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Event-Related Potentials, Emotion, and Emotion Regulation: An Integrative Review

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Progress in the study of emotion and emotion regulation has increasingly been informed by neuroscientific methods. This article focuses on two components of the event-related potential (ERP)—the P300 and the late positive potential (LPP)—and how they can be used to understand the interaction between the more automatic and controlled processing of emotional stimuli. Research is reviewed exploring: the dynamics of emotional response as indexed at early and late latencies; neurobiological correlates of emotional response; individual and developmental differences; ways in which the LPP can be utilized as a measure of emotion regulation. Future directions for the application of ERP/electroencephalogram (EEG) in achieving a more complete understanding of emotional processing and its regulation are presented.

INTRODUCTION

Research on emotion regulation has expanded at a rapid pace in recent years—and has become a popular topic in social, clinical, developmental, and cognitive psychology (Gross & Thompson, 2007); moreover, the current issue of *Developmental Neuropsychology* is consonant with the increased focus on neurophysiological and neurobiological measures related to emotion regulation (Lewis, Lamm, Segalowitz, Stieben, & Zelazo, 2006; Ochsner & Gross, 2005). Indeed, a growing body of work in cognitive/affective and social neuroscience utilizing functional magnetic resonance imaging (fMRI) has begun to shed light on the neural structures involved in emotion regulation (reviewed later). From a clinical perspective, interest in the neuroscience of emotion regulation has flourished, at least in part because of the belief that emotion *dysregulation* is a key mechanism underlying various psychopathologies (Davidson, 1998; Davidson, 2002; Phillips, Ladouceur, & Drevets, 2008a, 2008b). From a developmental perspective, emotion regulation stands at the intersection of developing cognitive and affective capabilities, and offers a unique opportunity to better understand their interaction (Lewis et al., 2006; Lewis & Stieben, 2004).

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Although the neuroscientific world of emotion regulation is dominated by fMRI studies, we aim to make a convincing case that specific scalp-recorded electrical activity of the brain can also be used to study emotion and emotion regulation. Electrodes placed on or near the scalp can be used to record the rapidly fluctuating electroencephalogram (EEG), which reflects continuous electrical changes in the brain. When the EEG is time-locked to specific events (i.e., the presentation of a stimulus or the execution of a response), the resulting positive and negative voltage changes over time are referred to as event-related potentials (ERPs). In terms of their neural basis, ERPs reflect the synchronous activity of populations of neurons—in particular, summated post-synaptic potentials (Fabiani, Gratton, & Federmeier, 2007; Luck, 2005). ERPs are typically distinguished by their timing, morphology, scalp topography, and response to experimental manipulations. The nomenclature of common ERPs often captures the polarity of the deflection and relative latency (e.g., the "P300" which reflects a positive deflection peaking around 300 msec following a stimulus).

The ERP technique has a number of advantages. For instance, unlike blood oxygenation measures derived from fMRI, ERPs *directly* reflect neural activity. Moreover, because the electrical activity of populations of neurons is volume-conducted through the brain to the scalp, scalp-recorded and neural activity occur nearly simultaneously. Because the EEG can be sampled on the order of milliseconds, ERPs have exceptional temporal resolution—and index early and rapid changes in neural processes. Moreover, ERPs are relatively inexpensive and might be better tolerated for research conducted with younger children.

This article will focus on very specific ERP components in response to particular types of stimuli. For the most part, the article focuses on studies that have utilized standardized emotional stimuli—mainly the International Affective Picture System (IAPS) (Lang, Bradley, & Cuthbert, 2005)—but also stimuli sets that include facial displays of emotion. We would note at the outset that faces are relatively weak emotional stimuli compared to IAPS pictures (Britton, Taylor, Sudheimer, & Liberzon, 2006). We begin by presenting a brief review on the P300 as an ERP component linked to stimulus salience. Next, data will be reviewed suggesting that emotional stimuli automatically capture attention and have been shown to increase the amplitude of the P300. More recent ERP data suggests that in addition to an increased P300, emotional stimuli are associated with a more sustained positivity in the ERP, referred to as the late positive potential (LPP). Similarities and differences between the P300 and the later and longer-lasting LPP are discussed. Collectively, these data suggest that emotional stimuli elicit a sustained increase in attention, receive increased processing resources—and that the facilitated processing of emotional stimuli can be indexed by modulation of positivities in the stimulus-locked ERP including the P300 and LPP. Next, we cover neurobiological correlates of the LPP, and suggest that the LPP might reflect neuromodulatory activity of the locus coeruleus norephinepherine system. The impact of individual, genetic, developmental and later-life differences on the LPP are also reviewed.

Although the facilitated processing of emotional stimuli appears relatively automatic, recent data suggests that measures of emotional processing are susceptible to a variety of top-down strategies that involve cognitive control. In the present article, we focus on attentional and cognitive change strategies of emotion regulation. Before discussing relevant ERP studies of emotion regulation, we present a brief overview of Gross' process model of emotion regulation, including a brief review of relevant neuroimaging studies on emotion regulation. Next, we discuss a sequence of recent ERP studies reporting that the LPP is sensitive to a variety of emotion regulation instructions that have been employed in the functional neuroimaging literature. Manipulations of meaning change, task relevance, spatial attention, and cognitive load are explored, and effect sizes of various manipula-

tions are compared. In addition, we propose that the time-course of the LPP might be an important metric for indexing emotion regulation, and present data demonstrating that the duration of the LPP can be quite prolonged following instructions to imagine recently viewed pictures. In summary, we suggest that the LPP indexes the dynamic level of arousal elicited by emotional stimuli. These data highlight the way in which the LPP might be utilized to study processes such as emotion regulation, across the lifespan and in disordered populations.

ATTENTION AND EMOTION: FROM THE P300 TO THE LPP

The P300 component of the ERP was first reported in 1965 (Sutton, Braren, Zubin, & John, 1965), and has been studied expansively for the past four decades (cf. Nieuwenhuis, Aston-Jones, & Cohen, 2005; Polich, 2007). In general, the P300 is observed as a rather broad positivity that is maximal along the midline at parietal recording sites between 300 and 500 msec following stimulus presentation (Sutton et al., 1965). The P300 has been studied most extensively in "oddball" tasks, in which participants are asked to count or otherwise keep track of certain *target* stimuli, which are presented infrequently among other *standard* stimuli; for instance, participants might hear beep and boop sounds on 80% and 20% of trials, respectively, and be instructed to count the relatively infrequent boops (Johnson, 1984, 1986; Magliero, Bashore, Coles, & Donchin, 1984; Squires, Donchin, Herning, & McCarthy, 1977; Sutton et al., 1965).

Figure 1 (top) presents ERP data recorded from posterior-superior recording sites (CP1/2, CP3/4, P1/2, P3/4, and PO3/4) and the scalp distribution of target minus standard effects (bottom) recorded from 39 participants during a typical oddball task in which auditory targets were presented on approximately 20% of trials. Consistent with Figure 1, target stimuli presented in this type of oddball task elicit larger P300s compared to standard stimuli. These effects seem to depend on participants' attending to the stimuli: when attention is occupied by a secondary task or when stimuli are ignored, target stimuli fail to elicit a P300 (Duncan-Johnson & Donchin, 1977; Hillyard, Hink, Schwent, & Picton, 1973). Moreover, the degree of P300 modulation by targets depends on subjective probability such that the P300 is larger when target stimuli are perceived as more unexpected or improbable (Duncan-Johnson & Donchin, 1977; Squires et al., 1977). However, even when equated for probability, targets will elicit a larger P300 than standard stimuli, suggesting that task-relevance itself is sufficient to potentiate the P300 (Duncan-Johnson & Donchin, 1977). Overall then, the P300 appears to reflect the allocation of capacity-limited resources toward motivationally salient environment stimuli.

In the type of oddball task described earlier, task-related demands and instructions dictate which stimuli are relevant. However, data from multiple measurements indicate that emotional stimuli *automatically* capture our attention. For instance, both pleasant and unpleasant stimuli are viewed longer than neutral pictures (Bradley, Codispoti, Cuthbert, & Lang, 2001; Bradley & Lang, 2000; Lang, Bradley, & Cuthbert, 1997, 1998a, 1998b; Lang, Greenwald, Bradley, & Hamm, 1993). More sophisticated studies that utilize eye-tracking find that individuals are more likely to look at unpleasant and pleasant compared to emotionally neutral images, measured in terms of initial and subsequent eye fixations (Calvo & Lang, 2004; Nummenmaa, Hyona, & Calvo, 2006)—even when instructed to only look at neutral images (Nummenmaa et al., 2006). Consistent with these data, individuals are faster to detect emotional stimuli among non-emotional distracters than vice-versa (Ohman, Flykt, & Esteves, 2001). Additionally, emotional com-
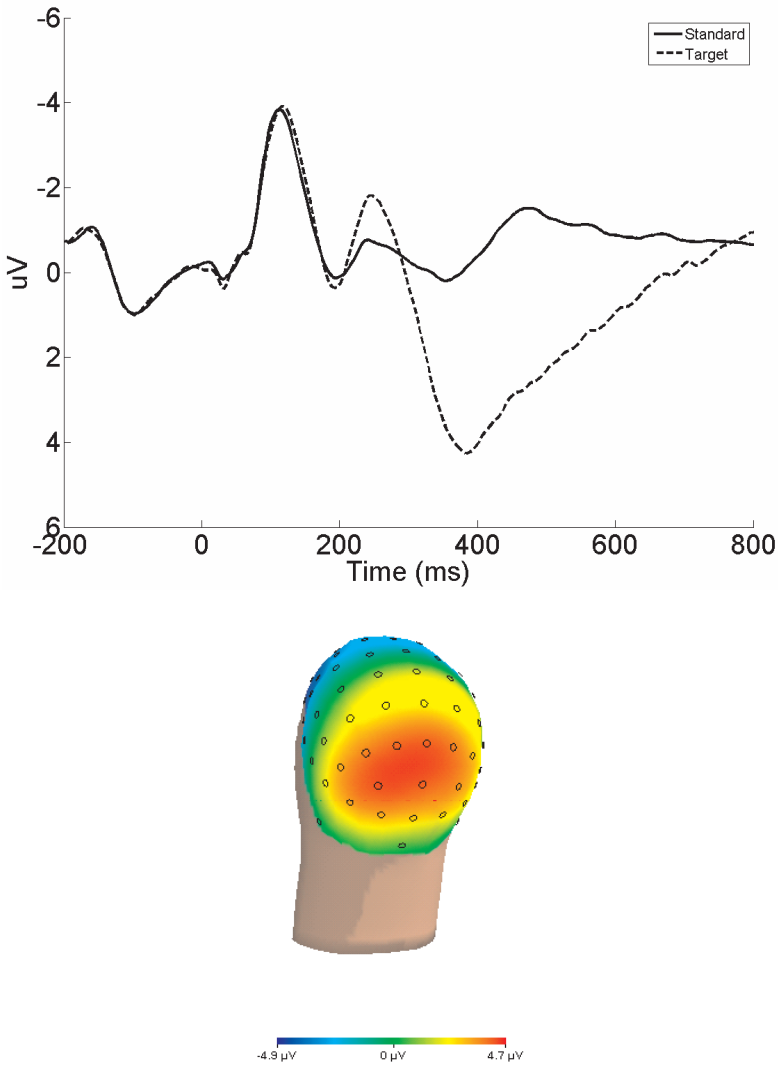
FIGURE 1   P300 component in response to a target and a non-target auditory tone at superior/posterior sites (top panel). Please note that negative is plotted upward. Scalp distribution of the difference between target and standard stimuli in the 300–600 msec post-stimulus period (bottom panel). Figure available in color online.

pared to non-emotional stimuli are less likely to be missed during target detection tasks (Anderson & Phelps, 2001; Vuilleumier & Schwartz, 2001).

The fact that emotional stimuli seem to automatically capture attention may depend on the relatively early detection of emotional compared to neutral information. Indeed, a number of ERP components that peak within 200–300 msec following stimulus onset have been shown to be larger following emotional compared to neutral visual stimuli (Carretie, Hinojosa, Martin-

Loeches, Mercado, & Tapia, 2004; Schupp, Junghöfer, Weike, & Hamm, 2003b, 2004; Schupp, Cuthbert et al., 2004; Schupp, Ohman et al., 2004).[1] The notion that emotion directs attention, and thereby facilitates subsequent processing, has been described as "motivated attention" (Bradley et al., 2003; Lang et al., 1997; Sabatinelli et al., 2005). In the language of the P300, emotional stimuli might be automatically processed as task-relevant, and because of their intrinsic motivational significance, emotional stimuli might be considered *natural targets.*

Consistent with this notion, a number of early studies reported an increased P300 in the 300–500 msec post-stimulus period following the presentation of emotional compared to neutral pictures (Johnston et al., 1986; Lifshitz, 1966; Mini et al., 1996; Radilová, 1982). These effects were observed for both pleasant (Lifshitz, 1966; Mini et al., 1996; Palomba, Angrilli, & Mini, 1997) and unpleasant (Lifshitz, 1966; Mini et al.,1996; Palomba et al., 1997; Radilová, 1982) pictures, suggesting that the emotional modulation of the P300 was independent of whether stimuli were aversive or appetitive. Similar results were reported for emotional adjectives (Naumann, Bartussek, Diedrich, & Laufer, 1992). Thus, although most theorizing about the P300 has focused on top-down manipulations of attention, even early data suggested that intrinsic motivational properties of visual stimuli can modulate the P300. Indeed, Johnston et al. (1986) interpreted both cognitive- and affective-related modulations of the P300 in terms of changes in the emotional value of stimuli.

Although most of the early studies reporting increased positivities following the presentation of emotional stimuli described the effects as modulating the P300, some authors also noted increased positivities extending beyond the traditional P300 (Johnston et al., 1986; Lang et al., 1997; Palomba et al., 1997). More recent work in emotion has focused on both the P300 and what has been referred to as the late positive potential (LPP).[2] The LPP is a midline ERP that becomes evident approximately 300 msec following stimulus onset, and is larger following the presentation of both pleasant and unpleasant compared to neutral pictures and words (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Dillon, Cooper, Grent-'t-Jong, Woldorff, & LaBar, 2006; Foti & Hajcak, 2008; Hajcak, Dunning, & Foti, 2007; Hajcak, Moser, & Simons, 2006; Hajcak & Nieuwenhuis, 2006; Hajcak & Olvet, 2008; Moser, Hajcak, Bukay, & Simons, 2006; Schupp et al., 2000; Schupp, Cuthbert et al., 2004; Schupp, Ohman et al., 2004; Schupp, Junghöfer, Weike, & Hamm, 2003a). Similar results have been obtained using threatening faces (Schupp, Ohman et al., 2004; Williams et al., 2007; Williams, Palmer, Liddell, Song, & Gordon, 2006) and facial expressions of other emotions (Eimer & Holmes, 2007; Eimer, Holmes, & McGlone, 2003). Figure 2 presents ERP data at posterior-superior recording sites (CP1/2, CP3/4, P1/2, P3/4, and PO3/4) from a recent study in which participants were shown pleasant, unpleasant and neutral pictures for 2,000 msec.[3] The LPP is evident as a rather sustained positive deflection in the stimulus-locked ERP following the presentation of pleasant and unpleasant compared to neutral images (Figure 2). The scalp distribution of the pleasant minus neutral and unpleasant minus neutral difference is depicted in Figure 3, from 400–800 (top), 800–1,400 (middle), and 1,400–2,000 msec (bottom) following picture onset. The LPP is evident as a broad superior-posterior positivity during the presentation of emotional pictures.

The increased LPP for emotional compared to neutral pictures has been shown to be larger for more intense stimuli (i.e., those rated as more arousing and prompting the largest skin conductance changes; Cuthbert et al., 2000), and is larger for highly arousing pleasant and unpleasant stimuli, such as erotica and threat scenes, respectively (Schupp, Junghöfer et al., 2004; Schupp, Ohman et al., 2004; Schupp, Cuthbert et al., 2004). Moreover, emotional effects of the LPP have been shown to be independent of stimulus size (De Cesarei & Codispoti, 2006) and perceptual characteristics of the stimuli (Bradley, Hamby, Low, & Lang, 2007).
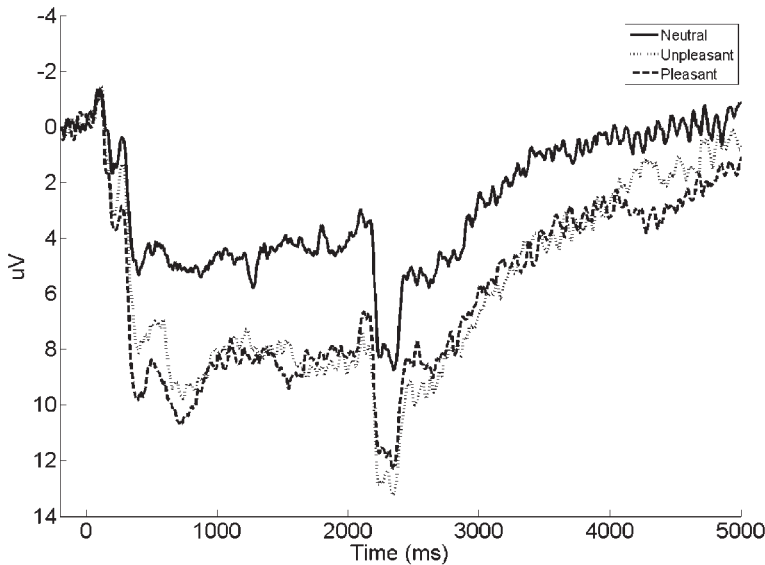
FIGURE 2   Event-related potentials following the presentation of pleasant, neutral, and unpleasant pictures at posterior/superior recording sites. Please note that negative is plotted upward; picture onset and offset occurred at 0 and 2,000 msec, respectively.

In addition, the increased LPP observed for emotional compared to neutral stimuli does not appear to habituate over repeated presentations of stimuli (Codispoti, Ferrari, & Bradley, 2006, 2007; Olofsson & Polich, 2007)—whereas many other measures that are sensitive to emotional compared to neutral stimuli, including skin conductance, heart rate, facial electromyography (EMG), and amygdala activation measured using fMRI, habituate (Breiter et al., 1996; Codispoti & De Cesarei, 2007; Codispoti et al., 2006, 2007). Unlike amygdala activation, which has been reported following the presentation of masked emotional faces (Whalen et al., 1998), the available data suggests that the LPP requires conscious recognition: although we are not aware of ERP studies that have examined masked presentations of IAPS images, masked presentations of facial expressions of emotion appear not to elicit an increased LPP (Williams et al., 2007). Finally, it is worth noting that the LPP appears relatively stable over time within individuals (Codispoti et al., 2006). Collectively, these data indicate that emotional influences on the LPP relate to the emotional intensity of stimuli, consistent with the notion that this effect is being driven by motivational salience; these effects do not, however, simply reflect stimulus novelty, low-level perceptual differences, or violations of expectation.

It is important to note that the increased positivity following emotional compared to neutral pictures extends well-beyond 1,000 msec (cf. Figures 2 and 4). In fact, an increased LPP is evident in some studies for the entirety of emotional picture presentation (Cuthbert et al., 2000; Foti & Hajcak, 2008; Hajcak et al., 2007; Hajcak & Nieuwenhuis, 2006; Hajcak & Olvet, 2008; Lang et al., 1997) and even in the period following picture offset (Hajcak & Olvet, 2008). Thus, emotional modulation of the LPP can extend for seconds. Much as the P300 has been interpreted in terms of a phasic increase in attention to task-relevant stimuli, the LPP appears to track the sustained increase in attention toward, and processing of, intrinsically motivating stimuli. This sustained pro-

Pleasant – Neutral	Unpleasant – Neutral

-0.5 µV 4.5 µV -0.5 µV 4.5 µV

Picture On (400-800 ms)

Picture On (800-1,400 ms)
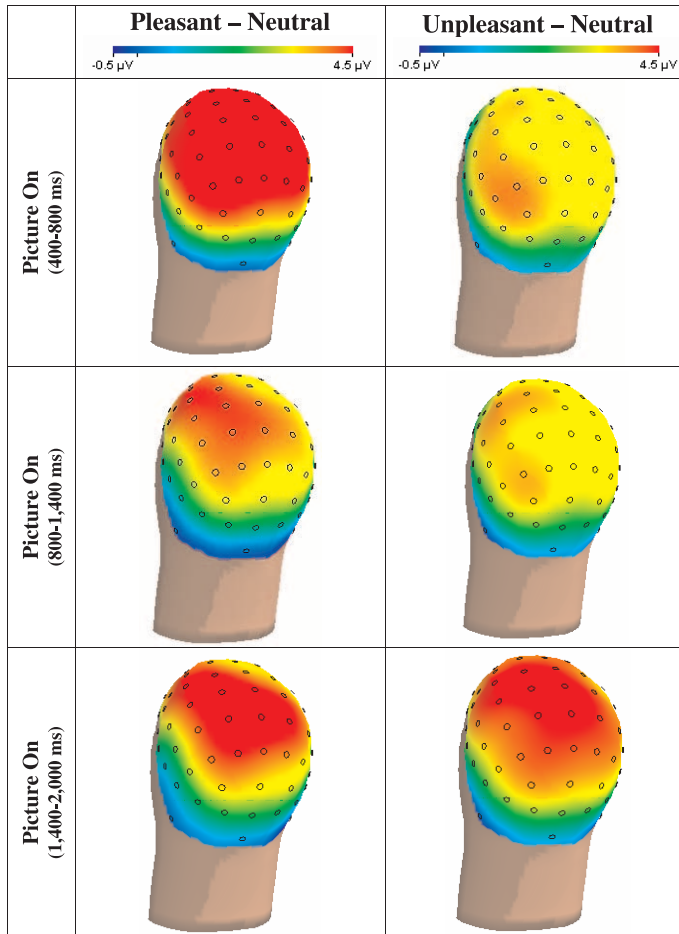
Picture On (1,400-2,000 ms)

FIGURE 3   Scalp distribution of the late positive potential to the pleasant minus neutral (left panel) and unpleasant minus neutral (right panel) difference during picture presentation from 400–800 (top), 800–1,400 (middle), and 1,400–2,000 msec (bottom) following picture presentation. Figure available in color online.

cessing has been linked to memory encoding and storage (Dolcos & Cabeza, 2002); a recent study by Koenig and Mecklinger (2008) found that although both pleasant and unpleasant pictures modulated posterior positivity in the 250–450 msec range, only later modulation of positive amplitudes predicted better memory for pictures.

Differentiating experimental effects on the P300 versus the LPP can be problematic, especially in the 300 to 1,000 msec time range. Complicating matters further is the fact that the P300 and LPP are quantified in different windows across studies: the P300 has been scored as the average activity between 300–400 msec, 400–480 msec (Keil et al., 2002), and 400–600 msec (Schupp et al., 2007); on the other hand, the LPP has been scored as the average activity 300–600 msec (Codispoti, et al., 2007), 350–600 msec (Moser et al., 2006), 416–456 msec (Schupp et al., 2003b), 350–750 msec (Schupp et al., 2000), 400–500 msec (Schupp, Ohman et al., 2004),
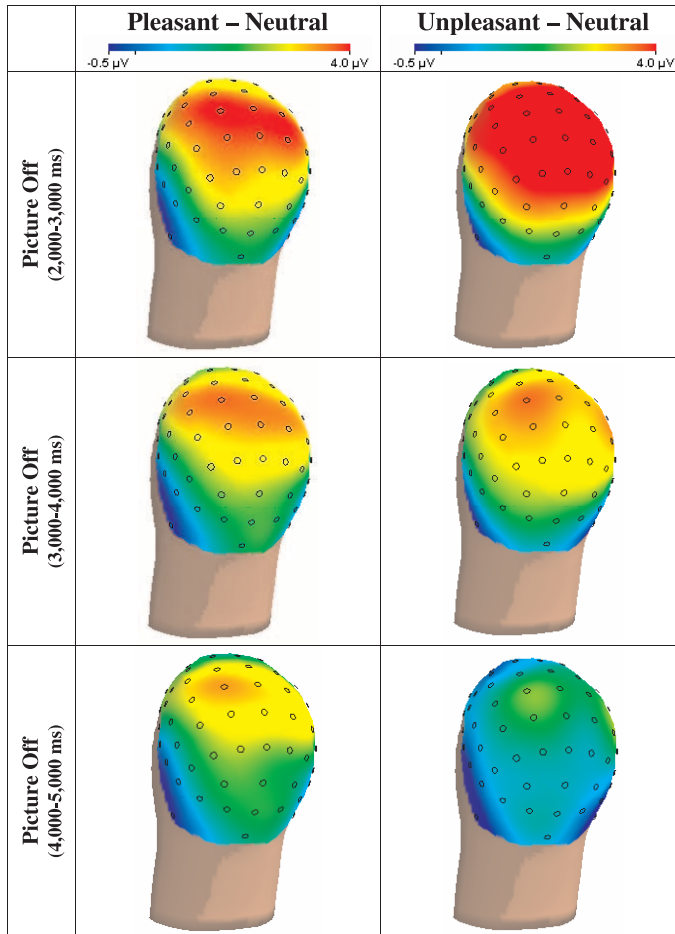
FIGURE 4   Scalp distribution of the late positive potential for pleasant (left panel) and unpleasant (right panel) pictures after picture offset; pictures were presented for 2,000 msec and the scalp distribution reflects the average activity between 2,000–3,000 (top), 3,000–4,000 (middle), and 4,000–5,000 msec (bottom) after picture onset. Figure available in color online.

500–650 msec (Hajcak et al., 2006), and 400–1,000 msec (Foti & Hajcak, 2008; Schupp, Cuthbert et al., 2004) following stimulus presentation. In fact, both area and peak measures of ERP components can be insensitive to component overlap and render it difficult to identify components that share temporal and spatial characteristics (Donchin & Heffley, 1979). However, the longer duration of the LPP suggests at least some distinction from the classic P300.

In terms of differentiating the P300 and LPP, a recent study from our group that employed temporospatial principle components analysis (PCA) found that emotional modulation of the P300 is evident predominantly at occipital-parietal sites around 350 msec following picture onset, whereas emotional modulation of the LPP appears evident at occipital to central recording sites with peaks about 850 and 1,600 msec following picture presentation; thus, the sustained positivity

observed following the presentation of emotional compared to neutral stimuli in the ERP likely reflects increases in multiple midline positivities—including the P300 and later-peaking positivities such as the LPP (Foti, Hajcak, & Dien, 2009). Our own suggestion is that researchers evaluate the P300/LPP in multiple windows following stimulus presentation, and at least examine more frontal/central activity later in the recording epoch. For the duration of the article, we use LPP coarsely to mean the sustained positive complex beginning in, and extending well-beyond, the time-range of the P300.

Neurobiological Correlates of the LPP

A recent study that combined ERP and fMRI methods indicated that the magnitude of the LPP elicited by emotional stimuli corresponded to increased blood flow in occipital, parietal, and inferotemporal regions in the brain (Sabatinelli, Lang, Keil, & Bradley, 2007). Consistent with these data, a study by Keil and colleagues estimated the source of the LPP in the occipital and posterior parietal cortex (Keil et al., 2002). In fact, functional neuroimaging studies have consistently reported increased activation of visual cortex following emotional compared to neutral images (Bradley et al., 2003; Breiter et al., 1996; Lane, Chua, & Dolan, 1999; Lane et al., 1997; Lang et al., 1998; Sabatinelli, Flaisch, Bradley, Fitzsimmons, & Lang, 2004).

The amygdala is also reliably implicated in processing emotional visual stimuli (Breiter et al., 1996; Phillips, Drevets, Rauch, & Lane, 2003; Sabatinelli et al., 2005; Whalen et al., 1998), projects to the occipital cortex (Amaral & Price, 1984; Freese & Amaral, 2005, 2006), and likely plays a role in biasing visual information so that emotionally significant information is preferentially processed (Bradley et al., 2003; Lane et al., 1999; Lane et al., 1997). In fact, it has been suggested that increased occipital activation may result from projections from the amygdala (Bradley et al., 2003). Although it is unlikely that the LPP would index activity of a structure shaped like the amygdala, it stands to reason that the LPP may index downstream processes resulting from increased activation of the amygdala.

To our knowledge, no studies to date have explicitly linked the LPP to the activity of specific neurotransmitter systems. However, Nieuwenhuis and colleagues have recently mounted a persuasive argument that the *P300* is an ERP manifestation of a phasic norepinepherine (NE) response to task-relevant stimuli (Nieuwenhuis et al., 2005). Insofar as the P300 and LPP may reflect the same neuromodulatory activity, it is an interesting—and testable—hypothesis that the LPP is also generated via the locus coeruleus (LC)–NE system in response to emotional stimuli. Although it is difficult to image small brainstem structures such as the LC, subliminal presentation of threatening stimuli have been shown to activate the LC using fMRI (Liddell et al., 2005), and consistent data has been reported in non-human animal research (Aston-Jones, Rajkowski, Kubiak, Valentino, & Shipley, 1996). Liddell and colleagues suggest that LC activation may be responsible for heightened attention and orienting toward emotional stimuli, and that the LC could receive input from initial emotional evaluation performed by the amygdala (Liddell et al., 2005).

Consistent with this possibility, intracranial ERP data suggest that the amygdala becomes active within 200 msec following the presentation of threatening stimuli; interestingly, in one study, threatening stimuli prompted a later, but sustained, effect from about 300 to 1,300 msec in occipito-temporal, anterior temporal, and orbitofrontal regions (Krolak-Salmon, Henaff, Vighetto, Bertrand, & Mauguiere, 2004). These intracranial recordings are consistent with the no-

tion that amygdala activation modulates visual processing (Morris et al., 1998; Pessoa, Kastner, & Ungerleider, 2002). Although the suggestion awaits validation, the LPP may reflect the activity of a brainstem-based alerting system that innervates large sections of the cortex via NE following the presentation of motivationally-salient stimuli.

Individual Differences in the LPP

Insofar as the LPP appears to index the facilitated processing of emotional compared to neutral information, certain types of stimuli ought to elicit larger responses based on individual differences. For instance, snakes and spiders appear to be detected relatively automatically among neutral distracters; moreover, individuals with phobias of these animals demonstrate a further attentional bias (Ohman et al., 2001). Consistent with these data, two studies to date have reported increased LPP amplitudes to pictures of spiders among spider phobic individuals (Kolassa, Musial, Mohr, Trippe, & Miltner, 2005; Miltner et al., 2005).

In addition to pictures of feared stimuli, pictures of desired objects also appear to elicit an increased LPP. Several studies on addiction have examined the LPP in response to drug cues. For instance, Franken and colleagues have reported that compared to control participants, abstinent cocaine-dependent participants demonstrate increased LPPs in response to cocaine pictures—and that increased LPPs predict cocaine craving (Franken et al., 2008; Franken, Hulstijn, Stam, Hendriks, & van den Brink, 2004; Franken, Stam, Hendriks, & van den Brink, 2003). We have recently reported similar LPP results in response to cocaine *cues* (Dunning et al., 2008). Collectively, these results suggest that individual differences in preference for stimuli relate to variation in the LPP: picture content that elicits intense desire or aversion based on individual differences elicits relatively large LPPs.

Although less studied in children than adults, the LPP has been used to track children's response to emotional facial stimuli; in fact, children as young as 7 months old show larger LPPs to fearful as compared to neutral faces (Leppanen, Moulson, Vogel-Farley, & Nelson, 2007). In recent work from our laboratory, we found increased LPPs in 18 children 5 to 8 years of age following the presentation of developmentally appropriate IAPS images (Hajcak & Dennis, 2009).

Positive-going amplitudes in the time range of the LPP may serve as markers of childhood traumatic experience. In a recent study by Shackman and colleagues (2007), abused children showed larger positive-going ERPs in the time range of the LPP when observing expressions of anger on their mothers' faces than did control children; skin conductance responses were also elevated among abused children and correlated with electrocortical response. In fact, amplitudes to angry faces accounted for 40% of the relationship between abuse and symptoms of anxiety (Shackman, Shackman, & Pollak, 2007). These results replicated past work showing that abused children exhibit larger LPPs to task-relevant angry (but not fearful or happy) facial stimuli (Pollak, Klorman, Thatcher, & Cicchetti, 2001). The LPP may also serve as a marker of attachment styles later in life. Compared to adults scoring low on attachment anxiety, adults characterized by anxious attachment styles had larger LPPs in response to unpleasant pictures, suggesting that attachment tendencies formed in childhood may relate to later emotional reactivity as indexed by the LPP (Zilber, Goldstein, & Mikulincer, 2007).

In addition to developmental work in children, there is increasing focus on the cognitive and affective neuroscience of aging which examines cognitive and neural changes that take place during later years (Hedden & Gabrieli, 2004; Mather et al., 2004; Mather & Carstensen, 2005). The

first evidence of age-related effects on the P300 dates back three decades (Goodin, Squires, Henderson, & Starr, 1978). Indeed more recent work confirmed initial reports that increases in age are associated with prolonged P300 latency and reductions in amplitude (Pfefferbaum, Ford, Roth, & Kopell, 1980; Pfefferbaum, Ford, Wenegrat, Roth, & Kopell, 1984; Picton, Stuss, Champagne, & Nelson, 1984; Walhovd, Rosquist, & Fjell, 2008). These changes are thought to reflect a slowing of cognitive processes and reduced availability of resources, respectively. Although there is a paucity of research on age-related changes and LPP responses to *emotional* stimuli specifically, a recent study found that the LPP to unpleasant images was reduced as a function of age, whereas the LPP to neutral and pleasant images was relatively invariant with respect to age (Kisley, Wood, & Burrows, 2007). These data are supported by a growing body of research indicating that aging is accompanied by a relative reduction in attention toward, and reactivity to, unpleasant stimuli (Mather et al., 2004; Mather & Carstensen, 2005)—and that the LPP might be a useful measure for assessing age-related changes in emotional processing.

In addition to individual difference variables and age-related changes in emotional processing, there is growing focus on how variation in candidate gene polymorphisms may relate to abnormal emotional processing (Canli, Omura et al., 2005; Hariri, Drabant, & Weinberger, 2006; Hariri, Goldberg et al., 2003; Hariri & Holmes, 2006; Hariri, Mattay, Tessitore, Fera, & Weinberger, 2003). The serotonin transporter (5-HTT) in particular has been extensively studied in the emotion literature. The 5-HTT protein is encoded by a gene (SLC6A4) that is located on chromosome 17. A linked polymorphic region (5-HTTLPR) in the promoter region has been identified, which includes a repetitive sequence that is expressed as either a short (s) or long (l) version of the gene. The 5-HTTLPR was initially shown to affect 5-HTT availability, with the s and l allele resulting in decreased and increased expression of 5-HT, respectively (Heinz et al., 2000), however, more recent studies suggest a much more complex relationship (Parsey et al., 2006; Praschak-Rieder et al., 2007; Reimold et al., 2007; Shioe et al., 2003).

Neuroimaging studies have shown that individuals carrying the 5-HTTLPR s allele have greater amygdala activity while processing unpleasant stimuli (Bertolino et al., 2005; Brown & Hariri, 2006; Hariri et al., 2005; Hariri et al., 2006). Canli and colleagues recently documented that greater reactivity to unpleasant compared to neutral stimuli among s allele carriers can be explained by *reduced* reactivity to neutral stimuli. (Canli, Omura et al., 2005). In addition, carriers of the s allele appear to have a dysfunctional coupling between the amygdala and prefrontal structures, such as the subgenual anterior cingulate cortex (Pezawas et al., 2005) and the ventromedial prefrontal cortex (Heinz et al., 2005). Therefore, individuals with the s allele may be characterized by altered emotional reactivity, abnormal brain circuitry supporting emotion regulation, or a combination of both that may serve as a risk factor for developing psychiatric disorders.

Another serotonergic polymorphism has been identified in the tryptophan hydroxylase 2 (TPH2) gene located in a transcriptional control region. TPH2 is a single nucleotide polymorphism (SNP) that results in a G to T switch (G-703T). Tryptophan hydroxylase (TH) is the rate-limiting enzyme of serotonin synthesis (Walther & Bader, 2003), therefore increased levels of TH would result in increased serotonin production and vice-versa. There has only been one study that has looked at the functional significance of this polymorphism in raphe nuclei cell cultures; however, that study did not find a relationship between the G-703T polymorphism and TH expression in the raphe (Scheuch et al., 2007). There have been no studies to date that have looked at the functional significance of this polymorphism in vivo; however, preliminary studies have shown that carriers of the T allele have increased amygdala activa-

tion in response to emotional stimuli (Brown et al., 2005; Canli, Congdon, Gutknecht, Constable, & Lesch, 2005).

There has only been one study that has examined the relationship between genetic polymorphisms and the LPP (Herrmann et al., 2007). Both the 5-HTTLPR and the TPH2 polymorphisms were assessed for their relationship to the early portion of the LPP and the early posterior negativity (EPN), which is an earlier ERP component related to increased emotional processing (Schupp, Junghöfer et al., 2003a, 2003b, 2004; Schupp, Ohman et al., 2004; Schupp et al., 2007). Although there was a significant finding in relation to the EPN (carriers of the s and T alleles had an increased EPN), these polymorphisms were not significantly related to the early portion of the LPP. Although research on imaging genetics has flourished, there is a relative paucity of work examining effects of genetic polymorphisms on ERP indices of emotional processing such as the LPP. It will be important for future studies to determine whether polymorphisms that relate to activity of other neurotransmitter systems, such as the NE system, may relate to variation in the LPP.

REGULATING EMOTION: CONCEPTUAL FRAMEWORK AND NEUROPHYSIOLOGICAL MEASURES

We acknowledge at the outset that there are many important ways emotion regulation can be conceptualized. For instance, Cole, Martin, and Dennis (2004) point out that emotion influences, and therefore *regulates,* a number of cognitive functions (e.g., memory)—and this impact of emotion on cognitive processes could rightly be called emotion regulation. In the present article, we focus on processes that influence when and how emotions are experienced (Gross, 1998; Gross & Thompson, 2007). This conception of emotion regulation is consistent with Thompson's (1994) definition of the term: "the extrinsic and intrinsic processes responsible for monitoring, evaluating, and modifying emotional reactions, especially their intensity and temporal features…" (pp. 27–28).

Gross and colleagues have conducted extensive research comparing the effectiveness and consequences of various emotion regulation strategies, and have formulated a process model of emotion regulation that has guided many recent studies. The most general distinction in Gross' model (1998, 2002) is between strategies that alter emotional responses before they are activated (i.e., antecedent-focused strategies) versus strategies that alter the actual *expression* of an emotional response, once initiated (i.e., response-focused strategies such as expressive suppression). Expressive suppression refers to inhibiting the behavioral expression of an emotional response. For instance, someone might suppress all fearful responses at a horror film in order to appear unafraid. On the other hand, antecedent-focused strategies refer to the ways in which the emotional impact of a stimulus might be mitigated. Reappraisal, for instance, is rooted in the work of Lazarus, who demonstrated that an emotional response is determined by the way a stimulus is interpreted (Lazarus, 1991). In this way, then, reappraisal involves consciously altering the meaning of an emotion-eliciting stimulus, for example, thinking about the fact that the bloody corpse in a horror movie is not real, and that the character is just an actor.

A growing body of research by Gross and colleagues suggests that response-focused strategies are not particularly effective (Gross & Levenson, 1997), are associated with physiological and cognitive costs (Gross, 1998, 2002; Gross & Levenson, 1997; Richards & Gross, 2000), and relate

negatively to measures of well-being and experiences of positive emotion (Gross & John, 2003). Cognitive forms of emotion regulation such as reappraisal, on the other hand, have been shown to decrease the intensity of self-reported negative affective experience (Gross, 2002; Hajcak & Nieuwenhuis, 2006; Ochsner, Bunge, Gross, & Gabrieli, 2002), but do not appear to cause increases in sympathetic nervous system activity (Gross, 1998) or negatively impact memory in the way that expressive suppression does (Richards & Gross, 2000).

Recent neuroimaging research has begun to shed light on the neural correlates of cognitive strategies of emotion regulation (cf. Ochsner & Gross, 2005). For example, reappraising unpleasant stimuli has been associated with increased activation in areas of the lateral and medial prefrontal cortex thought to support cognitive control; reappraisal is also accompanied by decreased activation of the amygdala, suggesting decreased emotional reactivity (Beauregard, Levesque, & Bourgouin, 2001; Eippert et al., 2007; Levesque et al., 2003; Ochsner, et al., 2002; Ochsner et al., 2004; Phan et al., 2005; Urry et al., 2006). Other research has documented similar patterns of neural activity when examining how attentional focus and evaluation at encoding influence emotional processing, such as categorizing unpleasant stimuli on non-affective versus affective dimensions (Hariri et al., 2003; Keightley et al., 2003; Mathews, Yiend, & Lawrence, 2004). Thus, multiple cognitive emotion regulation strategies appear to rely on a similar network of neural activation indicating diminished emotional processing and increased cognitive control.

In fact, emotion regulation may operate in a similar manner to extinction following the pairing of a conditioned stimulus (CS) with an aversive unconditioned stimulus (US). To investigate this similarity, Delgado et al. (2004) used a paradigm in which participants learned to pair shock (US) with colored stimuli (CS). On "regulation" trials, participants were asked to imagine a soothing scene from nature that incorporated the color of the CS, whereas in "attend" trials, participants attended to their emotions and sensations as normal. Using an emotion regulation strategy lessened conditioning effects, reduced amygdala responses to the CS, and enhanced activation in the left lateral PFC. This pattern is similar to activations observed during extinction learning (Phelps, Delgado, Nearing, & LeDoux, 2004), suggesting that the top-down regulation of emotion may operate via the same mechanisms involved in associative learning (Phelps, 2006). Comparable results have recently been demonstrated using a CS paired with reward (Delgado, Gillis, & Phelps, 2008).

In a series of studies, we have examined the sensitivity of the LPP to a variety of emotion regulation instructions derived from Gross' (1998, 2002) process model of emotion regulation. In an initial study, the LPP was reduced when participants were asked to decrease the intensity of their emotional response to unpleasant images (Moser et al., 2006). Because this study involved voluntary emotion regulation, participants were free to employ any method they chose to reduce the intensity of their emotional response; therefore, the mechanisms underlying modulation of the LPP were somewhat unclear.

In a follow-up study, Hajcak and Nieuwenhuis (2006) employed more directive reappraisal instructions. On a trial-by-trial basis, participants were instructed to either reinterpret unpleasant images in a less negative way, or to view unpleasant images as they normally would. In this study, the LPP was reduced for the duration of a 2,000 msec picture presentation following reappraisal instructions, beginning 200 msec following stimulus onset; moreover, participants reported less intense emotional responses following reappraisal, and the reduction in the LPP correlated with reductions in self-reported emotional experience following reappraisal (Hajcak & Nieuwenhuis, 2006).

Hajcak and Nieuwenhuis (2006) interpreted reappraisal-related reductions in the LPP as reflecting changes in stimulus meaning. However, reappraisal-related changes in the LPP might be attributable to other task-related differences (e.g., attentional focus, cognitive load). To more directly assess the role of stimulus meaning on the elicited LPP, Foti and Hajcak (2008) provided participants with descriptions of images prior to viewing them. That is, unpleasant pictures were either described in more negative (e.g., "Two people died in this horrendous car crash") or more neutral terms (e.g., "No one was seriously injured in this car accident") before they were viewed by participants. Results indicated that the LPP was smaller for neutrally described as compared to negatively described unpleasant pictures; 1,000 msec following picture presentation, the LPP following neutrally described unpleasant pictures did not differ from neutral pictures. This finding further suggests that meaning change is indeed capable of modifying LPP response to affective images.

MacNamara, Foti, and Hajcak (2009) also examined the effect of meaning change on the LPP, but by fully crossing picture and description type (i.e., by including both unpleasant and neutral pictures preceded by both neutral and negative descriptions), directly compared extrinsic (i.e., description type) and intrinsic (i.e., picture type) manipulations of emotional significance. Further, MacNamara et al. (2009) used temporospatial PCA, and reported components corresponding to the P300 (peaking at 334 msec), and the early and the late LPP (peaking at 1,066 msec and 1,688 msec, respectively). Analysis of these factors indicated that intrinsic and extrinsic effects contributed independently and additively to the P300 and the early LPP—and that extrinsic effects were solely responsible for modulation of the late LPP. In sum, these results suggest that early components corresponding to the P300 and the early LPP may be more sensitive to intrinsic factors related to emotional significance, while the later LPP may reflect deeper processing related to ongoing evaluations of stimulus meaning (cf. Schupp, Flaisch, Stockburger, & Junghöfer, 2006).

The MacNamara et al. (2009) study further suggests that reappraisal-related changes cannot be attributed to cognitive load: if modulation of the LPP is a result of the *effort* involved in reinterpreting an image, then amplitudes to neutral pictures preceded by negative descriptions should also have been decreased, as this combination should have required more effort to process than neutral pictures preceded by neutral descriptions. However, negative descriptions selectively *increased* the LPP, while neutral descriptions selectively *decreased* the LPP, regardless of picture type. Finally, these results also suggested that it is possible to *up-regulate* the LPP—in other words, that it is possible to increase the LPP elicited by *neutral* pictures. Previous studies had failed to report up-regulation effects, however, these studies used pleasant and unpleasant pictures in the regulation conditions, suggesting that a "ceiling effect" may have prevented further increases in response (Krompinger, Moser, & Simons, 2008; Moser, et al., 2006).

In addition to varying the meaning of stimuli, it is possible to vary their *relative importance* by manipulating the task-relevance of emotional versus neutral stimuli.[4] By asking participants to count pleasant, unpleasant, or neutral pictures, Schupp and colleagues (2007) created a target-like effect for each type of stimuli across experimental blocks. In this study, both task relevance and the effect of emotion increased positive amplitudes in the time range of the early LPP; however, these effects also *interacted* such that the amplitudes evoked by emotional as compared to neutral pictures were larger for task-relevant stimuli (Schupp et al., 2007). These results suggest that top-down manipulations of attention such as task relevance operate in conjunction with the more bottom-up effects of emotional salience as the significance of stimuli are evaluated.

The LPP also appears sensitive to *how* emotional stimuli are attended to and appraised: Hajcak et al. (2006) had participants make emotional or non-emotional decisions about pleasant and unpleasant images; the LPP elicited by emotional pictures was smaller in the non-emotional than emotional decision condition. Moreover, this pattern of results did not reflect task-difficulty as indicated by reaction times (Hajcak et al., 2006). These results are consistent with past research: for example, when participants were required to attend to facial gender (by counting either male or female faces) or to attend to facial expression (by counting the number of surprised faces), emotional faces elicited increased P300s only in the "attend-emotion" condition (Krolak-Salmon, Fischer, Vighetto, & Mauguiere, 2001). Taken together, these results indicate that automatic attention elicited by affective stimuli can be reduced by attending to non-emotional aspects of emotional stimuli.

Another question is the extent to which spatial attention modulates the electrocortical response to emotional stimuli. For example, Keil and colleagues asked participants to count dots that appeared intermittently under a flickering image on one side of the screen, while ignoring a picture on the other side. Results revealed that spatial attention and emotional modulation operated additively to influence electrocortical response (Keil, Moratti, Sabatinelli, Bradley, & Lang, 2005). However, *non-attended* emotional stimuli in this study also increased amplitudes in the left hemisphere, suggesting that spatial attention may amplify, but is not necessary for eliciting increased electrocortical response, at least in the left hemisphere. In contrast to these results, two studies (Eimer et al., 2003; Holmes, Vuilleumier & Eimer, 2003) found that emotional faces elicited larger electrocortical positivities than neutral faces only when faces occurred in spatially attended locations. Though the reasons for these inconsistent results are not immediately clear, one possibility is that differences in task difficulty may determine whether or not spatial attention modulates response to emotional stimuli (i.e., a more difficult task may leave less resources available for processing stimuli outside of spatial awareness).

As a means of emotion *regulation*, spatial attention can also function to decrease emotional response. For instance, van Reekum and colleagues (2007) measured patterns of gaze fixation and found that when instructed to decrease emotions to an unpleasant image, participants frequently looked at irrelevant or non-emotional areas of the picture; furthermore, gaze changes accounted for a significant amount of variance in brain areas responsive to the regulation task as measured by fMRI activity (van Reekum et al., 2007). Dunning and Hajcak (2009) similarly found that when participants had their gaze directed to a less emotional part of an unpleasant picture, the LPP was reduced compared to when participants viewed the same picture while their gaze was directed to a more emotional portion of the picture. These results suggest that spatial manipulations of attention can function effectively to regulate emotional response.

Although *reappraisal* may not affect the LPP via mechanisms of cognitive load, it is possible that under different circumstances, with sufficient cognitive load, emotional stimuli might fail to elicit increased attention because of a lack of available resources. To examine the role of concurrent task difficulty on the LPP, Hajcak, Dunning, and Foti (2007) recorded ERPs while individuals viewed pleasant, neutral, and unpleasant IAPS images under three conditions: no concurrent task, an easy concurrent task, or a difficult concurrent task. In the easy and difficult concurrent tasks, participants had to perform either relatively simple or more difficult mental mathematics, respectively. The LPP difference between emotional and neutral images was nearly identical across all three conditions—there was no indication that concurrent task difficulty itself reduces the emotional modulation of the LPP (Hajcak et al., 2007).

In sum, the LPP reflects an early electrocortical response to emotional stimuli that indexes stimulus salience and is sensitive to both relatively automatic (Hajcak et al., 2006) and conscious emotion regulation strategies (Hajcak & Nieuwenhuis, 2006; Moser et al., 2006); the LPP is sensitive both to the type of picture presented, but also to the affective context in which pictures are delivered (Foti & Hajcak, 2008; MacNamara et al., 2009), as well as where attention is directed within a given picture (Dunning & Hajcak, 2009). Indeed, these studies have found relatively large effects on the amplitude of the LPP: Table 1 presents effect sizes (in Cohen's *d*) for various studies that have assessed the influence of emotion regulation instructions on the LPP; as a point of comparison, effect sizes for emotional versus neutral pictures on the LPP during passive viewing are also presented, when applicable. Compared to the effect of emotion regulation instructions, passively viewing emotional pictures is associated with relatively greater effect sizes (cf. MacNamara et al., 2009). However, the effect sizes in the emotion regulation conditions tend to be quite large. Relative to other emotion regulation strategies, a comparison of effect sizes suggests that attentional manipulations are associated with the largest effects on the LPP.

Time-Course of the LPP: An Alternative Index of Emotion Regulation

As described earlier, studies typically find that the LPP is sustained for the duration of picture presentation (Cuthbert et al., 2000; Foti & Hajcak, 2008; Hajcak et al., 2007; Hajcak & Nieuwenhuis, 2006); moreover, there is evidence that the LPP indexes the continued processing of emotional stimuli following stimulus offset. For instance, Schupp and colleagues presented visual stimuli for 120 to 333 msec and found an increased LPP up to 300 msec after picture offset (Schupp et al., 2004a; Schupp et al., 2007). In a more recent study, the LPP was larger following pleasant and unpleasant pictures for 800 and 1,000 msec, respectively, after picture-offset, when visual stimuli were presented for 2,000 msec (Hajcak & Olvet, 2008). Therefore, initial evidence suggests that the LPP indexes a fairly sustained increase in neural activity following the presentation of emotional stimuli.

All of the studies described earlier that have examined the effects of emotion regulation on the LPP have quantified differences in terms of the *magnitude* of the LPP. However, the LPP lends itself toward other ways of measurement. Rothbart and Derryberry (1981) delineated several characteristics of emotional reactivity, which were later described by Davidson (1998) as metrics for quantifying *affective chronometry*. For instance, some emotional responses might reach their maximum very rapidly, whereas other responses may take a longer time to develop; Davidson refers to this metric as *rise time to peak*. Similarly, the time it takes to return from maximum response to baseline, *recovery time*, is another metric that can be used to characterize the time-course of emotional reactivity. Davidson also highlights *duration of response* as an additional aspect of affective chronometry—that is, the amount of time that responding stays above some threshold.

Along these lines, the duration of the LPP following picture offset could potentially be used to inform the characteristics of emotion regulation more generally. To examine whether the duration of the LPP could be extended based on experimental instructions, 22 undergraduate students (15 male, 7 female) viewed 40 pleasant, 40 unpleasant, and 40 neutral IAPS pictures for 2,000 msec; 3,000 msec following picture offset a tone occurred that was a cue to imagine the preceding picture as if it was still right in front of them (but without closing their eyes).[3] These data are presented in Figure 2. During picture presentation, the LPP at posterior/superior sites varied as a function of picture type ($F(2,42) = 24.18$, $p < .001$) and post-hoc paired-sample *t*-tests indicated

TABLE 1
Summary of LPP Studies That Employed Emotion Regulation Manipulations. Effect Sizes (Cohen's *d*) are Presented Both for the Effect of Emotion and for the Emotion Regulation Condition.

Paper	Manipulation	Emotion Regulation Strategy	Picture Type (* = target of regulation condition)	Viewing: Unpleasant	Viewing: Pleasant	Emotion Regulation
Dunning & Hajcak (2009)	Attention directed to more or less arousing aspects of unpleasant IAPS	Directed Attention	Unpleasant*, Neutral	Study 1: 1.60–1.82 Study 2: 1.30	N/A	Study 1: 1.68–1.87 Study 2: 2.65
Krompinger, Moser, & Simons (2008)	Increase, maintain, or decrease instructions	Cognitive Change	Pleasant*, Neutral	N/A	1.81	.95 (increase ns)
Foti & Hajcak (2008)	Negative or neutral descriptions precede unpleasant IAPS	Cognitive Change	Unpleasant*, Neutral	2.80–3.48	N/A	1.20 (posterior, early window)
Hajcak & Nieuwenhuis (2006)	Reappraisal instructions	Cognitive Change	Unpleasant*, Neutral	4.56	5.04	1.33
Hajcak, Moser, & Simons (2006)	Make affective or non-affective decisions about emotional stimuli	Appraisal	Unpleasant*, Pleasant*, Neutral	3.03	4.16	2.09
Moser, Hajcak, Bukay, & Simons (2006)	Increase, maintain, or suppress instructions	Cognitive Change	Unpleasant*, Neutral	2.96	N/A	.77 (increase ns)
Hajcak, Dunning, & Foti (2007)	No, easy, or difficult concurrent task	Distraction	Unpleasant*, Neutral*, Pleasant*	3.01	3.28	ns

IAPS = International Affective Picture System (Lang et al., 2005); N/A = not applicable; ns = not significant.

that the LPP was larger for pleasant and unpleasant compared to neutral pictures ($t(21) = 6.87$, $p < .001$ and $t(21) = 5.27$, $p < .05$, respectively); the LPP elicited by pleasant pictures did not differ from the LPP elicited by unpleasant pictures ($t(21) = .20$, $p > .84$). Consistent with previous work, the LPP was larger during the presentation of both pleasant and unpleasant emotional stimuli at posterior-superior sites.

In the picture offset period, we analyzed three 1,000 msec windows (Figure 4). In all three windows, the LPP continued to vary with picture type ($F(2,42) = 14.71$, $p < .001$, $F(2,42) = 6.91$, $p < .01$ and $F(2,42) = 3.46$, $p < .05$, respectively). Post-hoc paired sample t-tests confirmed that the LPP was larger for pleasant and unpleasant compared to neutral pictures in the early ($t(21) = 4.10$, $p < .01$ and $t(21) = 4.62$, $p < .001$, respectively) and middle ($t(21) = 3.08$, $p < .01$ and $t(21) = 3.30$, $p < .01$, respectively) windows. In the early and middle windows, the LPP elicited by pleasant and unpleasant pictures did not differ from one another ($t(21) = 1.49$, $p > .15$ and $t(21) = 61$, $p > .55$, respectively). By the late window, the LPP was larger for pleasant compared to neutral pictures ($t(21) = 2.61$, $p < .05$), however the LPP elicited by unpleasant pictures did not differ from neutral ($t(21) = 1.72$, $p > .10$) or pleasant ($t(21) = .70$, $p > .49$) pictures. In sum, the LPP was larger after picture offset following pleasant pictures for 3,000 msec and unpleasant pictures for 2,000 msec.

In a previous study in which participants were not instructed to imagine pictures, persistence of the LPP was only evident for a maximum of 1,000 msec following picture presentation (Hajcak & Olvet, 2008). Taken together, these data suggest that the *time-course* of the LPP elicited by emotional stimuli can be modulated by cognitive instructions. Along these lines then, future studies might further utilize the time-course of the LPP to index emotion regulation. For example, reappraisal instructions may not only reduce the size of the LPP, but they may also reduce the duration of the LPP. Duration of response to emotional stimuli might be particularly relevant in relation to psychiatric disorders such as depression (cf., Siegle, Steinhauer, Thase, Stenger, & Carter, 2002).

Other EEG/ERP Measures of Emotion and Emotion Regulation

In addition to examining the P300/LPP elicited by emotional compared to neutral stimuli, several laboratories have also measured the P300 to secondary stimuli while participants viewed IAPS images. Specifically, the P300 elicited by a task-irrelevant tone (the "probe P300") is attenuated while participants view emotional compared to neutral pictures (Bradley, Codispoti, & Lang, 2006; Cuthbert, Schupp, Bradley, McManis, & Lang, 1998; Schupp, Cuthbert, Bradley, Birbaumer, & Lang, 1997). This reduction in probe P300 amplitude has been interpreted as reflecting a reduced availability of attentional resources during emotional picture viewing. Insofar as it is a relatively easy addition to experimental designs, future studies might further examine how variation in probe P300 amplitude relates to the LPP as a function of emotion regulation instructions. For instance, probe P300 amplitude ought to be increased (reflecting greater availability of attentional resources) under conditions in which the LPP is reduced (e.g., while directing attention to non-emotional compared to emotional portions of unpleasant IAPS).

Although we have focused on the P300 and LPP, it is worth considering how future studies might further capitalize on EEG data during the type of emotional processing and regulation studies described earlier. In particular, relating the LPP and variation in the LPP as a function of emotion regulation instructions to frontal and parietal EEG power might be a fruitful direction for future research.

Frontal alpha (8–13 Hz) asymmetries have been used to index affective style and differences in emotionality (Allen, Urry, Hitt, & Coan, 2004; Coan & Allen, 2003, 2004; Davidson, 1998; Harmon-Jones, 2003, 2004; Harmon-Jones & Allen, 1998). In particular, greater right than left frontal activity (inversely related to alpha) is thought to be associated with an emotional and behavioral tendency to withdraw (e.g., experiencing fear, sadness, inhibition) while greater left than right frontal activity is believed to index approach-related motivation (e.g., as found in happiness, joy, anger, pleasure-seeking). A large literature has linked anger and the tendency to experience anger to increased activity of the left prefrontal cortex, indexed through alpha power (Harmon-Jones & Allen, 1997, 1998; Harmon-Jones & Sigelman, 2001; Harmon-Jones, Sigelman, Bohlig, & Harmon-Jones, 2003; Harmon-Jones, Vaughn-Scott, Mohr, Sigelman, & Harmon-Jones, 2004).

As a measure of affective style, resting frontal EEG asymmetries should be informative about emotionality, and it might be fruitful for future studies to relate resting EEG asymmetries to the LPP. Along similar lines, the LPP could be compared to "activation asymmetries"—that is, changes in frontal alpha during exposure to affective stimuli (Coan, Allen, & McKnight, 2006).

Although most work on individual differences has reported on alpha band activity, increased gamma band (30–50 Hz) activity has also been associated with emotional picture viewing (Keil et al., 2001). Future work might begin to explore the relationship between gamma activity and individual differences in emotional response and regulation. Indeed initial research has suggested that gamma response to emotional stimuli may relate to psychopathology—for example, affective pictures failed to elicit increased gamma activity in individuals with alexthymia as compared to controls (Matsumoto, Ichikawa, Kanayama, Ohira, & Iidaka, 2006).

SUMMARY

The LPP is evident as a positive-going sustained increase in the stimulus-locked ERP following emotional compared to neutral stimuli. We believe that the LPP reflects multiple and overlapping positivities beginning in the time range of the classic P300, and that these positivities reflect increased salience of stimuli. Indeed, the extent to which the LPP is increased for emotional stimuli relates to the subjective value/intensity of the stimuli—the degree to which stimuli prompt motivational activation. The magnitude of the LPP, however, is also sensitive to a variety of manipulations borrowed from the emotion regulation literature, highlighting the inextricable link between emotion and cognition, between bottom-up and top-down processes. The amplitude of the LPP is determined by: willful modulation of emotions, reappraisal instructions, preceding descriptions, the way in which stimuli are initially appraised, and manipulations of attention. Initial data further suggests that the time-course of the LPP (i.e., the duration of the LPP) might be an additional way to quantify emotional reactivity and regulation. The LPP stands as a viable neurophysiological measure for studying emotion and emotion regulation across the lifespan, and as a function of individual differences. The full potential of this measure, however, rests on its future application to studies that go beyond the basics of emotion response and regulation to inform our understanding of social, developmental, and individual differences—studies that are sure to capture our attention.

NOTES

1. Recent work suggests that variation in at least some of these earlier ERP components may be due to differences in the perceptual complexity of emotional compared to neutral stimuli (Bradley, Hamby, Low, & Lang, 2007).
2. Positive modulation of the ERP in this time range has also been described in terms of a slow wave (Keil et al., 2002) and the late positive complex (Naumann, Bartussek, Diedrich, & Laufer, 1992). Here, we intentionally do not refer to this as the slow wave, as earlier studies reported a slow wave that was not sensitive to emotional stimuli (Johnston, Miller, & Burleson, 1986).
3. The numbers of the IAPS pictures used were the following: pleasant (1340, 1440, 1441, 1460, 1601, 1710, 1750, 1811, 1920, 1999, 2040, 2091, 2160, 2209, 2530, 4006, 4142, 4150, 4180, 4520, 4533, 4542, 4561, 4599, 4608, 4659, 4660, 4680, 5260, 5460, 5623, 5628, 5833, 5910, 7430, 8185, 8200, 8370, 8470, 8490), neutral (2381, 2518, 2620, 5130, 5395, 5471, 5500, 5535, 5534, 5731, 5750, 5800, 5900, 7006, 7009, 7031, 7040, 7044, 7052, 7053, 7055, 7057, 7058, 7059, 7080, 7036, 7038, 7190, 7192, 7205, 7211, 7224, 7234, 7242, 7283, 7495, 7546, 7590, 8311, 9070), and unpleasant (1051, 1200, 1205, 1274, 1280, 1932, 2375.1, 2455, 2490, 2692, 2799, 2981, 3022, 3030, 3160, 3215, 3230, 3280, 3300, 3350, 3550, 5973, 6021, 6211, 6242, 6510,6540, 6550, 6555, 6821, 9001, 9006, 9040, 9120, 9181, 9265, 9415, 9432, 9530, 9910).
4. The studies presented here have displayed images in an overlapping manner so as to avoid confounds of spatial attention.

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