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Original

Repetition and ERPs during emotional scene processing: A selective review / Ferrari, Vera; Codispoti, Maurizio; Bradley, Margaret M.. - In: INTERNATIONAL JOURNAL OF PSYCHOPHYSIOLOGY. - ISSN 0167-8760. - 111:(2017), pp. 170-177. [10.1016/j.ijpsycho.2016.07.496]

Availability:

This version is available at: 11381/2825176 since: 2017-05-19T16:07:53Z

Publisher:

Elsevier B.V.

Published

DOI:10.1016/j.ijpsycho.2016.07.496

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Repetition and ERPs during emotional scene processing: A review

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Abstract

Studies are reviewed that investigate effects of repetition during picture perception on event-related potentials, elucidating perceptual, memory and emotional processes. Repetition suppression was consistently found for the amplitude of early frontal N2 and posterior P2 components, which was greatly enhanced for massed, compared to distributed, repetition. Both repetition suppression and enhancement of the amplitude of a centro-parietal positive potential (LPP) were found in specific contexts. Suppression was reliably found following a massive number of repetitions of few items, whereas enhancement is found when repetitions are spaced, and enhancement was apparent both during simple free viewing as well as on an explicit recognition test. Regardless of repetition, an enhanced LPP was always found for emotional, compared to neutral, scenes. Taken together, the data suggest that different effects of massed and distributed repetitions on specific ERP components index perceptual priming, habituation, and spontaneous episodic retrieval.

Keywords: repetition, emotion, perception, attention, memory, event-related potentials

There is considerable evidence that repeated exposure to a stimulus affects attentional and orienting processes (Bradley & Lang, 2000; Siddle, 1991; Sokolov, 1963), triggers spontaneous memory retrieval (Bradley et al., 2015; Hintzman, 2004, 2010), produces perceptual priming (Henson & Rugg, 2003; Tulving & Schacter, 1990), and leads to changes in subjective ratings of pleasantness and arousal (Bornstein, 1989; Codispoti, et al, 2006a; Fechner, 1876; Raymond, et al., 2003; Zajonc, 1968). In terms of neural response, repetition of a stimulus can prompt either suppression or enhancement effects, which have been widely investigated using electrophysiological (Ferrari, et al., 2015; Grill-Spector, et al., 2006), magnetoencephalographic (Huberle & Lutzenberger, 2013), and neuroimaging (Bradley et al., 2015; Segaert et al., 2013) measures. Here, we review a series of electrophysiological studies that were conducted in our laboratories in order to investigate repetition effects in the context of picture processing, highlighting parametric manipulations that provided multiple replication conditions across studies, and which help to elucidate perceptual, memory and emotional processes.

Previous studies have identified a number of different event-related potentials that are sensitive to novelty and repetition in visual perception. These include an early anterior N2 (and its posterior P2; Ferrari, et al., 2010; Gruber, et al., 2006; Penney, et al., 2001) component, as well as a late positive potential. The early N2 component is part of a family of negative subcomponents peaking around 250-300 ms after stimulus onset that is reliably enhanced for novel visual stimuli (see Folstein & Van Patten, 2008 for a review)¹. In addition to early components, a later, slower late positive potential measured over centro-parietal sensors is also reliably enhanced not only for novel, but also for significant stimuli. Here, we manipulate the number and type of repetition as well as the stimulus significance and the task context to elucidate cognitive processes in scene perception.

1. Repetition suppression: anterior N2/posterior P2

Repetition suppression effects in early ERP activity have long been described which include a reduction in the amplitude of a negative component in a 200-300 ms time window measured over fronto-central sensors (anterior N2). Early evidence of modulation was observed in the classic “oddball” paradigms (Donchin, et al., 1978; Squires, et al., 1977), in which an infrequent oddball stimulus prompts a larger N2, compared to a repetitive, frequently presented “standard” stimuli (e.g., Chong et al., 2008; Henson et al., 2004; Folstein & Van Patten, 2008; Schendan & Kutas, 2003; Wang et al., 2004). Because an infrequent oddball tends to be both perceptually more novel and task-relevant than the repeated standard, however, it is difficult to disentangle effects of novelty and stimulus significance on the N2. In a series of studies, we covaried these variables by presenting novel and repeated stimuli that were either significant or not. In these studies, significance was varied either by comparing emotionally evocative to neutral scenes (Ferrari et al., 2010; Ferrari et al., 2015) or repetitions that were informative about the upcoming stimulus to those that were not (Ferrari et al., 2010).

Results indicated that the amplitude of the fronto-central N2 was primarily modulated by novelty, rather than significance, with clear suppression of this component with repeated picture presentation. Suppression effects were similar for emotional and neutral stimuli, as well as for those that were informative or not, providing converging evidence that N2 modulation is not modulated by stimulus significance. And, although early ERP effects for novel visual stimuli are typically described in terms of the fronto-central N2, we found similar modulatory effects for a posterior P2 in the same time window (Figure 1), which was similarly reduced for repeated items, regardless of stimulus significance.

Whereas an enhanced N2/P2 for novel stimuli is often interpreted as reflecting a mismatch between the current stimulus and a mental template reflecting task-relevance (Daffner, Mesulam, et al.,

2000; Folstein, et al., 2008), the free viewing context in which natural scenes were presented in our studies is relatively task-free and lacks a clear mental template to which incoming stimuli must be matched. Rather, this perceptual context suggests an interpretation of N2/P2 modulation that places emphasis instead on the dramatic reduction in the N2 for a repeated stimulus, rather than on the enhanced amplitude found for novel scenes. One possibility is that the N2 primarily reflects perceptual fluency, in which the previous occurrence of a visual stimulus significantly facilitates or eliminates some perceptual processing, reducing the amplitude of these components.

We investigated this hypothesis by comparing N2/P2 suppression for massed repetitions, in which perceptual processing was recent and a representation presumably still available, to repetitions that were distributed at longer lags (average 90 items) in which the visual representation is no longer available in a short-term store (Ferrari et al., 2015). N2/P2 suppression was greatly enhanced for massed compared to distributed repetitions (Figure 1), such that, following a single massed repetition, N2/P2 attenuation is equivalent to when a picture is repeated for the fourth time. On the other hand, effects of repetition on these early components was also evident, but smaller, when repetitions were distributed at long lags (Ferrari et al., 2015). Taken together, if the N2/P2 complex indexes perceptual fluency, these data suggest that any previous occurrence instantiates a memory representation that can facilitate later perceptual processes.

2. Late positive potential

Repetition Suppression. Free viewing of natural scenes prompts a centro-parietal late positive potential (LPP), which is enhanced when pictures depict emotional, compared to neutral, contents (Cacioppo et al., 1994; Cuthbert et al., 2000; Johnston et al., 1986; Radilova, 1982; Schupp et al., 2006). The late positive potential begins around 300 ms after the onset of an emotional picture and is most enhanced for the pictures rated highest in emotional arousal, regardless of whether they depict

appetitive (e.g., erotica) or aversive (e.g., mutilated bodies) content (De Cesarei & Codispoti, 2011; Schupp et al., 2004; 2006). Occipital and posterior parietal regions have been suggested as the possible origin of the affective modulation of the LPP (Sabatinelli et al., 2013), which relies on the recognition process (i.e. categorization) of the emotional content of the stimuli (Codispoti et al., 2009; De Cesarei & Codispoti, 2011), and it is not due to low-level perceptual properties such as picture size, complexity, color, or spatial frequencies (Bradley et al., 2007; Codispoti et al., 2012; De Cesarei & Codispoti, 2006; 2011).

Affective modulation of the LPP is found regardless of whether pictures are presented during free viewing (Ferrari et al., 2013; Schupp et al., 2007), in the context of an affective categorization task (Cuthbert et al., 2000; Schupp et al., 2004) or as task-irrelevant distractors (Codispoti et al., 2006b; Ferrari et al., 2008; MacNamara et al., 2011; Wiens & Syrjanen, 2013), suggesting that it indexes a relatively obligatory process (Codispoti et al., 2006a,b; Ferrari et al., 2008). Since one important feature of an obligatory process is resistance to habituation, we have utilized stimulus repetition as a variable to better understand the nature of the processes associated with LPP modulation.

In an early study, 3 pleasant, 3 neutral and 3 unpleasant pictures were repeated up to 60 times and results showed that the overall amplitude of the late positive potential was attenuated across repetitions (Codispoti et al., 2006a). This decline was not due to refractory effects or a waning of alertness, as evidenced by the renewal of the LPP when a set of novel pictures was presented. In addition, both pleasant and unpleasant pictures continued to elicit larger late positive potentials than neutral pictures throughout the entire repetition phase. Conversely, in the same study, differentiation between emotional and neutral pictures in both skin conductance responses and heart rate change rapidly habituated, replicating results of a previous study (Bradley et al., 1993). The persistence of affective modulation of the late positive potential and the rapid decrease in differential autonomic

responses for emotional stimuli are consistent with theories suggesting that the orienting response is not a unitary process (Barry, 1996; 2006; Bradley, 2009).

Co-registration of autonomic reactions necessitates the use of a long inter-stimulus interval (e.g., 10–20 s), which might have contributed to the persistence of the LPP affective modulation by increasing the relative “novelty” of each picture, despite its continued repetition. Using a shorter ISI (2–3 s) to reassess the effects of picture repetition on the late positive potential, 5 picture exemplars of each content (pleasant, neutral, unpleasant) were presented for as many as 90 trials in a second study (Codispoti et al, 2007). Findings were similar to those obtained with a longer inter-picture interval, with the overall amplitude of the late positive potential diminished with repetition, whereas significant modulation of the late positive potential by emotion persisted to the last presentation (Figure 2).

In these early studies, a relatively low number of repeated pictures was always presented intermixed among other (repeated) pictures. Thus, although the pictures were highly familiar, initial encoding and attention allocation processes were still necessary for picture identification on each presentation, potentially prompting the continued LPP enhancement for emotional, compared to neutral, scenes. We tested this hypothesis in two experiments by repeatedly presenting the same picture with no intervening stimuli between repetitions (massed repetition; Ferrari et al., 2011). In one study, the same picture exemplar was repeatedly presented 6 times in a row, and these blocks of massed repetitions were alternated with blocks of novel pictures that were presented only once throughout the study. Results indicated that although massed repetition clearly prompted a reduction of the LPP amplitude, LPP amplitude again continued to be significantly larger when subjects viewed emotional, compared to neutral, pictures (Figure 3). In a second study, we extended the number of massed repetitions to 30 contiguous repetitions in order to more completely attenuate attentional resource allocation to emotional pictures (Ferrari et al., 2011). Despite a vast difference in the absolute

number of contiguous repetitions in two studies (i.e., 6 or 30), results were strikingly similar: Overall, the LPP was attenuated with massed repetition but a larger late positive potential continued to be associated with viewing emotional, compared to neutral, pictures (Figure 3). These data also disconfirmed a hypothesis that intermixing pictures in the early studies was responsible for the sustained modulation following repetition.

Additional indices of affective picture processing following repetition assisted in the interpretation of the continued LPP modulation for emotional scenes. Significant affective modulation of the reflexive blink response to a startle probe, in which blinks are enhanced when viewing unpleasant scenes and attenuated when viewing pleasant scenes, was preserved despite picture repetition, replicating a previous study (Bradley et al., 1993). Thus, even after 30 massed (i.e. contiguous) repetitions of the same picture, blink reflexes were significantly potentiated for startle probes presented during unpleasant picture viewing (relative to neutral) and attenuated when subjects viewed pleasant pictures (Ferrari et al., 2011). Persistence of startle modulation despite massive massed repetition is strong evidence of continued motivational activation.

Conversely, the amplitude of the probe P3 component, a measure of attention allocation to the secondary startle probe, significantly increased with massed repetition in both studies, consistent with the hypothesis that more attention is available for processing the startle probe when the picture has been recently processed. Thus, whereas probe P3 amplitude is typically attenuated when subjects viewed novel emotional, compared to neutral, pictures (Cuthbert et al., 1998), massed repetition effectively eliminated affective modulation of this electrocortical component in both experiments (6 or 30 contiguous repetitions, Ferrari et al., 2011). The attenuation of probe P3 modulation with stimulus repetition parallels the findings of other indices of attention allocation, such as reaction times (RT), in which the normal slowing of secondary RT decisions when viewing emotional, compared to neutral,

scenes (De Cesarei & Codispoti, 2008; Ferrari et al., 2014; Wangelin et al., 2012) disappears after only a few repetition of the same stimulus, suggesting that both probe P3 and RT reflect resource allocation, which decreases with stimulus repetition (Codispoti, et al., under revision).

Repetition Enhancement. Thus far, we have described effects of repetition suppression, in which the amplitude of the LPP is generally attenuated as repetitions increase. On the other hand, many ERP studies of recognition memory routinely “repeat” a previously presented stimulus in the context of new items during a recognition task, and find a robust repetition enhancement, such that “old”, compared to new, items prompt an enhanced ERP in a late positive component that is similar in timing and topography to the LPP (Curran & Doyle, 2011; Ferrari et al., 2013; Weymar et al., 2013; Wilding et al., 1995; Wilding & Rugg, 1996; Voss & Paller, 2008). These old–new ERP differences have often been attributed to specific episodic recollection, in which recognition decisions reflect activation or retrieval of a specific episodic trace (e.g. Curran & Doyle, 2011; Paller et al., 1995; Paller et al., 2003; Wilding & Rugg, 1996; Rugg, & Curran, 2007; Voss & Paller, 2008).

A number of important differences exist between our studies of repetition and the old-new recognition data that may mediate the different findings of repetition suppression and enhancement. One important factor concerns the relative temporal distance between repetitions: In many of our studies, repetitions are massed (Ferrari et al., 2011, Figure 3) or otherwise occur very closely in time (Codispoti et al., 2006; 2007, Figure 2), whereas the temporal interval between repetitions is typically longer in recognition studies. Second, in recognition studies, the ERP is measured on the first repetition (the “old” item), compared to a new item, whereas our studies routinely involve much more repetition. Third, the recognition task requires an overt episodic decision regarding prior presentation – in our repetition studies, the repeated stimulus does not require an explicit memory decision. Any or all

of these variables may be important in determining whether a repetition enhancement or suppression effect is obtained, and our next set of studies investigated each of these variables.

To assess effects of temporal distance, the ordinal number of the repetition, and task (e.g., explicit recognition), repetitions of emotional and neutral scenes were presented either 4 times in a row (massed) or temporally distant (distributed), and the LPP measured both during free viewing (encoding) and on a later recognition test (Ferrari et al., 2013; Ferrari et al., 2015). Consistent with our previous research, massed repetitions during encoding prompted significant repetition suppression of the LPP, whereas the LPP continued to be enhanced when viewing emotional, compared to neutral, scenes. On the other hand, distributed repetition, in which there was a temporal distance between subsequent presentations, prompted a significant repetition *enhancement* effect, with larger positivity for distributed repetitions, compared to either novel scenes or massed repetitions (Figure 4).

Importantly, the LPP was enhanced even on the first distributed repetition (Figure 4, inset), consistent with old-new recognition studies (e.g. Curran & Doyle, 2011; Wilding & Rugg, 1996; Voss & Paller, 2008) which find an enhanced LPP for items that had previously only been presented once during encoding. In addition to ERPs, an analysis of the oscillatory brain activity during repeated processing revealed a theta enhancement (see Ferrari et al., 2015) that was uniquely found for distributed, but not massed, repetitions, which is also often reported in studies of episodic retrieval (e.g., Carrier & Pashler, 1992; Karpicke & Blunt, 2011; Karpicke & Roediger, 2008; Nyhus & Curran, 2010; Nelson et al., 2013).

We next measured effects of massed or distributed repetition at encoding on a later recognition task. Following free viewing, a series of scenes was presented and the participant made “old” and “new” decisions for scenes previously presented in the context of massed or distributed repetition, or only once during encoding. Replicating the repetition enhancement effect for the LPP found in

previous recognition studies (e.g. Curran & Doyle, 2011; Wilding & Rugg, 1996; Voss & Paller, 2008), "old" scenes presented once prompted enhanced positivity compared to new scenes (Figure 4). More importantly, "old" items initially encoded with distributed repetition showed an enhanced ERP compared to "old" scenes presented only once, or to novel scenes (Figure 5). Finally, emotional scenes continued to prompt enhanced positivity, compared to neutral scenes, regardless of whether they were repeated or not, indicating that repetition and emotion have independent effects on the LPP.

The spacing effect, which has been known since the beginning of verbal learning research (e.g., Ebbinghaus, 1864; for reviews, see Cepeda, et al., 2006; Crowder, 1976; Dempster, 1988) is the classic finding that, compared to massed repetitions, repetitions that are spaced across the encoding episode enhance later memory performance. Consistent with this, recognition accuracy in our study was enhanced for scenes presented in the context of distributed repetitions at encoding, compared to scenes presented only once or with massed repetitions (Ferrari et al., 2013). Discriminating among the different theoretical accounts put forth to explain the spacing effect has proved difficult, however, as different theories make similar behavioral predictions.

For instance, multiple trace theory (Melton, 1970; Glenberg, 1979) suggests that distributed, but not massed, repetition results in multiple encoding traces, which subsequently benefit retrieval performance. Study-phase retrieval (Green, 1989) and recursive reminding (Hintzman, 2010) accounts hypothesize that distributed repetitions act as retrieval cues to earlier episodes, with this retrieval practice facilitating later memory performance. Study-phase retrieval accounts posit that an additional process - episodic retrieval - occurs during spaced, but not massed, repetitions, and event-related potentials provide a novel methodology for assessing this prediction. Consistent with this account, distributed, but not massed repetitions, uniquely prompt a repetition enhancement effect in the LPP that is similar in timing and topography to the classic old-new ERP routinely found on episodic retrieval

tasks, suggesting that spontaneous retrieval of early occurrences may mediate the memory advantage for distributed repetitions.

Summary

Taken together, the systematic variation of parameters related to stimulus novelty, including the number and type (massed, distributed) of repetition, as well as the task context, not only provided multiple opportunities to replicate effects of suppression and enhancement on ERPs, but also afford a better understanding of repetition effects.

For the early N2/P2 complex, massed repetition completely and immediately attenuates these potentials, such that the N2 on the first contiguous repetition is reduced to the same degree as that measured to subsequent repetitions. Because of this, we have suggested that, instead of signalling novelty, N2 attenuation may index perceptual fluency, in which a previous presentation results in a memory representation that facilitates perceptual processing. N2 attenuation is largest for massed repetitions, but still apparent for repetitions that are spaced, suggesting that, at least in the short-term, prior presentations are able to prime perceptual processes. Emotional significance had no effect on modulation of the N2/P2 complex by repetition, suggesting this modulatory component indexes early stages of sensory or perceptual processing.

The data also indicate that when repetitions are temporally adjacent or otherwise close in time, reliable "suppression" is found in the amplitude of the centro-parietal LPP such that it is attenuated, compared to when viewing novel scenes. When repetitions are distributed (spaced) in time, however, repetition enhancement, rather than suppression, is obtained. Thus, repetition enhancement was found for distributed repetitions during free viewing, and for all "old" items on a later recognition test, with the most enhancement for repetitions that were distributed at encoding. One interpretation of these data is that repetition enhancement of the LPP indexes an additional process in which the repeated stimulus

acts to retrieve the episodic memory representation of a prior occurrence. Whereas a hypothesis of episodic retrieval is well founded when repetition enhancement occurs in the context of an explicit recognition task, finding similar effects for scenes whose repetitions are simply distributed in a task that does not require episodic retrieval (e.g., free viewing) suggests that spontaneous retrieval probably occurs in many contexts that do not explicitly probe memory, and supports theories (Green, 1989) that suggest study-phase retrieval mediates the classic spacing effect in learning and memory. In fact, spontaneous retrieval, or “reminding” (Hintzman, 2010), has been proposed as a basic mode of memory retrieval that routinely occurs in everyday life, with moment-to-moment cognition relying on both internal and external cues reminding us of both past and future events.

Additional evidence that spontaneous retrieval is prompted by distributed repetitions are data from a recent fMRI study (Bradley et al., 2015) in which scenes presented with repetitions spaced across the encoding phase uniquely prompted increased BOLD activity in regions of the posterior parietal cortex (e.g., precuneus) that are typically found in neuroimaging studies of episodic memory (Donaldson et al., 2001; Guerin & Miller, 2009; Kompus et al., 2011; Wagner et al., 2005; Yassa & Stark, 2008). On the other hand, when repetitions were massed, posterior parietal activation was absent, and, as reviewed here, LPP suppression is also reliably found. Massed repetitions, as well as when a few items are repeatedly presented in an intermixed fashion, instantiate memory representations that are still active on subsequent presentations, ruling out the operation of a retrieval process. In this case, spontaneous retrieval does not occur, the LPP is attenuated, and continued presentations do not support better memory performance.

The amplitude of the LPP was always greater when viewing emotional, compared to neutral, pictures, and this affective modulation persists regardless of whether repetitions are massed or distributed, whether the context involves free viewing or recognition, and whether scenes are old or

new. We have interpreted these data as indicating that affective modulation of the LPP reflects automatic engagement of motivational systems, which continues to occur after multiple repetitions and regardless of task-relevance (Bradley, 2009). According to this interpretation, mere repetition of a scene does not change or reduce its motivational significance, which requires additional counter-conditioning or other learning that changes the associative links to the subcortical systems mediating appetitive and defensive behaviors. On the other hand, the similar effects of repetition suppression and enhancement for both emotional and neutral scenes are evidence of more general cognitive processes that operate regardless of motivational significance.

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Footnote

1. In contexts other than visual perception, such as those involving response inhibition and/or response conflict, anterior N2 components such as the ERN, go-nogo N2, conflict N2 and the FRN are also modulated and have been attributed to cognitive control, which is probably active in specific task contexts.

Figures

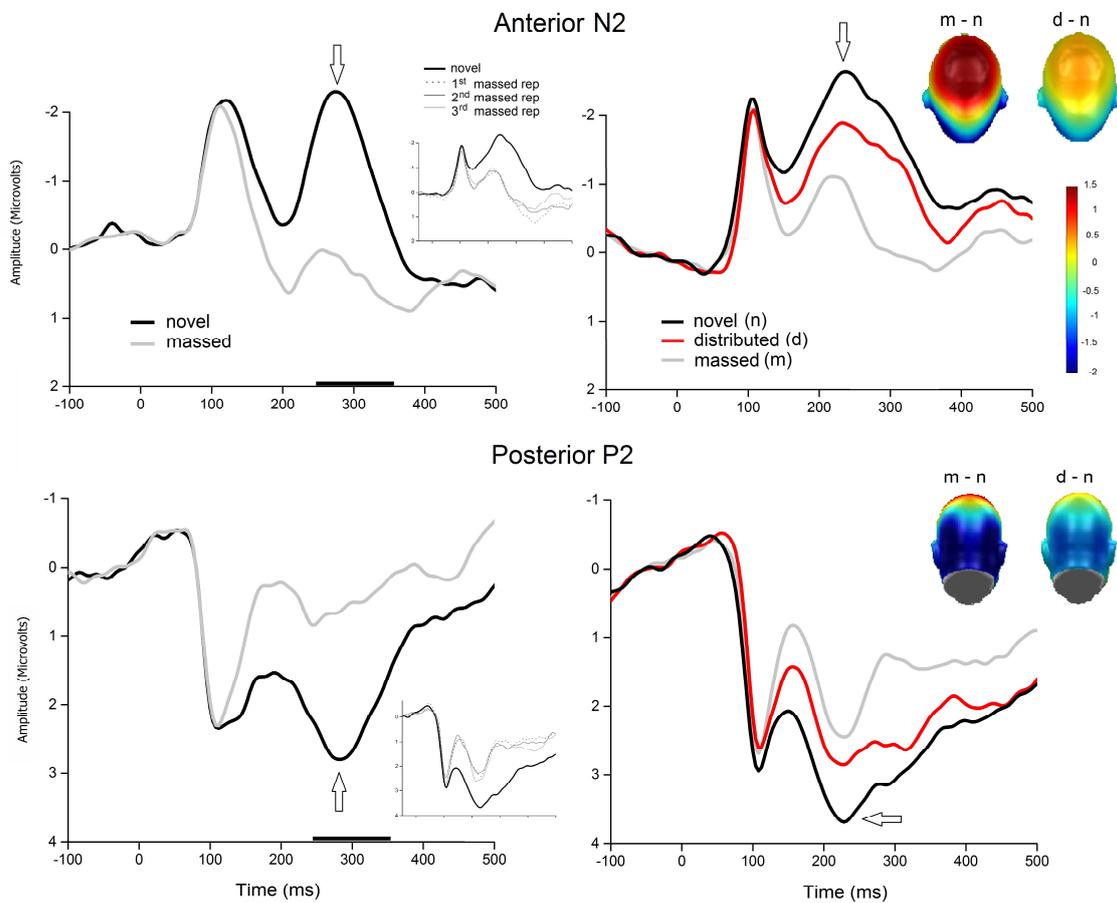


Figure 1: Left: Grand-average ERP waveforms when viewing novel pictures and pictures presented with massed repetitions for frontal (top) and posterior (bottom) sensors show the clear repetition suppression of both the anterior N2 and the posterior P2 (based on data from Ferrari, Bradley, Codispoti & Lang (2010), that is similar for each repetition (waveform inset, based on data from Ferrari, Bradley, Codispoti & Lang (2015)). Right: Grand-average ERP waveforms when viewing novel pictures and pictures presented with distributed and massed repetitions for frontal (top) and posterior (bottom) sensors show maximal attenuation for massed repetitions, and the topography of the differences (150-300 ms).

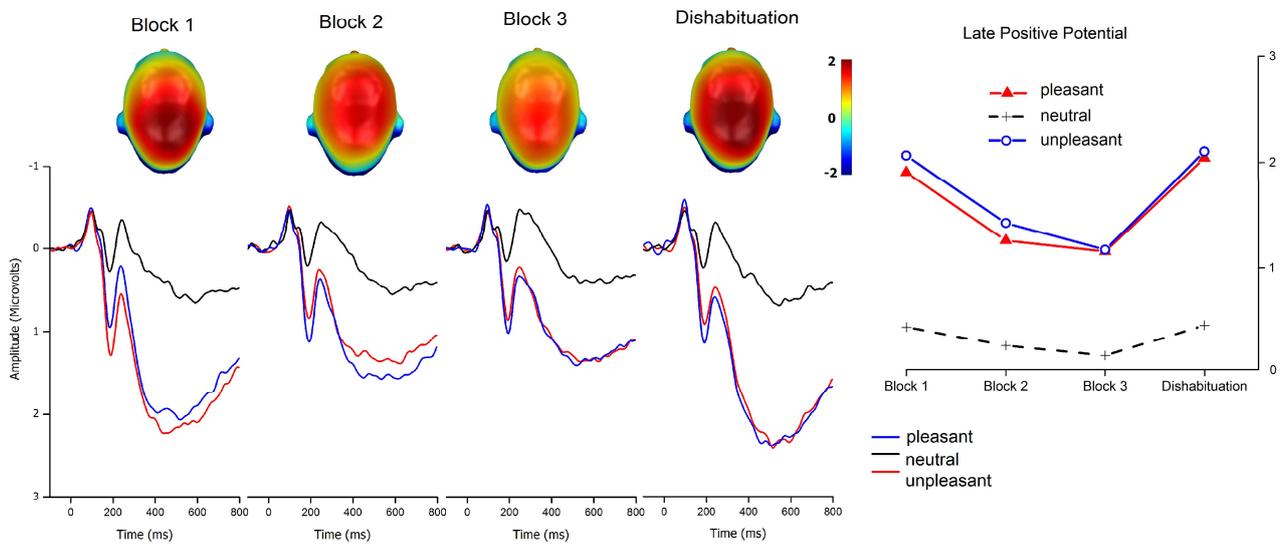


Figure 2. Grand-averaged ERP waveforms over centroparietal sensors during viewing of 5 picture exemplars of each content (pleasant, neutral, unpleasant) that were presented for as many as 90 trials across the three blocks of habituation phase followed by a block of dishabituation, during which a new set of pictures was presented and repeated 30 times. In this study (Codispoti, Ferrari, & Bradley, 2007) repetitions were closely spaced. The inset above each ERP waveform illustrates the scalp topography (top view) of the difference (in the window 300–600 ms) between emotional and neutral picture processing. Right: Mean ERP amplitude (in the window 300–600 ms) for centroparietal sensors shows a decrease across blocks of repetition (Block 1, 2 & 3), whereas significant modulation of the late positive potential by emotion persisted to the last presentation.

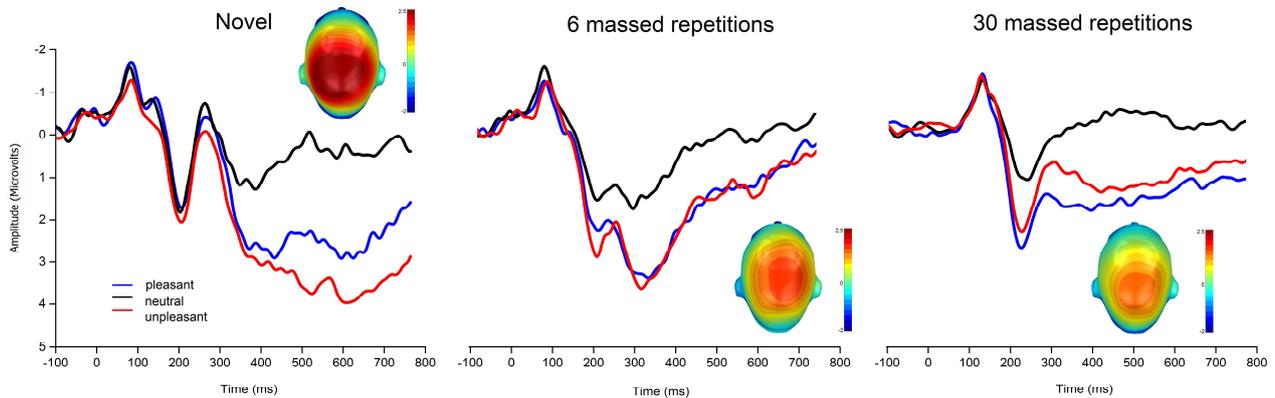


Figure 3. Grand-averaged ERP waveforms over centroparietal sensors when subjects viewed pleasant, neutral, and unpleasant pictures in the novel and massed (averaged over 6 or 30 repetitions) condition. Insets are the top view of the scalp distribution of the difference in the 400–700-ms window between emotional (pleasant and unpleasant) and neutral picture processing. Despite a vast difference in the absolute number of contiguous repetitions in two studies (i.e., 6 or 30), results were strikingly similar: The enhanced late positive potential when viewing emotional, compared to neutral, pictures persisted across massed repetitions. Based on data from Ferrari, Bradley, Codispoti & Lang (2011).

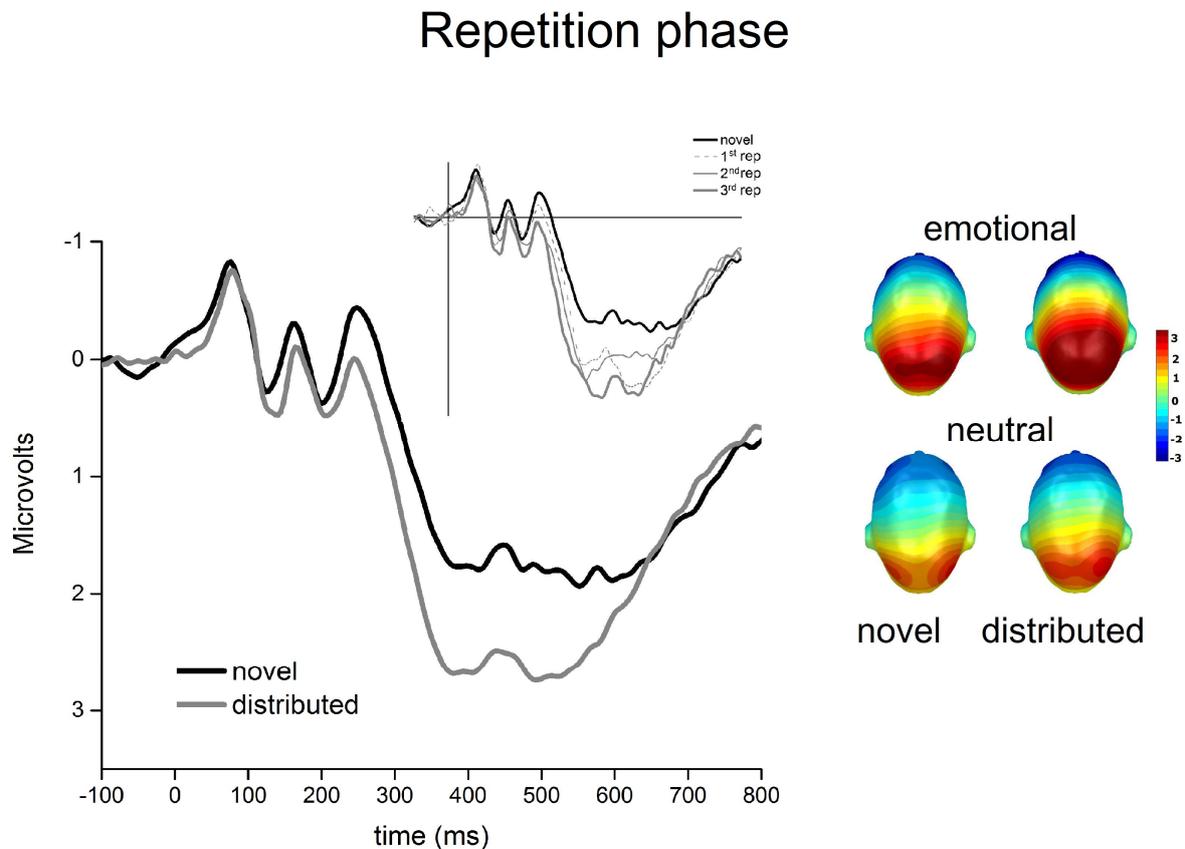


Figure 4. Grand-average ERP waveforms when viewing pictures that were novel or presented with distributed repetition (four repetitions) show an old-new ERP difference (350–600 ms) that is similar for each repetition (waveform inset). The topography (top view) of the ERP potentials in the old-new window shows that the enhanced positive potential for distributed repetitions, compared to novel presentations, was apparent for both emotional and neutral pictures. Based on data from Ferrari, Bradley, Codispoti & Lang (2015).

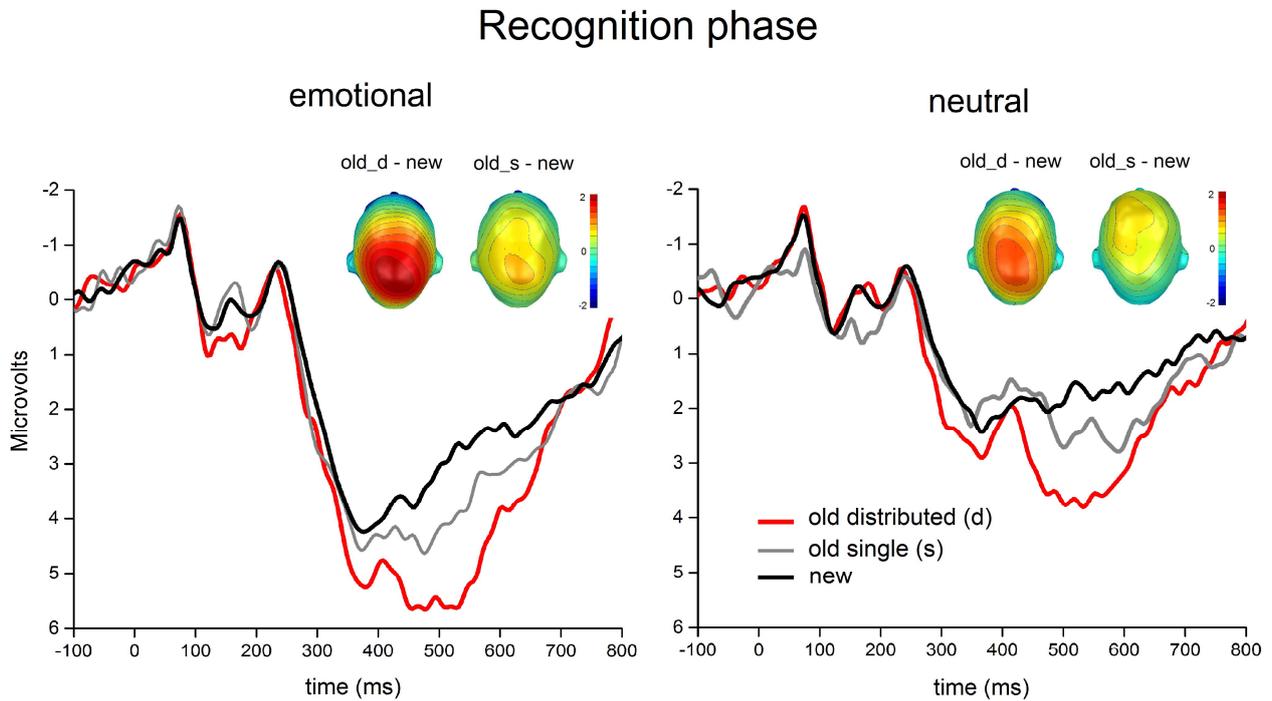


Figure 5. Grand average ERP waveforms over centro-parietal sensors when recognizing emotional (left panel) and neutral (right panel) old pictures presented once (s), or distributed (d) during encoding and new pictures. Insets show scalp topography (top view) of the difference in the 400–600 ms window between old pictures presented once (old_s – new) or distributed (old_d – new) during encoding and new pictures. Based on data from Ferrari, Bradley, Codispoti, Karlsson & Lang (2013).