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Electrophysiological Evidence of Auditory Temporal Perception Related to the Assimilation Between Two Neighboring Time Intervals

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Abstract

We conducted two event-related potential (ERP) experiments that examined the mechanisms of auditory temporal assimilation. Stimulus patterns consisted of two neighboring time intervals marked by three successive tone bursts (20 ms, 1000 Hz). Six stimulus patterns were used in which the first time interval (T1) varied from 100 to 280 ms, while the second time interval (T2) was fixed at 200 ms. Two other stimulus patterns consisted of different T1/T2 combinations were employed. Participants judged whether T1 and T2 had the same duration or not by pressing a button. ERPs were recorded from 11 electrodes over the scalp. Behavioral data showed symmetrical assimilation; the participants judged the two neighboring time intervals as equal when the difference between the time intervals (T1-T2) was -40 to +40 ms. Electrophysiological data showed that two ERP components (P300 and CNV) emerged related to the temporal judgment. The P300 appeared in the parietal area at 400 ms after the 2nd tone burst, and its amplitude decreased as a function of T1. The CNV component appeared in the frontal area during T2 presentation, and its amplitude increased as a function of T1. In Experiment 2, 11 stimulus patterns were presented. In seven stimulus patterns, T1 varied from 80 to 320 ms, and T2 was fixed at 200 ms. ERPs were recorded from 19 electrodes over the scalp. In this experiment, behavioral data showed asymmetrical assimilation; participants judged the two neighboring time intervals as equal when T1-T2 was -80 to +40 ms. Consistent with the results of Experiment 1, electrophysiological data showed the P300 and the CNV during T2. In addition, a slow negative component (SNCt) appeared in the right prefrontal area after the 3rd tone burst, and continued up to about 400 ms after the stimuli. The magnitude of this component was smaller when temporal assimilation occurred. These three ERP signatures seem to correlate with the process of temporal assimilation; (a) the P300 augmentation, which could be related to the participants' attention to the 1st interval and reflect the monitoring of the passage of time, (b) the CNV in the frontal area, which might have accompanied the process of memorizing the lengths of the time intervals, and (c) the SNCt in the right prefrontal area, which showed a reduction when temporal assimilation occurred. Our results showed spatiotemporal characteristics of the cortical processing of short time intervals and may assist the neurophysiological understanding of illusions in time and time perception in general.

Key Words: temporal perception, bilateral assimilation, unilateral assimilation, P300, CNV, SNCt

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1. Introduction

In recent years, the perception of time with regard to relatively short time intervals has been a matter of interest both in psychology and neurobiology (Eagleman, 2008; Meck, Penney, & Pouthas, 2008; ten Hoopen, Miyauchi, & Nakajima, 2008). It is argued that judgments at subsecond timing lead to various types of perceptual distortions — illusions — in several modalities. So far, we have found a couple of phenomena related to auditory temporal perception in short time intervals by means of psychophysical measurements (Nakajima, ten Hoopen, & van der Wilk, 1991; Sasaki, Nakajima, & ten Hoopen, 1998; Miyauchi & Nakajima, 2005, 2007; ten Hoopen, Sasaki, Nakajima, Remijn, Massier, Rhebergen, & Holleman, 2006). One is so-called 'temporal assimilation,' in which physically different, short time intervals are perceived as (almost) equal to each other when they neighbor each other (Nakajima, et al., 1991; Miyauchi & Nakajima, 2005; 2007). Despite the robustness of this phenomenon, its underlying neural mechanisms have not yet been clarified. In this study, we recorded event-related potentials (ERPs) of the human scalp to investigate brain processes involved in temporal assimilation.

ERPs have high temporal resolution, and are suitable to extract brain responses relevant to the perception of short time intervals from different brain areas at the same time. Previous studies with ERPs suggested that the perception of temporal intervals required several brain functions, such as working memory and attention (Gibbon, Malapani, Dale, & Gallistel, 1997; Grondin, 2001; Rubia & Smith, 2004). The ERP component related to these functions is often referred to as a contingent negative variation (CNV) (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV has been observed in temporal perception and estimation tasks; it is related to the memorization of time intervals (Pouthas, Garnero, Ferrandez, & Renault, 2000; Pfeuty, Ragot, & Pouthas, 2003), duration reproduction (Macar, Vidal, & Casini, 1999), and accumulation processes (Macar, et al., 1999; Pouthas, et al., 2000; Pfeuty et al., 2003). Another ERP component, the P300, (Picton, 1992) is also related to selective attention in temporal tasks (Le Dantec, Gontier, Paul, Charvin, Bernard, Lalonde, & Rebaï, 2007).

By presenting time intervals marked with three successive sounds, and by recording ERPs from the parietal and the frontal areas simultaneously, we might be able to extract several stages of temporal perception spatiotemporally.

In the present study, we used time intervals marked by three successive sounds, and recorded ERPs from the parietal and the frontal areas simultaneously. Following previous research, we first focus upon the CNV and the P300 generated from the frontal and the parietal areas. In order to eliminate effects that may have emerged irrelevant to the temporal judgment task, we compared the ERP components in a temporal judgment task with those obtained in a control task without judgments.

2. Experiment 1

The direct aim of Experiment 1 was to obtain electrophysiological indices of temporal assimilation. In order to measure the ERP correlates of temporal assimilation, we recorded ERPs from 11 electrodes over the scalp, while participants were engaged in a temporal judgment task.

2.1. Participants

Eight healthy volunteers participated. They were six females and two males, aged 21-35 years. All were right-handed and had no reported hearing deficits. Informed consent was obtained from each participant after an explanation of the purpose and the procedures of the experiment.

2.2. Apparatus and Stimuli

The experiment was conducted in an electromagnetically shielded soundproof room (Yamaha Music Cabin, SC-3 or SC-5). The background noise was kept below 30 dBA. Stimuli were synthesized with J software (the sampling frequency was 44.1 kHz) run on a Dell Dimension 4500C personal computer. They were diotically presented via headphones (Stax SR-303) to the participant by an AV tachistoscope (Iwatsu, IS-703), through low-pass filters (NF DV8FL with a cut-off frequency of 8 kHz) and a driver unit (Stax SRM-313). All stimuli consisted of two neighboring time intervals marked by three successive tone bursts of 1 kHz and 20 ms (5-ms rise/fall times and a 10-ms

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plateau). The sound pressure level of the tone bursts was 77 dBA. This level was measured as the level of a continuous tone of the same amplitude with a precision sound level meter (Node, type 2075), mounted with an artificial ear (Brüel & Kjær 4153). There were eight stimuli in total (Figure 1a): six standard stimuli, where the first interval (from the onset of the 1st marker to the onset of the 2nd marker: T1) varied from 100 to 280 ms (i.e., 100, 120, 160, 200, 240, and 280 ms), and the second interval (from the onset of the 2nd marker to the onset of the 3rd marker: T2) was fixed at 200 ms. There were two dummy stimuli, where the combinations of T1 and T2 were 240/240 and 200/100 (ms).
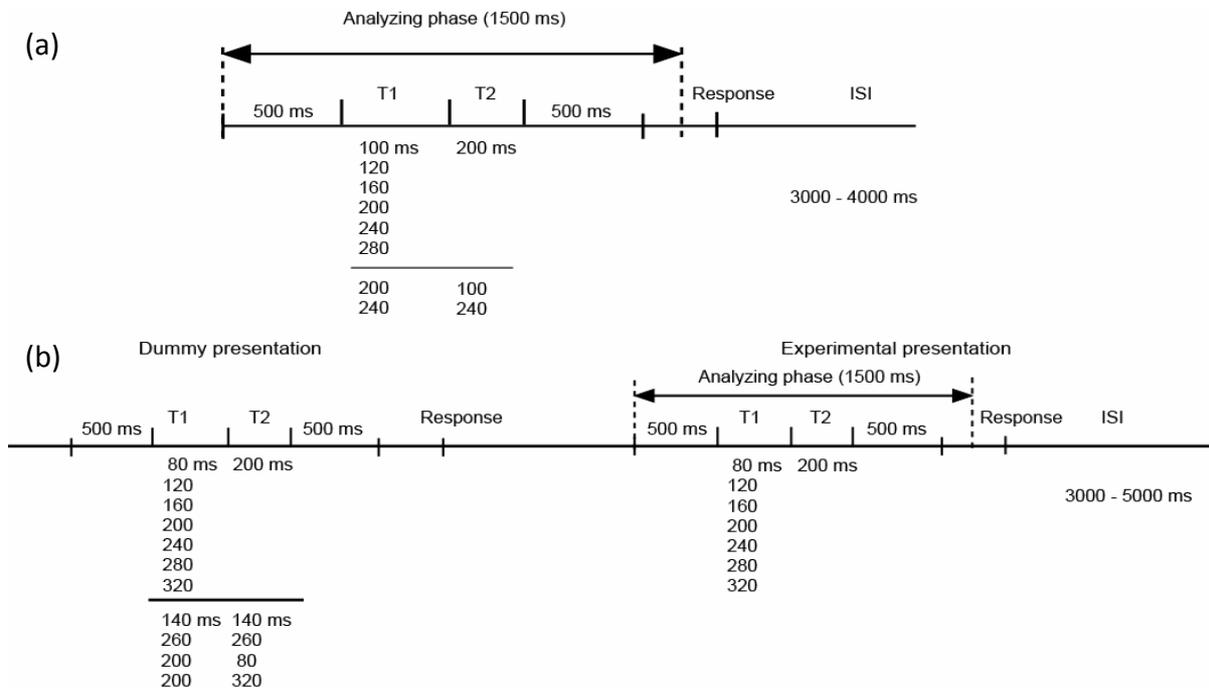
Figure 1. Procedures of Experiment 1 (a) and Experiment 2 (b). The stimulus epoch begins 500 ms prior to the onset of the 1st marker and continues 1000 ms after the onset of the 1st marker. Inter-stimulus intervals (ISIs) are randomly varied between 3 and 5 s.

2.3. Procedure

Two different tasks were performed in different sessions. In the *experimental task*, the participant judged whether the durations of T1 and T2 were the *same* or *different* by pressing quickly one of two buttons that were held in the right and the left hand. The *control task* consisted of passive listening to the stimuli and pressing one of the two buttons, chosen at the participant's own will, without making a judgment. For both the experimental and the control task, eight stimuli were presented about 95 times in pseudo-random order. The tasks were divided into 12 blocks of 64 trials (i.e., 8 stimuli × 7 or 8 presentations × 12 repetitions). Inter-stimulus intervals (ISIs) were varied randomly between 3 and 4 s. The allocation of the two buttons to the 'same' or the 'different' response was counterbalanced across participants. The participant first performed the control task and then the experimental task on different days.

2.4. ERP recording

ERPs were recorded by an EEG-1100 (Neurofax, Nihon Koden) from 11 scalp locations (Fz, F3, F4, Cz, C3, C4, Pz, P3, P4, T3, and T4, according to the international 10-20 system) referred to an electrode at the nose tip. Horizontal and vertical electro-oculograms (EOGs) were also recorded, using four electrodes placed over the outer canthi and in the superior and inferior areas of the orbit. The electrode impedance was kept below 5 kΩ. The ERP and EOG data were filtered with a bandpass of 0.27-300 Hz and sampled at a rate of 683 Hz. For the ERP analysis, each stimulus epoch began 500 ms prior to, and continued 1000 ms after, the onset of the 1st marker (Figure 1a). The participant was instructed to close his/her eyes and yet to stay alert. Trials that included artifacts defined as

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waves for which voltage exceeded ± 100 µ*V* at one or more electrodes were excluded from the analyses.

2.5. ERP analyses

ERPs were obtained by taking averages for each of the six standard stimuli. The 500-ms epoch prior to the beginning of the standard stimulus was used as a baseline to calculate the amplitude of the ERP waveforms. We analyzed the ERP components at the frontal (Fz) and parietal (Pz) areas to check spatiotemporal characteristics of the ERP components related to the temporal judgment. At Pz, a large positive component appeared about 500-950 ms after the stimulus onset in the experimental task. For the time being, we will call this component the P300, appearing after T1. We analyzed its peak latency and amplitude from the baseline. During the stimulus presentation, a CNV-like component appeared at Fz. In order to determine the neural activities regarding the temporal judgment, the mean CNV amplitudes in the experimental task and the control task were calculated over two successive 100-ms time windows (TW_{CNV}), from the onset of the 2nd marker to the onset of the 3rd marker (i.e., T2): $TW_{CNV}1$ and $TW_{CNV}2$. The CNV difference waves were calculated by subtracting the mean CNV amplitudes in the control task from those in the experimental task. The CNV difference waves were then averaged within each TW_{CNV} on Fz for each participant, and the averaged values were utilized for later statistical analyses. The data for the 240/240 and the 200/100 were not analyzed – these stimuli had been included to prevent the participant from expecting a fixed duration for T2.

3. Results

3.1. Response ratios

Figure 2 shows the results of the same-different temporal judgments averaged across participants. The participants judged the two neighboring time intervals as equal when -40 ≤ (T1-T2) ≤ +40 ms. The data from the experimental task were subjected to a one-way ANOVA. There was a significant main effect of stimuli; $F (5, 35) = 20.9$, $p < .001$. Dunnett's post-hoc *t*-tests revealed that the response ratios differed significantly from that obtained for the stimulus where T1 = T2 (200/200), when T1 =

100, 120, or 280 ms. This was not very far from our previous finding that T1 had been perceived as being equal to T2 when -80 ≤ (T1-T2) ≤ +50 ms (Miyauchi & Nakajima, 2005; 2007). However, the range of assimilation was symmetrical around zero in the present results.

3.2. ERPs

The grand averaged waveforms in the experimental and in the control task are shown in Figure 3. Figure 4 shows the ERP waveforms related to the six standard stimuli recorded from the three midline electrodes, Fz, Cz, and Pz. Electrophysiological data clearly showed that the same-different judgment task yielded a greater cognitive demand than the no-judgment task. Negative amplitude differences between the experimental and the control task began to appear after the 2nd marker, and continued until the 3rd marker appeared. Responses related to the same-different judgments were observed in the front-central slow negative component and in the parietal positive component not far from 300 ms after T1. These components, being defined as the CNV and the P300, respectively (Figure 3), must have reflected the cortical processing of temporal information.

3.2.1. P300 (Pz)

Latencies

The P300 latencies at Pz in each of the ERP waveforms related to the six standard stimuli (100/200, 120/200, 160/200, 200/200, 240/200,
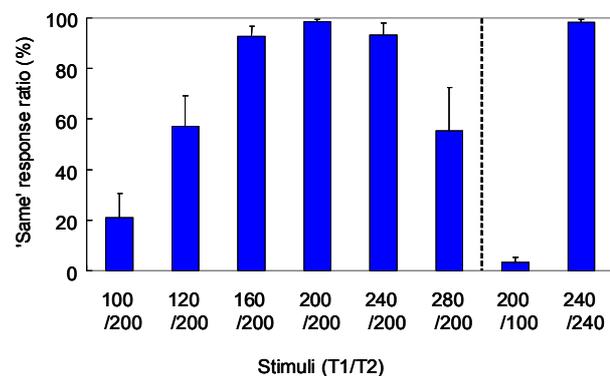
Figure 2. Results of the same-different judgments in Experiment 1. Each bar shows the ratio of the 'same' responses (i.e., the ratio in which T1 and T2 were perceived as having the same duration). T1 and T2 were perceived as equal when -40 ≤ (T1-T2) ≤ +40 ms. The results indicate that assimilation took place between T1 and T2. Error bars show the standard deviations.

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and 280/200) were analyzed with a one-way ANOVA. The main effect of stimuli was significant; $F (5, 35) = 10.40$, $p < .003$. A post-hoc analysis with Bonferroni correction showed that the P300 latencies to the 100/200 and the 120/200 stimulus were shorter than those for the other stimuli (Table. 1). The P300 latencies to the 100/200 and the 120/200 stimulus were 473 and 541 ms, respectively. The appearance of the P300 was about 400 ms after T1, which means that this component appeared after the 2nd marker; in the 100/200 pattern, the P300 emerged 373 ms after T1, while in the 120/200 pattern, it appeared 421 ms after T1. The results suggest that the participants paid more attention to the first interval (T1) than to the second interval (T2), especially when T1 was 100 or 120 ms.

Table 1.
Mean latencies and amplitudes of P300 in the judgment condition

Stimuli	Latency (ms)	Amplitude (μ V)
100/200	473.9 (30.5)	9.5 (4.0)
120/200	541.3 (78.4)	9.0 (4.6)
160/200	601.6 (75.0) [a]	7.7 (3.6)
200/200	694.0 (107.4) [a, b]	7.0 (4.0)
240/200	683.9 (89.2) [a, b]	6.3 (4.5)
280/200	763.7 (151.8) [a, b]	6.7 (5.0)

Note. Values represent the means (and the standard deviations) (n=8). Within each column, superscripts mark statistically significant differences compared with 100/200 ([a]) and 120/200 ([b]), p <. 05.

Amplitudes
The peak amplitudes of the P300 at Pz in each of the ERP waveforms related to the six standard stimuli (100/200, 120/200, 160/200, 200/200, 240/200, and 280/200) were subjected to a one-way ANOVA. The main effect of stimuli was significant; $F (5, 35) = 4.06$, $p < .05$. The P300 components for shorter intervals were larger than those for the longer intervals, irrespective of the judgment (same/different). In order to examine the relationship between stimuli and their P300 peak amplitudes, we additionally performed a linear regression analysis. A line was fitted to the averaged P300 amplitude data (Figure 5a). The P300 peak amplitude was negatively related to the length of T1: The longer the T1, the lower the P300 amplitude was. Its

slope was negative; $R^2 = .87$, and significant; Spearman's $r_s = .94$, $p < .05$.
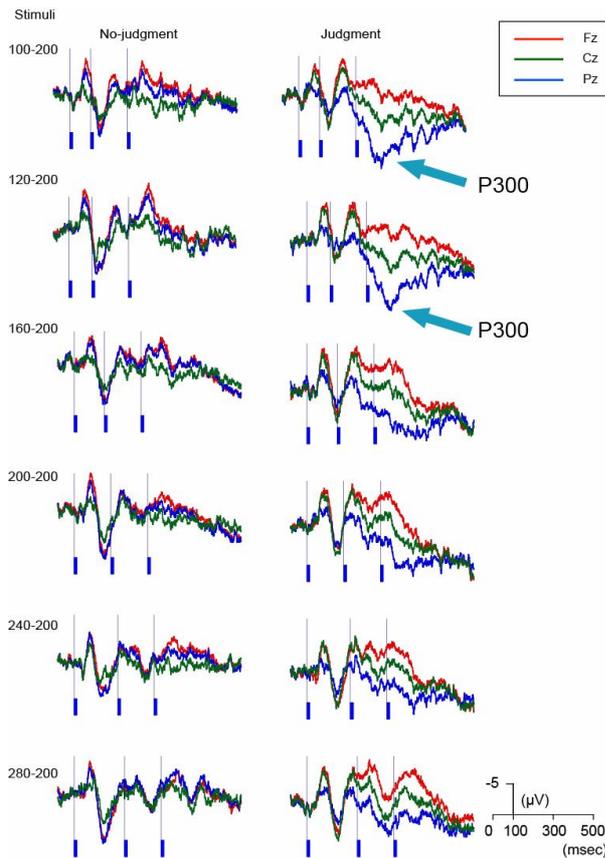
3.2.2. CNV (Fz)
The CNV difference waves at Fz in each of the ERP waveforms related to the six standard stimuli were also subjected to a one-way ANOVA for $TW_{CNV}1$ and $TW_{CNV}2$, respectively. Although the main effect of stimuli was not significant: $TW_{CNV}1$; $F (5, 35) = 0.89$, *n.s.*; $TW_{CNV}2$; $F (5, 35) = 0.24$, *n.s*; the linear regression line to the length of T1 in each of the six stimuli, was well fitted to the averaged CNV differences both in $TW_{cnv}1$ and in $TW_{CNV}2$ (Figure 5b). was positive; $R^2 = .79$ and significant; Spearman's $r_s = .84$, $p < .01$. The difference between the CNV amplitudes in the experimental and in the control task increased as T1 was lengthened.
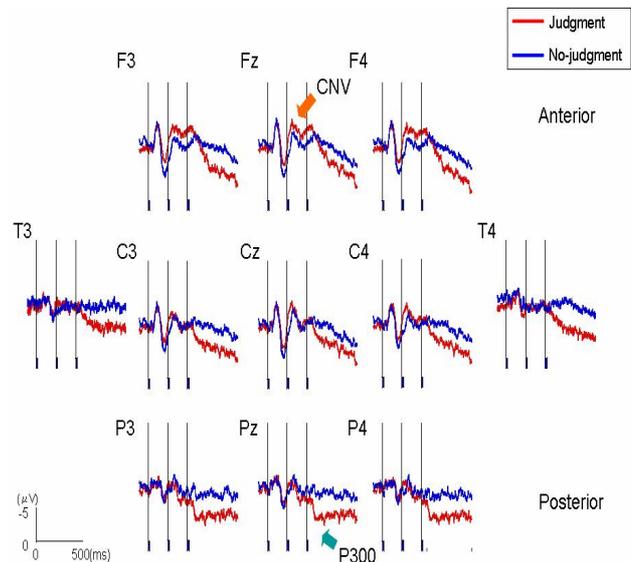
Figure 3. Averaged ERP responses elicited in the condition where T1 = T2 = 200 ms (physically equal) in Experiment 1. The two neighboring time intervals were perceived as equal. Red lines represent the ERPs obtained when the participants made same-different judgments, while the blue lines correspond to the control task, in which they listened to the stimuli passively. The CNV emerged in the frontal areas, whereas the P300 emerged in the parietal areas. This tendency was observed in all the other stimuli.

4. Discussion
Experiment 1 examined the neural processing of auditory temporal assimilation. We demonstrated that ERP components related to temporal perception could be extracted by contrasting the brain activations in the judgment condition and in the no-judgment condition.

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Figure 4. Averaged ERP waveforms related to the six standard stimuli recorded from the three midline electrodes, Fz, Cz, and Pz in Experiment 1. The left column indicates the no-judgment condition, and the right column the judgment condition. The P300 was especially large when T1 ≤ 120 ms.

Behavioral results showed a clear assimilation: participants judged the two neighboring time intervals as equal when -40 ≤ (T1-T2) ≤ +40 ms. One of our previous studies has confirmed that the range of temporal assimilation was clearly beyond the range indicated by the just noticeable differences (JNDs) of short time intervals (Sasaki et al., 1998). These data agree with the present behavioral data, in which the 'same' responses in a certain range around zero millisecond should have been caused by assimilation.

In our ERPs, two components, the CNV and the P300, appeared in response to the temporal judgment. Because the CNV has been associated with 'expectancy' of a subsequent stimulus (Walter et al., 1964, Tecce, 1972), we may assume that the CNV emerged when the participants processed and memorized the duration of the first interval (T1) to compare it
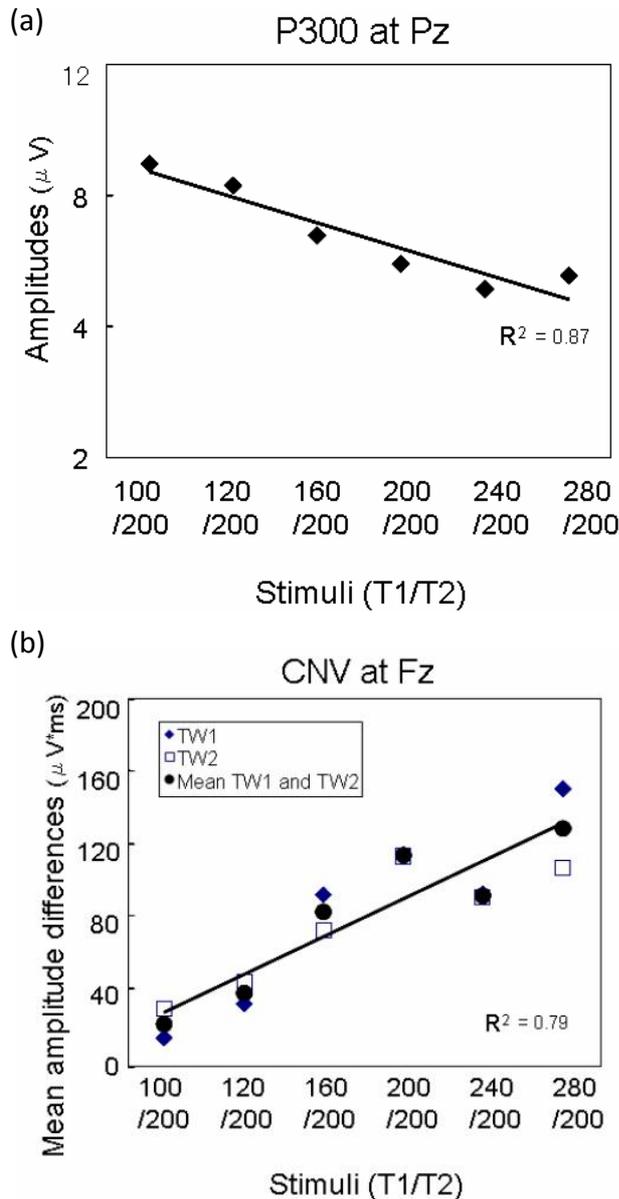
with the second interval (T2). It has been suggested that the CNV amplitude on the frontal electrode reflects the judged interval duration (Macar et al., 1999; Pfeuty et al., 2003), and larger CNV amplitudes have been obtained for longer memorized duration. These findings were in line with our result that the CNV amplitude in the experimental task increased as T1 was lengthened.

The P300 is known as an index of 'attention' (Picton, 1992). The positive component about 400 ms after T1 ≤ 120 ms in the parietal site may have been P3b, (Squires, Squires, & Hillyard, 1975) which occurred when the participants' were actively attending to the stimulus. This result suggests that the participants had difficulty in monitoring the arrival of the next marker; they may have needed more attention when T1 ≤ 120 ms.

Two questions still remain. Firstly, although the assimilation range obtained in the present experiment is not too far from the previous psychological finding that assimilation had taken place when -80 ≤ (T1-T2) ≤ +50 ms (Miyauchi & Nakajima, 2005; 2007; see also Nakajima, ten Hoopen, Sasaki, Yamamoto, Kadota, Simons, & Suetomi, 2004), the asymmetrical range around zero, which had appeared consistently in the previous research, did not appear. Secondly, the relative timing of the CNV and the P300 was sensitive to the timing at which the second sound marker was presented; they emerged corresponding to the physical duration of T1 but not to the judgment. A study indicated that a late positive component (LPCt) that directly related to temporal judgment appeared after two successive visual stimuli (Paul, Le Dantec, Bernard, Lalonde, & Rebaï, 2003). According to this study, an ERP component related to temporal judgment may be expected to appear after stimulus presentation. However, since T2 was fixed at 200 ms in the present experiment, the participants may have judged the equality of neighboring time intervals simply depending on a framework of 200 ms to be related to T1. If so, they could have discriminated the differences among stimuli mainly by focusing on T1. This strategy might have resulted in the absence of the asymmetrical temporal assimilation and assimilation-related components. In order to avoid such a strategy bias, we increased the

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number of dummy stimuli and widened the range of T1 in Experiment 2.

(a)

(b)

Figure 5. (upper) The peak amplitudes of P300 at Pz, and (lower) the amplitude differences of CNV between the judgment and the no-judgment condition in $TW_{CNV}1$ and $TW_{CNV}2$ in Experiment 1. The regression line in each panel was fitted to the means for $TW_{CNV}1$ and $TW_{CNV}2$.

5. Experiment 2

The aim of Experiment 2 was to further elucidate the processing of temporal assimilation. In Experiment 1, in which $-100 \leq (T1-T2) \leq +80$ ms, and only eight stimuli were employed, asymmetrical temporal assimilation as expected was not observed. In the present experiment, we utilized 11 temporal patterns with a widened time range of $-120 \leq (T1-T2) \leq +120$ ms. To check

brain activity in a broader area, we recorded ERPs from 19 electrodes instead of 11.

5.1. Participants

Nine healthy volunteers participated. They were seven females and two males, again 18-30 years old. None of them participated in Experiment 1. All were right-handed and reported no hearing deficits. Informed consent was obtained from each participant after an explanation of the purpose and procedure of the experiment.

5.2. Apparatus and Stimuli

The apparatus was the same as in Experiment 1 (Figure 1b). There were 11 stimuli: seven standard stimuli, in which the first interval (from the onset of the 1st marker to the onset of the 2nd marker: T1) varied from 80 to 320 ms in 40-ms steps (i.e., 80, 120, 160, 200, 240, 280, and 320 ms), and the second interval (from the onset of the 2nd marker to the onset of the 3rd marker: T2) was fixed at 200 ms. There were four dummy stimuli, where the combinations of T1 and T2 were 140/140, 260/260, 200/80, and 200/320 ms.

5.3. Procedures

The procedure was basically the same as in Experiment 1 except for the repetition. For both the experimental and the control task, the standard stimuli and the dummy stimuli were presented 100 times in pseudo-random order. The tasks were divided into 10 blocks of 40 trials and 10 blocks of 30 trials (i.e., 7 standard stimuli × 10 presentations × 10 repetitions). Dummy presentations, in which the dummy and the standard stimuli were employed, alternated with experimental presentations that were limited to the standard stimuli. ERPs were recorded only in the experimental presentations (Figure 1b). ISIs were varied randomly between 3 and 5 s. The participant first performed the control task and then the experimental task on four separate days in total.

5.4. ERP recording

ERPs were recorded by the same EEG machine from 19 scalp locations (Fp1, Fp2, F7, F8, Fz, F3, F4, Cz, C3, C4, Pz, P3, P4, T3, T4, T5, T6, O1, and O2, international 10-20 system) referred to an electrode at the nose tip. Horizontal and vertical electro-oculograms (EOGs) were also recorded

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using four electrodes placed over the outer canthi and in the superior and inferior areas of the orbit. The other recording details were the same as in Experiment 1.

5.5. ERP analyses

We first checked whether the two ERP components, the CNV and the P300 at the frontal (Fz) and parietal (Pz) areas, appeared again. Next, the mean CNV amplitudes in the experimental task and in the control task were measured over two successive 100-ms time windows ($TW_{CNV}1$ and $TW_{CNV}2$) from the onset of the 2nd marker to the onset of the 3rd marker. The CNV difference waves were calculated, and averaged within each TW_{CNV} at Fz for each participant. In addition, we picked out six frontal electrodes (Fp1, Fp2, F7, F8, F3, and F4) where a slow negative component (SNCt) after the stimuli emerged. Because any temporal comparison must have taken place after the participant had a chance to perceive both of the neighboring time intervals, the ERPs corresponding to the assimilation were expected to appear only after the 3rd marker (Paul et al., 2003). We assumed that the SNCt and the CNV reflect different functions regarding temporal judgment, and analyzed them separately. In order to obtain SNCt's, the stimulus epoch up to 400 ms after the end of the 3rd maker was divided into four time windows (TW_{SNCt}s) of 100 ms: $TW_{SNCt}1$ to $TW_{SNCt}4$. We calculated the SNCt difference waves by subtracting the mean SNCt amplitudes in the control task from those in the experimental task. The SNCt difference waves were averaged within each TW_{SNCt} on all of the 19 scalp electrodes, and the averaged values were utilized for statistical analyses.

6. Results

6.1. Response ratios

Figure 6 shows the results of the same-different judgments. The participants judged the two neighboring time intervals as equal when -80 ≤ (T1-T2) ≤ +40 ms. The data from the experimental task were subjected to a one-way ANOVA. There was a significant main effect of stimuli; $F (6, 56) = 39.17$, $p < .001$. Dunnett's post-hoc t-tests revealed that the response ratios differed significantly from that obtained for the stimulus where T1=T2 (200/200), when T1 was 80, 280, or 320 ms (200 ms vs. 80 ms; $p <$
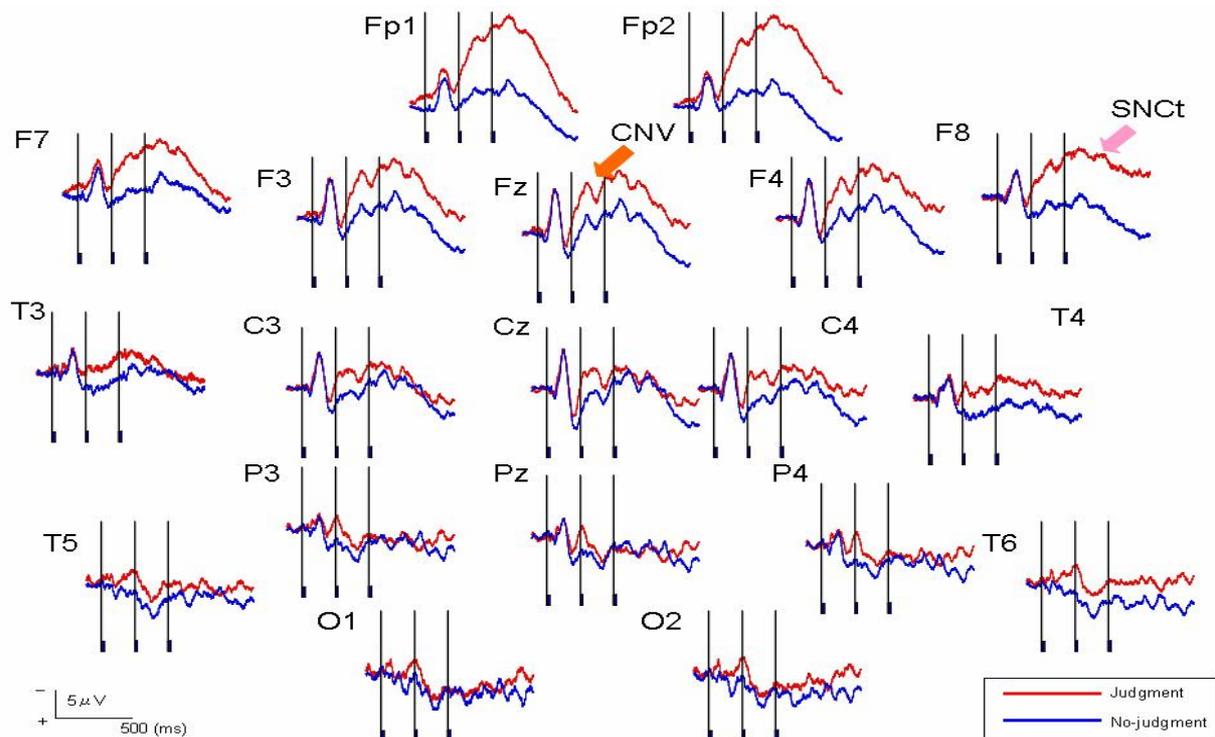
.001, 200 ms vs. 280 ms; $p < .001$, 200 ms vs. 320 ms; $p < .001$). T1 was perceived as equal to T2 when T1 was 120, 160, and 240 ms as well as when T1 = T2 = 200 ms —an asymmetrical temporal assimilation thus took place as in our previous reports (Miyauchi & Nakajima, 2005; 2007).
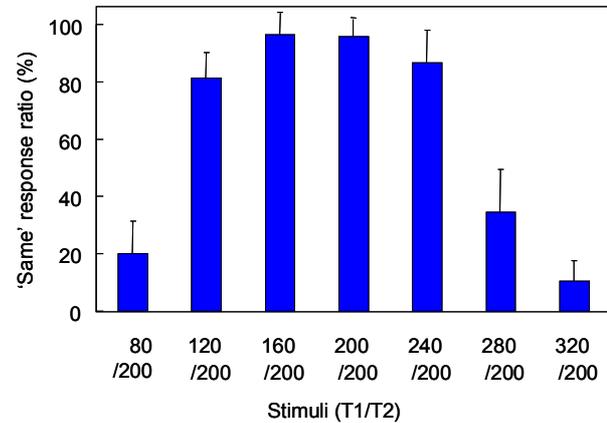
Figure 6. Results of the same-different judgments in Experiment 2. Each bar shows the ratio of the 'same' responses. T1 and T2 were perceived as equal when -80 ≤ (T1-T2) ≤ +40 ms. The results indicate that asymmetrical temporal assimilation indeed took place between T1 and T2. Error bars show the standard deviations.

6.2. ERPs

Figure 7 shows averaged ERP waveforms elicited in the condition where T1 = T2 = 200 ms, and Figure 8 shows ERP waveforms related to the six standard stimuli recorded from the three midline electrodes, Fz, Cz, and Pz. As seen in Figure 8, a P300-like positive component appeared in the parietal area not far from 300 ms after the first interval when T1 ≤ 120 ms. The amplitude differences between the experimental task and the control task emerged in the frontal area between the 2nd marker and the 3rd marker. The CNV was prominent in the experimental task, in which participants performed same-different judgments. In addition, a slow negative component (SNCt) in the right-prefrontal area was observed after the 3rd marker in the experimental task. It lasted until 400 ms after the stimuli. The amplitude was remarkably larger than the corresponding amplitude in the left prefrontal area. This prefrontal SNCt after the offset of the 3rd marker was assumed to contain components that reflect temporal judgments.

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Figure 7. Averaged ERP responses elicited in the condition where T1 = T2 = 200 ms (physically equal) in Experiment 2. The two neighboring time intervals were perceived as equal. Red lines represent the ERPs obtained when the participants made same-different judgments, while the blue lines correspond to the control task, in which they listened to the stimuli passively. The CNV emerged in the frontal areas and the SNCt emerged in the right-prefrontal areas.

6.2.1. CNV (Fz)

The CNV difference at Fz in each of the ERP waveforms related to the seven standard stimuli (80/200, 120/200, 160/200, 200/200, 240/200, 280/200, and 320/200) were also subjected to a one-way ANOVA for $TW_{cnv}1$ and $TW_{cnv}2$, respectively. The main effect of stimuli was significant for $TW_{cnv}1$; $F(6, 48) = 2.57$, $p <.05$; but not for $TW_{cnv}2$; $F(6, 48) = 0.85$, *n.s.* The length of T1 and the averaged CNV differences for $TW_{cnv}1$ and $TW_{cnv}2$ were linearly related. Its slope was positive; $R^2 = .83$, and significant; Spearman's $r_s = .54$, $p < .05$. (Figure 9). As in Experiment 1, the CNV amplitudes in the experimental task increased as T1 was lengthened.
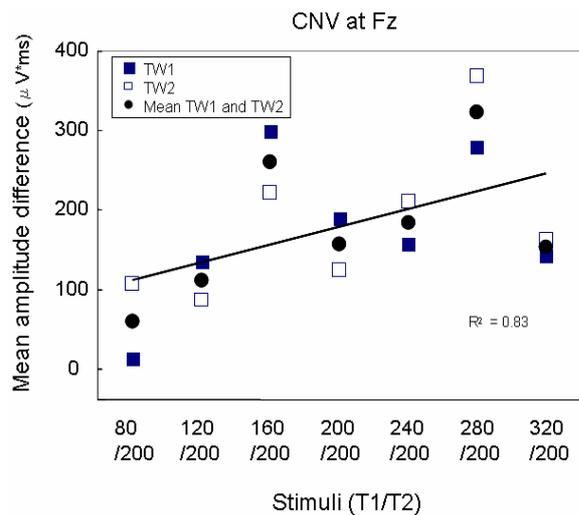
6.2.2. Neural correlates of temporal assimilation in SNCt

To check the relationship between the ERPs and the behaviorally shown temporal assimilation, we performed another type of selective averaging of the ERP data based on the behavioral results. We divided the ERPs into two groups: those obtained in the conditions where 'same' judgments dominated (i.e., T1 = 120, 160, 200, 240) and those obtained in the conditions where 'different' judgments dominated (i.e., T1 = 80, 280, 320). Figure 10 shows the color maps corresponding to the 'same' and the 'different' responses. A remarkable difference between these two ERP groups was observed in the right-prefrontal areas. We then compared the 'same' judgment ERPs with the 'different' judgment ERPs at the six frontal electrodes in each TW_{SNCt} individually. Two-sample *t*-tests were performed in terms of the two ERP groups in each of the four TW_{SNCt}'s over the six frontal electrodes (Fp1, Fp2, F7, F8, F3, and F4, respectively). In TW_{SNCt} 1 (i.e., from 0 ms to 100 ms after the offset of the 3rd marker), the neural activity derived from the F8 electrode was significantly smaller in the same-dominating group than in the different-dominating group (TW_{SNCt} 1; $t = -3.76$, $p < 0.001$).
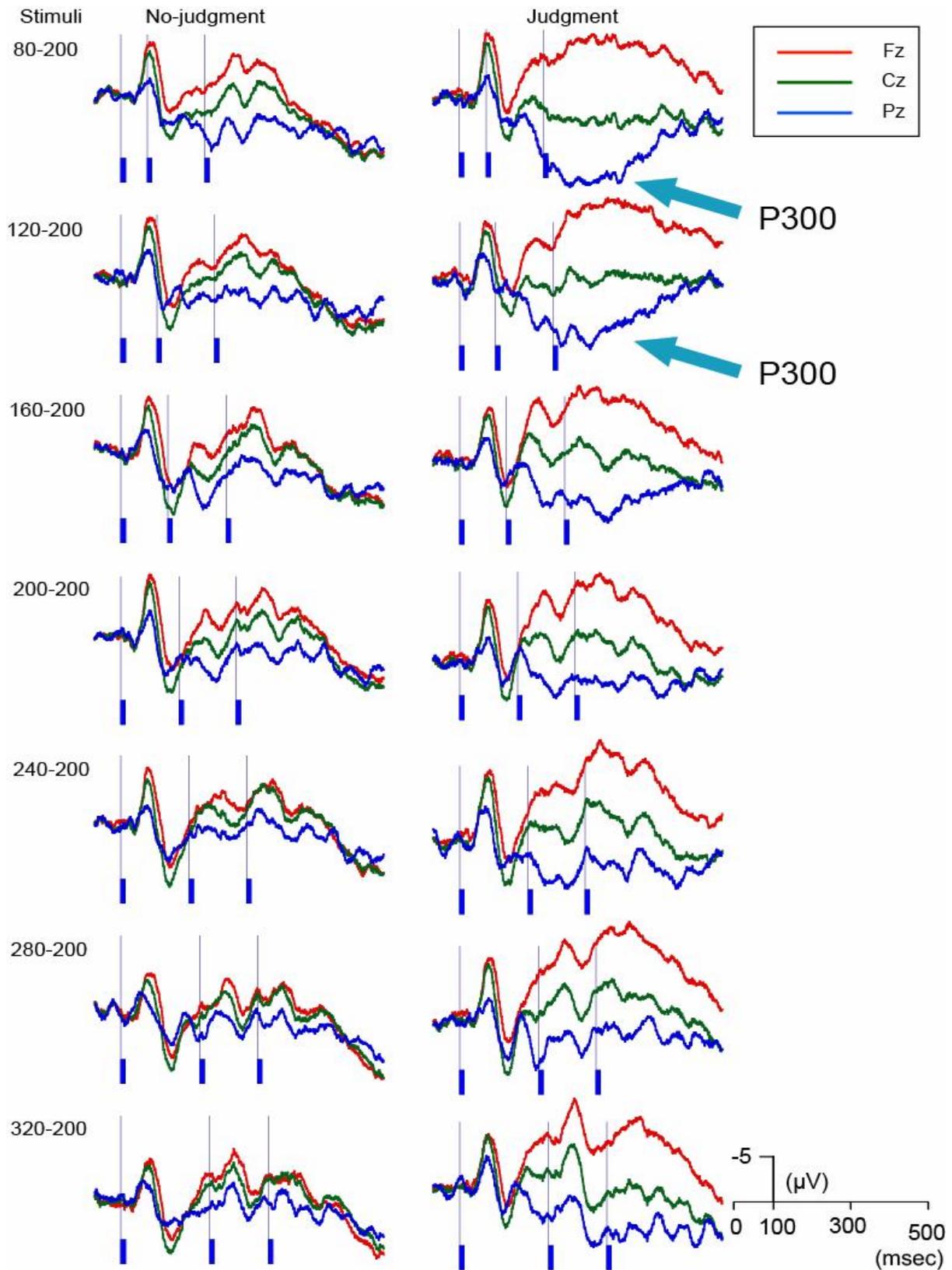
Figure 8. Averaged ERP waveforms related to the seven standard stimuli recorded from the three midline electrodes, Fz, Cz, and Pz in Experiment 2. The left column indicates the results in the no-judgment condition, and the right column the results in the judgment condition. The P300 was remarkable when T1 ≤ 120 ms.

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Figure 9. The amplitude differences of CNV between the judgment condition and the no-judgment condition in $TW_{CNV}1$ and $TW_{CNV}2$ in Experiment 2. The regression line was fitted to the means for $TW_{CNV}1$ and $TW_{CNV}2$ combined.

6.2.3. Laterality

For the ERP analysis, a three-way (7 T1 × 2 electrodes × 4 TW_{SNCt}'s) repeated-measures ANOVA was performed in order to check the effect of laterality for each of the three following pairs of homologous electrodes: Fp2/Fp1, F8/F7, and F4/F3. In the F3/F4 and F7/F8 pairs, the mean amplitude differences in the right side electrode tended to be larger than those in the left side electrode; F3/F4: F (1, 8) = 4.8, p = 0.06; F7/F8: F (1, 8) = 4.4, p = 0.06; but not in the Fp1/Fp2 pair: F (1, 8)= 0.3, p = 0.5.

7. Discussion

As observed in Experiment 1, the CNV and the P300 appeared again at the frontal area and the parietal area. The P300 was remarkable when T1 ≤ 120 ms; the P300 latency was shortened, and the amplitude tended to be augmented. In contrast, the CNV increased when T1 was longer. The activation of these components was quite similar to those observed in Experiment 1, despite different stimuli and participants. The elicitation of the two ERP components, the P300 and the CNV, throughout these experiments provides evidence that these ERPs were correlated with the processing of temporal information.

In the behavioral data, asymmetrical temporal assimilation took place when -80 ≤ (T1-T2) ≤ +40 ms. This is in accordance with previous psychophysical findings showing that temporal assimilation took place when -80 ≤ (T1-T2) ≤ +50

ms (Miyauchi & Nakajima, 2005; 2007; see also ten Hoopen et al., 2006). The ranges of assimilation in the previous studies and those in the present study fairly overlapped, although the time intervals adopted in our study somewhat differed. The difference between the results of Experiment 1 and Experiment 2 appeared unexpectedly. Probably a certain number of different stimuli should be employed to avoid the inadequate strategy of participants to attend only to the first time interval as in Experiment 1. The behavioral data in Experiment 2 showed the robustness of assimilation, and ensured the reliability of the experimental procedures.

In addition to the CNV and the P300 during stimulus presentation, the SNCt appeared after the 3rd marker in the right-prefrontal area. According to the ERP analysis, activity at the F8 electrode was prominent when the participants engaged in the same-different judgments. This is in line with the previous ERP and magnetoencephalographic literature which reported a crucial role of the right prefrontal area in time perception (Pouthas, et al., 2000; Pfeuty et al, 2003; Hairston & Nagarajan, 2007).

The SNCt activity was small when assimilation occurred. This may be explained by the economic use of cognitive resources (Casini & Macar, 1996; Casini, Macar, & Giard, 1999; Schubotz & Friederici, 1997). Recent reviews of functional magnetic resonance imaging studies reported that the right dorsolateral prefrontal cortex (rDLPFC) was involved in tasks of cognitive time estimation (Meck et al, 2008; Rubia & Smith, 2003), especially in comparison of time intervals (Rao, Mayer, & Harrington, 2001). The present results show that the ERP activation related to the same-different judgments emerged most prominently around F8, suggesting a relationship of the rDLPFC with the present temporal judgment task.

8. General Discussion

The present experiments comprised the first ERP study that visualized neural correlates of auditory temporal assimilation. Three ERP signatures were obtained as spatially and temporally separable components related to the process of temporal assimilation: P300 at Pz, CNV at Fz, and SNCt at F8. Each component is assumed to show a distinct brain process underlying the temporal assimilation.

Figure 10. ERPs obtained during the 'same' (top) and the 'different' (bottom) judgments of the standard stimuli. The maps show the brain activities in the time window of SNCt within 100 ms after the 3rd marker. The frontal areas' activation was small when assimilation took place. A significant difference between the same and the different responses emerged at F8.

The P300 and the CNV appeared during the stimuli. The P300 is assumed to reflect attention to T1; the participants focused on monitoring the passage of time. This is in accordance with a previous ERP study adopting a temporal judgment task (Le Dantec et al., 2007). The CNV reflected memory process for T1 (Macar et al., 1999; Pfeuty et al., 2003). The CNV

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between the onset of the 2nd marker and the onset of the 3rd marker (T2) must have changed depending on the memorized duration. The CNV activity observed over the frontal site was in line with previous studies, where the CNV amplitudes were larger when subjectively judged time was longer (Macar et al., 1999; Pfeuty et al., 2003; Le Dantec et al., 2007). Most remarkably, the SNCt at the right-prefrontal electrode was found to be related to the participants' temporal judgment. According to traditional models of interval timing, temporal judgment requires three psychological functions: attention, memory, and decision (Treisman, 1963, Gibbon et al., 1997, Grondin, 2001). The three above-mentioned components may be linked to these functions: P300 to attention, CNV to memory, and SNCt to decision.

The right-prefrontal SNCt that appeared up to 100 ms after the 3rd marker correlated with the behavioral performance; its activation was relatively small when the neighboring time intervals were perceived as equal. Earlier studies have documented that low frontal activation was linked to superior performances in some temporal judgment tasks, interpreted as a more economic use of cognitive resources (Casini & Macar, 1996; Casini et al., 1999; Schubotz & Friederici, 1997). Following these findings, the above attenuation of the SNCt activity can be explained by the economic information processing in the brain. The attenuation of SNCt observed in Experiment 2 in conditions where neighboring time intervals are mostly perceived as equal seems to have been caused by the occurrence of the unilateral or bilateral assimilation (Sasaki et al., 1998; Miyauchi &

Nakajima, 2005; 2007; Nakajima, et al., 2004; ten Hoopen et al., 2006). According to our psychophysical model of unilateral temporal assimilation (Nakajima, et al., 2004), the perceived difference between T1 and T2 should be reduced by cutting the processing time for T2 after the offset of the 3rd marker. If this model works in the present experimental paradigm, the whole processing, including the detection of the duration markers, may have continued a little longer than 80 ms after the 3rd marker in some stimulus conditions; the reduction of the SNCt in the assimilation conditions may appear longer than 100 ms. We are now examining this possibility utilizing a new set of data.

The most important finding in the present study was that the SNCt was strongly related to temporal judgment, which should be a decision making process involving assimilation or contrast. Thus, we presented an example of a brain-scientific representation of psychophysical models related to time perception.

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