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Visual Emotional Context Modulates Brain Potentials Elicited by Unattended Tones

Sayaka Sugimoto, Hiroshi Nittono, and Tadao Hori

Hiroshima University, Japan

*Corresponding Author:

Hiroshi Nittono, Ph.D.

Graduate School of Integrated Arts and Sciences, Hiroshima University

1-7-1 Kagamiyama, Higashi-Hiroshima 739-8521, Japan

Fax: +81-82-424-0759

E-mail: nittono@hiroshima-u.ac.jp

Abstract

To examine whether brain electrical responses to environmental stimuli were influenced by emotional contexts, event-related potentials (ERPs) elicited by nonstartle probe tones were recorded from 13 student volunteers while they were viewing emotionally positive, neutral, and negative slides of the International Affective Picture System. The auditory stimuli consisted of high-deviant (2000 Hz, $p = .08$), low-deviant (1050 Hz, $p = .08$), and standard (1000 Hz, $p = .84$) tones with a mean onset-to-onset interval of 600 ms. Participants were told to ignore the tones. High-deviant tones elicited a larger N1 (peaking around 100 ms) when participants were viewing negative slides than when viewing positive slides. The amplitude of the P2 elicited by standard tones (peaking around 170 ms) was smaller when participants were viewing positive slides than when viewing negative and neutral slides. The amplitude of the mismatch negativity (150–200 ms) tended to reduce during positive slide presentation, but this difference appeared to be due to reduction of the P2 elicited by standard tones. These findings suggest that visually induced emotional states have a sequential effect on auditory information processing, in that the influence of negative emotion appears at an earlier stage than that of positive emotion.

Keywords: event-related potentials, affect, mood, auditory information processing, N1, P2, mismatch negativity

1. Introduction

Emotion and mood can affect information processing of environmental events at multiple levels (Bower, 1981; Forgas, 1995). Negative emotion facilitates a systematic and detail-oriented analysis of specific information since it informs individuals that there is something bad in their environment and urges them to act specifically. In contrast, positive emotion facilitates a simple heuristic style of information processing and broadens the focus of thinking and actions since it informs that there is no urgent threat in the environment (Fredrickson, 2004; Schwarz, 1990). Generally, organisms respond more rapidly and intensely to negative events than to positive ones, and underlying neural processes probably differ between negative and positive emotions (Cacioppo and Gardner, 1999; LeDoux, 1998; Taylor, 1991).

Event-related potentials (ERPs) are voltage fluctuations that are associated in time with some physical and mental occurrence, and contain components that span a continuum between exogenous and endogenous potentials (Picton et al., 2000). Because each ERP component has different temporal and topographical characteristics and different sensitivities to experimental manipulations, it is assumed that each component reflects a different stage or aspect of information processing. The recording of ERPs can therefore reveal the processing stages that are influenced by emotion and mood.

Numerous studies have dealt with the ERPs elicited by visual emotional pictures (e.g., Cuthbert et al., 2000; Delplanque et al., 2006; Sabatinelli et al., 2007; Schupp et al., 2000). Most of the pictures were selected from the slide set of the International Affective Picture System (IAPS; Lang et al., 1999). These studies have consistently shown that the amplitude of the late positive potential (probably consisting of the P300 and subsequent positive slow wave component) is larger when the eliciting picture is arousing in both positive and negative directions, suggesting that arousing pictures attract greater attention than neutral pictures. However, the analysis and interpretation of ERP components earlier than the late positive potential may be difficult, because earlier ERP components reflect not only emotional processing but also processing of nonemotional physical aspects of stimuli like complexity, colorfulness, and spatial frequency. Since the IAPS slides contain various contents, clear separation of emotional processing from nonemotional processing seems unfeasible.

In the present study, we used the IAPS slides to induce emotional states and recorded ERPs to task-irrelevant, unattended probe tones (Papanicolaou and Johnstone, 1984). Since the eliciting stimuli were identical, ERP differences under various emotional contexts can be interpreted as the modulatory effect of emotional states on information processing of environmental stimuli.

Several ERP components elicited by acoustic probe stimuli have been shown to be influenced by visually induced emotional states. The N1 (N100) is a negative wave peaking around 100 ms after the auditory stimuli with a frontocentral scalp distribution (Näätänen and Picton, 1987). Several neural generators including the primary and secondary auditory cortices contribute to the N1 (Giard et al., 1994). Its amplitude is affected by physical stimulus attributes such as intensity and interstimulus intervals, and is also affected by internal states such as attention and arousal levels (Näätänen, 1992). Cuthbert et al. (1998) presented an 800-Hz pure tone (65 dB) or a burst of startle white noise (95 dB) while participants were viewing positive, neutral, and negative slides of the IAPS. Participants were told to either ignore the auditory stimuli or attend to them (i.e., memorize and compare them with a second stimulus presented later). Startle probes elicited a larger N1 than did the tone probes. Emotional slides affected the amplitude of the N1 only when it was elicited by the attended startle noise, in such a way that the N1 amplitude increased when participants were viewing negative slides than when viewing positive and neutral slides. Other studies showed that the amplitude of the N1 elicited by unattended startle probes was not influenced by viewing emotional slides (Bradley et al., 2006; Schupp et al., 1997). However, little is known about the modulatory effect of emotional context on the N1 elicited by nonstartle tone probes. If nonstartle tones are highly deviant, N1 amplitude may increase in a negative emotional state.

Following the N1, the P2 wave appeared over central scalp sites with a peak latency of around 200 ms. Although this potential was combined with the N1 as “N1–P2 complex” in early studies, the P2 reflects independent processes that can be differentiated from the N1 (Näätänen, 1992; Näätänen and Picton, 1987). The functional significance of the P2 has not yet been elucidated. It has been suggested that the P2 may consist of a modality-specific component, which is generated in the auditory cortex, and a nonspecific component, which reflects auditory driven output of mesencephalic reticular activating system (Crowley and Colrain, 2004). Schupp et al. (1997) reported that the P2 elicited by startle probes was smaller when participants were viewing positive and negative slides than when viewing neutral slides. However, this finding has not been replicated in other studies using similar protocols (Bradley et al., 2006; Cuthbert et al., 1998). Using an oddball counting task that contained nonstartle standard (1000 Hz, $p = .80$) and target tones (1500 Hz, $p = .20$), Mercado et al. (2006) reported that the P2 amplitude was larger when participants were viewing a negative slide (wolf jaw) than when viewing a positive (opposite sex nude) or a relaxing slide (landscape). This effect was found only for participants with high state anxiety. Participants with low state anxiety showed the opposite effect—the P2 tended to be larger for a positive slide than for a negative or a relaxing slide. However, it remains unclear why this effect occurred, because Mercado et al. did not show ERP waveforms separately for standard and target tones. In sum, the P2 might be affected by emotional context, although inconsistent findings of previous studies prevent predicting the direction of change.

Between the N1 and P2, which are exogenous in essence, mismatch negativity (MMN) occurs, usually superimposing on the descending slope of the N1. The MMN is an endogenous component that reflects a mismatch between the eliciting stimulus and the preceding stimulus context (Näätänen, 1992, 2000). Usually the MMN is best seen in difference waveforms in which ERPs elicited by standard tones were subtracted from ERPs elicited by deviant tones. Surakka et al. (1998) presented standard (1000 Hz, $p = .85$) and deviant tones (1050 Hz, $p = .15$) to participants who were passively viewing positive, neutral, and negative slides selected from the IAPS. When participants were viewing positive slides, the amplitude of the MMN was reduced compared with when they were viewing negative and neutral slides. Surakka et al. reported that there was no difference in the N1 amplitude. However, they did not examine the P2. Moreover, it remains unclear whether the MMN difference was only due to the difference in valence of emotional context, because the negative slides they used were significantly more arousing than the positive slides.

In addition to these early ERP components, the amplitude of the P300 (or the late positive potential) elicited by probe stimuli is affected by viewing emotional slides (Cuthbert et al., 1998; Schupp et al., 1997). Contrary to the N1, P2, and MMN mentioned above, the P300 is reduced when participants were viewing arousing stimuli irrespective of its emotional valence, although positive slides tend to have a greater effect (Bradley et al., 2006; Schupp et al., 2004). This reduction of the P300 elicited by auditory probe stimuli is associated with the enhancement of the late positive potential elicited by visual emotional slides (e.g., Cuthbert et al., 2000; Schupp et al., 2000), which is consistent with the framework of limited capacity model of attention (Donchin et al., 1986). Similar results of the P300 were obtained when the level of interest in background film stimuli was manipulated (Suzuki et al., 2005). Another line of research has also shown that the amplitude of the P300 is sensitive to reward magnitude of eliciting events rather than their emotional valence (Yeung and Sanfey, 2004).

Taken together, the effect of emotional context on auditory information processing has been mostly investigated using startle probes. There are only few studies using tone probes, which produced inconsistent results except in the case of the P300. In the present study, a three-tone passive oddball paradigm was used to examine the effect of emotional context on the N1, P2, and MMN components of the ERP. Highly deviant and less deviant tones were unpredictably presented as embedded in frequent standard tones. Since the N1 and MMN occur temporally overlapping with each other, it is helpful to use two types of deviant tones when examining these components in a single experiment (Nittono et al., 2001). While the N1 amplitude tends to be proportional to the magnitude of deviance from the preceding stimulus context, the MMN amplitude is relatively stable when the deviance exceeds a certain threshold (Näätänen, 1992). Thus, high-deviant tones are suitable for recording the N1, because they are expected to elicit a larger N1 than low-deviant tones. On the other hand, low-deviant tones are suitable for recording the MMN, because they are expected to elicit only a small N1. There were three predictions. (1) The amplitude of the N1 elicited by high-deviant tones would be larger when participants were viewing negative slides than viewing positive and neutral slides. (2) P2 amplitude would be influenced by emotional context in some way. (3) MMN amplitude would be reduced when participants were viewing positive slides compared with when they were viewing negative or neutral slides.

2. Methods

2.1. Participants

Thirteen student volunteers at Hiroshima University participated in the study (five men and eight women, 20–27 years old, mean 22.8 years). All of them were right-handed, assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). They had normal or corrected-to-normal sight according to self-report. Standard audiometry confirmed normal hearing. They gave written informed consent.

2.2. Stimuli

One hundred and twenty color slides (40 positive, 40 neutral, and 40 negative) were selected from the IAPS, based on their normative rating scores (Lang et al., 1999) [Footnote 1]. For ethical reasons, extremely negative and positive pictures (e.g., mutilated bodies or erotic nudes) were excluded [Footnote 2]. The resultant sets met the criteria that all categories differed from one another in normative valence scores (Positive: 6.00–8.00, Neutral: 4.00–6.00, Negative: 1.95–4.00), and that arousal scores of positive and negative slides did not differ significantly from each other but were higher than those of neutral slides (Positive and Negative: 3.00–6.00, Neutral: 2.00–4.00). The means and standard deviations of normative scores for the positive, neutral, and negative slide sets are shown in Table 1.

The auditory probe stimuli consisted of 1000 Hz ($p = .84$, standard), 2000 Hz ($p = .08$, high-deviant), and 1050 Hz ($p = .08$, low-deviant) pure tones with a duration of 50 ms including 10 ms rise/fall times. They were presented via headphones (Audio-technica, ATH-T2, Tokyo, Japan) at about 60 dB SPL in a quasi-random order, with the limitation that at least two standard tones were presented between adjacent deviant tones. The intensity of the tones was measured roughly by an ordinary sound level meter without using an artificial ear. Although the tone intensity could not be measured precisely, it kept constant across trials. The interstimulus interval varied between 500 and 600 ms (mean 550 ms).

2.3. Procedure

Experiments were conducted in a dimly-lit, sound-attenuated room. Participants were seated on a comfortable chair. Slides were presented one at a time with visual angles of 6.8° in height and 8.7° in width (18 × 23 cm) on a cathode ray tube (CRT) placed at 1.5 m before the participants' eyes. Three slide categories were presented in random order. Each slide lasted 16 s and a 9-s blank was inserted between the slides. The probe tones started 1 s after the slide onset and stopped at its offset. A total of 25 tones (2 high-deviant, 2 low-deviant, and 21 standard) were presented while each slide appeared on the CRT. The first four tones were always standard tones, so that deviant tones were presented from about 3 s after slide onset. Participants were told to look at a series of slides presented on the CRT and ignore the tones. After each slide went off, participants rated the experience evoked by the slide on valence and arousal dimensions using the Self-Assessment Manikin (SAM) with nine-point scales (Lang et al., 1999). After a 9-s rating period, the next slide appeared on the CRT. At the beginning of the experiment, participants received three practice trials using three different slides other than the slides used in the experiment. Then, three blocks of 40 trials each were conducted with short breaks in between. Each block contained 13 or 14 slides of respective emotional categories.

2.4. Electrophysiological recording

An electroencephalogram (EEG) was recorded from 33 scalp sites (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz, O2, M1, and M2 according to the 10–20 system) using an elastic cap with sintered Ag-AgCl electrodes (Electro-Cap International Inc., Eaton, OH). The average reference of C3 and C4 were used as a common reference at recording and the data were re-referenced to the nose tip offline. Horizontal and vertical electrooculograms (EOGs) were recorded from the outer canti of both eyes and from above and below them. Electrode impedance did not exceed 5 kΩ. At recording, a time constant of 10 s (high-pass 0.016 Hz) and a low-pass filter of 60 Hz were used. The sampling rate was 500 Hz.

2.5. Data reduction

Before ERP averaging, ocular artifacts in EEG records were corrected using Gratton et al.(1983)'s method, which was implemented in Brain Vision Analyzer 1.05 (Brain Products, Gilching, Germany). Then, a digital bandpass filter of 1–30 Hz was applied. ERP waveforms were calculated separately for each participant, slide category, and auditory stimulus type. The period between 100 ms before and 500 ms after the onset of auditory stimulus was averaged. Whenever EEG or EOGs exceeded ± 80 μV, the periods were excluded from the averaging. The first two tones of each tone sequence and two standard tone after each deviant tone were excluded from the averaging. Each ERP waveform was aligned to the 100-ms prestimulus baseline by subtracting the mean amplitude of this period from each point of the waveform.

The N1 was designated as the maximal negative deflection between 50 and 150 ms after the onset of each type of tone. The P2 was designated as the maximal positive deflection between 100 and 250 ms after the onset of standard or high-deviant tones. The P2 for low-deviant tones was not analyzed because it was indiscernible in most individual waveforms as well as in grand mean waveforms. Peak latencies of the N1 and P2 were measured at their dominant sites (Fz for N1, Cz for P2), and the amplitudes at the corresponding peak latencies were scored at all electrode sites. To examine the MMN, difference waveforms were calculated by subtracting the ERPs elicited by standard tones from the ERPs elicited by high and low deviant tones. To reduce the effect of the N1 on MMN measurement, MMN amplitude was scored as the mean amplitude of 150–200 ms after the stimulus onset, the period that was slightly later and shorter than the expected period of MMN elicitation.

2.6. Statistical analysis

Subjective rating scores and the amplitude and latency data of ERPs were submitted to repeated measures analyses of variance (ANOVAs). For ERPs, midline and lateral electrode sites were analyzed separately. For the midline site analysis, amplitude data of each ERP component were submitted to an ANOVA with factors of slide category, auditory stimulus type, and electrode site (Fpz, Fz, FCz, Cz, CPz, Pz, and Oz). For the lateral site analysis, the factor of hemisphere was added and an ANOVA with factors of slide category, auditory stimulus type, hemisphere (left and right), and electrode site (Fp1/2, F3/4, F7/8, FC3/4, FT7/8, C3/4, T7/8, CP3/4, TP7/8, P3/4, P7/P8, O1/2, M1/2) was conducted. Only the results of midline site analysis were reported here, because no sign of lateralization effect related to emotional context was found (i.e., no significant interaction of slide category and hemisphere in the lateral site analysis), and the remaining effects were similar to those in the midline site analysis. Following these overall ANOVAs, the effect of slide category was examined separately for each auditory stimulus type by a one-way ANOVA on the amplitude data at the most dominant site of each ERP component (Fz for the N1 and MMN, Cz for the P2). Whenever appropriate, Greenhouse–Geisser ε correction of degrees of freedom was made. Post hoc multiple comparisons were made using Shaffer's modified sequentially rejective multiple test procedure, which extends Bonferroni *t* tests to a stepwise fashion and increases the probability of detecting differences without changing the control of Type I error (Shaffer, 1986). The significance level was set at .05 for all statistical tests.

To deal with the problem of component overlapping, a temporal principal component analysis (PCA) was applied to the ERP data (Dien and Frishkoff, 2005). Because the peak latencies of the N1 and P2 differed between stimulus types, separate PCAs were applied for each stimulus type [Footnote 3]. A covariance matrix was calculated from the database consisting of 1,287 averaged waveforms (i.e., 13 participants × 3 slide categories × 33 electrode sites), each of which included 250 time points (from 0 to 500 ms). Only factors with eigenvalues greater than one were retained, and Varimax rotation was performed. Factor scores after rotation, which can be viewed as the amount of a component within a given ERP, were submitted to ANOVAs that were similar to those used in the peak and mean amplitude analysis described above. Because the two results corresponded well with each other, only a brief summary of the PCA results will be shown in the Results section.

3. Results

3.1. Slide ratings

Table 1 shows the mean valence and arousal rating scores for the three slide categories. ANOVAs with a factor of slide category showed significant differences between the slide sets in valence and arousal, *F*s(2, 24) = 105.16 and 17.56, *p*s < .001, εs = .61 and .94. Multiple comparisons showed that the three slide sets were significantly different from one another in valence rating and that the positive and negative slide sets were significantly more arousing than the neutral slide set, while they did not differ from each other in arousal ratings.

3.2. Event-related potentials

Figure 1 shows the grand mean ERP waveforms elicited by high-deviant, low-deviant, and standard tones. All types of tones elicited a negative wave (N1) about 100 ms after the stimulus onset. High-deviant and standard tones elicited positive waves (P2) with peak latencies of about 210 ms and 170 ms, respectively. No clear P2 wave could be seen after the low-deviant tones, probably because the MMN, a potential with the opposite polarity, overlapped with the P2. In difference waveforms, the MMN appeared for both high and low deviant tones, negatively at midline sites and positively at mastoids. Figure 2 shows scalp topographic maps of the N1, P2, and MMN. The N1 and MMN had a frontal dominant distribution, whereas the P2 had a central dominant distribution.

3.2.1. N1

Figure 3 illustrates the mean amplitudes of the N1s elicited by high-deviant, low-deviant, and standard tones. An ANOVA with factors of slide category (positive, neutral, and negative), stimulus (high-deviant, low-deviant, and standard), and site (Fpz, Fz, FCz, Cz, Cpz, Pz, and Oz) showed significant main effects of stimulus and site, $F(2, 24) = 12.48$, $p < .001$, $\varepsilon = .78$; $F(6, 72) = 47.28$, $p < .001$, $\varepsilon = .27$, respectively. Multiple comparisons showed that N1 amplitude was significantly larger at Fz and FCz than at Fpz, CPz, Pz, and Oz, and significantly larger for high- and low-deviant tones than for standard tones. The Slide Category × Stimulus and Stimulus × Site interactions were also significant, $F(4, 48) = 3.28$, $p = .032$, $\varepsilon = .75$; $F(12,144) = 15.30$, $p < .001$, $\varepsilon = .25$, respectively. Separate ANOVAs at the dominant site (Fz) showed that the effect of slide category on N1 amplitude was significant only for high-deviant and standard tones, Fs(2, 24) = 5.00 and 7.37, ps = .027 and .004, εs = .74 and .96. N1 amplitude for low-deviant tones was not affected by slide category, $F < 1$. Results of multiple comparisons are shown in Figure 3. The amplitude of the N1 elicited by high-deviant tones was significantly larger when participants were viewing negative slides than when they were viewing positive slides. In contrast, the amplitude of the N1 elicited by standard tones was significantly smaller for negative slides than for positive and neutral slides.

A Slide Category × Stimulus ANOVA of N1 latency data showed a significant effect of stimulus, $F(2, 24) = 6.67$, $p = .008$, $\varepsilon = .85$. Multiple comparisons showed that N1 latency was shorter for standard tones ($M = 93$ ms) than for high- and low-deviant tones (Ms = 108 and 110 ms, respectively). The main and interaction effects of slide category were not significant.

3.2.2. P2

The mean amplitudes of the P2s elicited by high-deviant and standard tones are shown in Figure 3. A Slide Category × Stimulus × Site ANOVA showed significant main effects of stimulus and site, $F(1, 12) = 12.58$, $p = .004$; $F(6, 72) = 30.81$, $p < .001$, $\varepsilon = .27$, respectively. P2 amplitude was larger for high-deviant than for standard tones. Multiple comparisons showed that P2 amplitude was significantly larger at Cz than at Fpz, Fz, CPz, Pz, and Oz. Separate ANOVAs at the dominant site (Cz) showed the effect of slide category on P2 amplitude was significant only for standard tones, $F(2, 24) = 4.65$, $p = .023$, $\varepsilon = .93$; $F < 1$ for high-deviant tones. Multiple comparisons showed that P2 amplitude was significantly reduced when participants were viewing positive slides than when they were viewing negative and neutral slides.

A Slide Category × Stimulus ANOVA of P2 latency data showed a significant effect of stimulus, $F(1, 12) = 15.57$, $p = .002$, suggesting that P2 latency was shorter for standard tones ($M = 170$ ms) than for high-deviant tones ($M = 209$ ms). The main and interaction effects of slide category were not significant.

3.2.3. MMN amplitude

The mean amplitudes of the MMNs for high-deviant and low-deviant tones are shown in Figure 3. A Slide Category × Stimulus × Site ANOVA showed a significant main effect of site, $F(6, 72) = 7.80$, $p = .003$, $\varepsilon =.32$. Multiple comparison showed that MMN amplitude was significantly larger at Fz than at Fpz. No significant main or interaction effects except for the interaction of stimulus and site, $F(6, 72) = 12.25$, $p < .001$, $\varepsilon = .30$. Tests of simple effects showed that the MMN amplitude significantly varied across sites only for low-deviant tones, $F(6, 72) = 28.20$, $p < .001$, $\varepsilon = .35$, where MMN amplitude was larger at Fz than at Fpz, Cpz, Pz, and Oz; $F = 1.94$ for high-deviant tones. Although the MMN appeared to be reduced during the positive slide presentation, this trend was not confirmed statistically. Separate ANOVAs at Fz showed no significant effect of slide category, Fs(2, 24) = 2.14 and 2.47, ps = .151 and .110, εs = .81 and .93.

3.2.4. Principal component analysis

Separate temporal PCAs for each stimulus type yielded 13, 17, and 16 factors for high-deviant, low-deviant, and standard tones, which were retained and rotated. On the basis of the latency and scalp topography of each factor, ERP components corresponding to the N1 and P2 were identified for all stimulus types, and a component corresponding to the MMN was identified for high- and low-deviant tones. ANOVAs on these factor scores confirmed the results obtained in the peak and mean amplitude analysis described above: (1) The N1 component for high-deviant tones was significantly larger when participants were viewing negative slides than when they were viewing neutral and positive slides. (2) The N1 component for standard tones was smaller when viewing negative slides than when viewing positive slides ($p = .04$) and neutral slides ($p = .06$). (3) The P2 component for standard tones was smaller when viewing positive slides than when viewing neutral slides ($p = .02$) and negative slides ($p = .07$). (4) The P2 and MMN for high- and low-deviant tones did not differ significantly among emotional slide categories. The P2 for low-deviant tones, which was indiscernible in averaged waveforms, could be identified by using PCA. However, no modulatory effect of emotional context was obtained.

4. Discussion

The results of valence and arousal ratings validated the adequacy of emotional context manipulation in this study. All pairs of slide categories differed from one another in valence, and the positive and negative slide sets were equivalent in arousal and were more arousing than the neutral slide set. The amplitude of the N1 elicited by high-deviant tones was enhanced when participants were viewing negative slides than when they were viewing positive slides. The amplitude of the P2 elicited by standard tones was smaller for positive slides than for negative and neutral slides. The MMN appeared to be reduced when participants were viewing positive slides, although the effect was not statistically significant. These ERP findings were confirmed by a temporal PCA, as well as by the traditional peak and mean amplitude analysis.

The enhancement of the N1 elicited by high-deviant tones in a negative emotional state replicates and extends the finding of Cuthbert et al. (1998) regarding the N1 elicited by attended startle probes. If auditory probe stimuli are highly deviant from the stimulus context, the emotional modulation of N1 amplitude can occur even when using unattended nonstartle tones. In contrast to the N1 elicited by high-deviant tones, the N1 elicited by standard tones was reduced in a negative emotional state. Since no previous study found this effect, further replication is needed. Nevertheless, this tendency is consistent with the general idea that negative emotion facilitates selective processing and narrows the focus of attention (Fredrickson, 2004; Schwarz, 1990), which involves sensitization to possibly significant deviant events and desensitization to normal regular events in the environment.

The effect of positive emotional state appeared in ERP waveforms after the N1. The P2 amplitude was reduced when participants were viewing positive slides compared with when they were viewing neutral and negative slides. The P2 was larger in amplitude and peaked later for deviant than for standard tones. The reason for this latency difference is not clear, but possibly because P2 generators were activated more extensively for deviant tones, by which the peak was delayed. Some studies have reported a similar result that unattended high-deviant sounds elicited a larger P2 with a longer latency compared with the P2 elicited by unattended standard tones (Ullsperger et al., 2001) [Footnote 4]. Because the functional significance of the P2 is poorly understood (Crowley and Colrain, 2004), we cannot specify the change in information processing underlying this attenuation. At least, the results suggest that part of brain responses to regular external events can be attenuated in a positive emotional state. Previous studies have suggested that the P2 (or another positivity in the vicinity of the P2) is enhanced by attention to the eliciting auditory stimuli (Goodin et al., 1983;

Näätänen, 1992). Clinical studies have shown that P2 amplitude was larger in patients with attention-deficit hyperactivity disorder (Oades, 1998; Wiersema et al., 2006). Therefore, the P2 reduction during the positive slide presentation might be seen as a sign of reduced attention to regular external events in a safe and comfortable environment. Moreover, the MMN in difference waveforms appeared to be reduced in a positive emotional state, which appears superficially similar to the report by Surakka et al. (1998). This effect is partly due to the reduction of the P2 elicited by standard tones and may not reflect the change in the MMN per se. A lack of significant effect may be due to lower arousal values of the slide set used in the present study, in which extremely negative and positive pictures were excluded. If more arousing slides are used, as in Surakka et al.'s study, the MMN change may be observed.

The effect of emotional context on acoustic startle reflex has been explained in terms of the motivational priming hypothesis (Lang, 1995). In this framework, defensive reflexes such as startle will be enhanced if they are elicited in the context of a negative emotional state, whereas appetitive reflexes will be enhanced if they are elicited in a positive emotional state. A negative emotional state activates the amygdala, which projects to the nucleus reticularis pontis caudalis in the startle circuit and potentiates the startle reflex (Davis, 1997; Lang et al., 1997). Interestingly, a similar type of explanation has been given to the modulatory effect of emotional state on ERP components, which are hardly regarded as defensive reflexes. Cuthbert et al. (1998) speculated that defensive motivation associated with negative emotion may prime and enhance early cortical processing of priority sensory input, which results in an ERP response similar to that prompted by an increase in stimulus intensity. Surakka et al. (1998) also suggested that positive emotional information attenuates the amygdala activity that, in turn, attenuates the mechanism responsible for detection of change in the auditory cortex.

The findings of the present study suggest that emotional states affect startle reflex and ERP responses in different ways. For startle reflex, the facilitating effect of negative emotion and the inhibitory effect of positive emotion exert on the same response measure (i.e., blink magnitude). However, the effect of negative emotion appeared mainly on the N1 component and the effect of positive emotion appeared mainly on the later ERP components, P2 and MMN. This pattern of results is consistent with previous findings (Cuthbert et al., 1998; Surakka et al., 1998). Besides ERPs to auditory probe stimuli, the amplitude of the N1 (N150) elicited by painful electric stimuli was enhanced when participants were viewing negative slides, but there was no comparable inhibition of the N1 when they were viewing positive slides (Kenntner-Mabiala & Pauli, 2005). This temporal difference in operation fits the general idea of positive–negative asymmetry suggesting that negative events prompt more rapid and intense responses than positive events (Cacioppo and Gardner, 1999; Taylor, 1991).

Unlike startle reflex, the neural mechanism underlying the emotional modulation of ERP components is far from clear. A possible clue may come from a neurochemical point of view. It is widely assumed that mood is modulated by neurochemical transmitters. In particular, negative mood is thought to be mediated by low serotonin function (Mitchell & Phillips, 2007). It is known that the primary auditory cortex receives dense serotonergic projections, which appear to exert an inhibitory effect on the neural activity evoked by auditory stimulation in this area (Hegerl et al., 2001; Hegerl and Juckel, 1993). An animal study showed that the administration of quipazine maleate (serotonin agonist) decreased N1 amplitude, whereas the administration of spiperone (serotonin antagonist) increased N1 amplitude (Manjarrez et al., 2005). That is, a lower serotonin level may be associated with a larger N1 amplitude. Although there is still controversy as to whether auditory evoked potentials reflect brain serotonin tone in humans (Dierks et al. 1999), it is possible that the effect of emotional context on N1 amplitude has a neurochemical background. Moreover, Kähkönen et al. (2005) suggested that MMN amplitude was also modulated by serotonergic activity. It is a subject of future investigation to examine whether serotonin or other neurotransmitters are responsible for the modulatory effect of emotional states on auditory ERPs.

5. Conclusion

The present study demonstrated that emotional states induced by visual slides modulate information processing of environmental acoustic stimuli reflected in ERPs. The effect appeared in a sequential fashion. Negative emotion increased the amplitude of the N1 elicited by highly deviant stimuli, whereas positive emotion reduced the amplitude of later ERP components, P2 and MMN. This study suggests that ERPs elicited by nonstartle tones may be an index of emotional states as well as startle blink reflex and ERPs elicited by startle probes.

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Footnotes

[1] The IAPS slide numbers were as follows: Positive: 1463, 1500, 1540, 1590, 1720, 1721, 1722, 1920, 1999, 2058, 2091, 2209, 2216, 2250, 2331, 2650, 2655, 2660, 4598, 5480, 5600, 5623, 5628, 5831, 5849, 5910, 7220, 7230, 7260, 7270, 7282, 7330, 7470, 7480, 7481, 7502, 8031, 8120, 8460, 8496; Neutral: 1670, 2880, 5390, 5510, 5530, 5740, 6150, 7000, 7002, 7004, 7006, 7009, 7020, 7025, 7030, 7034, 7035, 7040, 7050, 7080, 7090, 7100, 7140, 7150, 7170, 7185, 7186, 7187, 7190, 7217, 7224, 7233, 7235, 7490, 7491, 7500, 7705, 7710, 7950, 9210; Negative: 1220,1270, 1275, 1301, 2110, 2205, 2312, 2682, 2692, 2700, 2722, 2900, 6190, 6241, 6213, 6610, 6940, 7360, 9000, 9001, 9046, 9102, 9110, 9220, 9280, 9290, 9330, 9340, 9390, 9404, 9470, 9530, 9584, 9592, 9611, 9621, 9830, 9911, 9912, 9920.

[2] Excluding extremely negative and positive pictures may limit the scope of the present study. The arousal values of the slides used in this study may have been lower than those used in previous studies. The consequences of this limitation are twofold. First, because we controlled the valence and arousal values of the slide set carefully and confirmed that these values differed significantly among the three emotional slide categories, significant effects obtained in the present study can be seen as valid as those obtained in studies using more arousing slides. Second, if a prediction from previous studies was not supported statistically, this does not negate the original finding since the latter was obtained by using a more arousing slide set. We will get back to this point in the Discussion.

[3] We first performed a single, overall PCA on the data for the three stimulus types. However, the result was confusing and difficult to interpret. Specifically, a single principal component (peaking around 185 ms) had different scalp topographies for standard and deviant tones. For the standard tone, it had a central maximal scalp distribution, which resembles the P2 in the averaged waveform. On the other hand, for the high-deviant and low-deviant tones, it had a frontal scalp distribution, which resembles the MMN in the averaged waveform. Because we felt difficulty in designating a single principal component as different ERP components (P2 or MMN) in different contexts, we gave up the overall PCA and performed a separate PCA for each stimulus type, which produced a similar but clearer result compared with the overall PCA.

[4] The positive component elicited by the high-deviant tone is not P3a but P2. The mean peak latency of 209 ms is too short for the P3a. Moreover, when a deviant stimulus is unattended, a P3a often occurs as a discrete hump peaking around 300 ms, which follows the P2 peaking around 200 ms (Cuthbert et al., 1998; Ullsperger et al., 2001). In this study, only one trough can be seen in the waveform, suggesting that no P3a followed P2.

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Table 1. Means ± standard deviations of valence and arousal ratings for positive, neutral, and negative slide categories.

	Normative		Present experiment	
Slide category	Valence	Arousal	Valence	Arousal
Positive	$7.2 \pm 0.4_a$	$5.0 \pm 0.5_a$	$6.7 \pm 0.7_a$	$4.7 \pm 1.4_a$
Neutral	$5.1 \pm 0.3_b$	$2.8 \pm 0.4_b$	$5.0 \pm 0.2_b$	$3.0 \pm 1.1_b$
Negative	$3.2 \pm 0.5_c$	$4.8 \pm 0.6_a$	$3.1 \pm 0.7_c$	$4.8 \pm 1.3_a$

Note. Means in the same row that do not share subscripts differ at $p < .05$.

Figure Captions

Figure 1. Left: Grand mean ERP waveforms elicited by high-deviant, low-deviant, and standard tones during positive, neutral, and negative slide presentations. Right: Grand mean difference waveforms computed by subtracting the ERP elicited by standard tones from the ERP elicited by high-deviant and low-deviant tones ($N = 13$).

Figure 2. Scalp topographic maps of the N1, P2, and MMN. The corresponding peak latencies (means ± standard deviations) are shown.

Figure 3. Mean amplitudes of the N1 (at Fz), P2 (at Cz), and MMN (at Fz) during positive, neutral, and negative slide presentations. Bars indicate standard errors of means.

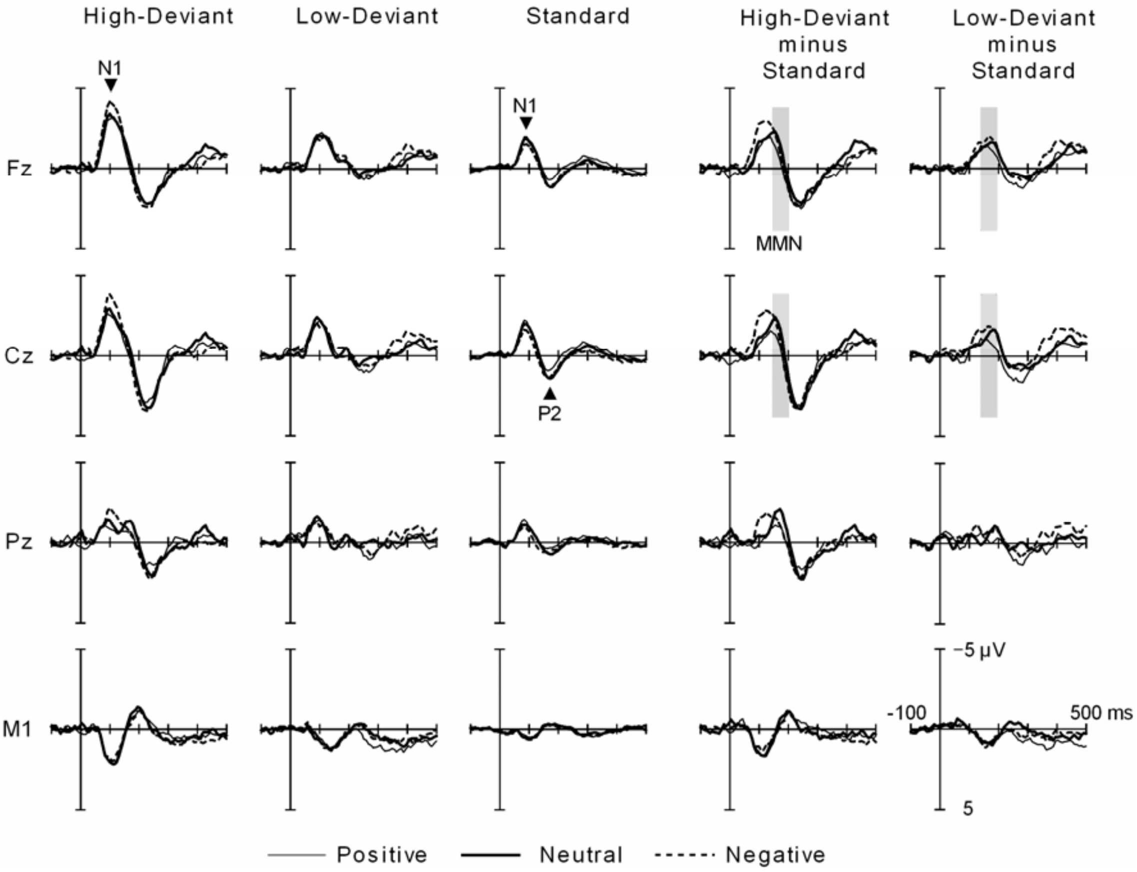
High-Deviant
Low-Deviant
Standard
High-Deviant minus Standard
Low-Deviant minus Standard
N1
N1
P2
MMN
Fz
Cz
Pz
M1
−5 µV
-100
500 ms
5
Positive
Neutral
Negative

Figure 1

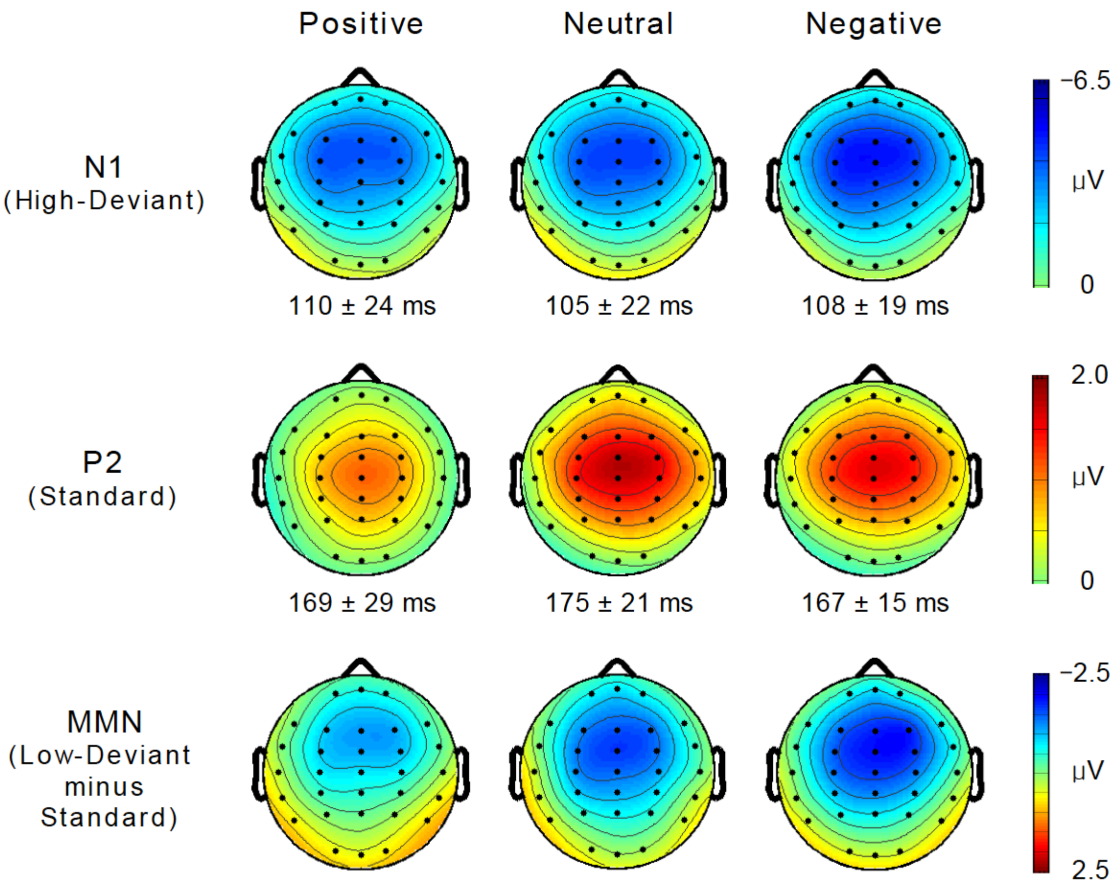
Positive
Neutral
Negative
N1
(High-Deviant)
110 ± 24 ms
105 ± 22 ms
108 ± 19 ms
−6.5
µV
0
P2
(Standard)
169 ± 29 ms
175 ± 21 ms
167 ± 15 ms
2.0
µV
0
MMN
(Low-Deviant
minus
Standard)
−2.5
µV
2.5

Figure 2

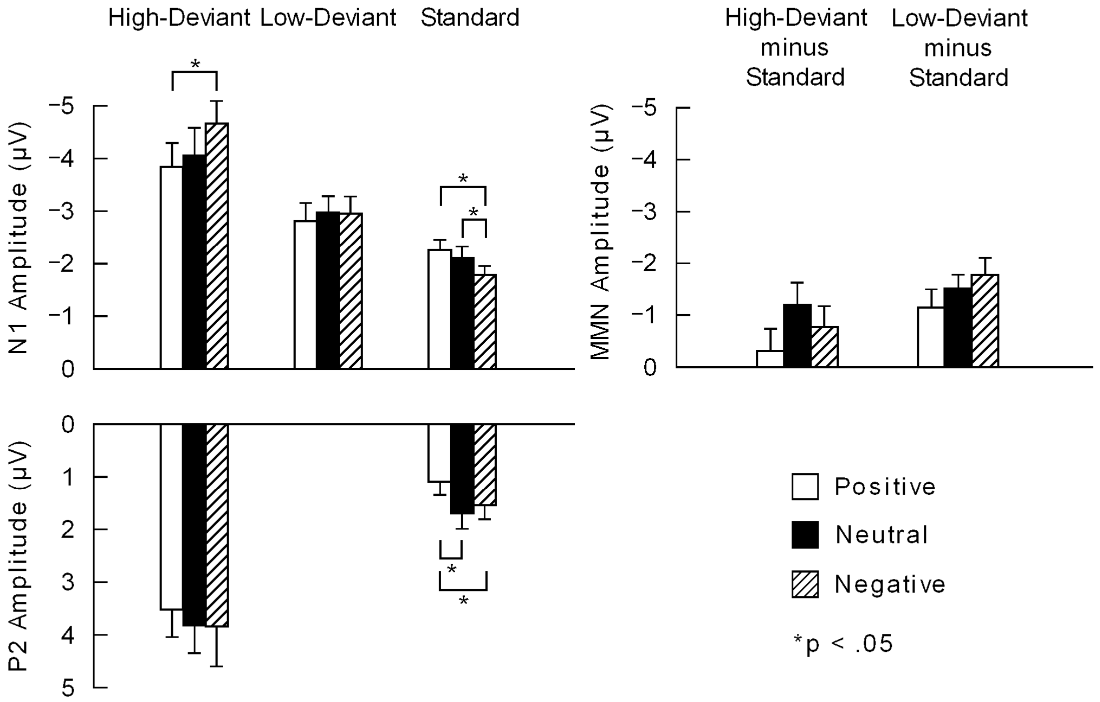
High-Deviant
Low-Deviant
Standard
N1 Amplitude (μV)
−5
−4
−3
−2
−1
0
*
*
*
P2 Amplitude (μV)
0
1
2
3
4
5
*
*
High-Deviant minus Standard
Low-Deviant minus Standard
MMN Amplitude (μV)
−5
−4
−3
−2
−1
0
Positive
Neutral
Negative
*p < .05

Figure 3