal component analysis.

Methods

The stimuli and task were the same as in Gontier et al. (2013), except for the combination of modalities and the durations to be discriminated. In the present experiment, we focused on the AA and AV modalities, and the difficulty of discrimination was manipulated by varying the longer duration while fixing the shorter duration (AA: 450/467 and 450/550; AV: 450/550 and 450/800; the combination of shorter/longer durations is indicated in milliseconds). When the difference between the two durations is small, discrimination would be difficult. When the difference is large, discrimination would be easy. By keeping the shorter duration fixed, the brain activity to the 450-ms intervals could be compared directly between the difficult and the easy conditions, because the stimuli for these two conditions are physically the same.

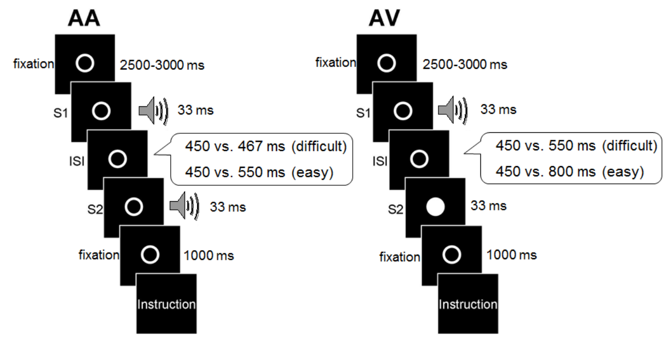

Figure 1: Schematic representation of the experimental paradigm. After the presentation of the stimuli, S1 and S2, and the fixation point, a visual instruction asked the participants to indicate whether the interval corresponded to the short or the long interval by pressing a button.

Participants

Fourteen right-handed employees or students at Laval University (4 men, 10 women, with a mean age of 26 years; ranged between 20-40 years), took part in this experiment[1].

Stimuli

An empty black circle (diameter: 1 cm) with white surrounds (1 mm, contrast 100%) displayed at the center of a 14-inch CRT monitor (refresh rate: 60 Hz) was used as the fixation point (0.95° of visual angle). The visual stimulus was a 33-ms flash (filled white circle on black background) with the same size and position as the fixation point. The auditory stimulus was a 33-ms sound (1 kHz pure tone burst) including a rise and a fall time of 5 ms that were raised-cosine shaped. Sounds were presented binaurally at 80 dB SPL via speakers placed on each side of the computer screen.

Procedure

The interval to be discriminated was a silent duration (empty duration) between two stimuli, S1 and S2 in this order. S1 was always an auditory stimulus while S2 was either auditory (AA; intra-modal) or visual (AV; inter-modal). There were two possible durations for the time interval; for the AA-difficult condition (AA-d), these intervals were 450 or 467 ms; for the AA-easy condition (AA-e), 450 or 550 ms; for the AV-difficult condition (AV-

[1] Data of two more participants were collected, but excluded from analyses because the percentage of correct responses in their behavioral data was lower for the easy condition than for the difficult condition. This exclusion was made for safety because the purpose of the study was to examine the effects of discrimination difficulty on the brain activity.

d), 450 or 550 ms; and for the AV-easy condition (AV-e), 450 or 800 m (Figure 1). These durations were determined by a pilot experiment, which was conducted to find the duration combinations that would have correct responses of above 80 % for the easy condition and around 60 % for the difficult condition. The task for the participants was to respond whether the presented time interval was the short one or the long one by pressing the button “1” or “2” respectively with their dominant (right) hand. In the practice blocks, participants received feedback after each response indicating whether the presented interval was short or long. In the experimental blocks, there was no feedback.

The experiment consisted of four sessions corresponding to the four modality-difficulty conditions. The order of the four sessions was counterbalanced over participants and the participants knew in advance what stimuli would delimit the interval. Each session was divided into four experimental blocks of 50 trials (25 short and 25 long intervals presented in a randomized order within each block) and was preceded by a practice block of 10 trials.

ERP Recordings

Scalp voltages were continuously recorded using a 32-channel Geodesic Sensor Net, connected to a DC-coupled 32-channel, high input impedance amplifier (NetAmps 300 TM, Electrical Geodesics, Inc., Eugene, OR). The net was adjusted so that the electrodes were correctly located according to the 10/20 system. EEG signals were recorded relative to a vertex reference electrode (Cz).

The EEG data were analyzed offline using Net Station 4.3 software (Electrical Geodesic Inc.) and digitally low-pass filtered at 30 Hz. The continuous EEG was segmented into epochs starting 200 ms prior to the onset of S1 and ending at 1 s after S2. The 200-ms prestimulus served as the baseline. After the segmentation, artifact detection was conducted with Net Station’s artifact detection tool, which automatically detected eye blinks, eye movements and marked bad channels in the input file. A channel with more than 100 μV between its minimum and maximum amplitude values for a given segment was identified as a bad channel for that segment. A channel was marked as bad throughout the entire recording if it was marked bad for more than 10% of the segments. Segments with eye-blink (> ± 100 μV), eye-movement (> ± 55 μV) or with more than 5 bad channels were excluded from further analyses. In the remaining segments, signal from rejected electrodes was replaced using the “bad channel replacement” algorithm in Net Station 4.3, which interpolates the signal of a bad channel from the signals of remaining channels using spherical splines. A baseline correction was applied and the average waveforms were re-referenced to averaged mastoids.

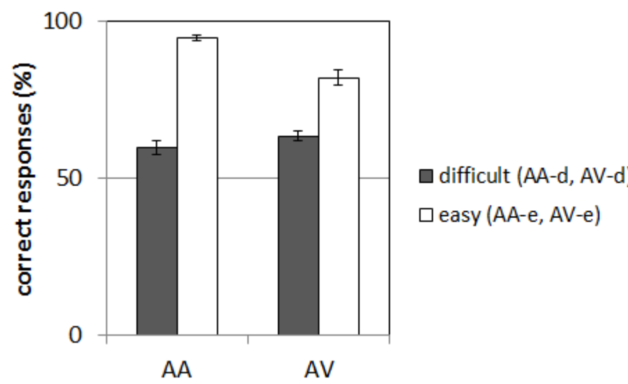

Figure 2: Percentages of correct responses. Error bars indicate standard errors.

Results and Discussion

Behavioral Data

Figure 2 shows the percentage of correct responses. The performance was better for the easy condition than the difficult condition for both modalities, as expected. The performance of the easy condition was better in the AA condition than the AV condition.

A two-way ANOVA (2 modalities × 2 difficulties) was performed on the percentages of correct responses, and the main effects of modalities and difficulties, as well as their interaction were significant (F [1, 13] = 4.736, p = .049, η_p^2 = .267; F [1, 13] = 698.087, p < .001, η_p^2 = .982; F [1, 13] = 29.813, p < .001, η_p^2 = .696, respectively). Ryan’s post-hoc test revealed that the effect of the modalities was significant in the easy condition (p < .001), but not in the difficult condition (p = .152). The effect of the difficulty was significant in both modalities (p < .001).

The behavioral results were similar to those obtained in previous studies (Gontier et al., 2013; Grondin & Rousseau, 1991), and the effects of difficulty appeared as expected.

ERP Data

Figure 3 shows the ERP waveforms for the short duration (450 ms), and Figure 4 the long duration (467 [AA-d], 550 [AA-e, AV-d], and 800 ms [AV-d]). In all conditions, there was an early negative component, N1, which peaked in amplitude at around 100 ms, and a following positive component, P2, which peaked at around 180 ms after the presentation of S1 (the auditory signal which marked the beginning of the interval to be discriminated). For both components, highest amplitudes appeared at midline frontal, central and parietal electrodes. These early waves were followed by a negative component, the Contingent Negative Variation (CNV), which developed mainly at fronto-central and parietal electrodes. After the CNV, N1 and P2 appeared after the presentation of S2 (which marked the end of the interval). The CNV amplitude seemed to increase until S2

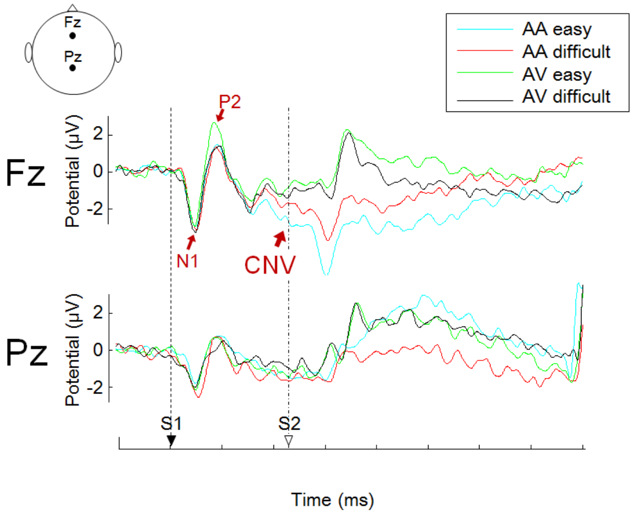

Figure 3: ERP activities recorded at Fz and Pz electrodes during the short interval.

for the AA intervals but not for the AV intervals (Figures 3 and 4).

CNV time course analysis To examine the increase in the CNV and to compare the CNVs between the two modalities and the two difficulty levels, we calculated the mean CNV amplitude over successive temporal windows of 48 ms each, for the short duration which was the same (i.e. 450 ms) for all modality and difficulty conditions; the component was divided into 4 temporal windows (tw1: 250-298, tw2: 300-348, tw3: 350-398, tw4: 400-448 [ms]). We looked at the CNV time course on the left (F3/C3), right (F4/C4) and medial (Fz/FCz/Cz) fronto-central electrodes grouping, as in Gontier et al. (2013).

A three-way ANOVA (2 modalities × 2 difficulties × 4 temporal windows) was carried out on the CNV amplitudes

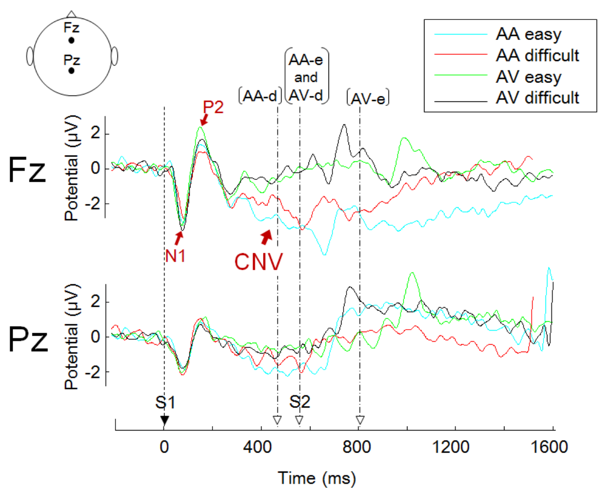

Figure 4: ERP activities recorded at Fz and Pz electrodes during the long interval.

at medial fronto-central electrodes grouping (Fz/FCz/Cz). None of the main effects were significant ($p > .05$), but the interaction between modalities and temporal windows was significant (F [3, 39] = 3.291, $p = .030$, $\eta_p^2 = .202$), and Ryan's post-hoc test showed that the effect of temporal windows was significant in the AA modality ($p = .040$), with significant difference between tw1 and tw4 ($p = .004$), but not in the AV modality ($p = .652$). Other interactions were not significant ($p > .05$).

A four-way ANOVA (2 modalities × 2 difficulties × 4 temporal windows × 2 lateralities) was performed at the lateral fronto-central electrode grouping (F3/C3 and F4/C4). The main effect of the temporal windows was significant (F [3, 39] = 3.756, $p = .018$, $\eta_p^2 = .224$), and Ryan's post-hoc test showed significant difference between tw1 and tw4 ($p = .001$). Other main effects and interactions were not significant ($p > .05$). The absence of the interaction between modalities and temporal windows suggested that the difference in the increase of CNV between modalities was limited to the medial electrodes.

The increase in CNV amplitude for AA intervals and its absence for AV intervals, which appeared at medial fronto-central electrodes, were in line with Gontier et al. (2013). The discrimination level did not influence the CNV amplitude significantly. It seemed that the increases in CNV observed only for AA intervals in the present results and in Gontier et al. (2013) were not caused by the easiness to judge the durations. It is possible that the time course of the CNV at the fronto-central sites reflects a processing that is specific to intra-modal auditory intervals.

Principal Component Analysis To analyze the activity patterns of all electrodes throughout the segmented epoch, we applied a principal component analysis (a spatial PCA, as described in Picton et al., 2000) to the grand-averaged

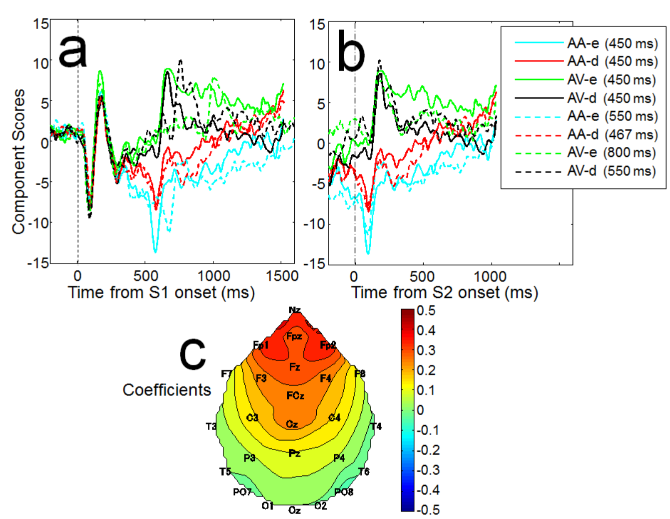

Figure 5: The time course of component scores (a, b) and the topography of component coefficients (c) of the first principal component.

data of all participants at all 29 electrodes for all conditions.

29 components were obtained from the analysis, and we decided to focus on the first three principal components whose eigenvalues were above 1. Figures 5-7 show the component scores and component coefficients of the first, second, and the third principal component, respectively. In each figure, the component scores are shown in two ways: aligned at the onset of S1 (a) and at the onset of S2 (b).

The first principal component showed frontal distribution, and the component coefficients were high in a wide area to Cz (Figure 5c). The coefficients for the second principal component were in opposite directions for the frontal polar sites (around Nz and Fpz) and the central sites (around FCz) (Figure 6c). The third principal component showed distribution at parieto-occipital regions with a peak in component coefficients at around Pz (Figure 7c).

The component scores of the first principal component showed peaks at about 100 and 200 ms after the S1 onset for all conditions (Figure 5a), which seemed to be related to the N1 and P2 to S1. Substantial differences between conditions began to appear after these peaks, and component scores increased for AV conditions while they decreased for AA conditions, resembling the CNV component. The decrease in the AA modality was larger for the easy conditions (the light blue lines in Figure 5a) than for the difficult conditions (the red lines in Figure 5a). To see whether these tendencies were statistically significant, we calculated the component scores for each participant's data using the component coefficients obtained from the grand-averaged data. Then, as in the CNV time course analysis, these component scores were divided into 4 temporal windows (tw1:250-298, tw2: 300-348, tw3: 350-398, tw4: 400-448 [ms]), and submitted to a four-way ANOVA (2 modalities × 2 difficulties × 2 duration × 4 temporal windows). None of the main effects were significant ($p > .05$), but the interaction between modalities and temporal windows was significant (F [3, 39] = 19.270, $p < .001$, $\eta_p^2 = .597$), and Ryan's post-hoc test showed that the effect of modalities was significant at tw4. The interaction between difficulties and temporal windows was also significant (F [3, 39] = 5.543, $p = .003$, $\eta_p^2 = .299$). Ryan's post-hoc test for this interaction did not show significant effects. Other interactions were not significant ($p > .05$).

The component scores for the second principal component showed a similar time course for all conditions until the presentation of S2 (Figure 6a). This was supported by the four-way ANOVA (2 modalities × 2 difficulties × 2 duration × 4 temporal windows) conducted with the same temporal windows as the first principal component analysis (described in the previous paragraph), which showed a significant main effect of the temporal windows (F [3, 39] = 19.254, $p < .001$, $\eta_p^2 = .597$) and no other significant main or interaction effects. It was surprising that the component scores showed such similarity for all conditions despite the diversity in the ERP waveforms. It is possible that this principal component, which appeared after extracting the large activities related to the sensory stimuli and discrimination difficulties as the first principal component, reflects the brain activity for purely temporal processing. When the time course of the component scores were examined aligned at the onset of S2 (Figure 6b), there seemed to be a small peak at around 200 ms after the onset of S2, and the scores after this peak showed a decrease in a similar pattern for all conditions. However, the decrease seemed slightly faster for the shorter durations, especially in the AA conditions (compare the solid and the dotted lines in Figure 6b). As we did with the component scores after S1, we divided the component scores from 250 ms to 998 ms after the onset of S2 into 15 temporal windows of 48 ms each, and conducted a four-way ANOVA (2 modalities × 2 difficulties × 2 duration × 15 temporal windows). The main effect of temporal windows was significant (F [14, 182] = 44.696, $p < .001$, $\eta_p^2 = .775$). Other main effects were not significant ($p > .05$). The interaction between modalities and duration was significant (F [1, 13] = 6.443, $p = .025$, $\eta_p^2 = .331$), and Ryan's post-hoc test showed that the effect of duration was significant only with the AA conditions ($p < .05$) and not with the AV conditions ($p > .05$). The interactions between difficulties and temporal windows and between duration and temporal windows were also significant (F [14, 182] = 3.366, $p < .001$, $\eta_p^2 = .206$; F [14, 182] = 4.584, $p < .001$, $\eta_p^2 = .261$ respectively), and for the latter interaction, Ryan's post-hoc test revealed that the effect of duration was significant at tw10-tw15, which corresponds to 700 to 998 ms after the onset of S2 ($p < .05$). Other interactions were not significant ($p > .05$).

The component scores for the third principal component showed peaks at around 100-200 ms after the onset of S2 for the AV conditions (Figure 7b). These peaks seemed to be related to the visual processing, since S2 was a visual stimulus in the AV conditions. There was also a slow peak at around 300 to 500 ms for the easy conditions in the AA

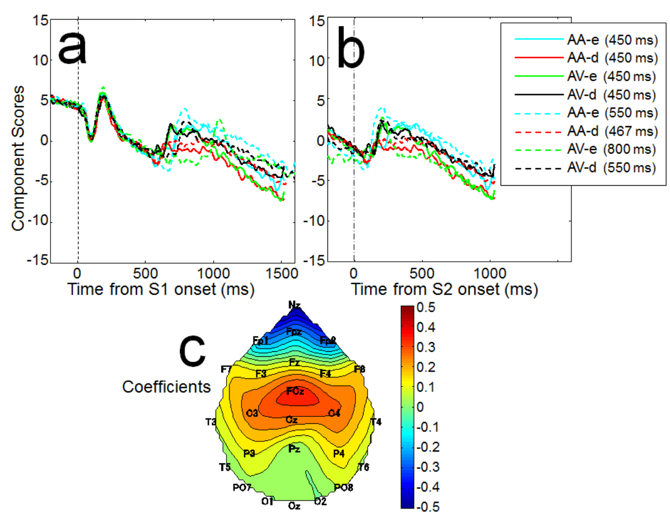

Figure 6: The time course of component scores (a, b) and the topography of component coefficients (c) of the second principal component.

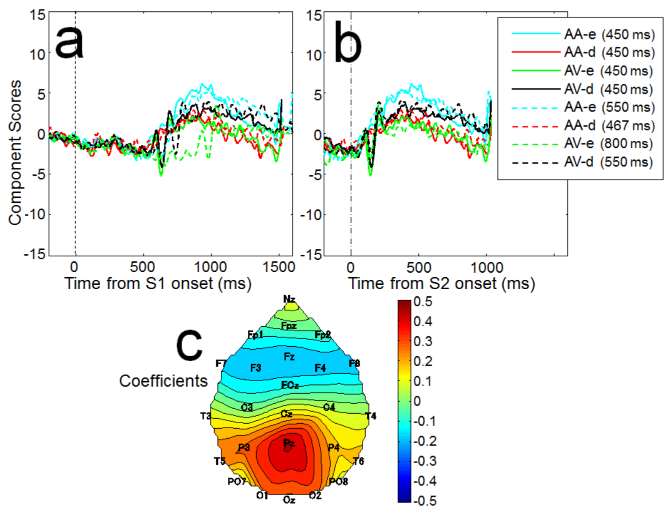

Figure 7: The time course of component scores (a, b) and the topography of component coefficients (c) of the third principal component.

modality after the onset of S2 (the light blue lines in Figure 7b). This slow peak was much smaller in the difficult conditions of the AA modality (the red lines in Figure 7b). This was supported by the three-way ANOVA (2 difficulties × 2 duration × 4 temporal windows) conducted with 4 temporal windows of 48 ms each dividing the component scores between 300-498 ms from the onset of S2. The main effect of the difficulties was significant (F [1, 13] = 7.104, p = .019, η_p^2 = .353), while the other main effects and interactions were not significant (p > .05). These analyses suggest that this peak could be related to the easiness to judge duration in the auditory modality.

Summarizing the results of the principal component analysis, the difference between the easy and the difficult condition in the AA modality seemed to have appeared at frontal polar sites after the N1/P2 peaks to S1 (as the first principal component, Figure 5), and at parieto-occipital sites at around 300-500 ms after the onset of S2 (as the third principal component, Figure 7). The second principal component, which had opposite tendencies for the frontal polar sites and the central sites, showed similar time course in the component scores for all conditions until the presentation of S2, possibly reflecting a common activity related to the temporal processing independent of the sensory modality (Figure 6).

Conclusions

The present study confirmed that the increase in CNV appeared only for auditory intra-modal (AA) interval, as in Gontier et al. (2013), and that this component at fronto-central sites was not influenced by the difficulty to discriminate duration. A principal component analysis of the data from all the electrodes seemed to separate brain activities specific to and common to intra- and inter-modal duration perception.

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