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When fear forms memories: Threat of shock and brain potentials during encoding and recognition

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Abstract

The anticipation of highly aversive events is associated with measurable defensive activation, and both animal and human research suggests that stress-inducing contexts can facilitate memory. Here, we investigated whether encoding stimuli in the context of anticipating an aversive shock affects recognition memory. Event-related potentials (ERPs) were measured during a recognition test for words that were encoded in a font color that signaled threat or safety. At encoding, cues signaling threat of shock, compared to safety, prompted enhanced P2 and P3 components. Correct recognition of words encoded in the context of threat, compared to safety, was associated with an enhanced old–new ERP difference (500–700 msec; centro-parietal), and this difference was most reliable for emotional words. Moreover, larger old–new ERP differences when recognizing emotional words encoded in a threatening context were associated with better recognition, compared to words encoded in safety. Taken together, the data indicate enhanced memory for stimuli encoded in a context in which an aversive event is merely anticipated, which could assist in understanding effects of anxiety and stress on memory processes.

Keywords

Emotion; Memory; Stress; Threat; ERPs

1. Introduction

Anticipating threat of shock elicits a variety of autonomic and somatic reactions that reflect activation of the brain's defense system (Bradley, 2000; Lang and Bradley, 2010). Defensive arousal in the context of imminent threat is apparent in skin conductance elevation, startle reflex potentiation and heart rate deceleration (Bradley et al., 2005, 2008; Grillon et al., 1991; Grillon and Davis, 1995; Melzig et al., 2008). Furthermore, both animal (Roozendaal and McGaugh, 1996) and human (Buchanan and Lovall, 2001; Cahill et al., 2003; Payne et al., 2007) research suggests that stress-inducing contexts not only activate defensive response mobilization but also facilitate later memory performance (Joëls et al., 2006; Diamond et al., 2007; Schwabe et al., in press). Indeed, there is evidence that both psychosocial stress and cold pressor stress induced prior to (Payne et al., 2007; Weymar et al., in press) or shortly after viewing emotional and neutral scenarios (Cahill et al., 2003) enhances long-time memory for these events. In the present study, rather than directly

imposing a physical stressor during encoding, we evaluate the effects of anticipating the presentation of an electric shock on subsequent recognition memory for emotional and neutral words encoded in a font color signaling shock threat – an anticipatory state in which an aversive event may or may not occur.

Recent Event-related potential (ERP) studies have reported differential processing of threat and safety cues. Cues that signal threat (either grating patterns or pictures), compared to safety, induce an enhanced P2 component over anterior brain regions (Baas et al., 2002; Bublatzky and Schupp, in press) and enhanced late positive potentials (P3 and LPP) over centro-parietal brain regions (Baas et al., 2002; Boöcker et al., 2004; Bublatzky and Schupp, in press), suggesting increased salience and resource allocation for these cues. On the other hand, whereas Shackman et al. (2011) also found heightened early components, they reported that P3 amplitude for task-relevant stimuli on a visual discrimination task was attenuated when participants were under (task-irrelevant) threat of shock, and that performance was also degraded, suggesting that a threat context can interfere with concurrent processing if the task-relevant stimuli do not serve a specific cuing function. In the current study, because the font color of the encoded words explicitly signaled threat (or safety) we expected enhanced P3 amplitude for threat cues, which also acts as a manipulation check.

Electrophysiological indicators of accurate recognition are seen in differences in the ERP when viewing old and new items during a recognition test (e.g., Gutchess et al., 2007; Maratos and Rugg, 2001; Weymar et al., 2009, 2010; Windmann and Kutas, 2001; for review see Rugg and Curran, 2007). When recognizing words, distinct ERP old/new effects have been linked to different types of mnemonic processes. An early frontal old/new difference (300–500 msec) is hypothesized to be sensitive to memory processes based on familiarity, while a later parietal old/new difference (>500 msec) has been proposed as a neural correlate of explicit retrieval, as it is enhanced by depth of processing, and for correct source and “remember” judgments in a recognition task (Rugg and Curran, 2007). Two hypotheses can be assessed: if threat of shock interferes at encoding, memory performance and old–new differences should be heightened for words encoded in a safe, compared, to threat context. On the other hand, if encoding items that signal the possibility of a painful event facilitates memory, we expected enhanced recognition and larger ERP old/new effects for words presented in the threat, compared to safe, context.

2. Material and methods

2.1. Participants

Participants were 28 healthy students (11 female, 17 male; mean age: 19.2 years; one left-handed) from a General Psychology course at the University of Florida who participated for course credit. They had normal or corrected-to normal vision and were native speakers of English. All participants provided informed written consent for the protocol approved by the UF Institutional Review Board. One subject (male) was excluded from the analyses due to a memory performance below chance level (50%) on the recognition test.

2.2. Materials and procedure

Overall, 240 nouns were selected from the Affective Norms for English Words (ANEW; Bradley and Lang, 1999), consisting of 48 unpleasant words (24 high arousal vs 24 low arousal words), 48 pleasant words (24 high arousal vs 24 low arousal words) and 24 neutral words. Two sets of 120 stimuli were matched on the basis of hedonic valence, arousal (see ANEW norms, Bradley and Lang, 1999) and word frequency (Kucera and Francis, 1967).¹ During encoding, approximately half of the participants received each of the two word sets.

Fig. 1 illustrates the encoding and recognition procedures. Of the 120 words presented at encoding, half were printed in a font color that signaled threat of shock (blue or yellow; counterbalanced across participants), and half were printed in a font color that denoted safety (blue or yellow). Each word was presented for 6 sec with no inter-trial interval (ITI). Threat and safety periods varied in duration from 12 to 36 sec (i.e., 2–6 words in the same font color). To encourage processing of the words, participants were told to press a button whenever the word “window” appeared (this word was never presented in the study). At the end of the encoding phase, one mild shock (5 mA, 32 msec duration) was delivered through the shock sensor using a constant current electro stimulator (Grass Instruments Co., Model SIU7, Quincy, Mass, USA) during a 6 sec threat period. This trial was not included in the analyses.

During recognition, each participant viewed both sets of words (240 words), resulting in 120 old words and 120 new words. Of the old words, half had been encoded in the context of threat of shock (half of each hedonic content), and half had been encoded in safe context. Each word was presented for 2 sec with a random ITI of 1.5, 2.0, or 2.5 sec containing a fixation cross.

The experiment took place in a reclining chair in a sound-attenuated dimly lit room. Participants were instructed that when a word was presented in one color, an electric shock could be delivered through a stimulating bar electrode attached to the inner surface of the right wrist, whereas no shock was possible if the word was presented in the other color. No mention of a memory test was made (incidental encoding). Immediately after encoding, the shock electrode was removed and the recognition memory task occurred, in which old and new words were presented. Participants were instructed to decide whether each word had previously been seen in the experiment or not. Following word offset² the question “Yes/No?” appeared, and the participants pressed a “yes” button if they remembered the word, or else a “no” button. The assignment of left and right button presses to yes/no responses was counterbalanced across participants.

2.3. EEG recording

Electroencephalogram (EEG) signals were recorded continuously from 128 electrodes using an Electrical Geodesic system and digitized at a rate of 250 Hz, using the vertex sensor (Cz) as recording reference. Scalp impedance for each sensor was kept below 50 k Ω , as recommended by the manufacturer guidelines. All channels were bandpass filtered online from .1 to 48 Hz. Off-line reduction was performed using Electro-Magnetic EncaphaloGraphy Software (EMEGS) (Junghöfer and Peyk, 2004) and included low-pass filtering at 40 Hz, artifact detection, sensor interpolation, baseline correction, and conversion to an average reference (Junghöfer et al., 2000). Stimulus-synchronized epochs were extracted from 100 msec before to 1200 msec after picture onset and baseline corrected (100 msec prior to stimulus onset).

2.4. Data analysis

ERPs were computed for each sensor and participant. In consideration of previous research and based on inspection of the waveforms (see Fig. 2), statistical analyses for encoding were computed using early (220–300 msec), middle (350–420 msec) and late (700–900 msec) time windows in which differences between threat and safety conditions were maximal.

¹Mean ratings from the ANEW (Bradley and Lang, 1999) did not differ for pictures in the two sets: Pleasure ratings: Unpleasant pictures 3.4, 3.5; Neutral pictures: 5.2, 5.1; Pleasant pictures: 6.8, 6.5. Arousal ratings: Unpleasant 5.2, 5.1; Neutral 3.5, 3.5; Pleasant 5.2, 5.2. In addition word frequency did not differ for emotional and neutral words in each of the two sets (set $\times$ content, $F_{(1,9)} < 1$).

²Behavioral recognition responses were delayed until the offset of the 2 sec picture presentation in order to avoid contamination by motor potentials. Reaction times are therefore not informative and were not analyzed.

Encoding-related ERP data were analyzed in a repeated measure analysis of variance (ANOVA) using cue (threat, safe) and hedonic content (5: unpleasant high, unpleasant low, pleasant high, pleasant low, neutral).

For recognition, only trials with correct responses were included in ERP averages. Based on inspection of the waveforms (Fig. 3), mean ERP amplitudes were analyzed in a window 500 and 700 msec over centro-parietal brain regions, where the difference between old and new conditions was maximal. Recognition-related ERP data were analyzed in a two-way ANOVA investigated the effects of anticipatory anxiety using cue (threat, safety) and hedonic content (5: unpleasant high, unpleasant low, pleasant high, pleasant low, neutral) as repeated measures. A second ANOVA included factors memory (old, new) and hedonic content (5).

For behavioral performance hit rate (H), false alarm rate (FA), recognition accuracy ($Pr = H - FA$), and response bias [$Br = p(FA)/p(1 - Pr)$] were analyzed using an ANOVA involving the factors context (2: threat, safe) and hedonic content (5: unpleasant high, unpleasant low, pleasant high, pleasant low, neutral).

For effects involving repeated measures, the Greenhouse–Geisser procedure was used to correct violations of sphericity.

3. Results

3.1. Manipulation check

Fig. 2 illustrates grand average ERPs for representative sensor clusters when encoding words in the context of color cues signaling threat or safety. Enhanced positivity when processing threat, compared to safety, cues was observed in the 220–300 msec window after stimulus presentation over midline frontal and centro-parietal scalp sites, context ($F_{(1,26)} = 6.93$, $p < .01$). Threat cues also elicited an enhanced P3 (350–420 msec) compared to safe cues, at midline centro-parietal and midline occipital electrode sites, ($F_{(1,26)} = 9.90$, $p < .01$). In the late 700–900 msec window a less positive-going wave was evident for threat cues, compared to safe cues, over frontal sensors, ($F_{(1,26)} = 4.49$, $p < .05$). In the same time window, a similar difference, with reversed polarity, was marginal over occipital sensors, ($F_{(1,26)} = 3.39$, $p = .07$). No effects of word hedonic content were observed in any of these analyses.

3.2. Recognition

Table 1 lists memory performance for old and new words presented in the context of threat and safe cues. For hits, a main effect of content, ($F_{(4,104)} = 7.07$, $p < .001$), indicated significantly overall higher accuracy when recognizing unpleasant words (whether high or low in arousal), compared to pleasant or neutral words (unpleasant vs pleasant: $F_{(1,26)} = 26.59$, $p < .0001$; unpleasant vs neutral: $F_{(1,26)} = 8.34$, $p < .0001$)³. Consistent with the hit rate, correct discrimination (Pr) between old and new words was better for unpleasant words, compared to neutral or pleasant words (content: $F_{(4,104)} = 4.26$, $p < .001$; unpleasant vs pleasant: $F_{(1,26)} = 5.62$, $p < .05$; unpleasant vs neutral: $F_{(1,26)} = 8.19$, $p < .0001$). On the other hand, unpleasant words were associated with a slightly more liberal response bias than pleasant or neutral words, (content: $F_{(4,100)} = 6.24$, $p < .0001$; unpleasant vs pleasant: $F_{(1,26)} = 37.17$, $p < .000$; unpleasant vs neutral: $F_{(1,25)} = 5.43$, $p < .05$). Overall, threat of shock did

³False alarms were slightly lower for pleasant words [content, $F_{(4,104)} = 7.22$, $p < .001$; pleasant (.22) vs unpleasant (.27): $F_{(1,26)} = 7.80$, $p < .0001$; pleasant (.22) vs neutral (.28): $F_{(1,26)} = 5.99$, $p < .05$].

not influence memory performance (context: for hit rate, $F_{(1,26)} = 1.44$, $p = .24$; for Pr, $F_{(1,26)} < 1$).

Table 2 lists the mean ERP amplitude changes during correct recognition of old and new words as a function of threat context and hedonic content. A main effect of hedonic content ($F_{(4,104)} = 5.82$, $p < .0001$) indicated overall greater positivity for highly arousing words (unpleasant = 3.1; pleasant = 2.8) compared to words rated lower in arousal (neutral = 2.1; pleasant = 2.0, unpleasant = 2.3), ($F_{(1,26)} = 14.86$, $p < .0001$).

Fig. 3 illustrates the grand average ERPs for correctly recognized words encoded in the context of threat of shock or safety and new words for representative sensor clusters. Correct recognition of old words, compared to new words, was accompanied by enhanced positivity that was most pronounced over centro-parietal scalp regions⁴ ($F_{(1,26)} = 17.15$, $p < .001$). More interestingly, recognition of words that were encoded in the context of shock threat showed an enhanced parietal positivity compared to words encoded in the context of safe cues ($F_{(1,26)} = 4.63$, $p < .05$). Although the interaction between threat context and hedonic content was not significant, the heightened parietal positivity for old words encoded in the context of shock threat, compared to safety, was reliable for emotional ($F_{(1,26)} = 4.90$, $p < .05$), but not for neutral words ($F_{(1,26)} < 1$), as illustrated in Fig. 3.

Recognition performance for words encoded in the context of threat, compared to safety, was not significantly heightened in the sample as a whole. To determine whether the enhanced parietal positivity for emotional words encoded under threat might be related to enhanced recognition of these stimuli for at least a subset of participants, the entire sample was ranked on the magnitude of the old–new difference for emotional words encoded under threat. Using a median split, participants showing the largest old–new difference ($n = 14$; 8 male) for emotional words encoded during threat (mean = $2.4 \mu\text{V}$; $F_{(1,13)} = 92$, $p < .0001$) also recognized significantly more emotional words encoded under threat (.78), compared to safety (.71), $F_{(1,13)} = 5.2$, $p = .04$. For the remaining participants ($n = 13$; 8 male), the old–new ERP difference was negligible ($-.04 \mu\text{V}$; $F < 1$), and there was no difference in performance when recognizing emotional words encoded during threat (.69) or safety (.71). Thus, participants showing a significant old–new difference in the ERP for emotional words encoded under threat also showed enhanced recognition of these items.⁵

3.3. Ratings

Overall, post-experimental ratings of aversiveness during anticipation confirmed greater aversion when processing cues that signaled threat of shock (Mean = 2.8, Standard Deviation – SD = 1.1) compared to cues signaling safe periods (Mean = 5.4, SD = 1.4) ($F_{(1,26)} = 58.05$, $p < .001$). More interesting, participants who showed a significant old–new difference in the ERP for emotional words encoded under threat (i.e., based on the median split) rated cues that threatened shock as significantly more unpleasant (Mean = 2.4, SD = .94) than participants who did not show an old–new difference in ERPs (Mean = 3.2, SD = 1.1) ($F_{(1,25)} = 3.5$, one-tailed $p < .05$).

⁴Based on previous studies reporting earlier frontal differences between old and new words (Rugg and Curran, 2007), we tested the ERP old/new difference in an earlier time window (300–400 msec). A significant difference was found in which correctly classified old words showed less negativity than correctly rejected new words ($F_{(1,26)} = 4.88$, $p < .05$). This frontally located old/new difference was not modulated by the content of the words ($F_{(4,14)} = 1.05$, $p = .38$), and whether a word was encoded in the context of threat of shock or safety did not affect the amplitude of this early frontal effect.

⁵P2, P3 and the late frontal positivity during encoding did not differ between participants showing a significant old–new difference in the ERP for emotional words encoded under threat (i.e., based on the median split) and participants who did not show an old–new difference in ERPs.

4. Discussion

ERPs were measured to assess the effects of a threatening context on later memory performance. During an incidental recognition test, correct recognition of words encoded in a threatening context, compared to words encoded during safety, evoked enhanced positivity over centro-parietal electrode sites in a 500–700 msec window, and this effect was most pronounced for emotional words. Moreover, although memory performance was not generally facilitated by a threatening context at encoding, following a median split based on the amplitude of old–new ERP differences, participants showing an enhanced late parietal old–new difference for words encoded under threat also showed significantly better recognition of emotional words encoded during threat, compared to safety. These participants also rated anticipated shock more highly aversive. Taken together, for a subset of participants, emotional words encoded in a threatening context prompted both better memory performance and an enhanced old–new ERP effect, compared to words encoded in a safe context.

During encoding, enhanced P2 and P3 components, as well as a less positive frontal slow wave, were found for cues signaling threat of shock, compared to safety, replicating previous studies (Baas et al., 2002; Bocker et al., 2004; Bublatzky and Schupp, in press) and providing a successful check of the instructed fear manipulation. Whereas ERPs during encoding were clearly different when processing threat and safe cues, there were no differences related to the hedonic content of the words, as often reported during encoding (Herbert et al., 2006; Fischler and Bradley, 2006). These effects, however, can be attenuated or altered depending upon the specific input task (see Fischler and Bradley, 2006; Hinojosa et al., 2010). In the current study, the font color that cued threat (or safety) was integrated with the lexical item at encoding, and differences in early ERPs appear to primarily reflect processing this perceptual feature, which cued threat or safety, rather than the meaning of the lexical item.

Consistent with this, modulation of early sensory components, such as the anterior P2 difference, are in line with other studies showing that a threat context increases perceptual vigilance (Shackman et al., 2011) as well as studies finding similar modulation for task-relevant perceptual cues (e.g., color target pop-outs; Luck and Hillyard, 1994). Relatedly, whereas Shackman et al. (2011) found a reduced P3 component when processing task-relevant stimuli in the context of a task-irrelevant (and previously instructed) threat (Shackman et al., 2011), the enhanced centro-parietal P3 found here is consistent with increased attention to the discrete cues signaling threat that is typically found for task-relevant (Duncan-Johnson and Donchin, 1982), and as well as motivationally relevant cues (Codispoti et al., 2007; Cuthbert et al., 2000; Herbert et al., 2006).

Correct recognition of previously presented, compared to new, words, was associated with enhanced ERP positivity over centro-parietal electrode sites from 500 to 700 msec after stimulus onset, replicating a late old–new effect reported in many previous studies when recognizing words (Maratos and Rugg, 2001; Windmann and Kutas, 2001; for review see Rugg and Curran, 2007). This late parietal old/new effect is typically described as an electrophysiological correlate of memory processes that reflect successful recollection (Rugg and Curran, 2007), rather than mere familiarity, as it is modulated by depth of processing, correct source memory, and “remember”, rather than “know” judgments. Because words encoded in the context of threat of shock showed enhanced parietal positivity compared to words encoded under safety, particularly for emotional items, an interpretation that these items were better recollected is supported.

Moreover, whereas memory performance across the entire sample was not different for words presented in threat, compared to safe, contexts, a median split based on the ERP old/new difference for emotional words encoded under threat showed that the group of participants showing enhanced parietal positivity for emotional words encoded during threat, compared to safety, also showed significantly better recognition performance for these words. In addition, post-experimental ratings of the aversiveness of shock anticipation for these participants was significantly greater than for those who did not show context differences in either the recognition-related ERPs or recognition performance. Taken together, for a subset of participants who found anticipating shock very aversive, items encoded in the context of shock threat show enhanced recognition in both performance and in the amplitude of the parietal old–new ERP difference, particularly for words with emotional content.

The finding that effects of threat on later recognition were most evident for emotional, compared to neutral, words is in line with recent data suggesting that memory for emotionally arousing stimuli is particularly enhanced in the context of stressful experiences (e.g., Joëls et al., 2006; Diamond et al., 2007). One line of research predicting specific enhancement is mood-congruent memory (Bower, 1987), which posits that encoding of stimuli congruent with a current mood state is better than for incongruent stimuli (Eich and Macaulay, 2000). The finding that recognition of both pleasant and unpleasant words was facilitated by a threat context here, however, would suggest that emotional arousal, rather than hedonic valence, may be the important congruent feature (Zillmann, 1996).

Although the amygdala is often assumed to mediate emotional learning, neuroimaging data suggesting the lack of amygdala activation in the context of shock threat (e.g., Mechias et al., 2010; Costa et al., 2009) is consistent with both animal and human conditioning research that suggests learning and memory can be mediated by other neural structures (e.g., Weinberger, 2007; Li et al., 2008). When neural activity is measured in the context of threat of shock, compared to safety, critical neural structures include the rostral anterior cingulate cortex (ACC), insula and prefrontal cortex areas (Mechias et al., 2010; Costa et al., 2009).

Anticipation of aversive events is a critical factor in disorders that involve catastrophizing, worry, and rumination (e.g., panic disorder, generalized anxiety disorder, depression or post-traumatic stress disorder). Recent reviews (Coles and Heimberg, 2002; McNally, 1997) and a meta-analysis (Mitte, 2008) of explicit memory performance in anxiety disorders, however, suggested inconsistent patterns across anxiety disorder groups and types of retrieval task. In the present study, stress and anticipatory anxiety at encoding enhanced both memory performance and old–new ERPs for emotionally arousing stimuli, suggesting that anxiety may facilitate memory for emotionally engaging, rather than only anxiety-related, information (cf., Martin et al., 1991).

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Fig. 1.

During encoding (top), emotional and neutral words were presented for 6 sec each with no ITI. Half of the words were printed in a font color that signaled threat of shock (blue or yellow), and half were printed in a font color that denoted safety (blue or yellow). During recognition, 120 old and 120 new words were presented for 2 sec each (1.5–2.5 sec ITI) for an explicit recognition decision. Of the old words, half had been presented in the context of threat of shock and half had been encoded in a safe context.

Fig. 2. Grand average ERP waveforms at representative sensor clusters for words encoded in a font color that signaled threat (thick line) or safety (thin line) periods.

Fig. 3.

Grand average ERP waveforms at representative sensor clusters for correctly recognized words that had been encoded in a font color that signaled threat of shock (thick line) or safety (thin line) and correctly classified new words (dotted line). The center of the figure highlights the centro-parietal sensor cluster where the memory difference (old – new) was largest. In the lower left of the center figure are displayed the scalp topographies of the ERP difference (old minus new; 500–700 msec) separately for words encoded under threat or safety. The upper bar graph illustrates the mean ERP (500–700 msec) when recognizing words encoded under threat or safety separately for emotional and neutral words.

Table 1

Recognition memory performance.

	Unpleasant		Neutral		Pleasant	
	Threat	Safe	Threat	Safe	Threat	Safe
Hits (H)						
High arousal	.77 (.17)	.74 (.12)			.65 (.20)	.65 (.13)
Low arousal	.75 (.14)	.76 (.14)	.67 (.18)	.69 (.16)	.67 (.21)	.65 (.19)
Mean	.76 (.12)	.75 (.11)	.67 (.18)	.69 (.16)	.66 (.18)	.65 (.14)
Discrimination index (Pr = H – FAs)						
High Arousal	.55 (.20)	.51 (.16)			.47 (.21)	.47 (.18)
Low Arousal	.45 (.19)	.47 (.18)	.39 (.24)	.42 (.21)	.42 (.23)	.39 (.20)
Mean	.50 (.17)	.49 (.14)	.39 (.24)	.42 (.21)	.44 (.19)	.43 (.15)
Response bias (Br)						
High Arousal	.55 (.28)	.46 (.23)			.37 (.25)	.33 (.20)
Low Arousal	.54 (.22)	.54 (.23)	.44 (.23)	.45 (.23)	.47 (.25)	.44 (.25)
Mean	.55 (.20)	.50 (.20)	.44 (.23)	.45 (.23)	.41 (.21)	.38 (.20)

Numbers represent percentages. Numbers in parentheses indicate SD. Higher Pr values indicate better discrimination ability between old and new items. Br values higher than .5 indicate liberal response criteria; lower Br values suggest conservative response bias; neutral bias yields Br = .5.

Table 2

Mean change (in μV) in a 500–700 msec window for centro-parietal sensors as a function of word content for words encoded in a font color that signaled threat or safety (“old”) and for new words on the recognition test (standard error of the mean).

	Old		New
	Threat	Safe	
High arousal			
Pleasant	3.67 (.82)	2.82 (.53)	2.05 (.45)
Unpleasant	3.61 (.54)	2.99 (.65)	2.68 (.43)
Low arousal			
Pleasant	2.96 (.60)	1.71 (.71)	1.20 (.46)
Unpleasant	2.75 (.52)	1.97 (.63)	2.23 (.51)
Neutral	2.57 (.78)	2.68 (.80)	.98 (.43)