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Effects of Sensory Modality and Task Relevance on Omitted Stimulus Potentials*

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Statements and Declarations

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Abstract

Omitted stimulus potentials (OSPs) occur when a sensory stimulus is unexpectedly omitted. They are thought to reflect predictions about upcoming sensory events. The present study examined how OSPs differ across the sensory modalities of predicted stimuli. Twenty-nine university students were asked to press a mouse button at a regular interval of 1–2 s, which was immediately followed by either a visual or auditory stimulus in different blocks. The stimuli were sometimes omitted ($p = 0.2$), to which event-related potentials (ERPs) were recorded. The results showed that stimulus omissions in both modalities elicited ERP waveforms consisting of three components, oN1, oN2, and oP3. The peak latencies of these components were shorter in the auditory modality than in the visual modality. The amplitudes of OSPs were larger when participants were told that the omission indicated their poor performance (i.e., they pressed a button at an irregular interval) than when it was irrelevant to their performance. These findings suggest that OSPs occur from around 100 ms in a modality-specific manner and increase in amplitude depending on the task-relevance of stimulus omissions.

Keyword: Event-related potential, Omission, Sensory modality, Task relevance, Prediction, Self-generation

Introduction

Event-related potentials (ERPs) can be observed not only when a sensory stimulus is delivered but also when a predicted sensory effect is unexpectedly omitted. These potentials have been referred to as omitted stimulus potentials (OSPs; Bullock et al. 1994; Hernández and Hernández-Sánchez 2017), missing stimulus potentials (MSPs; Simson et al., 1976), or omission responses (SanMiguel et al. 2013b; Braga and Schönwiesner 2022). We use the term OSPs throughout the manuscript. Recent research has suggested that oN1, oN2, and oP3 are elicited in response to the omission of self-generated sensory stimuli, which are analogous to N1, N2, and P3 elicited by actual sensory stimuli (Dercksen et al. 2020; SanMiguel et al. 2013a; Stekelenburg and Vroomen 2015; van Laarhoven et al. 2017), and these OSP components are assumed to reflect the processing of prediction errors that are not contaminated by sensory evoked potentials (Friston 2005; Arnal and Giraud 2012; SanMiguel et al. 2013a).

OSPs that occur in a latency range of less than around 200 ms are considered the processing of prediction errors in sensory areas of the brain (SanMiguel et al. 2013b; Stekelenburg and Vroomen 2015). If this is the case, OSPs should occur to reflect the difference in the sensory modalities of the predicted stimulus. It has been reported that the peak latencies of OSPs are shorter in the auditory modality than in the visual (Simson et al. 1976; Nittono 2005; Hernández and Hernández-Sánchez 2017) and somatosensory modalities (Hernández and Hernández-Sánchez 2017). These findings indicate that OSPs may reflect processing in modality-specific cortical areas. However, it remains unclear whether earlier OSPs occur in a modality-specific way, as previous studies have mainly dealt with time windows after around 200 ms. In the present study, we compared the time course of prediction-related neural responses to stimulus omission as a series, including early potentials such as oN1, between sensory modalities. The electrical sources of earlier OSPs were also compared between sensory modalities.

Most studies on OSPs have examined brain responses to stimulus omission by manipulating the physical contexts of the stimuli preceding the omission. Such studies have demonstrated that OSPs are attenuated when stimuli are randomly presented in terms of content (SanMiguel et al. 2013a; Kimura and Takeda 2018; Dercksen et al. 2020) or timing (van Laarhoven et al. 2017). These results suggest that OSPs are sensitive to the predictability of identity and timing of the upcoming stimulus. However, even when the physical contexts of stimuli are the same, the processing of stimulus omission should be affected when the reasons or contexts for stimulus omission differ. For example, Nittono and Sakata (2009) asked participants to press a button with a constant interval of 1–2 s. Each button press was followed by a visual stimulus, which was omitted infrequently. They also manipulated the meaning of the stimulus omission in the task instructions. The results showed that the amplitudes of oN2 (200–250 ms) and oP3 (300–500 ms) were larger when participants were told that stimulus omission occurred due to their irregular button press intervals than when participants were told that stimulus omission occurred randomly. Moreover, frontocentral feedback-related negativity (FRN) was elicited around 200–250 ms in addition to regular OSPs in the task-relevant condition, as stimulus omissions served as feedback on participants' button press performance (Walsh and Anderson 2012). These results suggest that OSPs can be affected by task instruction and the importance given to omissions.

In the present study, we examined the nature of OSPs by comparing sensory modalities (visual and auditory) and manipulating the task relevance of stimulus omission. Three hypotheses were tested. First, the latency of each OSP component would be shorter in the auditory modality than in the visual modality (H1). Second, the electrical sources of earlier oN1 and oN2 would be estimated in the sensory cortex corresponding to each sensory modality (H2). Third, the amplitudes of OSP components would be larger when stimulus omissions conveyed information about task performance in both visual and auditory modalities (H3).

Methods

Participants

Forty undergraduate and graduate students participated in the experiment. We used a sample size comparable to those used in recent OSP studies, for example, 31 participants in Dercksen et al. (2020) and 30 participants in Kimura and Takeda (2018). All participants self-reported having normal vision and hearing. Written informed consent was obtained before the experiment. The deception in the instruction (see below) was debriefed after the experiment, and only those who agreed to their data being used were included in the analysis (none withdrew). Participants received 2,000 Japanese yen as monetary compensation. The study protocol was approved by the Behavioral Research Ethics Committee of the Osaka University School of Human Sciences (HB021-106) in accordance with the Declaration of Helsinki. After excluding data based on the exclusion criteria described below, data from 29 participants (17 males and 12 females, 19–31 years old, $M = 22.9$ years old) were used for the analysis. All but two of them were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield 1971).

Stimuli and tasks

Fig. 1 shows the schematic representation of the experiment. Following Nittono and Sakata (2009), participants were asked to press the mouse button with their index finger at a constant interval of 1–2 s. Immediately after the button presses, a visual or an auditory stimulus was presented in separate blocks. The hands used for button pressing were counterbalanced across the participants. In the visual modality, an LED light (20 mm × 20 mm) was presented for 70 ms, and in the auditory modality, a 1000-Hz pure tone (rise/fall 10 ms) was presented for 70 ms. Prior to the experiment, participants were asked to match the volume of the tone to the light intensity (approximately 360 cd/m^2) so that the light and tone intensities were subjectively equal. The LED light was placed on a tabletop right in front of the participant and a viewing distance of 60 cm, and auditory stimuli were presented binaurally through earphones using the Ez-SOUND sound stimulus system (Nihon Santeku, Osaka, Japan). The experiment was controlled using Inquisit 6.5.1 (Millisecond Software, Seattle, WA, USA).

Procedure

A visual or auditory stimulus was presented after each button press when it was done within 800–2,400 ms after the previous button press. Participants were informed that occasionally the stimulus would not be presented, even after a button press. Following Nittono and Sakata (2009), we gave the participants two types of instructions regarding the reasons for the stimulus omission. In the relevant condition, they were told that stimuli would not be presented if the interval between button presses was irregular; they should keep the intervals constant so that as many stimuli as possible were presented. In the irrelevant condition, participants were instructed to continue the button press without worrying about stimulus omission, as it would occur randomly. In fact, both conditions used the same program in which the stimulus was omitted with the same probability of 20% regardless of participants' button press intervals, with the restriction that a stimulus was presented in the first two trials of the block and the trials after two consecutive omission trials. When the button was pressed outside the range of 800–2,400 ms after the previous button press, no stimulus was presented and this was counted as an error.

Participants performed all four types of tasks: Sensory Modality (visual and auditory) × Condition (relevant and irrelevant). Each task consisted of three blocks of 100 trials, that is, 240 stimulus trials and 60 omission trials. Fifteen practice trials were given at the beginning of each modality task to allow participants to learn the appropriate button press interval and to familiarize themselves with the change in the sensory modality of the feedback stimulus. The order of stimulus modalities and the order of conditions within the stimulus modality were counterbalanced across the participants. At the beginning and end of the experiment, participants were asked to press a button at a regular interval of 1–2 s without any stimulus following 60 times (120 times in total) as a motor control condition, the data of which were used to correct movement-related potentials in the ERP waveforms.

After completing each experimental task and motor control condition, participants were asked to rate the difficulty of the task and the degree of concentration during the task on a scale of 1–9. Moreover, they were asked to rate the degree to which they thought the button press was associated with stimulus presentation on a visual analog scale of 0–100 after each task.

Electroencephalogram recording

Electroencephalogram (EEG) was recorded from 64 sites using Ag-AgCl active electrodes (ActiveTwo system, BioSemi, Netherlands) at a sampling rate of 2048 Hz and with a 0–400 Hz bandpass filter. A reference electrode (Common Mode Sense [CMS], active electrode) and a ground electrode (Driven Right Leg [DRL], passive electrode) were also placed on the scalp. An electrode was placed on the nose tip for offline re-reference. Vertical and horizontal electrooculograms were recorded from four additional electrodes placed lateral to the outer canthi of the eyes and above and below the right eye (UltraFlat active electrodes).

Exclusion criteria

A total of 11 participants were excluded from the analysis based on the following criteria: those who recognized that the same program was used in the relevant and irrelevant conditions (n = 2) and those who had 10% or more error trials in any condition (n = 9). Thus, data from the remaining 29 participants were used for the analysis. The mean percentages of error trials were 1.43% in the visual relevant condition, 0.79% in the visual irrelevant condition, 1.24% in the auditory relevant condition, 1.05% in the auditory irrelevant condition, and 0.63% in the motor control condition. These error trials were excluded from the following analysis.

Data reduction

The mean subjective ratings and the mean button press intervals were calculated for each experimental task. For the motor control condition, the blocks conducted at the beginning and end of the experiment were pooled and the subjective rating scores were averaged. The EEG data were analyzed using Brain Vision Analyzer 2.2.2 (Brain Products, Germany). The data were resampled to 512 Hz, and digital high-pass filter of 0.1 Hz (12 dB/oct) and low-pass filter of 30 Hz (48 dB/oct) were applied. Eye blinks and eye-movement-induced artifacts were corrected using Gratton et al.'s (1983) method. The epochs 200 ms before and 800 ms after the button press of the omission trials were averaged per task and condition. Trials that contained a voltage step of greater than 100 μV between adjacent sampling points, a voltage difference of greater than 250 μV within an epoch, or a maximum voltage difference of less than 0.5 μV within 100-ms intervals were removed (Foti et al. 2009; Matsuda and Nittono 2018). The percentages of rejected trials were 1.9% in the visual relevant condition, 2.1% in the visual irrelevant condition, 4.4% in the auditory relevant condition, 4.2% in the auditory irrelevant condition, and 3.1% in the motor control condition. Baseline correction was performed by subtracting the mean amplitude of the initial 200-ms period from the amplitude of the entire averaged waveform at each point. Moreover, the ERP waveforms in the motor control condition were subtracted from the ERP waveforms in the omission trials to correct movement-related potentials.

To test the effect of sensory modality on the latencies of OSPs (H1), peak latencies were identified at the predominant site of each OSP component. oN1 was identified as the most negative peak in the time window of 50–150 ms at CP4 for the visual modality and T8 for the auditory modality. oN2 was identified as the most negative peak in the time window of 150–350 ms at T8 for both the visual and auditory modalities. oP3 was identified as the most positive peak in the time window of 250–550 ms at Cz for both the visual and auditory modalities. Peak latencies were compared between the visual and auditory modalities.

To test the effects of task relevance on the amplitudes of OSPs in the visual and auditory modalities (H3), five regions of interest (ROIs) were defined for analysis: left parietal (CP1, CP3, P1, P3), right parietal (CP2, CP4, P2, P4), left temporal (FC5, FT7, C5, T7, CP5, TP7), right temporal (FC6, FT8, C6, T8, CP6, TP8), and frontocentral (F1, Fz, F2, FC1, FCz, FC2, C1, Cz, C2), according to previous reports (Nittono, 2005; Nittono and Sakata, 2009; SanMiguel et al., 2013a). The oN1 amplitude was quantified as the mean voltage of 80–120 ms in the left and right parietal ROIs for the visual modality, and the left and right temporal ROIs for the auditory modality. The oN2 amplitude was quantified as the mean voltage of 200–250 ms for the visual modality, and 160–210 ms for the auditory modality in the left and right temporal, and frontocentral ROIs. The oP3 amplitude was qualified the time window of 300–450 ms for the visual modality, and 250–400 ms for the auditory modality in the frontocentral ROI.

To test the sensory modality effect on the electrical sources of OSPs (H2), sLORETA (Pascual-Marqui 2002) was conducted for the relevant condition in the oN1 and oN2 time windows. The relevant condition was selected because larger amplitudes were expected in this condition. The distribution of current densities in the brain was estimated from the distribution of scalp potentials of the mean amplitudes (after subtracting the motor control condition). The estimated three-dimensional current density magnitudes (sLORETA-xyz values) were compared to zero using the voxel-wise paired *t*-test. Statistical nonparametric mapping permutation tests (5,000 times) were performed to determine the critical values for a significant difference ($p < .05$).

Statistical analysis

Subjective, behavioral, and ERP measures were subjected to repeated measures analyses of variance (ANOVAs) with factors of sensory modality (visual and auditory) and condition (relevant and irrelevant). The significance level was set at .05 for all analyses.

Results

Subjective rating and behavioral results

Table 1 shows the subjective and behavioral measures. Sensory Modality × Condition ANOVAs were performed on the subjective and behavioral measures. The difficulty of the task, degree of concentration during the task, and association between the button press and stimulus presentation were significantly rated higher in the relevant condition than in the irrelevant condition in both the visual and auditory modalities [difficulty: $F(1, 28) = 33.22$, $p < .001$, $\eta_p^2 = .54$; degree of concentration: $F(1, 28) = 8.05$, $p = .008$, $\eta_p^2 = .22$; association between the button press and stimulus presentation: $F(1, 28) = 10.74$, $p = .003$, $\eta_p^2 = .28$]. The intervals of button presses were significantly shorter in the relevant condition than in the irrelevant condition, $F(1, 28) = 10.93$, $p = .003$, $\eta_p^2 = .28$. In the motor control condition, the mean ratings were 2.9 (*SD* = 1.4) and 6.3 (*SD* = 1.3) for the difficulty and the degree of concentration, respectively, and the mean button press intervals were 1,354 ms (*SD* = 186).

ERPs

Fig. 2 shows the grand mean ERP waveforms for the relevant, irrelevant, and motor control conditions, and the motor-corrected scalp topographies of the mean amplitudes in oN1, oN2, and oP3 time windows for the omission and stimulus trials in the visual and auditory modalities. In the omission trials, superimposed on the slow positive motor-related potentials, deflections corresponding to each component of OSPs can be observed in both modalities. In the auditory irrelevant condition, oN1 could not be clearly identified from the waveform, but could be identified in the temporal areas from the scalp topography. oN1 was predominant in the right parietal site in the visual modality and in the bilateral temporal sites in the auditory modality. oN2 was predominant in the right temporal areas in both modalities. oP3 had a centroparietal distribution but a slightly more posterior distribution in the visual modality than in the auditory modality. Only in the relevant condition did the frontocentral dominant FRN seem to be superimposed on the temporal dominant oN2 in both modalities. In the stimulus trials, N1, P2, and P3 were identified as responses to the stimulus, which differed from the component compositions in the omission trials.

Table 2 shows the peak latencies of each component of OSPs. oN1, oN2, and oP3 all showed shorter latencies in the auditory modality than in the visual modality. Sensory Modality × Condition ANOVAs were performed on the peak latencies of oN1, oN2, and oP3, respectively. oN1 peak latencies were numerically shorter in the auditory modality than in the visual modality, but the main effect of sensory modality was not significant, $F(1, 28) = 0.67$, $p = .422$, $\eta_p^2 = .02$. oN2 peak latencies were significantly shorter in the auditory modality than in the visual modality, $F(1, 28) = 37.01$, $p < .001$, $\eta_p^2 = .57$. oP3 peak latencies were also significantly shorter in the auditory modality than in the visual modality, $F(1, 28) = 36.47$, $p < .001$, $\eta_p^2 = .57$. None of the main effect of condition and the interaction effect were significant for oN1, oN2, and oP3 latencies, *ps* > .161. A Component × Condition ANOVA was performed on peak latency differences between modalities. The latency differences between the visual and auditory modalities significantly increased from oN1 (4 ms) to oP3 (64 ms), $F(2, 56) = 21.10$, $p < .001$, $\varepsilon = .86$, $\eta_p^2 = .43$. None of the main effect of condition and the interaction effect were significant, *ps* > .827.

Fig. 3 shows the mean amplitudes for the oN1, oN2, and oP3 time windows. Each of the visual and auditory OSP components was significantly greater than the baseline (i.e., 95% CI did not cross the baseline), although there were some ROIs with no significant difference from the baseline. Apart from visual oN1, the mean amplitudes tended to be larger in the relevant condition than in the irrelevant condition. The differences between the relevant and irrelevant conditions were significant in the visual oP3 and auditory oN1, oN2, and oP3 time windows.

Fig. 4 shows the electrical sources estimated by sLORETA based on the mean amplitude of the relevant condition of oN1 and oN2 time windows in the omission and stimulus trials. For visual oN1, none of the activities were significant. For visual oN2, the estimated source with maximum activity was the superior parietal lobule in the right parietal lobe (BA7). For auditory oN1, the estimated source with maximum activity was the precentral gyrus in the left frontal lobe (BA43), and activities in the superior temporal gyrus (BA22) and transverse temporal gyrus (BA42) were also significant. For auditory oN2, the estimated source with maximum activity was the middle temporal gyrus in the right temporal lobe (BA37). For the visual stimulus trials, the activities in the occipital lobe (BA18 and BA19) were significant as well as the activities in the temporal and parietal lobes in the time windows of oN1 and oN2. For the auditory stimulus trials, the activities in the temporal lobe (BA21, BA22, BA41, and BA42) were significant as well as the activities in the occipital and parietal lobes in the time windows of oN1 and oN2.

Discussion

The present study examined the effect of sensory modality on OSPs by comparing responses to unexpected stimulus omissions presented after the participants' button presses in the visual and auditory modalities. OSP components oN1, oN2, and oP3 were elicited by both visual and auditory stimulus omissions, and the peak latencies were shorter in the auditory modality than in the visual modality, which supported H1. Although sLORETA did not reveal any electric sources in the visual cortex, it showed significant activations in the auditory cortex in the latency ranges of oN1 and oN2, which partially supported H2. We also examined the effects of task relevance on omission responses. The results showed that the amplitudes of OSPs tended to be larger when participants were instructed that the omission was relevant to the button press task than when they were instructed that the omission was irrelevant to the task in both modalities. H3 was partially supported because the amplitude differences between conditions were only partially significant.

Subjective and behavioral measures showed that participants evaluated the task as more difficult, they were more concentrated on the task, and the button press was more strongly associated with the stimulus presentation in the relevant condition than in the irrelevant condition in both modalities. The mean button press interval was shorter in the relevant condition. These results are consistent with Nittono and Sakata (2009). Based on these results, we concluded that the participants perceived the relevant and irrelevant conditions as different.

The finding that the peak latencies of oN1, oN2, and oP3 were shorter in the auditory modality than in the visual modality is consistent with previous findings (Simson et al. 1976; Nittono 2005; Hernández and Hernández-Sánchez 2017). Sound transduction into electrical signals in hair cells of the inner ear is faster than phototransduction in the retina (King 2005). The differences in latencies of OSPs between the visual and auditory modalities are probably related to the difference in transduction speed between sensory receptors. This suggests that neural pathways containing sensory receptors corresponding to each sensory modality contribute to generation of OSPs. In the present study, peak latency differences between sensory modalities increased at later stages (4, 40, and 64 ms for oN1, oN2, and oP3, respectively). If they were purely cognitive components that were not specific to sensory modalities and were triggered by the initial detection of omission, the peak latency differences should have been constant across sensory modalities for later components. However, this was not the case. The finding suggests that all these components reflect somehow sensory-specific processing.

The electrical sources of auditory oN1 and oN2 were estimated in the right temporal lobe, where the auditory cortex is located. This is consistent with the findings of SanMiguel et al. (2013a) and Stekelenburg and Vroomen (2015) that the superior and middle temporal gyrus of the temporal lobe were the estimated sources of auditory oN1 and oN2. The source of visual oN2 was estimated in the superior parietal lobule of the right parietal lobe, which corresponds to the dorsal visual pathway, although no activity was found in the visual cortex. These results suggest that brain regions responsible for each sensory modality are likely to be involved in the occurrence of early OSPs. However, the distribution of the estimated sources was different between the omission and stimulus trials, as were the waveforms and topographies. This result is consistent with the findings of recent studies comparing response to omissions with response to actual stimuli (Dercksen et al. 2020; Fonken et al. 2019), and suggests that oN1 and oN2 in response to stimulus omissions do not fully share neural pathways with N1 and N2 in response to actual sensory inputs. Dercksen et al. (2020) discussed a possible explanation for the initial topography difference between omission and stimulus (sound) presentation in reference to the findings in other species (Carbajal and Malmierca 2018; Parras et al. 2017). Sound omission does not activate the lemniscal pathway, which feeds information about the sound itself, but involves the non-lemniscal pathway, which is thought to feed prediction errors. In contrast, actual stimulation activates both pathways. A similar thing should happen in the visual modality. Such differences in neural pathways may cause differences in electrical sources and topographies between OSPs and sensory evoked potentials.

Although the maximum sources of the omission trials differed between the visual and auditory modalities, the right temporal and parietal lobes showed significant activity in both modalities. This is in line with SanMiguel et al. (2013a), who reported source dominance in the right hemisphere for oN1 and oN2. Also, right hemisphere dominance is consistent with fMRI and MEG studies that investigated omission responses to auditory stimuli (Miyauchi et al. 1996). This right-hemisphere dominance was not due to motor-related factors, because the hands used for button pressing were counterbalanced across the participants. Because such right hemisphere dominance was not obvious during the same latency range in the stimulus trials, it may be specific to omission responses.

The amplitude of each OSP component was larger in the relevant condition than in the irrelevant condition except for visual oN1, and the differences between conditions were significant for visual oP3, and auditory oN1, oN2, and oP3, even though the physical contexts of stimuli were identical in both conditions. This is consistent with the well-known finding that attended stimuli elicit larger ERP responses (e.g., Luck and Kappenman 2012). In the present study, the information value of the omission was manipulated by prior instruction. The stimulus omission functioned as negative feedback on the task performance in the relevant condition. Thus, participants should have paid more attention to omissions so that they could use the omission event as useful information to accomplish the task of maintaining the button press interval constant. It has been reported that the amplitudes of OSPs increase in attended situations (Raij et al. 1997; Chennu et al. 2016); therefore, the larger oN1 and oN2 are likely attributable to attending to omissions.

Raggazoni et al. (2019) reported that a prefrontal P2 (pP2) was elicited by stimulus omission when the participants counted the number of stimulus omissions. However, we did not find a similar wave in this study. For instance, the scalp topography of a similar latency range (300–450 ms for the visual and 250–400 ms for the auditory) in the present study did not reveal any positivity in the prefrontal area. The lack of pP2 may be due to different experimental settings. For example, the SOA was 2,000 ms in Raggazoni et al., whereas it was approximately 1,300 ms in this study. Moreover, Raggazoni et al. reported that pP2 occurred only when participants were asked to count the number of omissions. As no counting was required in the present study, no pP2 may have been elicited.

The amplitude of oP3, which is probably the same as P300, likely increased because the omission contained more valuable information (Johnson 1986). The present study showed that participants' readiness to use omissions as feedback to judge their performance on the task strengthened OSPs. Only in the relevant condition, where the participants believed that stimulus omissions indicated their failure, the FRN was elicited in response to feedback that indicated their performance was worse than expected (Walsh and Anderson 2012). This is in line with Nittono and Sakata (2009) and suggests that participants performed the two conditions differently depending on the instruction given about task relevance.

The present study was not able to fully replicate the results of Nittono and Sakata (2009) since there was no significant amplitude difference in visual oN2 between the conditions, and a different result than expected for visual oN1. The smaller task-relevance effect in the visual modality may be related to the fact that OSPs in the auditory modality tended to be larger than in the visual modality in this study. In Nittono (2005), the amplitudes of oN2 and oP3 were at the same level across modalities. A possible explanation could be that the visual stimulus in this study (a small LED light) was not intense enough to make the omissions salient, although the subjective intensities of the visual and auditory stimuli were matched. It should be determined in future research whether OSPs in the visual modality are affected by the size of the predicted stimulus in the visual field such that larger OSPs are elicited when the participants expected a larger stimulus compared to a smaller stimulus.

There are several limitations in the present study. First, the motor control condition was used to control the motor-related potentials. This procedure has been commonly used in the previous studies (Dercksen et al. 2020; Kimura and Takeda 2018; Stekelenburg and Vroomen 2015). However, it may not be a perfect control condition. For example, the characteristics of the motor activity of the button press itself (e.g., speed and intensity of the button press) may differ depending on whether participants expect a stimulus after the button press. Indeed, the mean button press interval was longer in the motor control condition (M = 1,354 ms) than in the experimental conditions (M = 1,214 ms). Therefore, readiness potentials and somatosensory afferent potentials could be different between the experimental and the motor control conditions. Second, it is not evident that the OSPs recorded in the present study are comparable to the OSPs recorded in a non-motor task in which regularly presented stimuli were omitted infrequently (Simson et al. 1976; Bullock et al. 1994; Raij et al. 1997; Chennu et al. 2016; Hernández and Hernández-Sánchez 2017; Fonken et al. 2019; Raggazoni et al. 2019). Omissions after self-generated actions have advantage over omissions of periodical stimulation in terms of the accuracy of temporal expectation, which is beneficial to record OSPs by reducing the latency jitter across trials. However, the extent to which the findings of this study can be generalized to the other type of OSPs is a topic of future research.

In conclusion, the present study suggests that the processing of stimulus omission occurs in the neural pathways corresponding to each sensory modality, despite the absence of physical stimulation. Moreover, a higher-order cognitive framework that attempts to use omissions as useful information for the task (i.e., omissions were a sign of poor performance) may also influence the processing of omissions by allocating more attention to the omissions and subsequent processing. Therefore, the characteristics of OSPs may vary depending on experimental tasks. Further research on OSPs would lead to a better understanding of the human perceptual mechanism that works even without actual stimuli.

Declaration

Ethics approval and consent to participate: This study was performed in line with the principles of the Declaration of Helsinki. Approval was granted by the Behavioral Research Ethics Committee of the Osaka University School of Human Sciences (HB021-106). Written informed consent for participation was obtained from all participants included in the study.

Consent for publication: All participants provided written informed consent for publication of obtained data under anonymity.

Availability of data and materials: The datasets analyzed during the current study are publicly available at https://osf.io/rq9np/.

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Author's contributions

Tomomi Ishida: Conceptualization, Methodology, Investigation, Data curation, Formal analysis,

Visualization, Project administration, Writing–Original Draft
Hiroshi Nittono: Conceptualization, Methodology, Writing–Review & Editing

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Table 1 Means and standard deviations of post-block ratings and button press intervals in the relevant and irrelevant conditions

	Visual				Auditory			
	Relevant		Irrelevant		Relevant		Irrelevant	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Difficulty (1: *easy* – 9: *difficult*)	5.4	1.7	3.6	1.7	5.9	1.7	4.1	1.9
Concentration (1: *not concentrated* – 9: *concentrated*)	5.8	2.0	5.0	1.9	6.0	1.8	5.2	1.6
Association between button press and stimulus (0: *not associated* – 100: *associated*)	69.6	24.1	56.4	26.3	77.2	21.0	62.1	29.4
Button press interval (ms)	1,187	227	1,274	239	1,161	202	1,235	245

Table 2 Means and standard deviations of the peak latencies (ms) for oN1, oN2, and oP3 in the visual and auditory modalities

	Visual					Auditory					Difference (Visual − Auditory)	
	Site	Relevant		Irrelevant		Site	Relevant		Irrelevant		Relevant	Irrelevant
		M	*SD*	*M*	*SD*		*M*	*SD*	*M*	*SD*		
oN1	CP4	102	32	99	22	T8	95	19	98	25	7	1
oN2	T8	230	39	241	52	T8	191	21	201	37	39	40
oP3	Cz	405	68	413	66	Cz	345	67	346	63	60	67

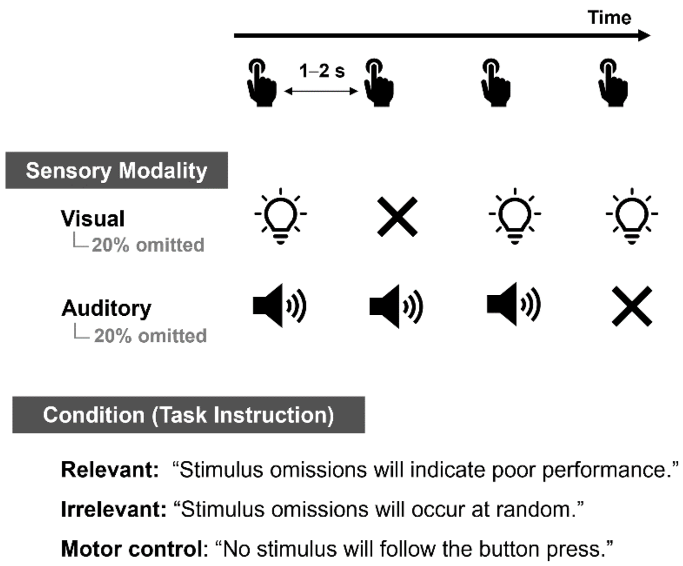

Fig. 1 Schematic representation of the experiment. Participants pressed a mouse button once per 1–2 s followed by a feedback stimulus. LED lights were presented in the visual modality and pure tones in the auditory modality, which were omitted in 20% of trials. In the relevant condition, participants were told that inconstant button press intervals would result in stimulus omission. In the irrelevant condition, participants were told that infrequent stimulus omissions would occur irrespective of button press intervals. In fact, the stimuli were omitted in 20% of the trials in both conditions. In the motor control condition, no stimuli were presented after button presses

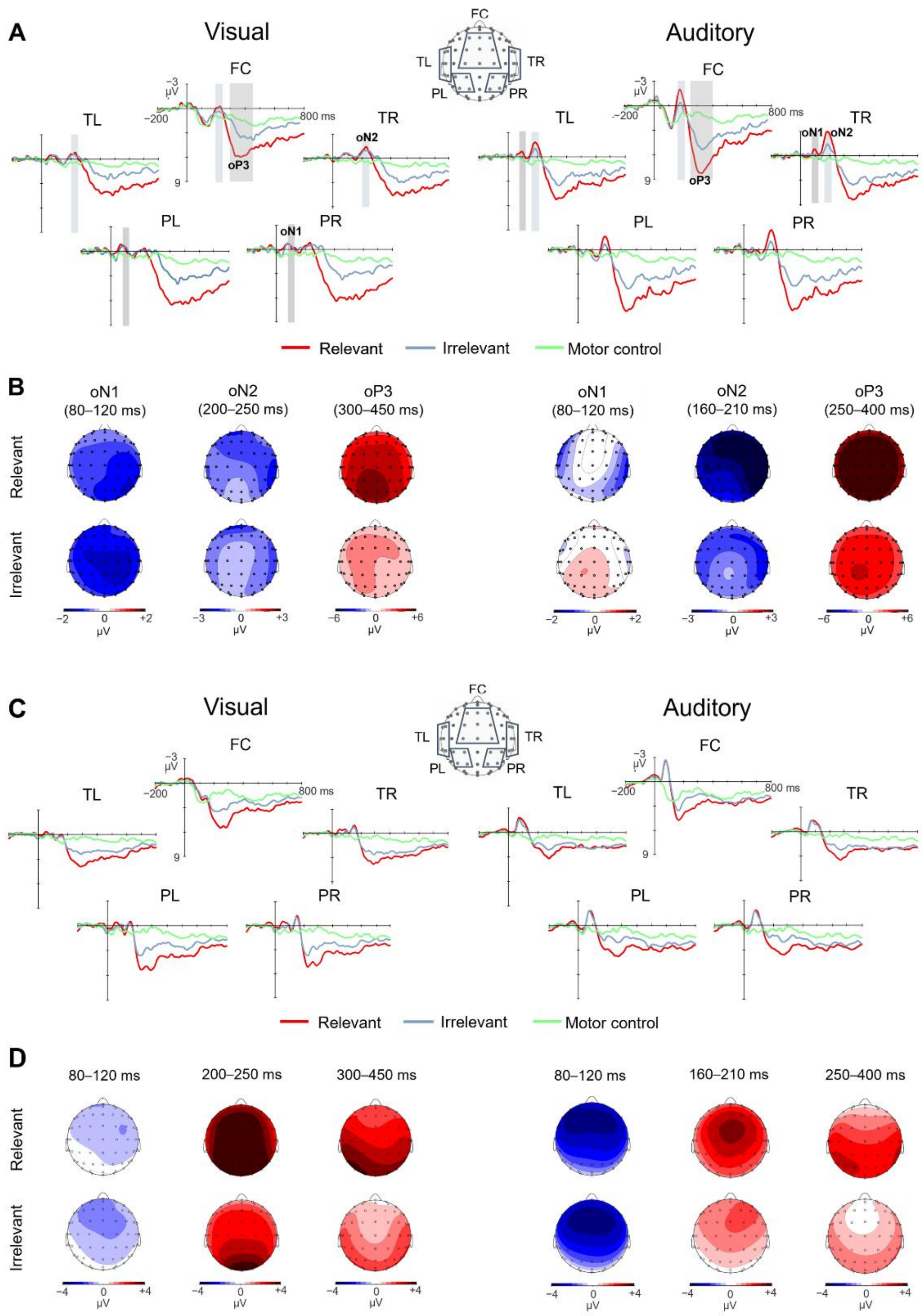

Fig. 2 Grand mean ERP waveforms of omission and stimulus trials, and motor-corrected scalp topographies in the visual and auditory modalities. Panel A: The waveforms of omission trials in the relevant (red), irrelevant (blue), and motor control (green) conditions averaged across electrode sites in five areas: FC (frontocentral), TL (temporal left), TR (temporal right), PL (parietal left), and PR (parietal right). Panel B: Scalp topographies for the omission trials after subtracting the motor control condition in the relevant (upper) and irrelevant (lower) conditions for oN1, oN2, and oP3 time windows as marked in gray on the waveforms. Panel C: The waveforms of the stimulus trials in the

relevant (red), irrelevant (blue), and motor control (green) conditions. Panel D: Scalp topographies for the stimulus trials after subtracting the motor control condition in the relevant (upper) and irrelevant (lower) conditions for oN1, oN2, and oP3 time windows.

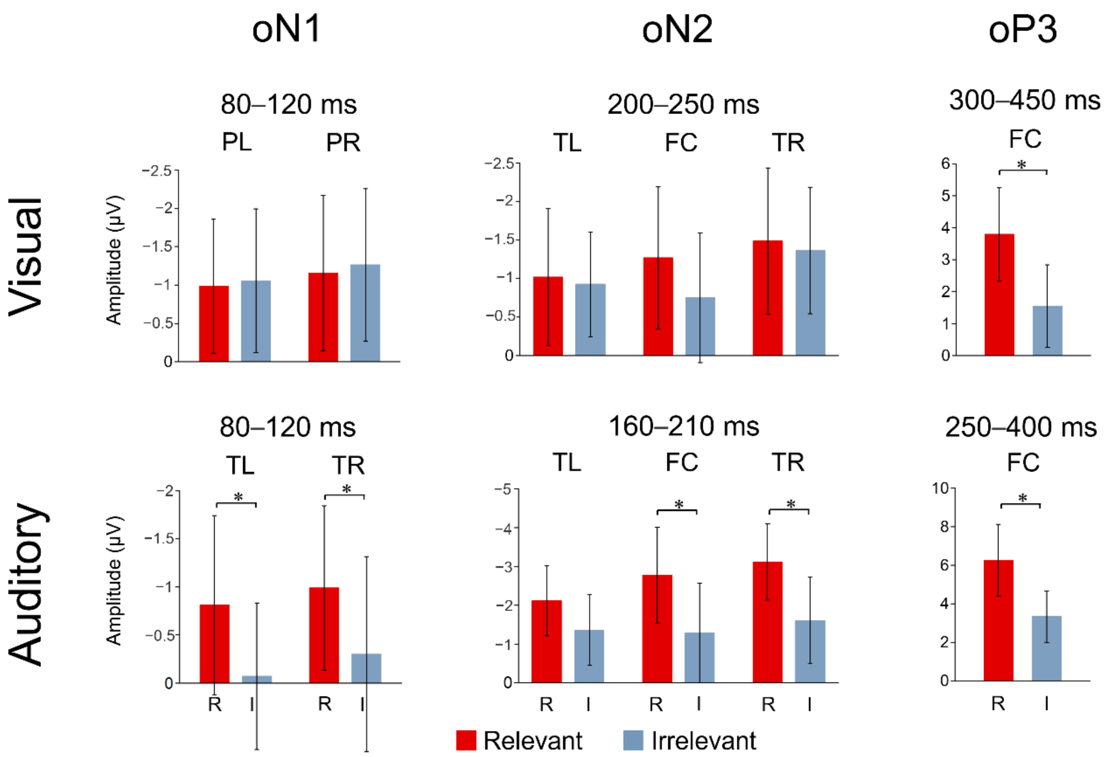

Fig. 3 Mean amplitude comparisons of the relevant (red) and irrelevant (blue) conditions for oN1, oN2, and oP3 time windows. Asterisk indicates a significant difference ($p < .05$). Error bars indicate 95% confidence intervals

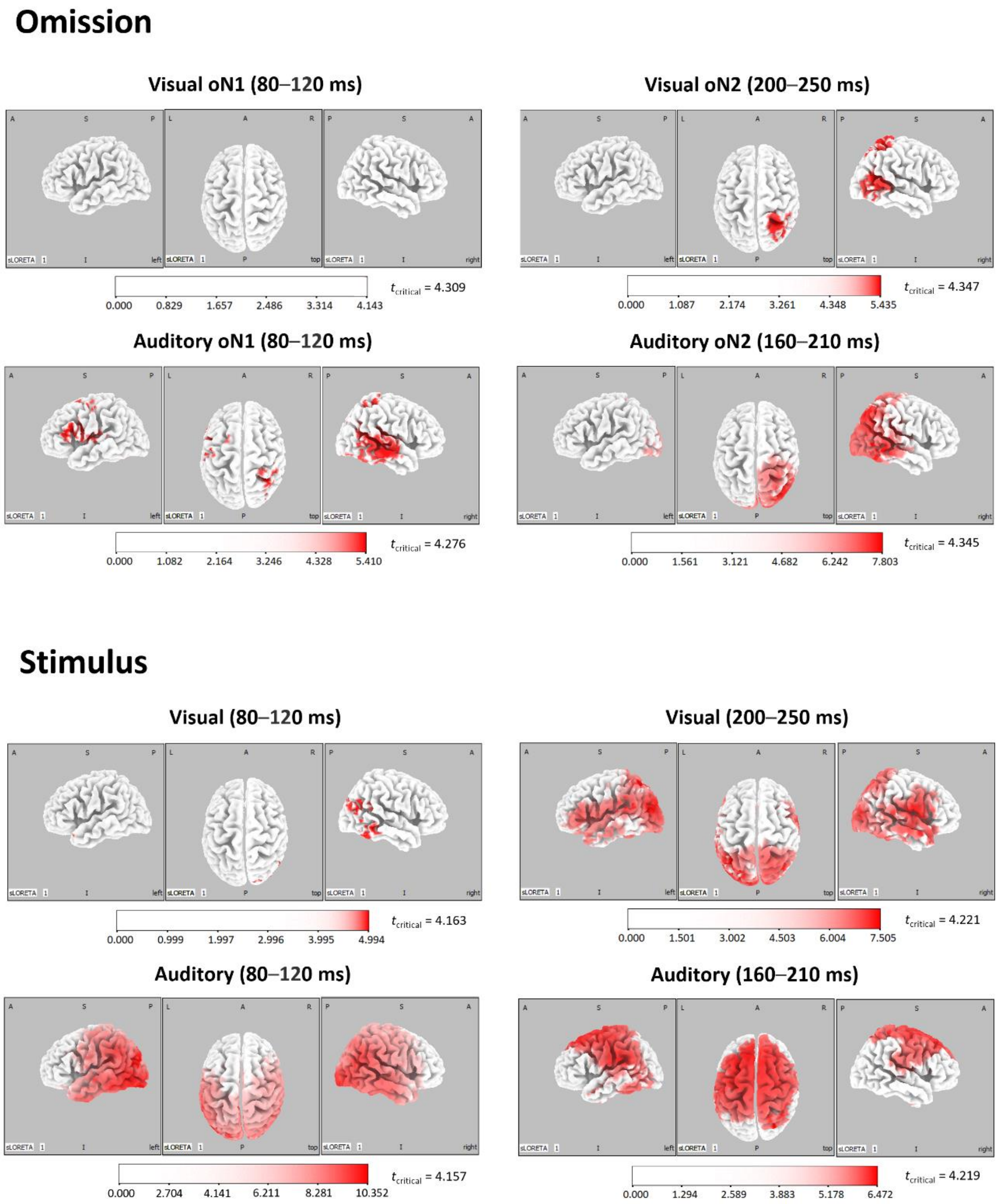

Fig. 4 sLORETA source estimation of the scalp potentials in the oN1 and oN2 time windows for the omission trials (upper) and stimulus trials (lower) in the visual and auditory relevant conditions. The upper limit of each color scale is the maximum *t*-value in the image. Only voxels that exceeded the critical *t*-values for the significant difference from zero calculated by statistical nonparametric mapping ($p < .05$) are colored. The critical *t*-values are indicated in the right side of the color scales.