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Transient gamma-band response is dissociated from sensory memory as reflected by MMN☆

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Abstract

The auditory gamma-band transient oscillatory response has been considered to reflect early cognitive processing and attention triggering, as has been suggested of the mismatch negativity (MMN). We examined whether the auditory gamma-band response was related to sensory memory as reflected by MMN. During the electroencephalogram (EEG) recordings, approximately 2000 click sounds were presented to nine healthy adult subjects with constant SOA of 120 or 170 ms in an ignored condition. At a probability of 10%, a click sound was randomly omitted from the stimulus sequence. EEG epochs responding to omitted clicks and to click sounds were averaged for analysis, respectively, and then those were convoluted by Gabor wavelet for the gamma-band response calculation. The MMN to a deviant omission in a sequence of click sounds was elicited with SOA of 120 ms which was shorter than the duration of temporal window of integration, whereas no MMN was elicited with SOA of 170 ms. In contrast with the MMN, the transient gamma-band response clearly commenced after the stimuli but not after the omissions, regardless whether SOA was short or long. The findings indicate that the brain process underlying the transient gamma-band response should be dissociated from the sensory memory function.

Keywords: MMN; Gamma-band response; Sensory memory; Omission; Temporal window of integration

The auditory gamma-band transient oscillatory response is elicited in the supratemporal auditory cortex by the onset of stimuli [4,11], is triggered by any auditory stimulus and lasts 100–200 ms [9]. The response is suggested to reflect the synchronization of oscillatory responses of feature-specific neurons for the perceptual integration of visual stimuli [3] and/or the temporal binding required for the unity of cognitive experience [2,7]. These findings indicate that the mechanism underlying the transient gamma-band response might be related to early cognitive processing [6]. Furthermore, Näätänen proposed that an attention-trigger mechanism might underlie the transient gamma-band response [9]. Tiitinen et al. demonstrated that the auditory gamma-band response is enhanced by selective attention [14].

The mismatch negativity (MMN) component of the event-related potentials (ERPs) is also related to early cognition and attention switching [1,8,9]. Tiitinen et al. examined the sensitivity of the auditory gamma-band response to occasional changes in stimulus features, in comparison with that of MMN [13]. MMN is generally considered to reflect change detection when a memory trace representing the homogeneous repetitive sound is different from the neural code of the incoming deviant sound [13]. Tiitinen et al. suggested that the gamma-band response might be dissociated from memory mechanisms because changes in qualitative stimulus aspects do not activate the generator mechanisms underlying the gamma-band response [13].

The best way to prove the existence of memory process is to demonstrate the brain activity in response to a stimulus omission. If a neuronal response can be generated by

☆ Excerpts of data from a chapter of our previously published book are employed in the present study for the new analysis [15].

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the information of omitted stimulus in spite of the absence of exogenous input, the mechanism underlying the response should require the storage of preceding stimuli, that is, a kind of memory process, because no afferent neuron could be activated by the physically absent stimulus [5]. Although no MMN can be elicited by a deviant omission in a sequence of repetitive tone pips or clicks in the ordinary oddball paradigm, MMN could be elicited only when the stimulus onset asynchrony (SOA) was as short as 150–170 ms [15–17]. The brain mechanism underlying the omission-MMN elicitation is termed the temporal window of integration (TWI) which integrates the compound sounds with temporal gap into a unitary event [1].

The aim of the present study is to examine whether or not the auditory gamma-band transient oscillatory response is related to memory function as reflected by MMN.

Nine healthy adults (ages 20–39 years; 2 males, 7 females) were studied in an electrically shielded, sound-attenuated chamber. Subjects gave informed consent after the nature of the study was explained to them. During the experiment, the subjects read a self-selected book in an ignore condition. Approximately 2000 click sounds of 0.1 ms in duration were presented to the subject's left ear through earphones at an intensity of 70 dB SPL with constant SOAs of 120 or 170 ms in a separate block. At a probability of 10%, a click sound was randomly omitted from the stimulus sequence.

The EEG was recorded from Ag/AgCl electrodes in 14 channels with nose reference. The electrode positions were Fp1, Fp2, F3, Fz, F4, C3, Cz, C4, P3, P4, T3, T4, left mastoid (LM), and right mastoid (RM). The scalp distribution of the MMN shows a fronto-central maximum, and polarity reversal in mastoid recordings. Such an inversion over the Sylvian fissure toward the mastoids has been confirmed for the MMN to various stimulus changes [10]. The electro-oculogram (EOG) was recorded from the outer canthi of both eyes. EEG and EOG were recorded with a time constant of 1.0 s and a high-frequency cut-off of 120 Hz. The analysis period was 256 ms, including 50 ms pre-stimulus interval. ERPs were separately averaged for omitted clicks (moments at which clicks should have commenced) and for click sounds. The averaged number of trials was around 120 for the omitted clicks and 200 for the clicks. EEG epochs contaminated by extra-cerebral artifacts (amplitude change exceeding 150 μV) were automatically rejected. Finally, both grand-average ERPs across all subjects were calculated. The baselines of ERPs were defined as the mean amplitudes ranging from pre-stimulus 20 ms to post-stimulus 20 ms. The early parts (20 ms) and late parts (20 ms) of ERP waveforms were lost in the figures as the result of ±20 ms moving average.

The EEG was digitally convoluted by Gabor wavelet, yielding a continuous measure of frequency-specific power over time (Gabor filter). The details of this Gabor filtering technique have been reported in the previous papers [12]. The Gaussian frequency gain function was centered at 40 Hz (S.D. 4.0 Hz) so that gamma band activity could be adequately enhanced. The continuous power changes were separately averaged for clicks and stimulus omissions, and quantified as a percentage. Statistics (Student's *t* tests) were obtained for the MMN and for the gamma-band response at the electrodes Fz, Cz, T3, T4, LM, and RM. The responses were quantified by averaging the ERP responses at 90–110 ms after click sound or its omission, and by calculating the peak amplitudes of the gamma-band responses at 20–40 ms.

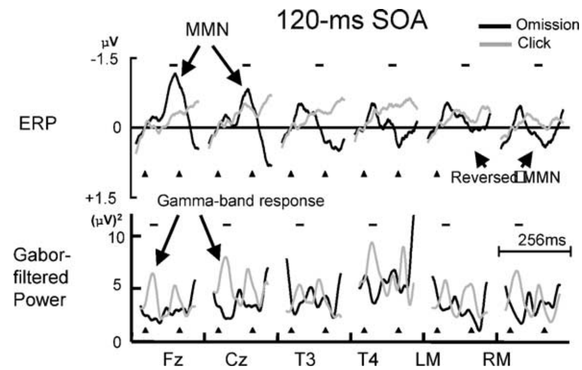

Fig. 1. Grand-average ERPs (top) vs. grand-average Gabor-filtered power waveforms (bottom) with 120 ms SOA in response to click sounds (gray) and omissions (black) at Fz, Cz, T3, T4, LM, and RM. A definite MMN at Fz and Cz and a reversed MMN at LM and RM are elicited by the omitted clicks but not by click stimuli (top). The transient gamma-band response is generated by the click sounds but not by the omissions (bottom). The filled triangles (▲) indicate the temporal points of omissions or clicks. The horizontal short bars indicate the measurement window for statistics, 90–110 ms for ERPs and 20–40 ms for the gamma-band responses.

Grand-average ERPs for the click sounds (gray) and the omitted clicks (black) are shown in the top row of Fig. 1 (120-ms SOA) and Fig. 2 (170-ms SOA). MMN was elicited only in the case of omission with 120-ms SOA (the ERP amplitudes to the omitted clicks with 120-ms SOA versus 170-ms SOA at Fz: $t(8) = 3.64$, one-tailed $p < 0.004$; Cz: $t(8) = 2.29$,

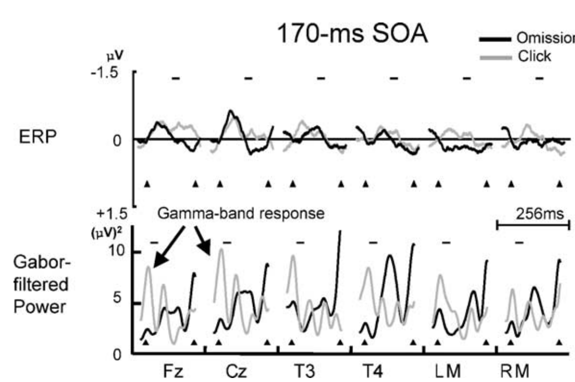

Fig. 2. Grand-average ERPs (top) vs. grand-average Gabor-filtered power waveforms (bottom) with 170 ms SOA in response to click sounds (gray) and omissions (black) at Fz, Cz, T3, T4, LM, and RM. The transient gamma-band response is generated by the click sounds but not by the omissions (bottom). No MMN is seen.

one-tailed $p < 0.03$; T3: $t(8) = 0.12$, ns; T4: $t(8) = 0.37$, ns; LM: $t(8) = 0.41$, ns; RM: $t(8) = 0.40$, ns; click versus omission with 120-ms SOA at Fz: $t(8) = 1.73$, one-tailed $p < 0.07$; Cz: $t(8) = 1.62$, one-tailed $p < 0.08$; T3: $t(8) = 0.45$, one-tailed ns; T4: $t(8) = 0.449$, ns; LM: $t(8) = 0.11$, ns; RM: $t(8) = 1.42$, one-tailed $p < 0.1$). Grand-average 'gamma-band Gabor-filtered power' waves to click sounds (gray) and omissions (black) are shown in the bottom row of the figure. Transient gamma-band responses were seen only in the case of click stimuli both with 120-ms (click versus omission at Fz: $t(8) = 1.13$, ns; Cz: $t(8) = 1.48$, one-tailed $p < 0.1$; T3: $t(8) = 0.72$, ns; T4: $t(8) = 1.71$, one-tailed $p < 0.07$; LM: $t(8) = 1.03$, ns; RM: $t(8) = 2.05$, one-tailed $p < 0.04$) and 170-ms SOAs (click versus omission at Fz: $t(8) = 1.42$, one-tailed $p < 0.1$; Cz: $t(8) = 1.77$, one-tailed $p < 0.06$; T3: $t(8) = 1.13$, ns; T4: $t(8) = 1.29$, ns; LM: $t(8) = 2.80$, one-tailed $p < 0.03$; RM: $t(8) = 1.13$, ns), but no responses in the case of omission.

Definite polarity inversion can be seen at RM in Fig. 1. The baseline period for analysis was limited to short by the peculiar stimulation.

The present results showed a clear MMN to omitted click sound when the constant SOA was 120 ms, whereas no MMN was elicited when the SOA was 170 ms. The previous studies revealed that the occurrence of the omission-MMN depends on the mechanism of the temporal window of integration (TWI) [1,9,15–17]. Based on TWI mechanism, if two stimuli are presented in close succession, the second stimulus enters the system within a period during which the integration process initiated by the onset of the first stimulus is still in the integration window. Therefore, the neural representation stored in auditory sensory memory was not a click itself but rather a compound event including the silent period of about 160 ms [15].

In contrast with MMN, the transient gamma-band response [3,7,4,9,11,14] definitely commenced after the click sounds but not clearly after the omissions, regardless of whether SOA is short (120 ms) or long (170 ms). The gamma-band response might not be elicited by the omission, or might be elicited but could not be seen because of time jitter. The event of "omission" may induce time jitter, because the gamma-band response when averaged may suffer from the uncertain estimation of time by the brain.

These findings suggest that the generator underlying the transient gamma-band response should be dissociated from the TWI mechanism in sensory memory as reflected by MMN. The dissociation between MMN and a transient gamma-band response implies that early cognition and attention switching as reflected by MMN does not require the activation of the mechanism underlying the transient gamma-band response. The present findings support Tiitinen et al.'s hypothesis that the transient gamma-band response serves detection of stimulus occurrence without responding to stored information of the preceding sounds [13].

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