

Repetition and Event-related Potentials: Distinguishing Early and Late Processes in Affective Picture Perception

Maurizio Codispoti¹, Vera Ferrari², and Margaret M. Bradley²

Abstract

■ A repetition paradigm was used to assess the nature of affective modulation of early and late components of the event-related potential (ERP) during picture viewing. High-density ERPs were measured while participants passively viewed affective or neutral pictures that were repeated up to 90 times each. Both ERP components were modulated by emotional arousal, with ERPs elicited when viewing pleasant and unpleasant pictures different than when viewing neutral pictures. On the other hand, repetition had different effects on these two components. The early occipitotemporal component (150–300 msec) primar-

ily showed a decrease in amplitude within a block of repetitions that did not differ as a function of picture content. The late centroparietal component (300–600 msec) showed a decrease both between and within blocks of repetitions, with neutral pictures eliciting no late positive potential in the final block of the study. The data suggest that the early ERP primarily reflects obligatory perceptual processing that is facilitated by active short-term memory representations, whereas the late ERP reflects increased resource allocation due to the motivational relevance of affective cues. ■

INTRODUCTION

Event-related potentials (ERPs) measured during affective picture viewing consistently vary with emotional arousal, with affective pictures (either pleasant or unpleasant) eliciting a larger, late positive potential (LPP) from about 300–600 msec over the centroparietal cortex (Schupp, Junghofer, Weiike, & Hamm, 2004; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Cacioppo, Crites, Gardner, & Bernston, 1994) compared with neutral pictures. In addition to the late positive potential, an earlier ERP component has been reported to vary with emotional arousal in a window from about 150–300 msec, with affective stimuli prompting significantly less negativity over frontal sites and less positivity over occipital sites compared with neutral pictures (e.g., Schupp et al., 2004). This earlier component sometimes differs only for pleasant pictures, or is most pronounced for pleasant pictures (De Cesarei & Codispoti, 2006; Schupp et al., 2004; Keil et al., 2002).

Both effects have been interpreted as reflecting enhanced attention to motivationally relevant pictures, but little is known regarding the precise nature of the mechanisms involved in these modulatory effects. In the current study, we utilize a repetition paradigm to explore the cognitive processes underlying the magnitude and

modulation of early and late ERPs by emotional arousal during picture viewing. There is considerable evidence that prior exposure to a stimulus affects subsequent attentional processes and orienting responses (Bradley, Lang, & Cuthbert, 1993; Siddle, 1991; Sokolov, 1963), with repetition prompting a decrease in responding due to a loss of novelty and salience. Habituation of responding to stimuli that are repeatedly processed is a central feature of stimulus orienting theories (Thompson & Spencer, 1966; Harris, 1943) and is held to reflect reduced attentional processing of a stimulus as its novelty wanes (Öhman, 1992; Siddle & Spinks, 1992; Kahneman, 1973). On the other hand, encoding processes related to sensory and perceptual intake are not expected to habituate, despite repetition, as they reflect the basic processing necessary for even recognizing that a stimulus has been previously presented. Thus, the nature of repetition effects on ERPs during picture viewing and how these impact affective modulation of early and late ERPs could shed light on the nature of the processes reflected in these ERP components.

If differential processing at the early stage of visual information processing is triggered by relevant perceptual features through a bottom-up, sensory-driven mechanism, modulation of this component should be less affected by picture repetition, particularly to the extent that it represents obligatory perceptual processing. On the other hand, to the extent that an ERP represents

¹University of Bologna, Italy, ²University of Florida

differential allocation of attentional resources, modulation of this component should decrease with picture repetition, reflecting less resource allocation to the picture as its novelty and salience decrease. According to this scenario, effects of repetition on the ERP provide a window to whether early and late effects of hedonic valence during picture viewing reflect perceptual or attentional processing.

The present research used a dense sensor (60 channels) electroencephalographic (EEG) array to measure early and late ERPs in a repetition paradigm. Participants viewed a set of 15 pictures (5 pleasant, 5 neutral, and 5 unpleasant) that were repeated 90 times each across three blocks in a habituation phase, in which each block was separated by a brief interblock interval (2 min). Within each block of 450 pictures, ERPs were assessed in three subblocks of 50 (10 repetitions per picture) for each picture content. This design allows an assessment of both within-block repetition effects, as well as habituation effects across blocks of repetition.

Attenuation of ERPs within a block of picture presentations could reflect differences in perceptual processing due to active short-term memory representations that facilitate initial processing. Several studies have demonstrated that behavioral reaction times are reduced by stimulus repetition (Delorme, Rousselet, Mace, & Fabre-Thorpe, 2004; Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001; Wiggs & Martin, 1998), presumably reflecting activation of short-term memory representations, which speed up perceptual processing via top-down influences that preset lower levels of the visual pathway to the currently activated stimulus features. On the other hand, attenuation of ERP magnitude across blocks in the habituation phase could reflect a longer term habituation process that reflects changes in resource allocation as the pictures become less novel with repetition. Assuming that neutral pictures elicit few attentional resources even when novel, we expect larger effects of repetition across blocks for affective pictures. To rule out interpretations of decreased amplitude (in either early or late ERPs) to fatigue, a new set of pictures was presented at the end of the habituation phase. We expected full recovery if ERP amplitude changes reflect stimulus-specific habituation.

We also assessed the temporal stability of both repetition and affective modulation of the early and late ERP components as an additional method for determining the mechanisms underlying early and late ERPs during picture viewing. Ten days after the initial study, participants returned to the laboratory and viewed a new set of affective and neutral pictures using the same repetition paradigm. If early affective modulation of the ERPs reflected a perceptual process triggered by the detection of object-relevant visual features (Ullman, Vidal-Naquet, & Sali, 2002), we expected less stability in this component, as the perceptual features and content of the pictures differ from one session to the next. On the other hand, because the new pictures in the second ses-

sion continued to depict pleasant, neutral, and unpleasant content, we expected a higher correlation between sessions for the late ERP, which is presumed to reflect heightened attention to motivationally relevant material.

Finally, to determine whether affective modulation of early and late ERPs reflects the operation of the same cognitive process, we assessed the covariation between these modulatory effects on a within-participant basis. If these ERPs reflected the same process, we expected a significant correlation in the magnitude of the modulatory effect obtained in the early and late ERP windows. To the extent that they reflect different perceptual and attentional processes, the magnitude of the modulatory effects should not be related.

METHODS

Participants

Participants were 24 students (12 men) from the University of Bologna ranging in age from 21 to 28 years. Blood phobia was evaluated by using the Mutilation Questionnaire (Klorman, Weerts, Hastings, Melamed, & Lang, 1974), and participants scoring above 18 were excluded. Informed consent was obtained from each participant; participants were not paid for their participation.

Materials and Procedure

Each person participated in two sessions separated by 10 days. In each session, 1800 pictures were presented for 1 sec each, arranged in three habituation blocks (450 pictures each) and one dishabituation block (450 pictures). The same 15 pictures (5 pleasant, 5 neutral, 5 unpleasant) were presented in each of the three habituation blocks; a new set of 15 pictures was presented in the dishabituation block. Between each block, a 2-min break was given. Within each of the three habituation blocks, pictures were presented in three subblocks consisting of 150 picture presentations (10 per picture; 50 per hedonic valence content).

Sixty pictures were selected from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005), depicting 20 unpleasant scenes (mutilated bodies), 20 pleasant scenes (erotic couples), and 20 neutral scenes (people). The 60 pictures were divided into four sets of 15 (five of each affective valence) and a different set of pictures was presented in Session 1 and Session 2 and during the habituation and dishabituation blocks. Sets of pictures were randomly assigned to each experimental condition.

In each session the experimental procedure was the same. Subjects were seated in a recliner in a dimly lit sound-attenuated room. After filling out the informed consent form (and, during the first session, the Mutilation Questionnaire), the electro-cap (Electro-Cap International, Inc., San Diego, CA) was attached. The participant

was instructed to simply view a series of pictures that would be presented on the screen. Pictures were presented for 1 sec on a white screen located approximately 80 cm from the participant's eyes. E-Prime software synchronized the presentation of the stimuli and triggered EEG recording on each trial. The order of picture presentation was pseudorandomized with the restriction that the same picture or a picture of the same valence could not occur on more than two consecutive trials. The inter-stimulus interval (ISI) varied between 2 and 3 sec.

EEG Recording and Data Processing

Electroencephalographic signals were recorded from 60-channel tin electrodes (Ag/AgCl) mounted in an elastic cap (Electro-Cap International, Inc.). Scalp impedance for each sensor was kept below 5 k Ω . Data were acquired referenced to CZ, and the average reference was calculated off-line. Vertical and horizontal eye movements were recorded using SensorMedics Ag/AgCl miniature electrodes. Data were low-pass filtered at 30 Hz and sampled at 250 Hz for 1500 msec (500 msec pre-stimulus and 1000 msec poststimulus onset).

Single-trial epochs were corrected for vertical and horizontal eye movements by using a correlative eye movement algorithm (Miller, Gratton, & Yee, 1988). Data editing and artifact rejection were done using statistical control of artifacts (Junghöfer, Elbert, Tucker, & Rockstroh, 2000). For each participant and picture valence, ERPs were averaged separately in three subblocks of 50 (10 repetitions \times 5 pictures) for each picture content for each of the three habituation blocks and for the dishabituation block.

A temporal principal components analysis conducted using all participants, all sensors, and all conditions resulted in two components that accounted for 94% of the variance. Accordingly, two time windows were selected and analyzed, including an early window between 150 and 300 msec and a later interval between 300 and 600 msec following picture onset.

In order to investigate the topography of the effects of repetition and emotion, voltages at 60 electrodes were averaged into eight clusters: frontal (left: Fp1, AF3, F7, F5; right: Fp2, AF4, F8, F6), centroparietal (left: F3, F1, FC5, FC3, FC1; right: F4, F2, FC6, FC4, FC2), centroparietal (left: C3, C1, CP1, CP3, P1, P3; right: C4, C2, CP2, CP4, P2, P4), and occipitotemporal sites (left: TP7, T5, P5, PO7, PO5, PO3, O1, POZ, OZ; right: TP8, T6, P6, PO8, PO6, PO4, O2).

These data were submitted to repeated measures analysis of variance (ANOVA; using the Greenhouse-Geisser correction) for factors of Region (four levels: frontal, frontocentral, centroparietal, and occipitotemporal), Hemisphere (two levels: left and right), Block (three levels: three blocks of the habituation phase), Subblocks (three levels: three subblocks within each block), and Valence (three levels: pleasant, neutral,

unpleasant) for the habituation phase. For the dishabituation, the same analyses, excluding the Block factor, were conducted.

RESULTS

Figure 1 illustrates averaged ERP waveforms for pleasant, neutral, and unpleasant pictures averaged across the habituation and the novel phase for each sensor. When session was included as a factor, this factor did not result in any significant main effects or interactions for ERPs analyzed in either early (150–300 msec) or late time windows (300–600 msec); thus, data were averaged across session in all analyses.

Early ERP Interval (150–300 msec)

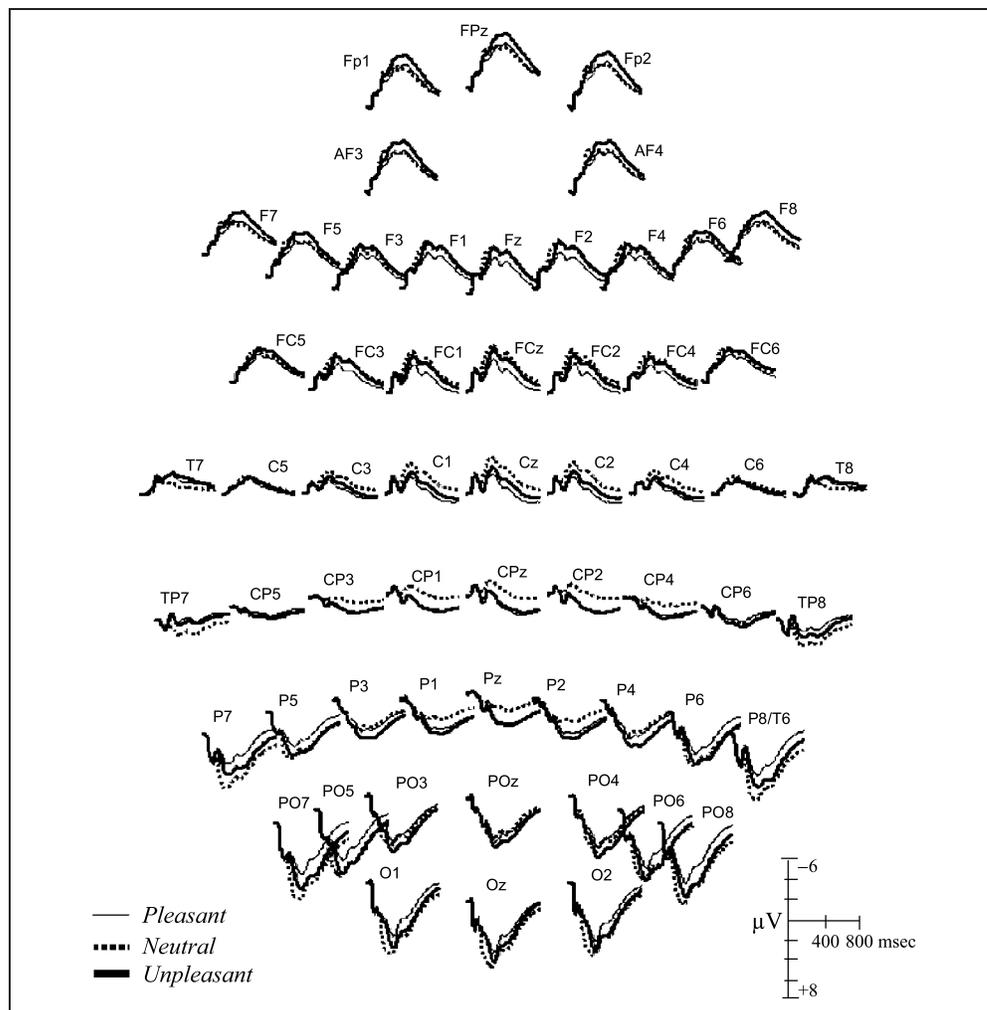
A significant Region \times Subblock interaction, $F(6,138) = 13.41$, $p < .0001$, $\eta^2 = .37$, indicated that repetition affected the magnitude of the early ERP component *within* a block of presentations. As Figure 2 illustrates, ERPs measured over occipitotemporal sites showed a linear decrease in positivity across picture repetitions within a block, $F(1,23) = 19.62$, $p < .0001$, $\eta^2 = .46$; in a related manner, ERP over frontocentral sites showed a linear increase in negativity across the picture repetitions within a block, $F(1,23) > 19$, $p < .0001$, $\eta^2 > .46$. On the other hand, as illustrated in Figure 2, the amplitude of these early ERP components fully recovered to initial levels following the brief interblock interval, as evidenced by the lack of a main effect across Block in the habituation phase, or any interactions involving Block.

A Region \times Valence interaction, $F(6,138) = 47.30$, $p < .0001$, $\eta^2 = .67$, indicated that, over occipitotemporal sites, emotional pictures prompted significantly less positivity than neutral pictures [quadratic: $F(1,23) = 69.93$, $p < .0001$, $\eta^2 = .75$], with less positivity for pleasant compared with unpleasant pictures, $F(1,23) = 30.16$, $p < .0001$, $\eta^2 = .56$. At frontocentral sites, the pattern was similar, but opposite in polarity, with emotional pictures prompting less negativity than neutral pictures [quadratic: $F(1,23) = 52.48$, $p < .0001$, $\eta^2 = .69$] and pleasant pictures prompting less negativity than unpleasant pictures $F(1,23) = 29.50$, $p < .0001$, $\eta^2 = .56$. Effects of valence in other regions included greater positivity for emotional (pleasant or unpleasant) compared with neutral pictures over centroparietal sensors [quadratic: $F(1,23) = 196.65$, $p < .0001$, $\eta^2 = .89$], and less negativity over frontal regions specifically for pleasant pictures compared to neutral pictures, $F(1,23) = 33.05$, $p < .0001$, $\eta^2 = .59$.

A Region \times Subblock \times Valence interaction, $F(12,276) = 2.49$, $p < .05$, $\eta^2 = .09$, primarily indicated that the decrease in ERP amplitude across subblocks in occipitotemporal and centroparietal regions was less pronounced for pleasant compared with neutral or unpleasant pictures.

No effects involving laterality were found.

Figure 1. Grand-averaged ERPs elicited by pleasant (thin line), neutral (dotted line), and unpleasant (thick line) pictures. Negative is plotted up and frontal electrodes are shown at the top of the figure. Waveforms reflect means across blocks and sessions for 24 participants.



Novel Phase

In the novel phase, ERPs in the early time window did not differ significantly from those elicited in the first block of the study for any picture content. Again, ERP amplitudes decreased across subblocks over centrofrontal and occipitotemporal regions, $F_s(2,46) > 11.1$, $p_s < .001$, $\eta^2 > .33$.

Late Interval (300–600 msec)

A Block \times Subblock \times Region interaction, $F(12,276) = 2.66$, $p < .05$, $\eta^2 = .09$, indicated habituation of the late component across both blocks and subblocks of picture repetition. As illustrated in Figure 3, a significant Block \times Subblock interaction over centroparietal sensors, $F(4,92) = 12.3$, $p < .001$, $\eta^2 = .35$, indicated (1) the late positive potential decreased across blocks of habituation, with a decrease from Block 1 to Block 2, $F(1,23) = 37.18$, $p < .0001$, $\eta^2 = .62$, and from Block 2 to 3, $F(1,23) = 5.59$, $p < .05$, $\eta^2 = .19$, and (2) the decrease in the late positive potential across subblocks

was most pronounced in the first block of habituation, $F(2,46) = 20.15$, $p < .0001$, $\eta^2 = .47$. Thus, the LPP decreased in magnitude across and within blocks in the habituation phase.

Differences as a function of picture content across blocks of habituation were signaled by a Valence \times Block \times Region interaction, $F(12,276) = 3.98$, $p < .001$, $\eta^2 = .15$. Over centroparietal sensors, a Block \times Valence interaction, $F(4,92) = 13.31$, $p < .0001$, $\eta^2 = .37$, was followed by simple main effect tests. ERPs were more positive when viewing emotional compared with neutral pictures in each of the three blocks of habituation, as illustrated in Figure 3, $F_s(2,46) > 76$, $p_s < .0001$, $\eta^2 > .77$. Moreover, there was a significant effect of Block for each picture content [pleasant: $F(2,46) = 27.5$, $p < .0001$, $\eta^2 = .54$; neutral: $F(2,46) = 6.14$, $p < .05$, $\eta^2 = .21$; unpleasant: $F(2,46) = 50.3$, $p < .0001$, $\eta^2 = .69$]. On the other hand, whereas late positive potential amplitude in Block 3 continued to decrease relative to Block 2 for emotional pictures, $F(1,23) = 6.1$, $p < .05$, $\eta^2 = .21$, there was no further reduction between Blocks 2 and 3 for neutral pictures; in fact, late positive potentials

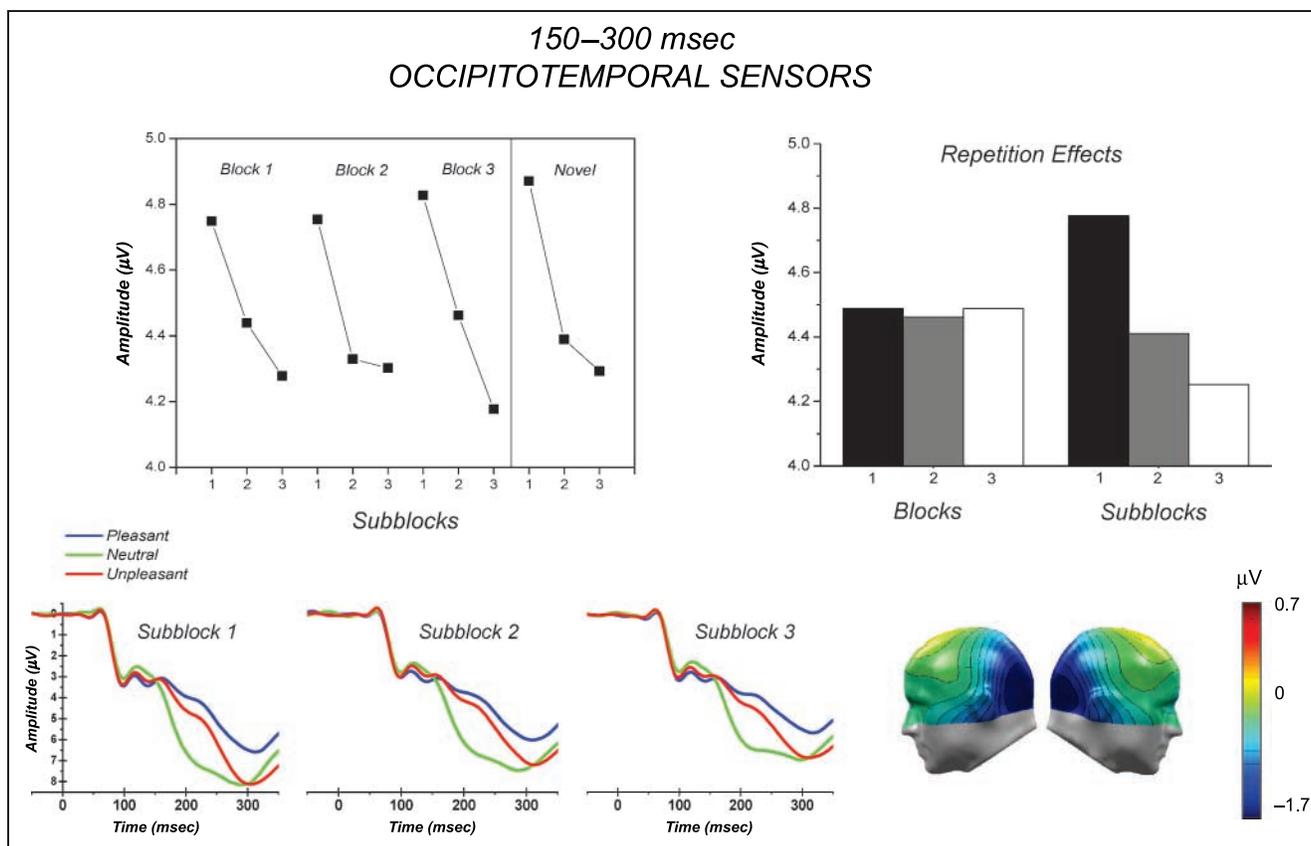


Figure 2. Top left: Mean ERP amplitude in the early window (150–300 msec) for occipitotemporal sensors decreases across subblocks in each of the three blocks of habituation and in the dishabituation (novel) block. Top right: Mean early ERP amplitude shows a decrease within (i.e., subblock) but not across blocks of repetition. Bottom right: Grand-averaged ERP waveforms for occipitotemporal sensors in each of the three subblocks (averaged over block) for pleasant, neutral, and unpleasant pictures. Bottom left: Scalp topography of the difference in early ERP amplitude between the last and first subblock illustrates the within-block habituation effect for the early ERP.

elicited in the third block of neutral picture viewing were not significantly different than zero.

Over frontal sites, a significant Block \times Valence interaction, $F(4,92) = 3.69$, $p < .05$, $\eta^2 = .13$, similarly indicated that neutral pictures showed a smaller decrease (in negativity) across blocks (mean: Block 1 = -4.29 , Block 2 = -3.82 , Block 3 = -3.74), compared to emotional pictures (mean: Block 1 = -5.17 , Block 2 = -4.26 , Block 3 = -4.11), $F_s(1,23) > 4$, $p_s < .05$, $\eta^2 > .21$.

A three-way interaction involving Region, Subblock, and Valence, $F(12,276) = 2.7$, $p < .05$, $\eta^2 = .11$, primarily indicated that a decrease in late positive potential amplitude across subblocks over occipitotemporal and centroparietal regions was less pronounced for pleasant pictures compared with neutral or unpleasant pictures.

An interaction of Region and Laterality, $F(1,23) = 14.1$, $p < .001$, $\eta^2 = .38$, resulted from the fact that potentials were overall more positive over the right hemisphere compared with the left hemisphere for sensors in the centroparietal (mean: right = 1.20, left = 0.92) and occipitotemporal (mean: right = 4.6, left = 3.90) regions. There were no effects of laterality involving picture content, block, or subblock.

Novel Phase

In the novel phase, the late positive potential was equivalent in magnitude to that elicited in the first block of the habituation phase, with emotional pictures again prompting a larger late positive potential over centroparietal sensors than neutral pictures, $F(2,46) = 135.3$, $p < .0001$, $\eta^2 = .85$, that were significantly larger than those elicited in the last block of habituation ($p_s < .005$).

Temporal Stability

To determine the temporal stability of the late positive potential effects, a correlation was conducted using the group means, 3 (picture content) \times 3 (habituation blocks) \times 3 (subblocks), from the initial session and from the session conducted 10 days later. Figure 4 illustrates the high temporal stability of the late positive potential across sessions: In each session, picture repetition decreased the magnitude of the late positive potential, and, in both sessions, affective pictures prompted larger late positive potentials than neutral pictures. In addition, the intra-individual temporal stability of the late positive

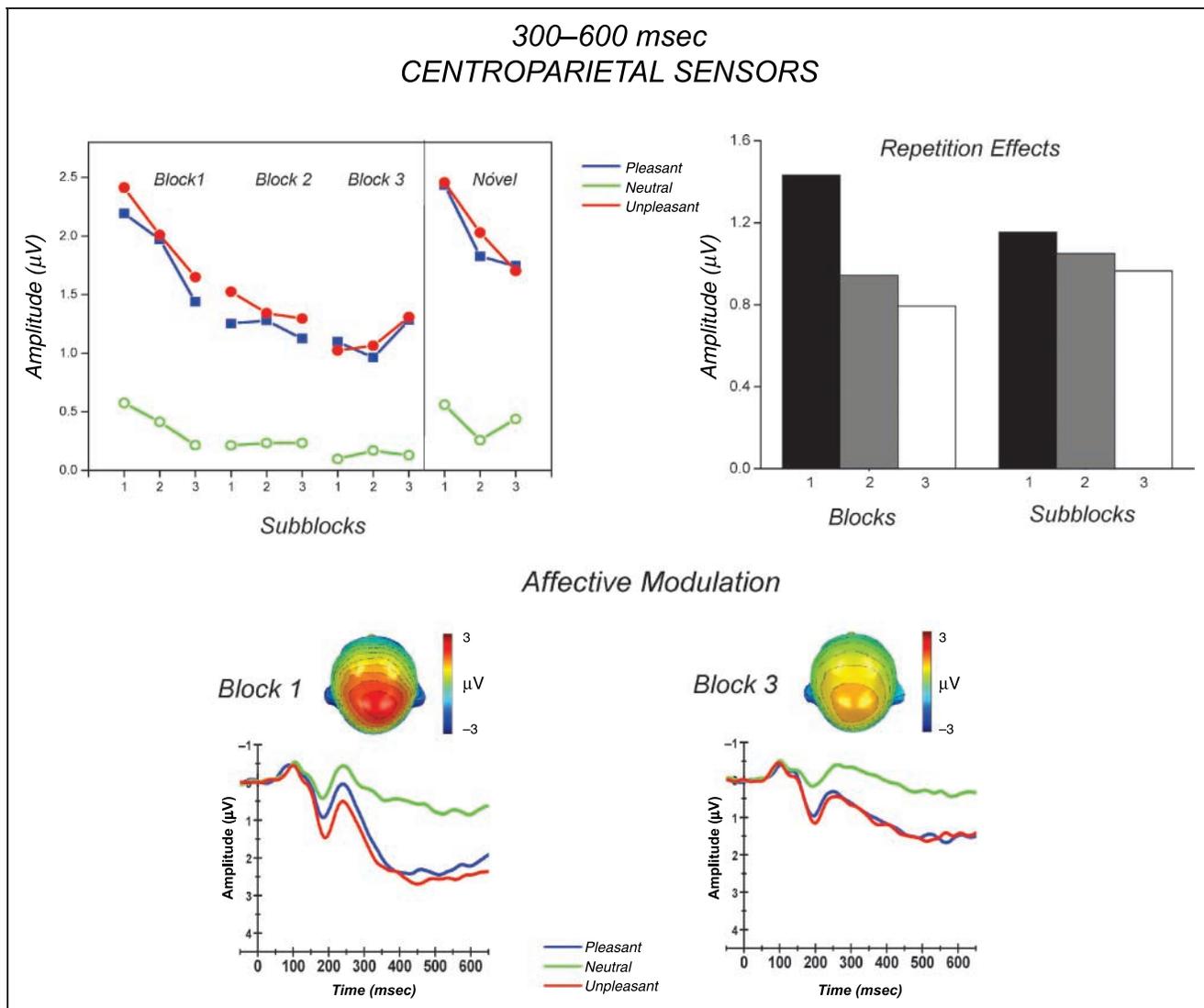


Figure 3. Top left: Mean ERP amplitude in the late window (300–600 msec) for centroparietal sensors decreases across both blocks and subblocks in the habituation and in the dishabituation (novel) block. Top right: The mean late positive potential shows a decrease as a function of repetition both within (i.e., subblock) and across blocks of repetition. Bottom: Grand-averaged ERP waveforms over centroparietal sensors for pleasant, neutral, and unpleasant pictures in the first, second, and third blocks of repetition in the habituation phase. The inset in each graph illustrates the scalp topography of the difference between emotional and neutral picture processing.

potential modulation was calculated for each participant, using the same data. As shown in the inset of Figure 4, 91% of the participants showed a statistically significant correlation between the modulatory effects of repetition and emotion on the late positive potential in Session 1 and Session 2, and the mean of the individual correlations was significant ($r = .55, p < .001$). For the early component, on the other hand, the mean correlation across participants was weak and not significant.

Correlation between Early and Late ERP Components

To determine the relationship between the effects of picture content on the early and late ERPs, a correlation analysis was conducted for each participant using

the difference between emotional and neutral pictures for the early and late ERP components (over occipital and centroparietal sensors, respectively) measured during each block of the study in each session. The correlation, averaged over participants, was low ($r = .03$) and not significant, suggesting that different processes contribute to these modulatory effects in the early and late ERPs.

DISCUSSION

In this study, we used a picture repetition paradigm to assess the cognitive processes underlying affective modulation of early and late ERPs and to determine how repetition affects short- and long-term habituation of each

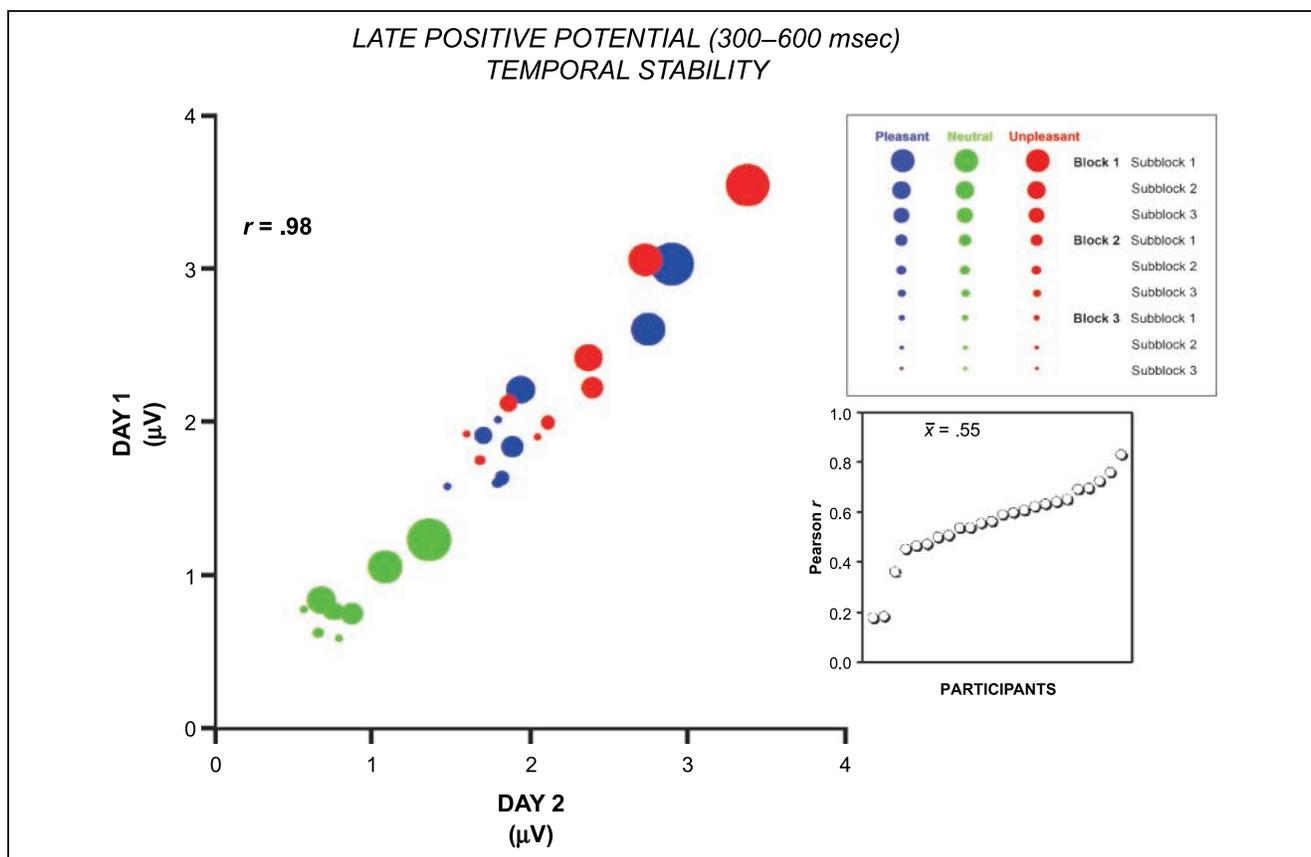


Figure 4. The correlation between the average (group) amplitude of the late positive potential (300–600 msec) over centroparietal sensors in each block and subblock of repetition across Sessions 1 and 2 (separated by 10 days) for pleasant, neutral, and unpleasant pictures. The inset shows the distribution of ranked within-subject correlations of the late positive potential, using the same data.

component. The data indicate that these two ERP components may reflect different stages of picture processing. Although both components were similarly modulated by emotional arousal, picture repetition had different effects. Moreover, there was no correlation between the magnitude of modulation by emotion in the early and late ERP windows within individuals, and, whereas the late positive potential showed stability between sessions, the early component did not. Taken together, the data are consistent with an interpretation that the early and late ERPs reflect different cognitive processes.

The late positive potential, maximal in a 300- to 600-msec window over centroparietal sensors, decreased in magnitude across both subblocks and blocks of habituation, consistent with a hypothesis that fewer resources were allocated to these pictures as their novelty and salience declined. Nonetheless, emotional pictures continued to elicit larger late positive potentials than neutral pictures, suggesting that affectively engaging pictures continue to draw attentional resources, despite previous presentation. For neutral pictures, on the other hand, the late positive potential was relatively small in the first block of the study, and was on the floor by the third block, with no change in its amplitude from Block

2 to Block 3. These data suggest that relatively few resources are allocated to neutral pictures, even when they are novel, and further presentation attenuates late positive potential amplitude even more.

Differences in attentional resource allocation to emotionally engaging pictures compared with neutral pictures is hypothesized to reflect activation in subcortical motivational circuits (Lang, Bradley, & Cuthbert, 1997) that elicit orienting activity, in which the individual allocates attention to the external and internal milieu in preparation for selecting and executing an appropriate response. Finding between-session stability in affective modulation of the late positive potential—when completely new pictures were presented in Session 2—supports the idea that this component reflects processing specific to the affective nature of the stimuli rather than to specific pictures. Moreover, that affective modulation for emotionally engaging pictures is sustained despite multiple presentations suggests that activating mental representations with strong associations to motivational circuits may reflexively heighten attention and intake.

This conclusion is similar to that reached in a previous study in which, using a smaller electrode array and longer intertrial intervals (20–30 sec), we also observed

For theories of emotion, perhaps the most surprising result is that, despite massive repetition, differential neural processing of emotional, compared with neutral, pictures continues to occur both early (150 msec) and late (300 msec) in the processing stream. However, these modulatory effects appear to reflect different processes. If early ERP differences reflect obligatory perceptual processing, the data suggest that photographs of natural scenes, unlike simpler sensory cues (i.e., letters, words, geometric figures), are visually complex stimuli that continue to demand measurable encoding on each presentation. Nonetheless, this processing can be facilitated by the activation of short-term representations of visual stimuli, increasing perceptual fluency, as suggested by the strong within-block habituation of this early occipitotemporal ERP component.

The late positive potential, on the other hand, does appear to reliably index affective significance; its sustained presence through multiple repetitions presumably occurs due to continued motivational activation by the visual cue, via long-standing associations to the subcortical appetitive and defensive systems that reflexively direct and orient attention. Although effects of emotion for these complex picture stimuli generally occur relatively late in the processing stream, greater centroparietal positivity during affective picture viewing was also obtained in the earlier time window, suggesting that repetition may facilitate the speed in allocating “natural selective attention” to motivationally relevant cues (Bradley, 2002). Attention can also be strategically directed to relevant stimuli via task or instructions, and studies of directed attention generally find that the centroparietal positive potential to a task-relevant cue similarly shows no habituation, whereas habituation to a task-irrelevant cue occurs quickly (Polich & Criado, 2006; Bennington & Polich, 1999; Roth, 1983). One hypothesis is that “cold” cognition has hijacked the attentional circuits that initially evolved to protect and sustain the life of the individual and the species, with the result that motivationally relevant cues and task-relevant (neutral) cues will tend to have similar effects on the late positive potential.

Reprint requests should be sent to Maurizio Codispoti, Department of Psychology, University of Bologna, Bologna, Italy, or via e-mail: maurizio.codispoti2@unibo.it.

REFERENCES

- Bennington, J. Y., & Polich, J. (1999). Comparison of P300 from passive and active tasks for auditory and visual stimuli. *International Journal of Psychophysiology*, *34*, 171–177.
- Berridge, C. W., & Waterhouse, B. D. (2003). The locus coeruleus–noradrenergic system: Modulation of behavioral state and state-dependent cognitive processes. *Brain Research Reviews*, *42*, 33–84.
- Bouret, S., & Sara, S. J. (2004). Reward expectation, orientation of attention and locus coeruleus–medial frontal cortex interplay during learning. *European Journal of Neuroscience*, *20*, 791–802.
- Bouret, S., & Sara, S. J. (2005). Network reset: A simplified overarching theory of locus coeruleus noradrenaline function. *Trends in Neurosciences*, *28*, 574–582.
- Bradley, M. M. (2002). *Natural selective attention: Emotion in perception*. Presidential address, 42nd annual meeting of the Society for Psychophysiological Research, Washington, DC.
- Bradley, M. M., Löw, A., & Lang, P. J. (in press). Perception and emotion: Stimulus complexity, hedonic arousal, and brain potentials. *Psychophysiology*.
- Bradley, M. M., Lang, P. J., & Cuthbert, B. N. (1993). Emotion, novelty, and the startle reflex: Habituation in humans. *Behavioral Neuroscience*, *107*, 970–980.
- Cacioppo, J. T., Crites, S. L., Jr., Gardner, W. L., & Bernston, G. G. (1994). Bioelectrical echoes from evaluative categorizations: I. A late positive brain potential that varies as a function of trait negativity and extremity. *Journal of Personality and Social Psychology*, *67*, 115–125.
- Codispoti, M., Ferrari, V., & Bradley, M. M. (2006). Repetitive picture processing: Autonomic and cortical correlates. *Brain Research*, *1068*, 213–220.
- Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: Covariation with autonomic arousal and affective report. *Biological Psychology*, *52*, 95–111.
- De Cesarei, A., & Codispoti, M. (2006). When does size not matter? Effects of stimulus size on affective modulation. *Psychophysiology*, *43*, 207–215.
- Delorme, A., Rousselet, G. A., Mace, M. J., & Fabre-Thorpe, M. (2004). Interaction of top-down and bottom-up processing in the fast visual analysis of natural scenes. *Cognitive Brain Research*, *9*, 103–113.
- Fabre-Thorpe, M., Delorme, A., Marlot, C., & Thorpe, S. (2001). A limit to the speed of processing in ultra-rapid visual categorization of novel natural scenes. *Journal of Cognitive Neuroscience*, *13*, 171–180.
- Foote, S. L., Aston-Jones, G., & Bloom, F. E. (1980). Impulse activity of locus coeruleus neurons in awake rats and monkeys is a function of sensory stimulation and arousal. *Proceedings of the National Academy of Sciences, U.S.A.*, *77*, 3033–3037.
- Goffaux, V., Gauthier, I., & Rossion, B. (2003). Spatial scale contribution to early visual differences between face and object processing. *Cognitive Brain Research*, *16*, 416–424.
- Harris, J. D. (1943). Habituation response decrement in the intact organism. *Psychological Bulletin*, *40*, 385–422.
- Herve-Minvielle, A., & Sara, S. J. (1995). Rapid habituation of auditory responses of locus coeruleus cells in anesthetized and awake rats. *NeuroReport*, *6*, 1363–1368.
- Jacoby, L., & Dallas, M. (1981). On the relationship between autobiographical memory and perceptual learning. *Journal of Experimental Psychology: General*, *3*, 300–324.
- Junghöfer, M., Elbert, T., Tucker, D., & Rockstroh, B. (2000). Statistical control of artifacts in dense array EEG/MEG studies. *Psychophysiology*, *37*, 523–532.
- Kahneman, D. (1973). *Attention and effort*. Upper Saddle River, NJ: Prentice Hall.
- Keil, A., Bradley, M. M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P. J. (2002). Large-scale neural correlates of affective picture processing. *Psychophysiology*, *39*, 641–649.
- Klorman, R., Hastings, J. E., Weerts, T. C., Melamed, B. G., & Lang, P. J. (1974). Psychometric description of some specific fear questionnaires. *Behavioral Therapy*, *5*, 401–409.

- Kok, A. (2001). On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, *38*, 557–577.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation, and action. In P. J. Lang, R. F. Simons, & M. T. Balaban (Eds.), *Attention and orienting: Sensory and motivational processes* (pp. 97–135). Hillsdale NJ: Erlbaum.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2005). *International Affective Picture System (IAPS): Affective rating of measures and instruction manual* (Tech. Rep. A-6). Gainesville, FL: University of Florida.
- Macé, M. J., Thorpe, S. J., & Fabre-Thorpe, M. (2005). Rapid categorization of achromatic natural scenes: How robust at very low contrasts? *European Journal of Neuroscience*, *21*, 2007–2018.
- Miller, G. A., Gratton, G., & Yee, C. M. (1988). Generalized implementation of an eye movement correction procedure. *Psychophysiology*, *25*, 241–243.
- Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3, and the locus coeruleus–norepinephrine system. *Psychological Bulletin*, *131*, 510–532.
- Öhman, A. (1992). Orienting and attention: Preferred preattentive processing of potentially phobic stimuli. In B. A. Campbell & H. Hayne (Eds.), *Attention and information processing in infants and adults: Perspectives from human and animal research* (pp. 263–295). Hillsdale NJ: Erlbaum.
- Pineda, J. A., Foote, S. L., & Neville, H. J. (1989). Effects of locus coeruleus lesions on auditory, long-latency, event-related potentials in monkey. *Journal of Neuroscience*, *9*, 81–93.
- Polich, J. (1990). Probability and inter-stimulus interval effects on the P300 from auditory stimuli. *International Journal of Psychophysiology*, *10*, 163–170.
- Polich, J., & Criado, J. R. (2006). Neuropsychology and neuropharmacology of P3a and P3b. *International Journal of Psychophysiology*, *60*, 172–185.
- Romero, R., & Polich, J. (1996). P300 habituation from auditory and visual stimuli. *Physiology & Behavior*, *59*, 517–522.
- Roth, W. T. (1983). A comparison of P300 and the skin conductance response. In A. W. K. Gaillard & W. Ritter (Eds.), *Tutorials in ERP research—endogenous components* (pp. 177–199). Amsterdam: North-Holland.
- Schupp, H. T., Junghofer, M., Weike, A. I., & Hamm, A. O. (2004). The selective processing of briefly presented affective pictures: An ERP analysis. *Psychophysiology*, *41*, 441–449.
- Siddle, D. A. (1991). Orienting, habituation, and resource allocation: An associative analysis. *Psychophysiology*, *28*, 245–259.
- Siddle, D. A. T., & Spinks, J. A. (1992). Orienting, habituation, and the allocation of processing resources. In B. A. Campbell, H. Hayne, & R. Richardson (Eds.), *Attention and information processing in infants and adults: Perspectives from human and animal research* (pp. 227–262). Hillsdale, NJ: Erlbaum.
- Sokolov, E. N. (1963). *Perception and the conditioned reflex*. New York: Macmillan.
- Swick, D., Pineda, J. A., & Foote, S. L. (1994). Effects of systemic clonidine on auditory event-related potentials in squirrel monkeys. *Brain Research Bulletin*, *33*, 79–86.
- Thompson, R. F., & Spencer, W. A. (1966). Habituation: A model phenomenon for the study of neuronal substrates of behavior. *Psychological Review*, *73*, 16–43.
- Ullman, S., Vidal-Naquet, M., & Sali, E. (2002). Visual features of intermediate complexity and their use in classification. *Nature Neuroscience*, *5*, 682–687.
- Vankov, A., Herve-Minvielle, A., & Sara, S. J. (1995). Response to novelty and its rapid habituation in locus coeruleus neurons of the freely exploring rat. *European Journal of Neuroscience*, *7*, 1180–1187.
- Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology*, *8*, 227–233.