Electrophysiological Substrates of Auditory Temporal Assimilation Between Two Neighboring Time Intervals

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ABSTRACT

Brain activities related to temporal assimilation, a perceptual phenomenon in which two neighboring time intervals are perceived as equal even when their physical difference is substantially larger than the difference limen, were observed. The neighboring time intervals (T1 and T2 in this order) were marked by three successive 1000-Hz pure-tone bursts of 20 ms. Event-related potentials (ERPs) were recorded from 19 scalp locations while the participants listened to the temporal patterns. Thirteen participants just listened to the patterns in the first session, and judged the equality/inequality of the neighboring intervals in the next session. The participant made his/her judgments on perceived equality/inequality by pressing one of two buttons. First, T1 was varied from 80 to 320 ms in steps of 40 ms, and T2 was fixed at 200 ms. About one year later, the same participants took part in another experiment in which the procedures remained the same except that the temporal patterns were reversed in time. Behavioral data showed typical temporal assimilation; equality appeared in an asymmetrical categorical range T1-T2 = -80 to 50 ms. Electrophysiological data showed a contingent negative variation (CNV) during T2 in the frontal area, which might reflect the process of memorizing the length of T1. A slow negative component (SNCt) after the presentation of T1 and T2 appeared in the right-frontal area, and continued up to about 400 ms after the end of T2; this component was larger when perceptual inequality took place.

I. INTRODUCTION

Our current purpose was to elucidate the mechanism of human auditory temporal perception. A phenomenon called "auditory 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., 2004; Miyauchi & Nakajima, 2007), was taken up for this purpose. We reported an ERP (event-related-potential) component closely related to this phenomenon in a previous study (Mitsudo, et al., 2009). In Mitsudo et al. (2009), we recorded ERPs while participants were judging equality/inequality of two neighboring time intervals, T1 and T2. An SNCt (slow negative component) appeared in the right-prefrontal area shortly after T2, and continued up to 400 ms. The magnitude of this component was larger for stimuli that were associated with subjective inequality between T1 and T2. Equality perception, including auditory temporal assimilation, seemed to correlate with smaller SNCt.

In the present study, we aimed at confirming the robustness of auditory temporal assimilation, and at exploring the mechanism of human rhythm perception more systematically in the same paradigm. ERPs were recorded while participants judged the equality/inequality of two neighboring time intervals. We first conducted an experiment employing the same stimulus patterns as in the previous study (Mitsudo, et al., 2009), but with new participants. About one year later, we conducted another experiment with the same participants, in which the stimulus patterns were reversed in time. If the SNCt in our previous study had really reflected the brain mechanism of rhythm perception, it should appear in another group of participants and for different stimulus patterns, and should be larger for the stimulus patterns in which the subjective inequality between T1 and T2 was dominant, i.e., when T1-T2 ≤ -80 ms or T1-T2 ≥ 50 ms.

Of our particular interest was the SNCt related to the judgment of equality/inequality to be made after T2. We compared the magnitudes of the SNCt after T2 between conditions in which equality/inequality judgments were and were not required.

II. EXPERIMENT

A. Participants

Thirteen healthy volunteers with normal hearing (Mean age 20.5 years, 1 male and 12 females) participated in each of Experiments 1 and 2. None of them were musically trained. Informed consent was obtained from each participant after an explanation of the purpose and procedures of the experiment, which were approved by the Ethics Committee of the Graduate School of Medical Sciences, Kyushu University.

B. 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 presented diotically from an AV tachistoscope (Iwatsu, IS-703) via a low-pass filter (NF DV8FL with a cutoff frequency of 8 kHz), an amplifier (Stax SRM-313), and headphones (Stax SR-303). All stimulus patterns consisted of two neighboring time intervals marked by three successive pure-tone bursts of 1 kHz and 20 ms with rise and fall times of 5 ms. 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 on an artificial ear (Brüel and Kjær 4153). In Experiment 1, we employed seven standard stimulus patterns, in which T1, as defined as the inter-onset interval between the 1st and the 2nd marker, varied from 80 to 320 ms in 40-ms steps, whereas T2, the inter-onset interval between the 2nd and the 3rd marker, was fixed at 200 ms. In Experiment 2, the same apparatus was utilized, and the stimulus patterns were reversed in time; T1 was fixed at 200 ms, and T2 varied from 80 to 320 ms. In each of these experiments, we employed four dummy stimulus patterns to prevent the participants from memorizing the fixed 200-ms duration. Indicating the neighboring time intervals as T1/T2 ms, the dummy patterns were 140/140, 260/260, 200/80, and 200/320 ms in Experiment 1, and the same patterns reversed in time in Experiment 2 (Figure. 1).

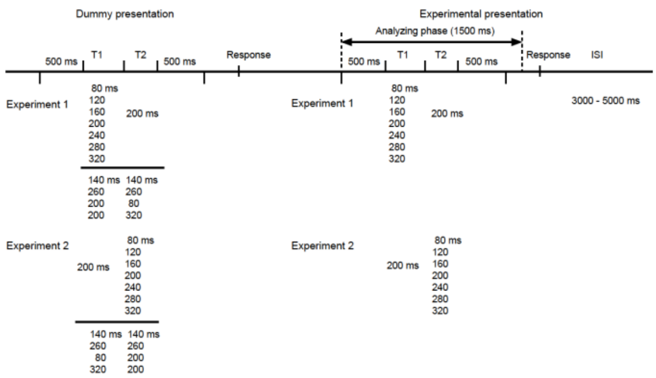

Figure 1. Experimental procedures. Stimulus epochs begin 500 ms prior to the stimulus and continue 1000 ms after the stimulus offset. Inter-stimulus intervals (ISIs) are randomly varied between 3 and 5 seconds. The procedures of the Experiments 1 and 2 were exactly the same except that the temporal patterns were reversed in time.

C. Procedure

We first conducted Experiment 1. Experiment 2 was conducted about one year after Experiment 1 with the same participants. Each experiment consisted of an experimental session and a control session. The task in the experimental session was to judge whether the durations of T1 and T2 were equal or unequal and to respond quickly by pressing one of two buttons held with both hands. The task in the control Figure. 1. Experimental procedures. Stimulus epochs begin 500 ms prior to the stimulus and continue 1000 ms after the stimulus offset. Inter-stimulus intervals (ISIs) are randomly varied between 3 and 5 seconds. The procedures of the Experiments 1 and 2 were exactly the same except that the temporal patterns were reversed in time. session was to listen passively to the stimuli and to press one of the two buttons, chosen at the participant's own will, without making a judgment. For both the experimental and the control session, the 7 standard stimuli and 4 dummy stimuli were each presented 100 times in random order. Dummy presentations, in which the dummy and the standard stimuli were employed, alternated with experimental presentations that were limited to the standard stimuli (Figure. 1). The sessions were divided into 10 blocks of 40 trials and 10 blocks of 30 trials (i.e., 7 standard stimuli × 10 blocks × 10 trials). ERPs were recorded only in the experimental presentation. ISIs were varied randomly between 3 and 5 s. The participant first performed the control session and then the experimental session on four separate days in total.

D. ERP recordings

ERPs were recorded 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, using EEG-1100 (Neurofax, Nihon Koden). 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 kW. The ERP and EOG data were band-pass filtered between 0.27 and 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 1). The participant was instructed to close his/her eyes and yet to stay alert. Trials that included artifacts defined as waves for which voltage exceeded ± 100 μV at one or more electrodes were excluded from the analyses.

E. ERP analysis

ERPs were obtained by taking averages for each of the seven stimulus patterns. 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 focused on 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). In order to examine SNCt, the stimulus epoch up to 400 ms after the end of the 3rd maker was divided into four time windows (TWSNCts) of 100 ms: TWSNCt1 to TWSNCt4. We calculated the SNCt difference waves by subtracting the mean SNCt amplitudes in the control session from those in the experimental session. The SNCt difference waves were integrated within each TWSNCt on all of the 19 scalp electrodes. In the current study, the integrated values of 6 frontal electrodes (Fp1, Fp2, F7, F8, F3 and F4) were utilized for further statistical analyses.

III. RESULTS

A. Behavioral data

Figure. 2 shows the results of the equal/unequal judgments. For each of Experiments 1 and 2, one-way (T1-T2 : -120, -80, -40, 0, +40, +80, +120 ms) ANOVA was conducted to analyze the behavioral data. 1 There were significant main effects of T1-T2 [Experiment 1: $F(6,84) = 46.3$, $p < .001$, Experiment 2: $F(6,84) = 64.6$, $p < .001$]. Dunnett's post-hoc t-test was performed for each experiment to check whether the equal response ratios obtained from 6 stimulus patterns (T1-T2 = -120, -80, -40, +40, +80, +120 ms) differed from that for the stimulus pattern of physically equal time intervals (T1-T2 = 0 ms). The response ratios differed significantly from that obtained for T1-T2=0 ms when T1-T2 was -120, +80, or +120 ms both in Experiment 1 (200/200 vs. 80/200: $p < .001$, 200/200 vs. 280/200: $p<.001$, 200/200 vs. 320/200: $p<.001$) and in Experiment 2 (200/200 vs. 200/80: $p < .001$, 200/200 vs. 200/120: $p < .001$, 200/200 vs. 200/320: $p < .001$). In both experiments, T1 was mostly perceived as equal to T2 when the difference between T1 and T2 (T1-T2) was in an asymmetrical range from -80 to 40 ms. The asymmetrical temporal assimilation indeed occurred.

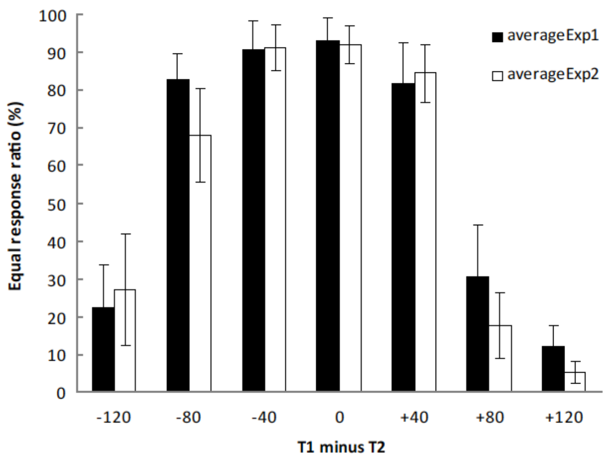

Figure 2. Results of equal-unequal judgments. Each bar shows the ratio of equal responses (i.e., T1 and T2 are perceived as having the same duration).The white and the black bars show the results of Experiment 1 and Experiment 2, respectively. T1 and T2 were perceived as equal when -80 ≤ (T1-T2) ≤ +40 ms. The results indicate that asymmetrical temporal assimilation took place between T1 and T2 in both experiments.

B. ERPs

A CNV-like component appeared at Fz during the stimulus presentation. The CNV was assumed to contain components reflecting the process of memorizing the length of T1 (Mitsudo, et al., 2009). The SNCt emerged in the frontal area at approximately 300 ms after the 1st marker and lasted until 400 ms after the 3rd marker. The SNCt amplitudes in the experimental session were greater in the right-frontal areas than those in the left corresponding areas.

1) Brain activities derived from equal-dominant/unequal dominant stimulus patterns. First, we divided the ERPs into two groups: those obtained in the conditions where equal judgments dominated (i.e., T1-T2 = -80, -40, 0, +40 ms) and those obtained in the conditions where unequal judgments dominated (i.e., T1-T2 = -120, +80, +120 ms).

Figure. 3 shows the color maps of the brain activities corresponding to equal- and unequal- dominant stimulus patterns in Experiment 1 (Top panel) and Experiment 2 (Bottom panel). A remarkable difference between these two groups was observed in the frontal area. A three-way (4 Time windows (TWs) × 2 laterality × 2 equality) repeated-measures ANOVA was performed over left- (Fp1, F7, and F3) and right- (Fp2, F8, and F4) frontal electrodes, to check the effect of laterality and equal/unequal judgment in each TW. The means (SDs) of the SNCt difference waves are shown in Table 1.

In Experiment 1, the main effect of equal/unequal judgment was significant [$F(1,12) = 5.95$, $p < .03$]. SNCt in the unequal-dominant stimulus patterns was significantly larger than that for the equal-dominant stimulus patterns. The interaction between equal/unequal judgment and laterality was also significant [$F(1,12) = 4.90$, $p < .04$]. The SNCt in the right-frontal area was larger for unequal-dominant stimulus patterns than for equal-dominant stimulus patterns ($p < .01$).

In Experiment 2, the main effect of laterality was significant [$F(1,12) = 10.38$, $p < .007$]. In addition, the interaction between laterality and TWs was significant [$F(3,36) = 4.61$, $p < .03$]. The neural activity derived from the right-frontal electrodes was larger compared to the left-frontal electrodes between 0 to 400 ms after the onset of the third marker (TW1: $p<.02$, TW2: $p<.008$, TW3: $p<.009$, and TW4: $p<.004$).

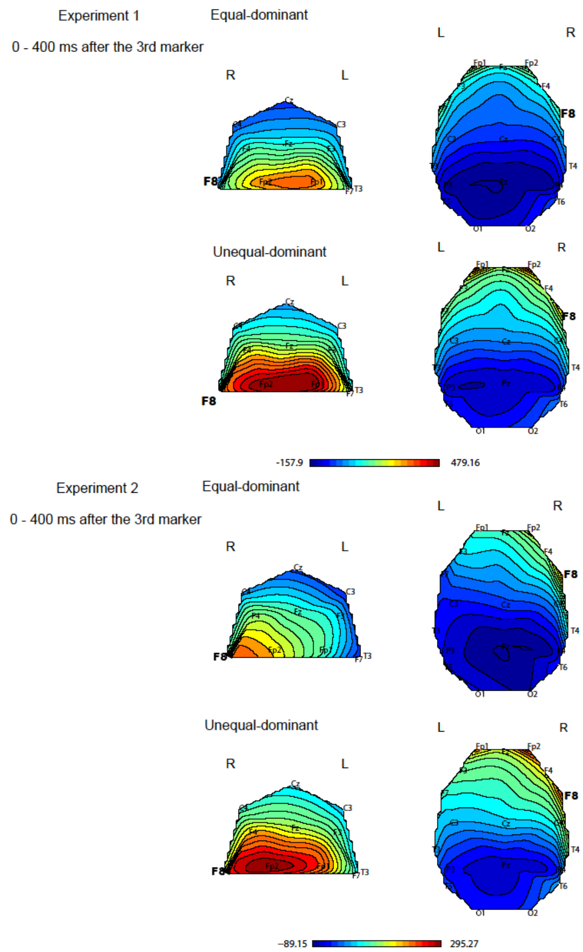

Figure 3. Topographical mapping of the brain activities during equal and unequal judgments of the standard stimuli. The maps show the brain activities in the time windows within 400 ms after the 3rd marker. In both Experiments 1 and 2, the right-frontal areas' activation is significantly larger for unequaldominant stimulus patterns than for the equal-dominant stimulus patterns. In Experiment 2, the SNCt derived from the right-frontal electrodes is significantly larger than that from the left.

Table 1. The means (SDs) of the SNCt difference waves categorized by the equal-dominant and the unequal-dominant stimulus patterns at left (FP1, F7, and F3) and right (FP2, F8, AND F4) frontal electrodes.

Time Windows (ms)	0-100		100-200		200 -300		300 -400	
Behavioral response	Equal	Unequal	Equal	Unequal	Equal	Unequal	Equal	Unequal
Experiment 1								
Left	281.5 (428.1)	353.5 (499.5)	330.3 (463.9)	387.4 (535.8)	254.6 (433.6)	358.9 (488.6)	213.1 (475.6)	340.0 (482.5)
Right	232.0 (436.8)	407.1 (477.8)	271.1 (469.2)	448.5 (498.8)	239.7 (409.9)	405.1 (489.0)	185.1 (447.1)	386.6 (527.3)
Experiment 2								
Left	37.3 (187.2)	140.5 (427.5)	62.5 (271.3)	203.9 (558.1)	-15.7 (269.4)	176.6 (631.0)	-27.5 (287.5)	120.6 (577.6)
Right	140.8 (304.3)	215.7 (427.1)	196.8 (363.8)	279.1 (541.8)	136.3 (374.2)	264.5 (592.3)	134.2 (385.7)	230.8 (583.4)

Note. Values are µV.

2) Neural correlates of perceptual equality/inequality. To check the relationship between the ERPs and the behaviorally shown perceptual equality/inequality, we performed another type of selective averaging of the ERP data. Trials in which participants responded equal or unequal were separated and averaged selectively.

We took the data of T1/T2 = 280/200 and 200/280 because of the following reasons. First, in these patterns, the temporal differences between T1 and T2 were both physically 80 ms. Second, behavioral data showed that the perception for these temporal patterns had some degrees of ambiguity: these patterns caused both “equal” and “unequal” judgments to substantial amounts, although the “unequal” judgment dominated for 280/200, while the “equal” judgment dominated for 200/280. Selective average waveforms were calculated for the “equal” and “unequal” response trials for each temporal pattern for each participant.

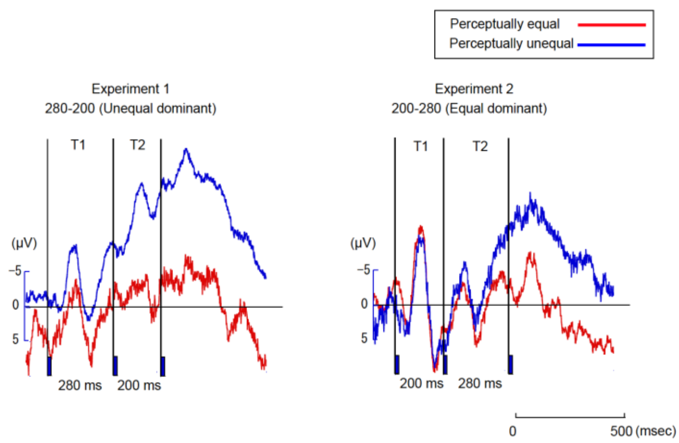

Figure 4. Averaged waveforms obtained from 3 right-frontal electrodes (Fp2, F8, and F4) in Experiments 1 and 2. Blue lines represent the ERPs when participants perceived two neighboring time intervals as unequal, while red lines correspond to participants’ equal perception. The SNCt is large when participants judged two time intervals as subjectively “unequal”. This tendency is observed both in 280/200 (an unequal-dominant stimulus pattern) and 200/280 (an equal-dominant stimulus pattern).

Figure. 4 showed the averaged ERP waveforms of T1/T2 = 280/200 and 200/280, obtained from 3 right-frontal electrodes (Fp2, F8, and F4). The SNCts at right-frontal electrodes showed larger activities when the brain process perceptual inequality of the rhythm. This tendency was observed both in 280/200 (an unequal-dominant stimulus pattern) and 200/280 (an equal-dominant stimulus pattern). Moreover, these SNCt differences between equality and inequality judgments were larger at right-frontal than at left-frontal electrodes.

IV. DISCUSSION

Behavioral result showed that assimilation took place in an asymmetrical time range of $-80 \leq (T1-T2) \leq +50$ ms. This is in accordance with previous psychophysical findings (Nakajima, et al., 2004; Miyauchi & Nakajima, 2007; Mitsudo, et al., 2009), and showed the robustness of this phenomenon. The slow negative component (SNCt) could be related to temporal judgment. SNCt repeatedly appeared in new group of participants at the right-frontal brain area 0-400 ms after the 3rd marker, even by different stimulus patterns. When the ERPs were divided into equal-dominant/unequal-dominant stimulus patterns, the SNCt derived from the right-frontal brain area was larger for the unequal-dominant stimulus patterns. The analyses based on the stimulus patterns indicated that the right-frontal brain area plays crucial role for perceiving time and rhythm (Pfeuty, Ragot, & Pouthas, 2003; Hairston & Nagarajan, 2007).

The most interesting finding in the current study was that the SNCts obtained from the right-frontal electrodes were larger when the brain processed perceptual inequality of the rhythm. The tendency was observed both in Experiments 1 and 2. Earlier studies have documented that the brain attenuated its activities when the temporal task was performed more efficiently (Casini & Macar, 1996). The magnitudes of SNCt can be explained by the economic information processing in the brain (Nakajima, et al., 2004). When the successively presented sounds are assumed to create regular time intervals, the brain is probably able to save its activity. This may have resulted in the low SNCt amplitude at the right-frontal areas in the equal responses. Previous literature reported that the right dorsolateral prefrontal cortex was involved in tasks of cognitive time estimation (Rubia & Smith, 2004), especially in comparison of time intervals (Rao, Mayer, & Harrington, 2001). The SNCt, which is related to the equal/unequal judgments emerged most prominently around the right-prefrontal electrodes (i.e., Fp2 and F8), suggesting the right dorsolateral prefrontal cortex could be a possible generator of the SNCt (Figures. 3 and 4). Another imaging technique like magnetoencephalography can confirm the spatio-temporal characteristics of this component.

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