Affective visual event-related potentials: Arousal, valence, and repetition effects for normal and distorted pictures

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Abstract

Event-related potentials (ERPs) were used to assess arousal (low, high), valence (negative, positive), and stimulus repetition effects for normal and distorted images from the International Affective Pictures System (IAPS). Distorted stimuli were constructed by dividing each image into 108 one cm squares and rearranging the segments randomly to produce a "scrambled" picture. Event-related potentials (ERPs) were elicited by presenting the normal and scrambled images as target stimuli, with a repeated visual pattern used as the standard stimulus. Participants (N=32) were instructed to press a button to the targets and ignore the standard. Stimulus repetition effects were assessed by presenting each stimulus twice in the normal and scrambled condition. High arousal stimuli yielded larger late positive components for both the normal and scrambled pictures. No overall valence effects were obtained, but arousal and valence influenced component amplitudes for middle-latency ERPs from the scrambled stimuli. For the normal pictures, stimulus repetition was associated with increased component amplitudes for all potentials and decreased RTs of all affective categories. For the scrambled pictures, no repetition changes were obtained. The findings suggest that stimulus arousal level contributes more than valence to affective ERP measures for normal as well as perceptually distorted pictures. Stimulus repetition engages memory for previous normal picture items but is not influenced by affective category[jo1]. Theoretical implications are discussed.

1.0 Introduction

The perceptual system utilizes information gained through previous exposure to affective events thereby facilitating subsequent processing of similar stimuli. As event-related potentials

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(ERPs) can provide fine-grain temporal resolution of the underlying mechanisms, this neuroimaging method has become highly useful for assessing affective neural processing (Bradley et al., 1992; Dolcos and Cabeza, 2002; Ito et al., 1998; Lang et al., 1993, 1999). Although affective ERPs can be generated automatically by motivationally relevant picture motifs (appetitive, fearful, sexual), emotional stimuli also modulate ERPs even if the image content is not readily perceived (Codispoti et al., 2006; Schupp et al., 2006). The present study employs a stimulus repetition paradigm to characterize these issues by comparing affective pictures with "scrambled" image controls.

1.1. ERPs from affective picture stimuli

The International Affective Picture System (IAPS) often is used to provide visual images for assessing emotional outcomes (Lang et al., 1999). These pictures are rated for valence (unpleasant to pleasant) and arousal (calm to exciting) level, and these dimensions have been related to ERP modulations. The temporal course of valence and arousal effects differs, however, as valence influences are observed for early (100-250 ms) whereas arousal influences occur for later (250-850 ms) components (Codispoti et al., 2007; Olofsson et al., 2007). Similar outcomes have been obtained from a wide range of tasks, and as affectively potent stimuli modulate ERPs even when presented subconsciously these effects appear to occur automatically (Bernat et al., 2001; Cuthbert et al., 2000; Delplanque et al., 2006; Roschmann and Wittling, 1992).

Affective ERP effects have been obtained from passive viewing, affect discrimination procedures, and for images presented as distracting or target stimuli in an oddball task (Delplanque et al., 2004, 2005; Keil et al., 2002; Mini et al., 1996; Schupp et al., 2000). In general, negative affective valence produces stronger ERP modulation than positive affective valence pictures (Cacioppo et al., 1999; Crawford and Cacioppo, 2002; Öhman and Mineka, 2001). This "negativity-bias" may reflect rapid amygdala processing of aversive information (LeDoux, 1995; Morris et al., 1998; Ohman and Soares, 1998). Moreover, these early affective ERPs appear related to affective disposition such as trait anxiety and trait fearfulness (Dien, 1999), whereas late affective ERPs are sensitive to individual variation from emotional reappraisal and evaluation strategies (Hajcac et al., 2006, Moser et al., 2006).

In addition, when a P300 component from an affective stimulus is elicited, amplitudes are larger over the parietal cortex and increase with increases in arousal level. Hence, emotional arousal may amplify activity in cortical structures that are normally engaged for target processing (Polich, 2007; Sabatinelli et al., 2007). When arousal level across stimuli is well controlled valence can modulate P300 from frontal sites (Cano et al., 2007; Conroy and Polich, 2007; Delplanque et al., 2005, 2006), although it is unclear whether these effects consistently obtain when both factors are manipulated within the same session (Cuthbert et al., 2000). Despite evidence for ERP modulations from picture valence and arousal (Delplanque et al., 2004, 2006; Olofsson and Polich, 2007; Schupp et al., 2006), these fundamental affective factors are not typically varied systematically. For example, positive/negative valences with generally high arousal level often are compared with neutral valence stimuli that are low-arousing in a fashion that confounds their ERP assessment by differential stimulus probability.

1.2. Stimulus repetition effects

When a stimulus is presented repeatedly, processing changes can be expected because of variation in stimulus novelty, priming mechanisms, and habituation. Recognition memory ERP studies using neutral and affective stimuli have found increased amplitudes for late positive components when a stimulus reoccurs within the stimulus series (Bentin et al., 1992; Friedman, 1990; Olofsson and Polich, 2007; Rugg, 1990; Segalowitz et al., 1997; Smith and Halgren, 1989). Several affective studies have presented stimuli multiple times but collapsed over

presentations to obtain their ERP averages, so that repetition effects cannot be assessed directly (Aftanas et al., 2001; Brazdil et al., 2003; Carretie et al., 2004a, 2004b; Ito et al., 1998; Keil et al., 2001; Schupp et al., 2000, 2004).

Olofsson and Polich (2007) found that successive repetition of affective target stimuli within an oddball sequence produced larger positive amplitudes for pleasant, unpleasant, and neutral stimuli from around 150 ms as well as evidence of priming with shorter P300 and response latencies across repetition trials. This repetition effect occurred independently of stimulus arousal level, with larger positivity from around 200 ms for high compared to low arousing stimuli. Further, N2 and P3 amplitude decreased overall across the experimental session, implying that amplitude habituation was independent of stimulus arousal level. Taken together, these findings suggest that arousal, repetition, and habituation appear to be produced independently of one another and overlap in time, although the time-course of affective stimulus repetition-induced memory effects over longer intervals is unknown.

1.3. Stimulus distortion

Current theories of affective ERP modulation emphasize stimuli with high evolutionary significance as automatic triggers of basic motivational systems whenever the stimuli are perceived (e.g., Schupp et al., 2006). Most ERP studies using affective pictures have employed stimulus durations of >500 ms, enabling a clear perception of picture contents. However, affective information also can be extracted during conditions of limited perception, such that ERP effects of arousal are conveyed in a stream of rapidly (120-333 ms) presented pictures (Junghöfer et al., 2001; Schupp et al., 2003, 2004, 2006). This method alters perceptual processing of affective content and alters higher-level semantic analysis of the picture content. This interpretation is supported by recent findings that physical attributes such as featural composition and complexity modulate affective ERPs perhaps by employing attentional mechanisms not specific to emotion (Bradley et al., 2007; Codispoti et al., 2006, 2007; Cano et al., 2007; Delplanque et al., 2007). Thus, if ERP affective modulations are preserved even when image is distorted the emotional information must be mediated by other perceptual processes.

1.4. Present study

The goals of the present study were to characterize affective valence and arousal processing across stimulus repetition of highly distinct IAPS stimuli and compared to visually distorted controls. IAPS images were selected in a way that the stimuli were either rated as comparatively low or high on arousal level, and relatively strong negative and positive valences selected within each arousal category. No neutral stimuli were employed. The chosen stimuli were presented as targets in an oddball paradigm, with normal pictures compared to their "scrambled" counterparts; and each stimulus occurred twice in each condition.

This approach was devised in order to: (1) assess valence and arousal effects under repetition circumstances within a target detection task[jo2], and (2) temporally track affective ERP effects for these variables across the waveform to characterize when and where they occur. As stimulus repetition is a common procedure and the physical stimulus properties contribute to outcomes, these factors were systematically manipulated to characterize the resulting ERP effects relative to previous studies. It was hypothesized that arousal would modulate the later ERP components, whereas valence would modulate the early ERP components. Valence effects should be found primarily over frontal electrodes, whereas arousal effects should be manifest over parietal areas. Stimulus repetition should produce larger later potentials for normal but not for unrecognizable scrambled pictures that also demonstrated an absence of affective outcomes.

2.0 Method

2.1. Participants

A total of 32 right-handed undergraduates (16 female) were employed as participants. All reported being free of neurological/psychiatric disorders, having normal or corrected-to-normal vision, and provided informed, written consent. Participants were compensated with course credit or $10 per hour.

2.2. Stimuli and procedure

The image stimuli for each of the four categories varied in arousal (low to high) and valence (negative to positive) according to the IAPS ratings, which were obtained using a 1-9 point scale by large cohorts of female and male undergraduates (Lang et al., 1995). The stimuli obtained consisted of 16 images of the four categories based on the mean female and male ratings. The mean (SD) arousal and valence ratings, respectively, were as follows: Low arousal-negative valence=4.46 (0.25) and 2.63 (0.30), high arousal-negative valence=6.76 (0.32) and 2.48 (0.30); low arousal-positive valence=4.45 (0.27) and 7.36 (0.29); high arousal-positive valence=6.68 (0.32) and 7.33 (0.29). Arousal and valence ratings were assessed with separate two-factor (2 arousal × 2 valence) analyses of variance. Low arousal pictures were rated lower on arousal than high arousal pictures, $F(1,60)=4242.1$, $p<.00001$; negative valence pictures were rated more negative than positive valence pictures, $F(1,60)=971.8$, $p<.00001$; no interactions were obtained ($p>0.40$, both cases).

These pictures were organized into a 9×12 cm format and served as target stimuli presented to each subject in an oddball task, with $p=0.40$ for a picture. A red and white checked standard image of equal size and a pattern designed to equate visual spatial frequency to the target occurred with $p=0.60$. This stimulus was adapted from previous reports (Delplanque et al., 2004, 2005, 2006). Additional "scrambled" target images were constructed by randomly rearranging 0.75 cm^2 areas of each image (192 square blocks), which largely maintains the picture's visual characteristics (color, spatial frequency, intensity) but eliminates its content. The Appendix lists the IAPS number of each stimulus and presents examples of a normal and scrambled stimulus from each category.

The subjects sat in a chair with 75 cm between the front edge of the chair and the computer screen. All stimuli were displayed for a duration of 1000 ms at the center of a computer screen on a light grey background at normal viewing luminance. A 2000 ms inter-stimulus interval was used. Participants were instructed to respond with a mouse-click using their dominant right hand when a target image was presented and to refrain from responding when the standard stimulus was presented. The 64 target pictures (16 for each of the four affective stimulus types) occurred randomly among 96 presentations of the standard image, resulting in a total of 160 trials. The scrambled pictures occurred as targets in a separate condition. Each stimulus set was presented twice using a different random order to yield 32 ERP trials for each subject and stimulus type, with half the subjects receiving the normal pictures first and the other half receiving the scrambled pictures first. Error rate and response time were recorded.

2.3. Recording conditions

Electroencephalographic (EEG) activity was recorded from 21 electrode sites including Fz, Cz, Pz, Fp1/2, F3/4, F7/8, C3/4, T7/8, P3/4, P7/8, O1/2, referenced to linked earlobes, a forehead ground, and impedances of 10KΩ or less, with the reference electrodes balanced. Additional electrodes were placed at the outer canthi as well as above and below the left eye to assess electro-ocular (EOG) activity with a bipolar recording. The bandpass was 0.01-30 Hz (6 dB/octave), and the EEG was digitized at 4.0 ms per point for 1024 ms, with a 100 ms pre-stimulus baseline. Waveforms were averaged off-line, such that trials on which the EEG or

EOG exceeded ±100 µV were rejected. Single-trial data also were subjected to an EOG correction procedure to remove any remaining artifact. Rest periods were provided as needed.

3.0 Results

3.1 Behavioral data

Error rate (ER) was defined as the percent of incorrect responses, was less than 1%, and is not considered further. Response time (RT) was defined as the time from stimulus onset to the button press response, and the mean RT was computed over stimulus trials for each subject from each condition across stimulus blocks. RT was assessed with a four-factor (2 arousal × 2 valence × 2 repetition × 2 stimulus type) analysis of variance. Mean RT did not differ among arousal ($p > .70$) or valence ($p > .30$) conditions (low arousal-negative valence=509, low arousal-positive valence=502, high arousal-negative valence=504, high arousal-positive valence=502 ms, respectively, $p > .15$). RT was longer for the first compared to second repetition, $F(1,31) = 12.7$, $p < .002$, and longer for the normal compared to scrambled stimulus items, $F(1,31)=16.2$, $p < .001$. RTs for normal pictures demonstrated a significant 45 ms decrease across repetitions, whereas scrambled pictures resulted in a non-significant change (5 ms decrease), yielding a repetition by stimulus type interaction, $F(1,31)=6.7$, $p < .02$. Further, RT from the normal stimuli decreased similarly across arousal and valence levels, but the scrambled stimuli yielded short RT and a stronger decrease for negative stimuli with longer $RT_{[jo3]}$ and less of a decrease for positive stimuli to produce a three-way interaction among arousal by valence by stimulus type, $F(1,31)=4.8$, $p < .05$. The origin of this weak behavioral interaction is unknown.

3.2 ERP analyses

After excluding error and artifact trials, the mean number of ERP averages for each stimulus condition across stimulus type for repetition block-1 was 14.7, 14.9, 14.7, 14.9, and for repetition block-2 was 15.1, 14.8, 14.8, 14.8, trials for the low arousal-negative, high-arousal negative, low-arousal positive, and high arousal-positive waveforms, respectively. A four-factor (2 arousal × 2 valence × 2 repetition × 2 stimulus type) analysis of variance performed on the number of trials found no differences for arousal ($F < 1$, $p > 0.80$), valence ($F < 1$, $p > 0.50$), repetition ($F < 1$, $p > 0.15$), or stimulus type ($F = 2.5$, $p > 0.12$). Thus, trial number did not differ among conditions.

Figure 1 illustrates the grand averages from the normal picture images. Figure 2 illustrates the grand averages from the scrambled images for each arousal and valence category. Averages from each repetition block overlapped for each of the midline electrodes. The ERP components were analyzed by measuring mean waveform amplitude relative to the pre-stimulus baseline within component time windows: N1=120-160 ms, P2=160-220, N2=220-300, P3=300-450 ms, early slow wave=550-700, late slow wave=700-850 ms.

Figure 3 and Figure 4 illustrate the mean component amplitude from the normal and scrambled images, respectively, for each experimental variable at the midline electrode location. Preliminary analyses were conducted to assess the extent to which arousal and valence outcomes were affected by repetition and stimulus type manipulations. No reliable effects for stimulus type order (normal vs. scrambled) were obtained, and this factor will not be considered further. Data were then assessed for the normal and scrambled conditions separately to facilitate interpretation of the findings by applying a four-factor repeated measures analysis of variance (2 arousal × 2 valence × 2 repetition × 3 midline electrodes) on the mean component amplitude from each subject. Greenhouse-Geisser corrections to the *df* were applied as needed, with the corrected probabilities reported. Additional analyses of hemispheric, frontal, and occipital electrodes were performed, but these did not reveal outcomes that differed appreciably from the overall findings.

Table 1 summarizes the results of the primary analyses of variance performed separately on the data from the normal and scrambled stimulus presentations. The table is organized to permit direct comparison between the two stimulus types with respect to the major independent variables of arousal, valence, and repetition. The electrode main effect reflected increased amplitudes from the frontal to parietal sites for all potentials across normal and scrambled stimulus conditions and will not be considered further.

Arousal—As evident from Figures 3 and 4, high arousal stimuli produced larger late positive potentials compared to low arousal stimuli, for both the normal and scrambled stimulus conditions. These arousal effects were more robust for the normal compared to scrambled images. Arousal and electrode position evinced interactions, such that the largest arousal effects were observed over the parietal electrode for potentials in the normal and scrambled conditions.

Valence—No main effects for valence category were obtained for any potential for either the normal or scrambled stimulus conditions. However, for the scrambled stimulus condition arousal and valence interacted reliably for the P2, N2, and P3 potentials. In general, the component amplitude differences for low compared to high arousal stimuli were somewhat greater for negative compared to positive valence stimuli. The valence and electrode factors yielded interactions for the later potentials only in the normal stimulus condition: Larger differences between valence categories appeared to occur over parietal compared to the frontal and central electrode locations.

Repetition—For the normal image pictures, the first stimulus repetition produced smaller potentials for all components compared to the second stimulus repetition as shown in Figure 3. No main effect of repetition was obtained for the scrambled pictures as shown in Figure 4. For the later components from the normal stimuli, repetition and electrode position interacted, such that repetition amplitudes were larger over the parietal compared to frontal/medial electrodes. The repetition factor also yielded interactions with valence effects for a few potentials from both the normal and scrambled stimuli. However, these interactions were statistically weak and evinced no discernible pattern.

4.0 Discussion

This study employed IAPS images that varied systematically in arousal (low vs. high) and valence (negative vs. positive) as targets in an oddball task to elicit ERPs. Since all stimuli occurred twice, the neuroelectric characteristics of stimulus repetition were obtained for these two affective parameters. Further, stimuli were presented in a separate session as scrambled images to investigate whether stimulus affect can be conveyed from the IAPS without access to global picture motifs. The major findings were that stimulus arousal modulated amplitude of the later components for both normal and scrambled pictures. No overall valence amplitude effects were obtained. Repetition of normal pictures was associated with increased amplitudes for all ERP components and decreased RTs independently of affective stimulus category. For normal stimulus pictures, strong arousal and repetition effects were obtained in the absence of independent valence effects. For the scrambled pictures, arousal effects were found in ERP amplitudes. Repetition of scrambled pictures had no effect on ERPs or RTs.

4.1. Arousal and valence

High-arousal stimuli evinced larger mean amplitudes compared to low-arousal stimuli (Carretie et al., 2004b; Delplanque et al., 2006; Schupp et al., 2000). These effects began approximately with the N2, became appreciably stronger for the P3 and early SW component, and were still robust for the late SW portion of the waveform as has been previously found (Olofsson and Polich, 2007). Arousal level also increased the amplitude of the later potentials

for the scrambled pictures, although the effects were statistically weaker than those from the normal pictures. No overall valence effects were obtained for either stimulus type, but arousal level and valence interacted for several components elicited by the scrambled stimuli.

A novel finding in this study is that highly arousing pictures still produce an elevated late ERP positivity for the scrambled stimulus images. The distorted pictures were made from the same IAPS pictures; with each picture segmented into squares and randomly rearranged. These distorted stimuli are unrecognizable and yielded no repetition memory effects for either RT or ERPs components, which were found for the normal pictures. These outcomes are consistent with previous studies that altered stimulus perception by quick serial presentation of affective pictures, as arousing stimuli appear to cause rapid cortical modulations even when picture content cannot be accessed due to perceptual limitations (Junghöfer et al., 2001; Schupp et al., 2003, 2006). These and the present results imply that physical stimulus properties (e.g., color, contrast, texture) can produce arousal ERP effects. Although the exact mechanisms of these influences are unknown, relatively low-level perceptual features of affective pictures appear to contribute to ERP arousal outcomes (Codispoti et al., 2006; Delplanque et al., 2007).

4.2. Stimulus repetition

Stimulus repetition of the normal pictures produced increased component amplitudes from the first to the second trial block, with no repetition main effects found for scrambled images. Recognition memory ERP studies have demonstrated increased amplitudes for late positive components when a stimulus is recognized as having been presented previously in the series (Bentin et al., 1992; Friedman, 1990; Rugg, 1990). Successively repeated emotional stimuli used as targets in an oddball task produced similar amplitude increases from the first to second repetition (Olofsson and Polich, 2007). The current results corroborate previous findings and extend the repetition effect to non-successive and unpredictable stimulus sequences (Aftanas et al., 2001; Carretie et al., 2001a, 2003, 2004a; Ito et al., 1998; Keil et al., 2001; Schupp et al., 2000, 2004). Moreover, the lack of interaction with the arousal or valence factors indicates that the modulation of rapid brain responses to affective images is stable over repetitions, so that ERP modulations from reoccurring affective picture stimuli are unlikely to be confounded by repeated stimulus presentations. That the repetition effects of ERP amplitudes and RTs occurred for the normal but not the scrambled images suggest that only normal images that can be recognized are subject to amplitude increase due to repetition.

4.3. Theoretical perspective

The straightforward nature of the present task with the same response for each target stimulus in the absence of any emotive judgments implies that the obtained ERP effects were produced automatically (Bernat et al., 2001; Olofsson and Polich, 2007; Schupp et al., 2000). Stimulus arousal influenced late component amplitudes from both normal and scrambled stimuli and implies that fundamental perceptual attributes are possible causes of arousal-related processing modulations, which were statistically weaker for the scrambled stimulus conditions. The variation for component amplitude between arousal and valence levels observed for the scrambled stimuli in the middle latency range also seem to reflect automatic featural processing of affective properties.[jo4] The exact mechanisms by which arousal-related ERP modulations are preserved in distorted images are unknown. However, the results from this and other studies suggest that physical stimulus characteristics (e.g., color, spatial frequency, local/global features) can convey arousing properties (Bradley et al 2007; Cano et al., 2007; Codispoti et al 2006, 2007). A systematic integration of these findings should emerge as additional results accumulate (Olofsson et al. 2007).

Although the origins of arousal/valence interaction effects in the scrambled images remain vague, they may result in part from the use of the extreme negative- and positive-valence ratings

coupled with the extreme low- and high-arousal levels used to select the present stimuli. Perhaps normal picture stimuli did not yield this interaction because these images are necessarily perceived as a whole percept rather than the individual components seen in scrambled images. Capturing the image in its entirety could override basic perceptual influences by which valence and arousal interacts (e.g., hue or brightness). Further, cognitive operations are likely to be utilized more efficiently for normal pictures compared to scrambled images, which would enhance memory performance and increase P300/slow wave amplitude (Azizian and Polich, 2007; Karis et al., 1984; Paller et al., 1988). Such ERP amplitude changes have been obtained when affective memory formation is assessed (Dolcos and Cabeza, 2002; Palomba et al., 1997). The present results indicate that emotional stimulus properties also can be conveyed without access to affective content, such that stimulus cues apparently can modulate ERPs when perceptual quality is limited or altered.

Acknowledgements

Appendix

Stimulus Category, Numbers of Selected IAPS Pictures, and Sample Normal and Scrambled Picture Stimuli[*] The images were presented in color.

Arousal-Valence Category	Selected IAPS Images	Normal
Low- Negative	2205, 2276, 2375.1, 2455, 2750, 2900.1, 3300, 9000, 9220, 9265, 9280, 9290, 9320, 9330, 9342, 9561	
High-Negative	2730, 3030, 3400, 6230, 6250, 6260, 6300, 6313, 6350, 6370, 6510, 6530, 6550, 8485, 9250, 9600	
Low-Positive	1463, 1500, 1510, 1590, 1721, 1920, 2080, 2224, 2331, 2395, 2530, 5594, 5820, 7280, 7480, 8461	
High-Positive	4607, 4608, 4660, 4670, 4680, 5621, 5629, 8030, 8080, 8180, 8185, 8186, 8370, 8400, 8490, 8501	

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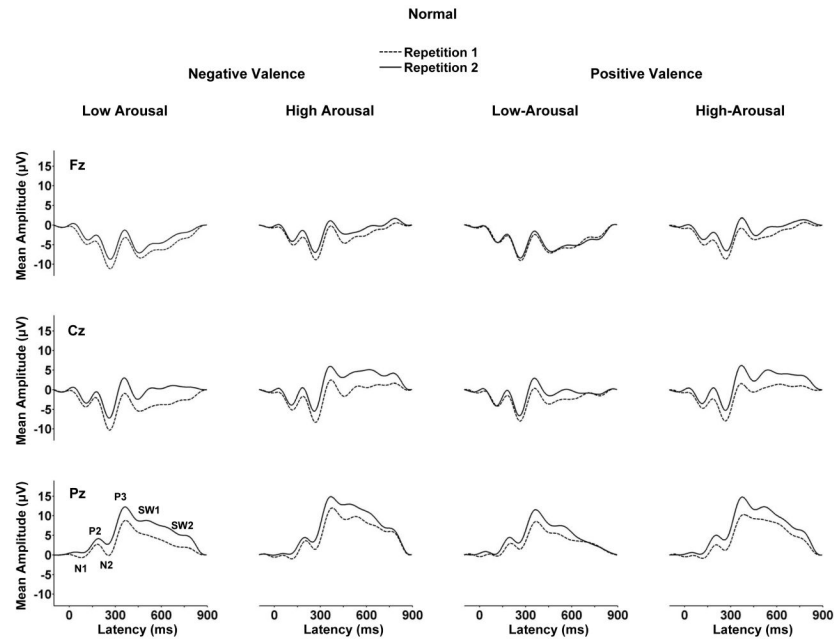
Figure 1.
Grand averages of the normal picture low-arousal and high-arousal stimuli for the negative valence and positive valence conditions from the repetition 1 and repetition 2 trial blocks (n=32).

Figure 2.
Grand averages of the scrambled picture low-arousal and high-arousal stimuli for the negative valence and positive valence conditions from the repetition 1 and repetition 2 trial blocks (n=32).
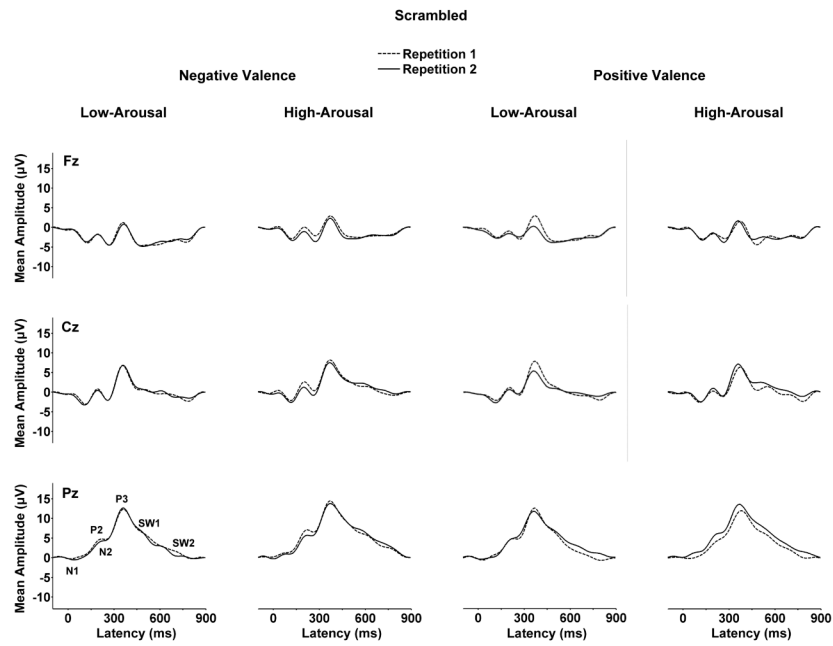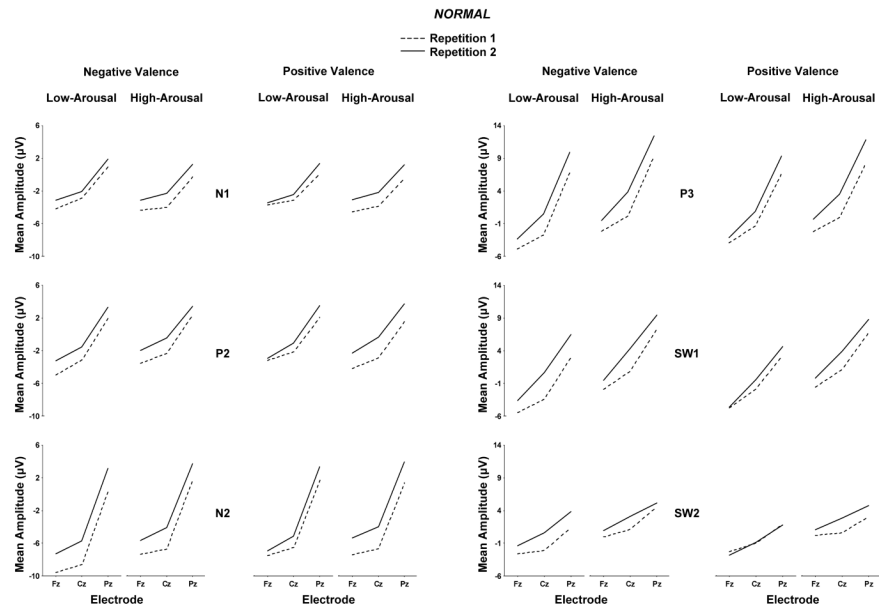
Figure 3.
Normal pictures: Mean amplitude for the N1, P2, N2, P3, early slow wave, and later slow wave components from the low-arousal and high-arousal for the negative valence and positive valence stimulus conditions as a function of midline electrode with repetition 1 and repetition 2 trial blocks overlapped.

Figure 4.
Scrambled pictures: Mean amplitude for the N1, P2, N2, P3, early slow wave, and later slow wave components from the low-arousal and high-arousal for the negative valence and positive valence stimulus conditions as a function of midline electrode with repetition 1 and repetition 2 trial blocks overlapped.
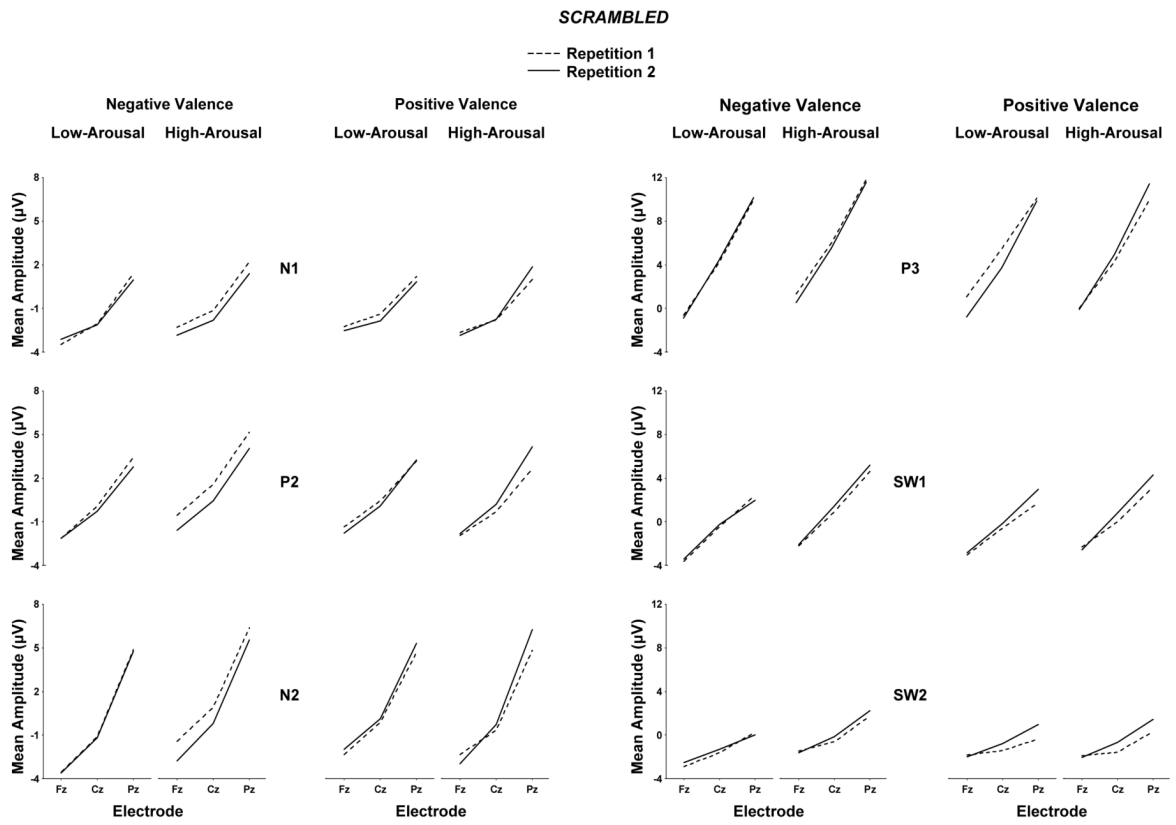
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Table 1

Summary of analyses of variance (2 arousal × 2 valence × 2 repetition × 3 electrodes) performed separately on the mean amplitude data for each component and stimulus type (normal vs. scrambled) separately.

	Normal						Scrambled					
	N1	P2	N2	P3	SW1	SW2	N1	P2	N2	P3	SW1	SW2
Arousal (1,31)	--	--	8.4**	41.6***	75.8***	44.2***	--	--	--	4.4*	12.4**	5.5*
Valence (1,31)	--	--	--	--	--	--	--	--	--	--	--	--
Repetition (1,31)	17.2***	19.9***	34.1***	39.9***	23.4***	11.2***	--	--	--	--	--	--
Electrode (2,62)	51.7***	56.0***	118.5***	189.8***	156.6***	49.7***	42.5***	51.9***	96.2***	182.6***	73.9***	28.4***
A × V (1,31)	--	--	--	--	--	--	--	6.6*	4.5*	6.2*	--	--
A × R (1,31)	--	--	--	--	--	--	--	--	--	--	--	--
V × R (1,31)	--	--	--	--	--	--	--	--	--	--	--	--
A × E (2,62)	--	--	5.9**	--	--	3.6*	--	--	--	--	5.6**	3.3*
V × E (2,62)	--	--	--	8.9***	4.9*	4.2*	--	--	--	--	--	--
R × E (2,62)	--	--	--	13.5***	11.1***	7.8**	--	--	--	--	--	--
A × V × R (1,31)	--	--	--	--	--	--	--	--	--	--	--	--
A × V × E (2,62)	--	--	--	--	--	--	--	--	4.4*	--	--	--
A × R × E (2,62)	--	--	--	--	--	--	--	--	--	--	--	--
V × R × E (2,62)	--	3.5*	--	--	--	--	--	3.8*	--	--	--	3.5*
A × V × R × E (2,62)	--	--	--	--	--	--	--	--	--	--	--	--

*p<0.05
**p<0.01
***p<0.001