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The interplay between attention and long-term memory in affective habituation

Vera Ferrari¹, Serena Mastria², Maurizio Codispoti²

¹ Department of Medicine and Surgery, University of Parma, Parma, Italy

² Department of Psychology, University of Bologna, Bologna, Italy

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Abstract

Previous studies have consistently shown that repeated exposure to emotional stimuli leads to a reduction in cortical and autonomic responses (affective habituation). These findings emerge from studies conducted within a single experimental session, preventing the possibility of disentangling short-term from long-term habituation effects. The present study investigated whether affective habituation reflects a short-living learning process, or a more stable change involving long-term memory. Participants went through a preliminary habituation phase consisting of 80 repetitions of the same set of emotional and neutral pictures, while event-related potentials and oscillatory activity were measured. Crucially, after a 1-day interval, the same participants were exposed to a second habituation phase with the same stimuli that had been seen before. Results showed that the attenuation of the LPP affective modulation prompted throughout repetitions of Session 1 remained unchanged after a 1-day interval, and this between-session habituation effect, which was specific to repeated exemplars, was consistent across different emotional contents. Alpha desynchronization was clearly enhanced for pictures of erotica and mutilation and this modulatory pattern remained fairly stable over repetitions. Altogether, these findings suggest that LPP affective habituation is not a short-living learning process, but, rather, reflects a strengthened long-term memory representation of specific repeated stimuli.

1. Introduction

The initial reaction to the presence of any new, unfamiliar, or potentially dangerous/rewarding stimulus is a reflexive orientation that prompts behavioral and physiological reactions collectively called the orienting response (OR; Bradley, 2000; 2009; Öhman, 1992; Öhman, Hamm & Hugdahl, 2000; Graham & Hackley, 1991; Siddle 1991; Sokolov, 1963). After this initial mobilization of resources to a new stimulus, responses rapidly habituate if the stimulus occurs repetitively. The habituation pattern, detectable in various components of the orienting response, is an instance of elementary learning that occurs in virtually all animals (Groves & Thompson, 1970; Rankin et al., 2009; Thompson & Spencer, 1966), and it reflects CNS plasticity that allows animals to adapt to a dynamic and constantly changing environment, thus helping them to focus on important information.

Studies exploring physiological indices of the orienting response to emotional visual stimuli have measured a cascade of cortical, autonomic, and somatic changes reflecting enhanced stimulus processing together with preparation for action: both critical processes in motivationally relevant contexts. Consistent with the typical habituation pattern of the orienting response, most of these physiological responses undergo attenuation as the stimulus is repeatedly presented. The more pronounced autonomic changes to both pleasant and unpleasant stimuli, compared to neutral ones, rapidly decline once the stimulus becomes familiar, consistent with the idea that no action is required (Bradley, Lang, & Cuthbert, 1993; Codispoti, Ferrari, & Bradley, 2006b). In terms of cortical changes, the heightened late positive potential (LPP) that develops over centro-parietal regions during the presentation of pleasant or unpleasant pictures, compared to neutral ones (e.g. Codispoti, Ferrari, De Cesarei, Cardinale,

2006a; Codispoti, De Cesarei & Ferrari, 2012; De Cesarei & Codispoti, 2011b; Ferrari, Codispoti, Cardinale, & Bradley, 2008; Schupp, et al., 2006; Johnston, Miller, & Burleson, 1986), is attenuated across repetitions, albeit maintaining a reliable affective modulation throughout an extensive habituation phase (Codispoti, De Cesarei, Biondi, & Ferrari, 2016; Ferrari et al., 2016; Mastria, Ferrari, & Codispoti, 2017). However, the mechanisms underlying affective habituation remain poorly understood.

The essence of memory is the traces left by passing experience, and it is well established that habituation is a form of implicit memory that allows people to tune out information after frequent exposure in order to effectively select relevant stimuli (Cowan 1988; Squire 2009; Milner, Squire, Kandel, 1998). As proposed by Sokolov (1963), habituation is caused by a representation of the stimulus being active in memory and can reflect short-term and long-term processes (Konorski, 1967; Wagner 1979; Thompson 2009). Habituation of the orienting response is typically observed within a session of stimulus repetitions. When a stimulus is repeatedly presented, it establishes a transient trace, possibly related to short-term processes. In “Comparator theories” of habituation (Ohman, 1992; Sokolov, 1964; Ramaswami, 2014; Siddle 1991), the current sensory input is compared against a “neural model” of the past stimulation in memory, and the stronger the match between the two, the more the orienting response is inhibited. Indeed, after several repetitions, no further information is necessary, and, therefore, allocation of attention to repeated stimuli is reduced. However, if the stimulus is not repeatedly presented, the short-term representation may be lost quite rapidly, and the response recovers immediately. Spontaneous recovery of the orienting response reveals that habituation might rely on

a transient memory trace, and it is considered one of the main characteristics of habituation (see Rankin et al., 2009; Thompson, 2009). On the other hand, the repeated exposure might also promote a consolidation of the trace in long-term memory, which instead leads to a more persistent habituation for long intervals such as days or months (long-term habituation, Ohman, Hamm & Hugdahl, 2000; Rankin et al., 2009). Recently, a task force of the main experts in the field (Rankin et al., 2009) included long-term effects as an additional characteristic of habituation (characteristic #10). Long-term retention of habituation has been demonstrated for autonomic responses (Ohman, Hamm & Hugdahl, 2000), and recent studies have shown long-term habituation (up to 48 hrs) of automatic orienting of attention as well as oculomotor capture by irrelevant distractors (Chelazzi, et al., 2019; Turatto & Pascucci, 2016; Turatto, Bonetti & Pascucci, 2018).

Since most of the habituation studies on emotional processing have been conducted within a single experimental session (Codispoti et al., 2006b; 2007; Ferrari et al., 2011; 2015; Ferrari, Codispoti, & Bradley, 2016), in the present study, the LPP affective habituation was measured in a between-session repetition paradigm in order to reveal whether it reflects a short-lived learning process, or a more stable change involving long-term memory. Thus, the same set of emotional pictures that prompted a decrease in the LPP throughout the single session habituation phase was then presented again in a subsequent session (one day apart), with the hypothesis that if the affective habituation of the LPP reflects only the involvement of short-term memory processes, we expected the 1-day interval to be sufficient to generate a spontaneous recovery of this cortical emotional response. Differently, we may argue that extensive

experience with repeated emotional stimuli prompts reliable and long-lasting effects in terms of attention and memory.

Considering that previous studies on the effects of repetition on LPP have mostly employed a restricted number of picture categories (e.g., Codispoti, et al., 2006; 2007; Ferrari, et al., 2016b), that is, the most effective, generally, in terms of autonomic and brain responses (e.g., erotica and mutilation, Bradley, Codispoti, Sabatinelli, & Lang 2001; Codispoti & De Cesarei, 2007; De Cesarei & Codispoti, 2011a), in the present study we aimed to extend the assessment of affective habituation to other affective contents (i.e., pictures of romantic couples and human threat) that are also known to be effective in capturing attention and prompting reliable brain responses.

Cortical responses can be characterized not only in the time domain for the study of ERPs, but also in the time-frequency domain in order to study oscillatory activity. Recently, a number of studies have assessed event-related oscillations associated with emotional processing, and it has been demonstrated that the processing of emotionally arousing (both pleasant and unpleasant) pictures, compared to neutral stimuli, is associated with an enhanced alpha event-related desynchronization (alpha-ERD; De Cesarei & Codispoti, 2011a; Ferrari et al., 2015). Schubring & Schupp (2019) reported that the enhanced decrease in power in the alpha band for high emotional stimuli as compared to low arousing images was similar between passive viewing and during an explicit categorization task, suggesting that the alpha modulation as a function of stimulus arousal is independent of task stimulus relevance. Little is known in terms of emotional habituation of alpha-ERD; with few repetitions (four), albeit consecutive, Ferrari and colleagues (2015) did not find any repetition

effect on the affective modulation of alpha-ERD. However, if the alpha-ERD to emotional stimuli mostly reflects attention allocation, with a massive repetition we should observe an evident habituation pattern. Thus, in this study, alpha-ERD will be tested in an extensive within- and between-session repetition context to investigate the role of attention and memory in the affective modulation of LPP as well as of alpha-ERD.

2. Method

2.1 Participants

Participants were 27 students (16 females) from the University of Bologna, who were compensated with a small amount of money (10 euros) for taking part in the two-session study. All participants had normal or corrected-to-normal vision, and none of them reported current or past neurological or psychopathological problems. They had no previous experience with the materials used in this experiment. The experimental protocol conformed to the Declaration of Helsinki and was approved by the Ethical Committee of the Department of Psychology at the University of Bologna. Due to technical problems, two participants (one female and one male) were excluded from the EEG analysis.

2.2 Materials and procedure

The visual stimuli were 126 images selected from various sources, including the International Affective Picture System (IAPS; Lang et al. 2008), and public domain pictures available on the Internet. Of these pictures, 42 depicted pleasant contents (erotica and romantic couples), 42 unpleasant contents (mutilated bodies and human attack) and the remaining 42 were neutral pictures depicting a variety of

images of people in daily contexts. All images (22.6° h x 17.1°) were equated for brightness and contrast, using a MATLAB-based toolbox (SHINE; Willenbockel et al., 2010).

A picture with a black circle (2° x 2°) located in the center of a grey background was selected to serve as “dummy” target in order to make sure that participants were paying attention to the pictures on the screen.

Participants took part into two different experimental sessions (one day apart, see Figure 1). The procedure was very similar across the two sessions. In Session 1, upon arrival at the laboratory, participants signed an informed consent form. Then, the subject was seated in a recliner in a small, sound-attenuated, dimly-lit room, and the EEG sensor net was attached. The task instructions were to look at the pictures on the screen, and to press the key space any time a black circle appeared at the center (low probability, 1 out of about 10 trials). No decision task was required for the images, except to look at them. Session 1 began with a block of 60 novel pictures (plus 10 trials with a dummy target) that had never been presented before, and then followed by a series of four blocks of 120 trials each (habituation phase), in which the same set of 6 pictures (2 pleasant, 2 neutral and 2 unpleasant) were repeated 20 times in each block, for a total of 80 repetitions of the same picture exemplar by the end of Session 1. Session 2 started with the habituation phase, where the same set of pictures that had been repeatedly presented the day before were again repeated across additional four blocks, for a total of 160 repetitions of the same picture by the end of Session 2. After the habituation phase, one block of all novel pictures was presented. Between each block, a 2-min break was given. The order of picture presentation was pseudo-randomized with the restriction that no more than two times consecutively the same

picture or a picture of the same content occurred. The specific set of pictures serving as novel or repeated varied across participants, such that, across subjects, all pictures were used in all conditions. During each trial, the picture remained on the screen for 2s, and was then followed by a grey screen lasting between 1500 and 2500 ms (intertrial interval, ITI). In each session, stimulus presentation lasted about 42 minutes.

Visual stimuli were presented on a 21" CRT monitor located approximately 100 cm from the participant's eyes, at 800×600 resolution and a refresh rate of 155 Hz, controlled by an IBM computer and E-Prime software synchronized the presentation of the stimuli and triggered EEG recording on each (Schneider, Eschman, & Zuccolotto, 2002).

-----INSERT FIGURE 1 ABOUT HERE-----

2.3 EEG recording and processing

EEG was recorded at a sampling rate of 512 Hz from 257 active sites using an ActiveTwo Biosemi system. An additional sensor was placed below the participant's left eye, to allow for detection of blinks and eye movements. All signals were recorded in single-ended mode. The EEG was referenced in real time to a feedback loop, which comprises a common mode active electrode located near Cz (CMS=common mode sense), and a passive electrode (DRL=driven right leg). A hardware fifth-order low-pass filter with a -3dB attenuation factor at 100 Hz was applied online. Off-line analysis was performed using Emegs (Peyk, De Cesarei, & Junghöfer, 2011). EEG data were filtered (0.1 Hz high-pass and 40 Hz low-pass), and eye movements were corrected by means of an automated regressive method (Schlögl et al., 2007). Trials and sensors containing artifactual data were detected through a statistical procedure specifically developed for dense-array EEG (Junghöfer, Elbert, Tucker, & Rockstroh,

2000). This procedure detects global and individual electrode artifacts and replaces artifact-contaminated sensors with spline interpolation, statistically weighted on the basis of all remaining sensors. The rejection of artifact-contaminated trials and sensors relies on the calculation of statistical parameters for the measured absolute potentials over time, their standard deviation over time, the maximum of their gradient over time (first temporal derivative), and the determination of boundaries for each of these three parameters. Across conditions, an average of 10% of the trials were rejected due to artifact contamination. The signal was then re-referenced off-line to the average of all channels (average reference). Baseline correction was calculated by subtracting the mean of the 200 ms preceding stimulus onset from each waveform. Based on previous studies and on a visual inspection of the ERP waveforms, the late positive potential (LPP) was scored as average amplitude of the ERPs in the time windows 400–800 ms over centro-parietal sensor sites.

For time-frequency analysis, no low-pass filtering was applied on the raw EEG signal, but then the correction of eye movements as well as the artifact detection and sensor interpolation was similar to the ERP analysis (Junghöfer, Elbert, Tucker, & Rockstroh, 2000). Across conditions fewer than 17% of the trials were excluded. Data were convolved using complex Morlet's wavelet varying in time and frequency with a Gaussian shape. The time frequency analysis was performed on single trial data using FieldTrip software through EMEGS (Peyk, De Cesarei, & Junghöfer, 2011). The Morlet wavelet has a Gaussian shape, where the ratio between the center frequency and its standard deviation was set to 7 (c parameter), and the number of wavelet cycles (m parameter) was set to 5 (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1997). The range of analysis was from 4 to 80 Hz in the time window from 3,000 ms before

picture onset to 4,000 ms after picture onset in steps of 10 ms. As frequency resolution is maximal for low frequencies and minimal for high frequencies (Roach & Mathalon, 2008), the step between successive frequencies varied linearly from 0.5 Hz for the lowest frequencies to 5 Hz for the highest frequencies. All data were baseline corrected by subtracting the average alpha power of the prestimulus baseline (-1500 to 1000 ms) from each data point. The baseline was calculated slightly earlier from stimulus onset to avoid the burst of oscillatory activity that starts before the onset of the stimulation, due to the artifact of the filter algorithm (Hermann, Grigutsch, & Busch, 2004). The resulting event-related change in total power values (relative to baseline) are in decibels (dB) (Delorme & Makeig, 2004). For alpha-ERD (8-12 Hz), statistical analyses were performed on the mean value of the occipito-temporal sensor group (see Figure 4) over the same temporal window of the LPP¹.

Data Analysis

Separate analyses were conducted to assess effects of emotional arousal (emotional versus neutral) and effects of specific picture categories (erotica, romance, neutral people, human threat, mutilation) for each measure (the LPP and the alpha-ERD). In the first set of analyses, effects of emotional arousal were assessed by averaging responses over different emotional contents, and analyzed in a repeated measure analysis of variance (ANOVA) using Emotional arousal (2: emotional and neutral) and Block (10: Novel 1, Blocks of repeated pictures from 1 to 8, Novel 2) as factors. Based on previous habituation studies (Ferrari et al., 2015), we expected the impact of picture repetitions to be evident since the very beginning of the habituation phase. Following this reasoning, the habituation of the affective modulation (emotional minus neutral stimuli) was initially tested by comparing the initial novel

phase and the first block of repeated pictures (Novel 1 vs. Block 1); subsequently, in order to evaluate the progression of repetition effects over trials we performed an ANOVA followed by a linear trend test of affective modulation (emotional minus neutral) over the four blocks of the habituation phase of Session 1. To test whether the habituation of the affective modulation was a temporary reduction (within-session effect) or whether it reflected a more persistent effect (between-session effect), we assessed the contrast between the last block of the habituation phase (Block 4) and the first block of Session 2 (Block 5): if we observed a significant recovery of affective modulation, it would support the within-session habituation hypothesis; differently, the absence of a recovery would be consistent with a long-term habituation account. To test whether more repetitions in Session 2 prompted further habituation, we planned an ANOVA followed by a linear trend test of affective modulation (emotional minus neutral) over the four blocks of the habituation phase of Session 2. We also assessed the persistence of the effect in the last block (Block 8; after 160 repetitions) in order to replicate and extend previous LPP studies. Finally, a comparison between Block 8 and Novel 2, as well as between the two novel phases, was performed to assess whether the introduction of a change in picture exemplars would determine a recovery of the response for emotional and neutral stimuli.

In a second set of analyses, we further examined repetition effects on different emotional categories (see introduction). Specifically, a repeated measure analysis of variance (ANOVA) was performed on the specific picture Category (5: erotica, romance, neutral people, human threat, mutilation) and the Block (10: Novel 1, Blocks of repeated pictures from 1 to 8, Novel 2) as factors. The statistical plan (and

the rationale) behind this analysis is similar to that described for the previous analysis that was performed with all emotional contents collapsed together.

Greenhouse-Geisser corrections were applied where relevant. For each ANOVA test, we reported the partial eta squared statistic (η^2_p) indicating the proportion of variance that is explained by experimental conditions over the total variance.

The detection of the dummy target (circle), used only to keep subject attention on the screen, was highly accurate (average 98%) and remained stable over trials of both sessions.

3. Results

3.1 The Late Positive Potential

Emotional Arousal. As illustrated in Figure 2, a significant Emotional arousal (2) x Block (10) interaction, $F(9, 216)=17.42$, $p<.001$, $\eta^2_p=.421$, indicated that the affective modulation of the LPP (emotional minus neutral) varied across blocks. In the first novel block (Novel 1), as expected, emotional pictures elicited a larger LPP compared to neutral stimuli, $F(1, 24)=102.75$, $p<.001$, $\eta^2_p=.811$, and this emotional effect was reduced during the first habituation block, Emotional arousal x Block (2: novel 1 and block 1), $F(1, 24)=12.47$, $p<.01$, $\eta^2_p=.342$. During the habituation phase of session 1, a significant Emotional arousal (2) x Block (4) interaction, $F(3, 72)=4.87$, $p<.01$, $\eta^2_p=.169$, Emotional arousal by linear interaction $F(1, 24)=7.6$, $p<.05$, indicated that the LPP affective modulation was further reduced across the four habituation blocks. Specifically, the difference between emotional and neutral pictures decreased between block 1 and block 2, Emotional arousal x Block, $F(1, 24)=9.267$, $p<.01$, η^2_p

=.279. Critically, during the first habituation block of session 2 (block 5), the habituation of LPP affective modulation was preserved, in fact it did not differ from the last block (block 4) of session 1, $F(1, 24)=.025$, $p=.875$, $\eta^2_p=.001$, but it remained reduced compared to the first habituation block (Block 1) of Session 1, $F(1, 24)=10.01$, $p<.01$, $\eta^2_p=.294$. The affective modulation of the LPP was not further reduced across the habituation phase of Session 2 (Emotional arousal x linear trend of four blocks, $F(1, 24)=1.16$, $p=.292$, $\eta^2_p=.046$). In the last block of the habituation phase (Block 8), after 160 repetitions, the affective modulation continued to be highly reliable, $F(1, 24)=30.15$, $p<.001$, $\eta^2_p=.557$.

Finally, when new pictures were presented in the Novel 2 block, the affective modulation of the LPP recovered completely, Emotional arousal x Block (2: Block 8 and Novel 2), $F(1, 24)=32.68$, $p<.001$, $\eta^2_p=.577$, and did not differ compared to Novel 1, $F(1, 24)=.97$, $p=.334$, $\eta^2_p=.039$. Specifically, only for emotional pictures did the introduction of new exemplars (Novel 2) determine an enhancement of the LPP compared to the last block of the habituation phase, $F(1, 24)=32.55$, $p<.001$, $\eta^2_p=.583$, as this enhancement was not observed for neutral stimuli, $F(1, 24)=0.17$, $p=.896$, $\eta^2_p=.001$.

The repetition effect on the LPP to neutral pictures was small and did not reach significance with the main analysis (blocks of 20 repetitions, main effect of Block, $F(1, 216)= 1.79$, $p=.131$; linear trend across all repetition blocks including the first novel phase, $p=.208$). When ERPs were averaged across blocks of 10 repetitions, a significant linear trend across all blocks of both sessions was found ($F(1,24)=4.65$, $p<.05$, $\eta^2_p=.162$), showing a rapid decrease in the LPP amplitude in the first few repetitions.

-----INSERT FIGURE 2 ABOUT HERE-----

Specific emotional categories. Figure 3 illustrates centro-parietal ERP waveforms and scalp topographies of the LPP for each picture category during viewing of novel pictures and across the habituation phase of the two sessions (figure 3b). The overall ANOVA—5 (Category) x 10 (Blocks)—revealed a significant main effect of Category, $F(4,96)=40.9$, $p<.001$, $\eta^2_p=.63$, Block $F(9,216)=14.51$, $p<.001$, $\eta^2_p=.377$, and their interaction, $F(36, 864)=5.253$, $p<.001$, $\eta^2_p=.18$.

During the viewing of novel pictures (novel 1), a significant category effect was observed, $F(4,96)=35.386$, $p<.001$, $\eta^2_p=.596$. All emotional pictures prompted a larger LPP compared to neutral pictures, $F_s(1,24)>18.8$, $p_s<.001$, $\eta^2_{ps}>.44$, with erotic pictures prompting the largest LPP, which was statistically different also compared to pictures of mutilations $F(1, 24)=17.87$, $p<.001$, $\eta^2=.427$. The LPPs for pictures of mutilations prompted a larger LPP compared to threat pictures $F(1, 24)=10.538$, $p<.01$, $\eta^2=.305$, and both led to a significantly larger LPP compared to pictures of romantic couples, $F_s(1,24)>8.879$, $p_s<.05$, $\eta^2_{ps}>.197$.

The Category effect was reduced during the first habituation block compared to the initial novel phase, Category x Block (2: Block 1 and Novel 1), $F(4, 96)=8.587$, $p<.001$, $\eta^2_p=.264$. Specifically, this LPP decrease was largest for erotic pictures compared to all other contents, $F_s(1,24)>10.232$, $p_s<.005$, $\eta^2_{ps}>.299$. On the other hand, across the habituation blocks of Session 1, the LPP was similarly attenuated for all emotional picture categories, linear trend, $F_s(1,24)>8.879$, $p_s<.05$, $\eta^2_{ps}>.197$. At the end of the habituation phase (Block 4) of Session 1, all emotional picture categories continued to elicit a larger LPP compared to neutral ones, $F_s(1,24)>7.311$,

$p < .05$, $\eta^2_{ps} > .234$. After the one-day break, the affective modulation did not recover for any stimulus category, specific Category (2) x Block (2: Block 4 and Block 5), $F(1, 24) < 2.259$, $p > .146$, $\eta^2_{ps} < .086$. More repetitions in Session 2 prompted a further decrease in the LPP only for erotic pictures, compared to neutral ones, linear trend of Category (2) x Block (4), $F(1, 24) = 7.395$, $p < .05$, $\eta^2_p = .236$.

Compared to the last block of the habituation phase, the introduction of novel pictures at the end of Session 2 prompted a recovery of the LPP for emotional contents, but not for neutral pictures, Category (5) x Block (2: Block 8 and Novel 2), $F(4, 96) = 10.641$, $p < .001$, $\eta^2_p = .307$. The recovery was observed for all emotional categories, $F(1, 24) > 8.936$, $p < .01$, $\eta^2_p > .271$, but the LPP recovery to new erotic pictures was larger compared to the other contents ($F(1, 24) > 8.703$, $p < .01$, $\eta^2_p > .266$). The category effect in the Novel 2 did not differ compared to Novel 1, Category (5) x Block (2: Novel 1 and Novel 2), $F(1, 24) = 1.213$, $p = .310$, $\eta^2_p = .048$.

-----INSERT FIGURE 3 ABOUT HERE-----

3.2 Alpha band (8-12 Hz)

Emotional Arousal. As illustrated in Figure 4, emotional pictures elicited a larger alpha-ERD compared to neutral stimuli, Emotional arousal, $F(1, 24) = 19.12$, $p < .001$, $\eta^2_p = .44$. The Emotional arousal (2) x Block (10) interaction was marginally significant, $F(9, 216) = 2.19$, $p = .054$, $\eta^2_p = .084$, and the affective modulation of alpha-ERD was not reduced during the first habituation block compared to the initial novel block, Emotional arousal x Block (2: Novel 1 and Block 1), $F(1, 24) = .822$, $p = .376$, $\eta^2_p = .033$. Moreover, the affective modulation (emotional minus neutral) did not decrease

throughout the habituation phase (linear $F(1,24)=.433$, $p=.517$, $\eta^2_p=.018$; $F(1,24)=.001$, $p=.971$, $\eta^2_p=.000$, respectively for Session 1 and Session 2). However, new pictures presented in the novel block of Session 2 prompted a larger affective modulation of the alpha-ERD compared to the last block of the habituation phase, Emotional arousal x Block (2: Block 8 and Novel 2), $F(1,24)=8.59$, $p<.01$, $\eta^2_p=.264$, as well as compared to Novel 1, $F(1, 24)=8.41$, $p<.01$, $\eta^2_p=.259$, which was mainly driven by emotional pictures $F(1, 24)=52.117$, $p<.001$, $\eta^2_p=.685$, as no change in alpha-ERD was found for neutral stimuli, $F(1, 24)=2.176$, $p=.153$, $\eta^2_p=.083$.

Specific emotional content. As illustrated in Figure 4d, alpha-ERD was affected by specific picture category, $F(4,96)=11.67$, $p<.001$, $\eta^2_p=.327$, with the strongest decrease for pictures of erotica and mutilations, which differed significantly from all the other categories, $F_s(1,24)>5.79$, $p_s<.05$, $\eta^2_{ps}>.194$, but not from each other $F(1,24)=2.403$, $p=.134$, $\eta^2_p=.091$. Pictures of romance also prompted a larger desynchronization compared to neutral pictures, $F(1,24)=5.87$, $p<.05$, $\eta^2_p=.197$, whereas no difference was found between threat and neutral stimuli, $F(1,24)=1.97$, $p=.17$, $\eta^2_p=.076$.

The impact of specific picture content did vary across blocks in the overall design, Category (5) x Block (10), $F(36,864)=1.18$, $p=.287$, $\eta^2_p=.047$. The Category effect was not reduced during the first habituation block compared to the initial novel phase, Category x Block, $F(4, 96)=.948$, $p=.440$, $\eta^2_p=.038$. Moreover, affective modulation of each specific category (compared to neutral) was also tested using linear trends during the habituation blocks of Sessions 1 and 2, but, again, no significant effects were observed, $F_s(1,24)<.954$, $p_s>.338$, $\eta^2_{ps}<.038$. Finally, the increase in alpha-ERD prompted by new pictures (Novel 2), compared to Block 8, was

similar for all emotional categories, Category x Block (2: Block 8 and Novel 2), $F(3,72)=.496$; $p=.686$, $\eta^2_p=.020$.

-----INSERT FIGURE 4 ABOUT HERE-----

4. Discussion

Previous studies have consistently shown that the enhanced late positive potential relative to the viewing of emotional scenes gradually habituates as the stimulus becomes familiar with repetition. Here we investigated whether this effect, triggered by mere stimulus repetition, implies a temporary change or, rather, a long-lived plasticity mechanism. In a between-session study, the attenuation of affective modulation of the LPP, prompted by extensive within-session repetitions, did not show any hint of spontaneous recovery after the one-day break. Indeed, when the same picture exemplars were presented again in session 2, the affective modulation of the LPP was similar to that measured at the end of the habituation phase of session 1, and this long-term habituation pattern occurred similarly for all emotional picture contents.

Despite the stable and long-lasting habituation of the LPP affective modulation, the present study has also confirmed that the LPP affective modulation is highly resistant to reaching full habituation (i.e., no difference between emotional and neutral stimuli). Several previous studies have manipulated stimulus novelty with massive repetitions (up to 90 repetitions of the same exemplar, Codispoti et al., 2007) and even with consecutive (i.e., massed) repetitions (Ferrari et al., 2015), and the LPP was always modulated by picture emotional content regardless of the high familiarity with the stimulus. Session 1 of the present study is clearly a good replication of these

previous studies, providing a further confirmation of the persistence of the LPP affective modulation to picture repetition. Compared to previous repetition studies (Codispoti et al., 2006b; 2007; Ferrari et al., 2011) that started with blocks of repetitions, the present one allowed us to investigate more closely the gradient of habituation going from a novel phase (stimuli never repeated) at the beginning of the study through an extensive habituation phase across two sessions. Moreover, here the number of repetitions was even higher over the two sessions (i.e., 160 repetitions of the same exemplar) and again, emotional pictures showed a reliable larger positivity compared to neutral stimuli at the end of the habituation phase. These findings support a two-process account of the LPP modulation during affective picture viewing, in which the resistant core reflects a mandatory process implied in the detection of stimulus motivational significance, while attentional allocation to emotional stimuli wanes with stimulus repetition (Bradley, 2009; Codispoti et al., 2016; Ferrari et al., 2011; Micucci, Ferrari, De Cesarei, Codispoti, 2020).

Another relevant question to address here concerns the type of memory representation that drives the emotional habituation pattern. How specific is it? Interestingly, our findings suggest that response inhibition was finely tuned regarding the specific stimulus used throughout the habituation phase and did not apply to similar emotional exemplars, as shown by the full recovery of the LPP amplitude as soon as new pictures of the same category were presented in the final novel phase. We interpreted the absence of generalization of the LPP habituation as due to the specificity of the neural memory trace built throughout repetitions. Indeed, as long as a specific emotional exemplar was repeated, the LPP amplitude was reduced, but the presentation of a new exemplar, although belonging to the same emotional and

semantic category, prompted a complete recovery of the LPP response. Clearly, this response recovery suggests that the specific perceptual features of the memory representation are critical in prompting attentional allocation to emotional stimuli (for both LPP and Alpha-ERD). After all, it can be advantageous to thoroughly monitor and detect any specific change that might belong to emotional scenes, and promote further “information gathering” (Näätänen, 1992).

Since previous repetition studies have employed a restricted number of emotional picture categories (erotic couples and mutilation pictures), in the present study we aimed to extend the assessment of affective habituation to other affective contents (i.e., pictures of romantic couples and human threat). The findings suggest that the affective habituation pattern is highly consistent across different emotional picture categories, ruling out the hypothesis that the persistence of the affective modulation of the LPP observed in previous studies applied only to certain picture exemplars with specific emotional features (i.e., bloody body parts and women’s breasts). Although the LPP elicited by erotic pictures, in the initial novel phase, was the largest among emotional contents, it quickly decreased as soon as pictures were repeated, to such an extent that in block 1 the LPP was already similar for erotica and mutilations. Again, the higher sensitivity to stimulus repetition for erotic contents was also evident in session 2, in which the habituation pattern continued only for this category, and not for the other emotional contents. In fact, except for erotic pictures, all the other picture exemplars belonging to emotional categories were highly heterogeneous in terms of both perceptual features as well as semantic contents (e.g., in the threat category, a picture could depict a knife or a gun pointed towards the observer or towards other people in the scene), making the formation of a completely new memory trace

necessary with no benefit of previous experience with other within-category exemplars. This finding seems consistent with previous studies that show that the level of heterogeneity of the stimuli is critical in determining the decrease in attentional capture (Kelley & Yantis, 2009). In particular, Kelley and Yantis (2009) have shown that attention allocation declines faster across trials when stimuli are consistent in appearance, compared with when they are more variable. Moreover, the large recovery for emotional pictures, especially for those depicting erotic content, in the novel block following the habituation phase seems to suggest that the memory trace, which was repeatedly activated during the habituation phase (and that was possibly active because stimuli had been recently presented) was effective for those specific exemplars but not for dissimilar new exemplars (less generalization) introduced in the novel phase (Kelley & Yantis, 2009). Future parametric studies are needed to further clarify whether the LPP response to repeated stimuli, and the recovery when presented with novel stimuli, is modulated by their level of perceptual and semantic heterogeneity.

On the other hand, the LPP response prompted by stimulus novelty does not seem to work in the same way for neutral pictures. The LPP decrement across repetitions was detectable only within the first few repetitions, but this trend habituated quickly. More surprising is the absence of a response recovery when new neutral pictures were presented at the end of the extensive habituation phase of Session 2. One hypothesis is that, while it might be fundamental to detect any specific perceptual change in an emotional stimulus, a change in the perceptual features of a neutral scene might be less critical in triggering an enhancement of attention, thus prompting a generalization of the habituation. Alternatively, the absence of a response recovery for neutral pictures

could be due to the presence of emotional stimuli, which makes novel neutral stimuli somehow less relevant.

Although habituation is usually considered a form of non-associative learning, Wagner's proposal (1979) together with recent findings on the habituation of behavioral interference (Turatto, Bonetti, & Pascucci, 2018) emphasized the important role of the surrounding context in terms of learned association between contextual cues and representation of the habituation stimulus. Turatto et al. (2018) found evidence of a long-lasting habituation (i.e., at least two weeks) of attentional capture due to a stored representation of the distractor onsets in relation to their context. In our study the experimental context (i.e., the experimental room, the display layout and the task) remained stable over the two sessions, thus we cannot exclude the role of context in facilitating the persistent habituation over time. In fact, at the beginning of session 2, the high familiarity with the context could have helped in making the memory representation of each specific picture immediately available, and this might impact both attention allocation (overall LPP amplitude) and emotional engagement (the affective modulation of the LPP) towards repeated pictures. Future studies could examine whether a change in the context between the two sessions causes a weakening of memory trace that would imply a partial recovery of the habituated response.

In the present study we also examined how picture repetition affects alpha oscillations, which play a fundamental role in information processing (Klimesch, 2018). Consistent with the literature (De Cesare & Codispoti, 2011a; Schubring & Schupp, 2019; Vagnoni, Lourenco, & Longo, 2015), in our picture viewing paradigm posterior alpha-ERD was stronger in response to both erotic, romance and mutilation pictures compared to neutral ones. Unexpectedly, the affective modulation of alpha-

ERD did not varied throughout the habituation phase of the two sessions, despite the high number of repetitions. Previous studies suggest that alpha-ERD might reflect increased excitability of early visual areas in response to increased attentional demands (Iemi, Chaumon, Crouzet & Busch, 2018; Klimesch, 2018; Scheeringa, Koopmans, van Mourik, Jensen, & Norris, 2016). While these previous studies focused on the overall alpha suppression, here we examined how stimulus repetition affects the affective modulation of alpha-ERD. The absence of any repetition effect on this modulatory pattern seems to suggest that the affective modulation of alpha-ERD does not reflect attentional processing to emotional stimuli, which should decrease with stimulus repetition. This finding was unexpected, and more studies are needed to examine the impact of stimulus repetition on alpha-ERD. Since previous studies have shown that alpha activity reflects several processes including inhibition of irrelevant stimuli and memory (Hanslmayr et al., 2012; Klimesch et al., 2011), one hypothesis is that other processes might differentially modulate alpha activity for neutral and emotional stimuli (i.e., memory processes; Klimesch et al., 2011; 2012). It should be noted, however, that the introduction of new emotional pictures after a sustained repetition phase determined a strong alpha-ERD enhancement which, as for the LPP, was not evident for new neutral scenes. This strong desynchronization, which was possibly enhanced by the previous habituation context, may support the need to detect any specific change regarding emotional stimuli in order to enhance attentional allocation (see Codispoti et al., 2016, for similar findings with behavioral interference).

Previous research suggests that both alpha-ERD and the LPP reflect attentional selection (Codispoti et al., 2006a; Ferrari et al., 2008; Mastria et al., 2017; Klimesch et

al., 2012), and they are similarly affected by emotional picture content, but it is still not clear whether they reflect similar neural mechanisms (De Cesarei & Codispoti, 2011a). Previous functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG) studies indicated that the LPP is possibly generated and modulated by an extensive brain network including occipital, inferior temporal, medial parietal, and prefrontal cortices (Moratti, Saugar, Strange, 2011; Sabatinelli, Lang, Keil & Bradley, 2007), suggesting an overlap with documented attentional networks that undergo habituation (Sabatinelli, Keil, Frank & Lang, 2013). While visual perception studies suggest that event-related modulation of alpha power reflects top-down mechanisms (task-specific associative networks) that regulate information flow in the sensory cortex (cortical excitability; Klimesch, 2012; Scheeringa et al., 2012; Palva & Palva, 2007), less is known regarding the neural processes involved in the affective modulation of the alpha-ERD. Future studies should further examine the role of attention and learning in the affective modulation of these two cortical measures (Alpha and LPP) and their specific neural underpinnings.

Although it is more common to think of how attention improves memory, there is a growing body of literature showing how memory and learning affect attention and perception (Chelazzi, et al., 2019; Chen & Hutchinson, 2018; Chun & Turk-Browne 2007; Henderson & Hollingworth 1999; Kelley & Yantis, 2009; Theeuwes, 2019). The present LPP findings suggest that long-term memory traces influence attentional deployment towards emotional cues, consistent with the idea that it is advantageous to rely on past experience to optimize the processing of incoming information and guide adaptive behavior (Nobre & Stokes, 2019).

Footnotes

¹ Similar findings were observed using a longer window (500 to 2500 ms after picture onset) where ERD-desynchronization was maximal (see Figure 4a). Results indicate that the affective modulation of alpha-ERD was not reduced during the habituation phase, but new emotional pictures determined a strong alpha-ERD enhancement, which was not evident for new neutral scenes.

Long-term affective habituation

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References

- Bradley, M. M. (2009). Natural selective attention: Orienting and emotion. *Psychophysiology*, *46*, 1–11. <https://doi:10.1111/j.1469-8986.2008.00702.x>
- Bradley, M. M., Lang, P. J., & Cuthbert, B. N. (1993). Emotion, novelty, and the startle reflex: Habituation in humans. *Behavioral Neuroscience*, *107*, 970–980. <https://doi:10.1037/0735-7044.107.6.970>.
- Bradley, M.M., Codispoti, M., Sabatinelli, D., & Lang, P.J. (2001). Emotion and motivation II: sex differences in picture processing. *Emotion*, *1*(3), 300-19. <https://doi.org/10.1037/1528-3542.1.3.300>
- Chelazzi, L., Marini, F., Pascucci, D., & Turatto, M. (2019). Getting rid of visual distractors: The why, when, how and where. *Current Opinion in Psychology*, *29*, 135–147. <https://doi.org/10.16/j.copsyc.2019.02.004>
- Chen, D., & Hutchinson, J. B. (2018). What is memory guided attention? How past experiences shape selective visuospatial attention in the present. In M. Geyer, B. Ellenbroek, & C. Marsden (Eds.), *Current topics in behavioral neurosciences*, (pp. 1-28.). Berlin: Springer Nature.
- Christoffersen, G. R J. (1997). Habituation: Events in the history of its characterization and linkage to synaptic depression. A new proposed kinetic criterion for its identification. *Progress in Neurobiology*, *53*, 45-66. [https://doi.org/10.1016/S0301-0082\(97\)00031-2](https://doi.org/10.1016/S0301-0082(97)00031-2) .

- Chun, M.M., & Turk-Browne, N.B. (2007). Interactions between attention and memory. *Current Opinion in Neurobiology*, 17, 177-84.
<https://doi.org/10.1016/j.conb.2007.03.005>
- Codispoti, M., De Cesarei, A., & Ferrari, V. (2012). The influence of color on emotional perception of natural scenes. *Psychophysiology*, 49, 11-6.
<https://doi.org/10.1111/j.1469-8986.2011.01284.x>.
- Codispoti, M., & De Cesarei, A. (2007). Arousal and attention: Picture size and emotional reactions. *Psychophysiology*, 44, 680–686.
<https://doi.org/10.1111/j.1469-8986.2007.00545.x>
- Codispoti, M., De Cesarei, A., Biondi, S., & Ferrari, V. (2016). The fate of unattended stimuli and emotional habituation: Behavioral interference and cortical changes. *Cognitive Affective and Behavioral Neuroscience*, 16, 1063-1073. <https://doi.org/10.3758/s13415-016-0453-0>
- Codispoti, M., Ferrari, V., De Cesarei, A., Cardinale, R. (2006a). Implicit and explicit categorization of natural scenes. *Progress in Brain Research*, 156, 57–69.
[https://doi.org/10.1016/S0079-6123\(06\)56003-0](https://doi.org/10.1016/S0079-6123(06)56003-0)
- Codispoti, M., Ferrari, V., & Bradley, M. M. (2006b). Repetitive picture processing: Autonomic and cortical correlates. *Brain Research*, 1068, 213–220.
<https://doi.org/10.1016/j.brainres.2005.11.009>.
- Codispoti, M., Ferrari, V., & Bradley, M. M. (2007). Repetition and event-related potentials: Distinguishing early and late processes in affective picture perception. *Journal of Cognitive Neuroscience*, 19, 577–586.
<https://doi.org/10.1162/jocn.2007.19.4.577>.

- Cowan, N. (1988). Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information processing system. *Psychological Bulletin*, 104, 163-191. <https://doi.org/10.1037/0033-2909.104.2.163>
- 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. [https://doi.org/10.1016/S0301-0511\(99\)00044-7](https://doi.org/10.1016/S0301-0511(99)00044-7).
- De Cesarei, A., & Codispoti, M. (2011a). Affective modulation of the LPP and α -ERD during picture viewing. *Psychophysiology*, 48, 1397-404. <https://doi.org/10.1111/j.1469-8986.2011.01204.x>.
- De Cesarei, A. & Codispoti, M. (2011b). Scene identification and emotional response: which spatial frequencies are critical? *Journal of Neuroscience*, 31, 17052-7. <https://doi.org/10.1523/jneurosci.3745-11.2011>.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics. *Journal of Neuroscience Methods*, 134, 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Ferrari, V., Bradley, M. M., Codispoti, M., & Lang, P. J. (2011). Repetitive exposures: Brain and reflex measures of emotion and attention. *Psychophysiology*, 48, 515–522. <https://doi.org/10.1111/j.1469-8986.2010.01083.x>.
- Ferrari V, Bradley MM, Codispoti M, Karlsson M, Lang PJ. (2013). Repetition and brain potentials when recognizing natural scenes: task and emotion differences.

Social Cognitive and Affective Neuroscience, 8(8):847-54.

<https://doi.org/10.1093/scan/nss081>.

Ferrari, V., Bradley, M. M., Codispoti, M., & Lang, P. J. (2015). Massed and distributed repetition of natural scenes: brain potentials and oscillatory activity.

Psychophysiology, 527, 865–872. <https://doi.org/10.1111/psyp.12424>

Ferrari, V., Codispoti, M., & Bradley, M.M. (2016a). Repetition and ERPs during emotional scene processing: A selective review. *International Journal of Psychophysiology*, 111, 170-177. <https://doi.org/10.1016/j.ijpsycho.2016.07.496>.

Ferrari, V., Codispoti, M., Cardinale, R., & Bradley, M.M. (2008). Directed and motivated attention during processing of natural scenes. *Journal of Cognitive Neuroscience*, 20, 1753-61. <https://doi.org/10.1162/jocn.2008.20121>.

Ferrari, V., De Cesarei, A., MASTRIA, S., Lugli, L., Baroni, G., Nicoletti, R., & Codispoti, M. (2016b). Novelty and emotion: Pupillary and cortical responses during viewing of natural scenes. *Biological Psychology*, 113, 75–82. <https://doi.org/10.1016/j.biopsycho.2015.11.008>.

Graham, F. K., & Hackley, S. A. (1991). Passive and active attention to input. In J. R. Jennings & M. G. H. Coles (Eds.), *Handbook of cognitive psychophysiology: Central and autonomic nervous system approaches* (pp. 251–356). New York: John Wiley and Sons Ltd.

Groves, P. M., & Thompson, R. F. (1970). Habituation: A dual-process theory. *Psychological Review*, 77, 419–450. <https://doi.org/10.1037/h0029810>

- Hanslmayr, S., Staudigl, T., & Fellner, M.C. (2012). Oscillatory power decreases and long-term memory: The information via desynchronization hypothesis. *Frontiers in Human Neuroscience*, 6 (74).
<https://doi.org/10.3389/fnhum.2012.00074>
- Henderson, J. M., & Hollingworth, A. (1999). High-level scene perception. *Annual Review of Psychology*, 50, 43-71.
<https://doi.org/10.1146/annurev.psych.50.1.243>
- Herrmann, C.S., Grigutsch, M., & Busch, N.A. (2005). EEG Oscillations and Wavelet Analysis. In: Handy, T. (Ed.), *Event-Related Potentials: a Methods Handbook* (pp. 229–259). Cambridge. MIT Press.
- Iemi, L., Chaumon, M., Crouzet, S.M., & Busch, N. (2017). Spontaneous Neural Oscillations Bias Perception by Modulating Baseline Excitability. *Journal of Neuroscience*, 25, 807-819. <https://doi.org/10.1523/jneurosci.1432-16.2016>.
- Johnston, V. S., Miller, D. R., & Burleson, M. H. (1986). Multiple P3s to emotional stimuli and their theoretical significance. *Psychophysiology*, 23, 684–694.
<https://doi.org/10.1111/j.1469-8986.1986.tb00694.x>.
- Junghöfer, M., & Peyk, P. (2004). Analyzing electrical activity and magnetic fields in the brain. *Matlab News & Notes*, 2/04, 14– 15.
<https://doi.org/10.1155/2011/861705>
- Junghöfer, M., Elbert, T., Tucker, D. M., & Rockstroh, B. (2000). Statistical control of artifacts in dense array EEG/MEG studies. *Psychophysiology*, 37, 523– 532.
<https://doi.org/10.1111/1469-8986.3740523>

- Kelley, T. A., & Yantis, S. (2009). Learning to attend: Effects of practice on information selection. *Journal of Vision*, 9 (7), 1-18. <https://doi.org/10.1167/9.7.16>
- Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, 16, 606–617. <https://doi.org/10.1016/j.tics.2012.10.007>
- Klimesch, W. (2018). The frequency architecture of brain and brain body oscillations: an analysis. *European Journal of Neuroscience*, 48, 2431-2453. <https://doi.org/10.1111/ejn.14192>.
- Konorski, J. (1967). *Integrative activity of the brain: An interdisciplinary approach*. Chicago: University of Chicago Press.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International Affective Picture System (IAPS): Affective Rating of Measures and Instruction Manual*, (Tech. Rep. No. A-6). Gainesville, FL: University of Florida.
- Mastria, S., Ferrari, V., & Codispoti, M. (2017). Emotional Picture Perception: Repetition Effects in Free-Viewing and during an Explicit Categorization Task. *Frontier in Psychology*, 8, 1001. <https://doi.org/10.3389/fpsyg.2017.01001>.
- Miller, G. A., Gratton, G., & Yee, C. M. (1988). Generalized implementation of an eye movement correction procedure. *Psychophysiology*, 25, 241-243. <https://doi.org/10.1111/j.1469-8986.1988.tb00999.x>

- Milner, B., Squire, L. R. & Kandel, E. R. (1998). Cognitive neuroscience and the study of memory. *Neuron*, 20, 445- 468. [https://doi.org/10.1016/s0896-6273\(00\)80987-3](https://doi.org/10.1016/s0896-6273(00)80987-3)
- Micucci, M. Ferrari, V., De Cesarei, A., & Codispoti, M. (2020). Contextual Modulation of Emotional Distraction: Attentional Capture and Motivational Significance. *Journal of Cognitive Neuroscience*, 32(4), 621-633. https://doi.org/10.1162/jocn_a_01505
- Moratti, S., Saugar, C., & Strange, B.A. (2011). Prefrontal-occipito-parietal coupling underlies late latency human neuronal responses to emotion. *Journal of Neuroscience*, 31, 17278–17286. <https://doi.org/10.1523/jneurosci.2917-11.2011>
- Näätänen, R. (1992). *Attention and brain function*. Hillsdale, NJ: Lawrence Erlbaum.
- Nobre, A. C., & Stokes, M. G. (2019). Premembering experience: A hierarchy of timescales for proactive attention. *Neuron*, 104(1), 132–146. <https://doi.org/10.1016/j.neuron.2019.08.030>.
- O'Brien, F., & Cousineau, D. (2014). Representing error bars in within-subject designs in typical software packages. *The quantitative methods for psychology*, 10, 56-67. <https://doi.org/10.20982/tqmp.10.1.p056>.
- Öhman, A. (1992). Orienting and attention: Preferred preattentive processing of potentially phobic stimuli. In B. A. Campbell, H. Haynes, & R. Richardson (Eds.), *Attention and information processing in infants and adults: Perspectives from human and animal research* (pp.263-295.), Hillsdale, NJ: Lawrence Erlbaum Associates, Inc..

- Öhman, A., Hamm, A. & Hugdahl, K. (2000). Cognition and the autonomic nervous system: orienting, anticipation, and conditioning. In: Cacioppo, J.T., Tassinary, L.G. and Bernston, G.G. (Eds.), *Handbook of Psychophysiology* (2nd edn.). (pp.533-575). Cambridge, UK: Cambridge University Press.
- Palva, S., & Palva, J.M. (2007). New vistas for alpha-frequency band oscillations. *Trends in Neuroscience*, 30, 150-158. <https://doi.org/10.1016/j.tins.2007.02.001>
- Peyk, P., De Cesare, A., & Junghöfer, M. (2011). Electromagnetoencephalography software (EMEGS): Overview and integration with other EEG/MEG toolboxes. *Computational Intelligence and Neuroscience*, 861705. <https://doi.org/10.1155/2011/861705>
- Ramaswami, M. (2014). Network plasticity in adaptive filtering and behavioral habituation. *Neuron*, 82, 1216–1229. <https://doi.org/10.1016/j.neuron.2014.04.035>
- Rankin, C. H., Abrams, T., Barry, R.J., Bhatnagar, S., Clayton, D.F., Colombo, J., et al., (2009). Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory*, 92, 135-8. <https://doi.org/10.1016/j.nlm.2008.09.012>.
- Roach, B. J., & Mathalon, D. H. (2008). Event-related EEG time-frequency analysis: an overview of measures and an analysis of early gamma band phase locking in schizophrenia. *Schizophrenia Bulletin*, 34, 907-26. <https://doi.org/10.1093/schbul/sbn093>.
- Sabatinelli, D., Keil, A., Frank, D.W., & Lang, P. J. (2013). Emotional perception: Correspondence of early and late event related potentials with cortical and

subcortical functional MRI. *Biological Psychology*, 92, 513–519.

<https://doi.org/10.1016/j.biopsycho.2012.04.005>

Sabatinelli, D., Lang, P. J., Keil, A., & Bradley, M. M. (2007). Emotional perception: correlation of functional MRI and event-related potentials. *Cerebral Cortex*, 17, 1085-1091. <https://doi.org/10.1093/cercor/bhl017>

Scheeringa, R., Koopmans, P.J., van Mourik, T., Jensen, O., & Norris, D.G. (2016). The relationship between oscillatory EEG activity and the laminar-specific BOLD signal. *Proceedings of the National Academy of Sciences*, 113, 6761-6. <https://doi.org/10.1073/pnas.1522577113>.

Schlögl, A., Keinrath, C., Zimmermann, D., Scherer, R., Leeb, R., & Pfurtscheller, G. (2007). A fully automated correction method of EOG artifacts in EEG recordings. *Clinical Neurophysiology*, 118, 98–104, <https://doi.org/10.1016/j.clinph.2006.09.003>.

Schubring, D., & Schupp, H.T. (2019). Affective picture processing: Alpha- and lower beta-band desynchronization reflects emotional arousal. *Psychophysiology*, 56, e13386. <https://doi.org/10.1111/psyp.13386>.

Schupp, H. T., Flaisch, T., Stockburger, J., & Junghöfer, M. (2006). Emotion and attention: Event related brain potential studies. *Progress Brain Research*, 156, 31–51. [https://doi.org/10.1016/S0079-6123\(06\)56002-9](https://doi.org/10.1016/S0079-6123(06)56002-9)

Siddle, D. A. T. (1991). Orienting, habituation, and resource allocation: An associative analysis. *Psychophysiology*, 28, 245-259. <https://doi.org/10.1111/j.1469-8986.1991.tb02190.x>

- Sokolov, E. N. (1960). Neuronal models and the orienting influence. In: Brazier, M. A., editor. *The central nervous system and behavior: III*. Macy Foundation; New York.
- Sokolov, E. N. (1963). Perception and the conditioned reflex. New York: Macmillan.
- Squire, L. R. (2009). Memory and brain systems: 1969-2009. *Journal of Neuroscience*, 29, 12711–12716. doi: 10.1523/JNEUROSCI.3575-09.2009
- Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1997). Oscillatory gamma-band (30–70 Hz) activity induced by a visual search task in humans. *Journal of Neuroscience*, 17, 722–734. <https://doi.org/10.1523/jneurosci.17-02-00722>
- Theeuwes, J. (2019). Goal-driven, stimulus-driven and history-driven selection. *Current Opinion in Psychology*, 29, 97–101. <https://doi.org/10.1016/j.copsyc.2018.12.024>
- Thompson, R. F. (2009). Habituation: A history. *Neurobiology of Learning and Memory*, 92, 127–134. <https://doi.org/10.1016/j.nlm.2008.07.011>
- Thompson, R. F., & Spencer, W. A. (1966). Habituation: A model phenomenon for the study of neuronal substrates of behavior. *Psychological Review*, 73, 16–43. <https://doi.org/10.1037/h0022681>
- Turatto, M., & Pascucci, D. (2016). Short-term and long-term plasticity in the visual-attention system: Evidence from habituation of attentional capture. *Neurobiology of Learning and Memory*, 130, 159-169. <https://doi.org/10.1016/j.nlm.2016.02.010>

- Turatto, M., Bonetti, F., & Pascucci, D. (2018). Filtering visual onsets via habituation: A context-specific long-term memory of irrelevant stimuli. *Psychonomic Bulletin & Review*, 25, 1028-1034. <https://doi.org/10.3758/s13423-017-1320-x>.
- Vagnoni, E., Lourenco, S.F., & Longo, M.R. (2015). Threat modulates neural responses to looming visual stimuli. *European Journal of Neuroscience*, 42, 2190-202. <https://doi.org/10.1111/ejn.12998>.
- Wagner, A. R. (1979). Habituation and memory. In A. Dickinson & R. A. Boakes (Eds.), *Mechanisms of learning and motivation: A memorial volume for Jerzy Konorski*, (pp. 53–82). New York: Erlbaum.
- Willenbockel, V., Sadr, J., Fiset, D., Horne, G.O., Gosselin, F., & Tanaka, J.W. (2010). Controlling low-level image properties: the SHINE toolbox. *Behavioral Research Methods*, 42, 671-684. <https://doi.org/10.3758/BRM.42.3.671>

Figure Captions

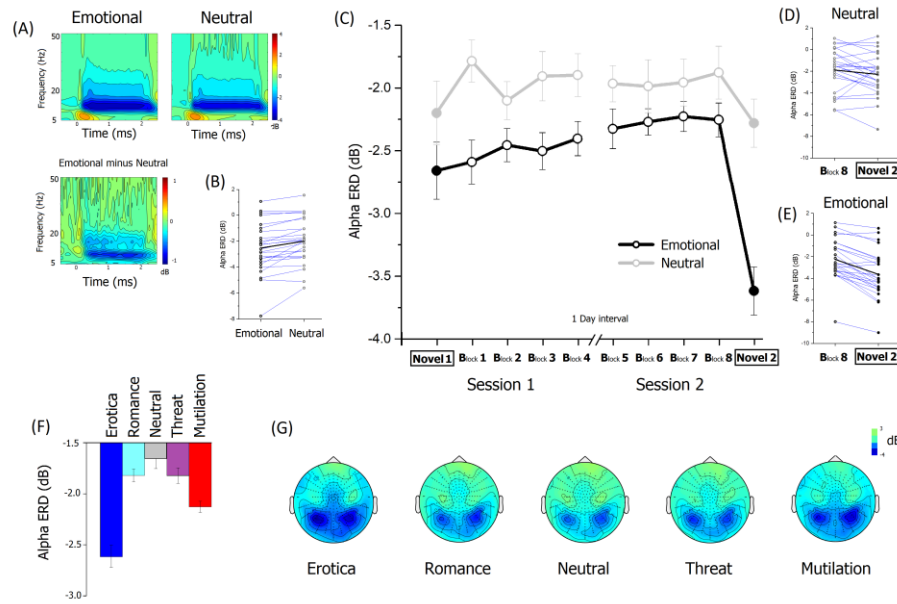
Figure 1. Schematic diagram showing the sequence of events in the present study. Session 1 started with a block of all novel pictures, depicting a variety of contents (erotic couples, romance, neutral people, human threat, and mutilations), followed by the habituation phase. After a one-day break the session started again with the same set of repeated pictures that continued to be presented throughout a new habituation phase, and the session ended with a new novel phase. Participants were instructed to look at the pictures and press a button any time a black circle (.15 probability) appeared on the screen.

Figure 2. (A) Centro-parietal ERP waveforms for emotional and neutral pictures in the novel blocks (average of Novel 1 and 2). (B) Single-subject line plot of the LPP mean amplitude (window 400-800ms from picture onset) for emotional and neutral pictures in the novel blocks. (C) Mean LPP amplitude for emotional and neutral pictures across the novel blocks (N1 and N2) and the habituation phases (from B1 to B8) of the two sessions. Scalp topographies (top view) of the difference between emotional and neutral LPP potentials are shown for each block. (D) Single-subject line plot of the affective habituation of the LPP. (E) Single-subject line plot of the recovery of the LPP for novel emotional pictures and (F) for novel neutral pictures. Bold line shows average across participants.

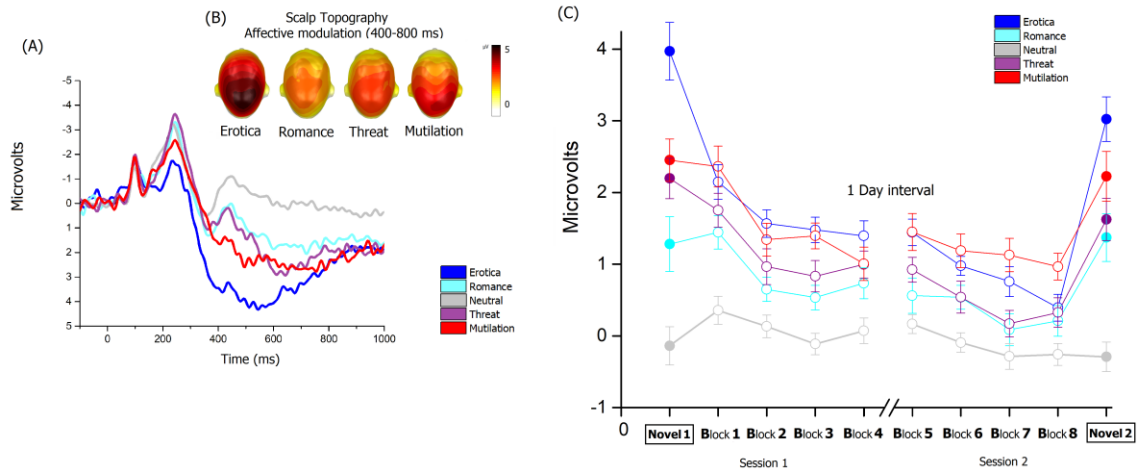
Figure 3. (A) Centro-parietal ERP waveforms for each picture content in the novel blocks (average of Novel 1 and 2). (B) Scalp topography (top view) in the LPP window of the difference between each emotional content and neutral pictures. (C) Mean LPP amplitude over centro-parietal region for each emotional content across the novel blocks (N1 and N2) and the habituation phases (from B1 to B8) of the two sessions.

Figure 4. (A) Time-frequency plot for emotional pictures (average of all contents) and neutral pictures, and their difference, over occipito-temporal regions. (B) Single-subject line plot of the mean of Alpha-ERD (8-12 hz) in the window 400-800 ms after picture onset for emotional and neutral pictures (C) Mean Alpha-ERD for emotional and neutral pictures across blocks of novel and repeated pictures. (D) Single-subject line plot of Alpha-ERD for emotional and (E) neutral pictures, in the last block of repeated pictures and the final novel phase. Bold line shows average across participants. (F) Mean of Alpha-ERD over occipital regions and (G) scalp topography for each picture content averaged across blocks.

Alpha Desynchronization



Late Positive Potential: Specific picture content



Late Positive Potential: Emotional Arousal

