Article

What's in a Face?

The Late Positive Potential Reflects the Level of Facial Affect Expression

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Abstract. Morphed faces depicting varying degrees of affect expression can be used to investigate the processing of ambiguous and thus more ecologically valid facial stimuli. Event-related brain potentials (ERPs) were measured while participants viewed a series of faces ranging in 10% increments from prototypically happy to prototypically neutral to prototypically angry. Results revealed that the late positive potential (LPP) – an ERP reflecting later stages of stimulus processing – followed the degree of expression of facial affect such that faces depicting a greater amount of affect elicited larger LPPs as compared to faces depicting less affect. The enhanced LPP to faces depicting greater amounts of affect was also more sustained for angry compared to happy faces – in general, angry faces elicited larger LPPs. Overall, these results demonstrate the sensitivity of the LPP to more ecologically valid facial expressions and thus the visual system's finely tuned discriminability of important social signals.

Keywords: event-related potentials, late positive potential, affective face processing, morphing

Faces convey a rich array of information about individuals (age, gender, ethnicity, emotional state) and the environment (approach/avoid intentions). Facial expressions of emotion are particularly relevant to the survival of social animals. The circumplex model of emotion (Posner, Russell, & Peterson, 2005; Russell, 1980) provides a parsimonious structure for organizing facial expressions of emotion by positing that all emotions derive from two higher-order, orthogonal, dimensions: hedonic valence and arousal. Valence refers to the degree of pleasure a stimulus evokes and arousal refers to the level of activation evoked. This organization of emotions serves as the basis for much of the research on facial expressions of emotion and thus represents the foundation for the present study.

Despite the omnipresence of faces and their survival value, many studies examining face processing use prototypical faces, depicting emotional extremes. However, facial expressions in daily life are fluid and consist of a multitude of combinations and degrees of affect expression. Therefore, the facial expressions processed in every-day social situations are often more ambiguous and dynamic than the prototypes used in the laboratory. One method to investigate responses to more ecologically valid emotional expressions is to morph prototypical expressions to create stimuli depicting varying degrees of facial affect. Recent research suggests that healthy individuals seem quite accurate at identifying the primary emotion displayed by morphed faces. Signal detection methods reveal that when presented with faces depicting varying degrees of emotional expression along angry-neutral, fear-neutral, and angry-fear spectrums, adults were able to accurately identify facial emotion along a continuum (Thomas, De Bellis, Graham, & LaBar, 2007).

Little is known, however, about the underlying neural mechanisms involved in the possessing of morphed – that is, more ecologically valid – facial expressions. Event-related brain potentials (ERPs) provide an ideal complement to behavioral measures because their excellent temporal resolution allows for the examination of the sequence of constituent neural operations involved in stimulus- and response-processing of the order of milliseconds. In this way, ERPs aid in separating out stimulus- from response-related neural processes that are confounded in behavioral measures. A number of studies have already demonstrated ERP modulations during the processing of faces depicting

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prototypical emotional expressions (see Eimer & Holmes, 2007 for a review).[1] For instance, several studies have reported an early-to-middle latency (< 300 ms) positive shift in frontal regions in response to prototypical emotional (positive and negative) compared to neutral faces, indicative of the recognition of emotional expression by areas of the frontal cortex (Eimer & Holmes, 2007). Studies reporting on the modulation of later (> 300 ms) ERP components also find an effect of prototypical facial affect. The Late Positive Potential (LPP) is of particular interest in the current study because it is sensitive to the emotional content of a broad range of stimuli (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). The LPP is a centro-parietally maximal positive shift that reaches its maximum amplitude between 300 and 1,000 ms following stimulus onset. It has been proposed to index attention, perception, and memory processes elicited by various types of motivationally relevant stimuli (Bradley, 2009; Donchin, 1981; Donchin & Coles, 1988; Nieuwenhuis, Aston-Jones, & Cohen, 2005, Schupp et al., 2000).

To date, several studies (e.g., Eimer, Holmes, & McGlone, 2003) suggest that the LPP is particularly sensitive to the arousal quality of emotional faces, reporting that the LPP is equally enhanced to both prototypical positive and negative facial expressions compared to neutral faces. Schupp et al. (2004), on the other hand, suggest that the LPP may also be sensitive to the valence of stimuli. They demonstrated larger LPPs during the processing of prototypical angry faces compared to prototypical happy and prototypical neutral faces, consistent with the so-called "negativity bias hypothesis." This hypothesis states that threatening/negative faces are processed more thoroughly than friendly/positive faces, which has been supported in a number of other studies using both real and schematic prototypical faces (Ito, Larsen, Smith, & Cacioppo, 1998; Kanouse & Hansen, 1971; Ohman, Lundqvist, & Esteves, 2001; Peeters & Czapinski, 1990; Skowronski & Carlston, 1989; Tipples, Atkinson, & Young, 2002).

More important to the current investigation, all face processing studies reviewed above used faces portraying prototypical affective expressions that depict the extreme end of the emotion. Only a few studies have investigated whether morphed faces modulate early and late ERP components (Achaibou, Pourtois, Schwartz, & Vuilleumier, 2008; Campanella, Quinet, Crommelinck, & Guerit, 2002; Cavanagh & Geisler, 2006; Sprengelmeyer & Jentzsch, 2006). The results of previous studies using morphed faces suggest that both early and late ERP components are modulated by the degree of facial affect expression. Campanella et al. (2002), Cavanagh and Geisler (2006), and Sprengelmeyer and Jentzsch (2006) reported ERP modulations between 200 and 600 ms while participants viewed faces depicting varying degrees of affective expression. Specifically, the P3 was larger when participants viewed two faces reflecting different emotions compared to the same emotion (Campanella et al., 2002), and was smaller and slower in depressed participants compared to controls for all faces, especially morphed faces displaying low levels of happy affect (Cavanagh & Geisler). Sprengelmeyer and Jentzsch also found that ERP positivities were larger between 200 and 600 ms for morphed faces displaying greater amounts of affect compared to neutral faces, with faces depicting intermediate levels of affect resulting in intermediate increases in the ERP. However, these studies examined only three morph levels (Cavanagh & Geisler, 2006; Sprengelmeyer & Jentzsch, 2006) or presented two faces at the same time within the context of a discrimination task (Campanella et al., 2002). Thus, the findings to date do not provide a clear understanding of ERP modulations during, and therefore the information processing stages involved in, the viewing of a continuum of morphed faces.

The purpose of the current study, then, was to build upon previous findings by investigating the modulation of early and late positivities, including the LPP, during the viewing of morphed affective faces. To extend previous studies, a broader range of facial expressions were created depicting varying levels of affective expression. This resulted in prototypical angry, neutral, and happy faces with 18 additional faces depicting 10% differences in affective expression along the happy-neutral and angry-neutral spectrum. Participants also rated stimuli using the Self-Assessment Manikin (SAM; Bradley & Lang, 1994) to assess both valence and arousal dimensions on a 1 (*very unpleasant*; low arousing) to 9 (*very pleasant*; highly arousing) scale. We predicted an effect of arousal on ERP components. Specifically, we predicted that the happiest and angriest expressions would result in the largest increase in ERP positivity measured at frontal recording sites in early time windows (< 300 ms; Eimer & Holmes, 2007) and at parietal recording sites during the LPP time windows (> 300 ms; Schupp et al., 2004) and the most neutral faces would result in the smallest ERP positivity. Intermediate faces depicting varying degrees of happiness and anger would result in an increase in ERP positivity consistent with the degree of affect expressed. Given past results supporting the negativity bias hypothesis (e.g., Schupp et al., 2004), we also considered the possibility of a valence effect in the LPP, such that a larger LPP would be elicited during the processing of angry compared to happy and neutral faces in general.

For SAM valence ratings, we predicted that the happiest faces would be rated as the most positive, the angriest faces would be rated as the most negative, and ratings for intermediate faces would coincide with the level of affect expressed. For SAM arousal ratings, we predicted that faces depicting greater amounts of affective expression (both positive and negative) would be rated as the most arousing, with ratings for intermediate faces coinciding with the level of affect expressed.

[1] The N170 is often analyzed within the context of face processing, but it is unclear at present if it indexes affective or structural aspects of face stimuli (Eimer & Holmes, 2007). Because the primary purpose of the current study was to examine early and late ERP positivities that show consistent modulations by emotional faces, our review of the existing literature focuses exclusively on these components.

Table 1. Average number of control points used for morphing

Facial region	Happy/neutral morph	Angry/neutral morph	Average
Eyebrows	17.0	17.0	17.0
Eyes	14.0	14.2	14.1
Mouth	24.0	20.6	22.3
Nose	12.0	12.0	12.0
Cheek/chin	11.0	11.0	11.0
Forehead	6.8	6.8	6.8
Face circumference	46.0	46.0	46.0
Hair/neck	20.5	20.6	20.6

Method

Participants

Twenty-nine undergraduate students (16 female) recruited through the University of Delaware Psychology Department participant pool took part in the current study for course credit.

Stimuli and Morphing Procedures

In line with the circumplex model of emotion (Posner et al., 2005; Russell, 1980), our goal was to create a series of images spanning both valence and arousal dimensions. Thus, we aimed to create faces ranging from prototypically happy to prototypically neutral to prototypically angry, each expressing slight differences in affective expression. The stimulus set comprised 30 pictures of five male and five female models each posing angry, happy, and neutral facial expressions taken from Ekman and Friesen's (1976) Pictures of Facial Affect. For each model, happy-neutral and angry-neutral morphs were performed. The happy-neutral morphs were created using the happy and the neutral faces to create a series of nine composite images expressing varying degrees of happiness. The angry-neutral morphs were created using the angry and neutral faces to create a series of nine composite images expressing varying degrees of anger. SmartMorph (http://logicnet.dk/SmartMorph/) picture-morphing software was used for all morphing procedures.

The techniques outlined in Steyvers (1999) were used as the basis for morphing the facial stimuli in the current study. In preparation for morphing, control points were placed on the corresponding regions of both faces (e.g., prototypical happy and neutral). The facial regions were defined as the eyebrows, eyes, mouth, nose, cheek/chin, forehead, circumference of face, and hair/neck (see Table 1). The number of points on each facial region was determined based on methods described in Steyvers and modified for each face as needed so as to minimize the amount of blurriness around the eyes and mouth during morphing. The eyes and mouth were given special attention, as a number of studies suggest that these regions of the face are most important for facial affect expression and recognition (e.g., Adolphs, 2002; Adolphs et al., 2005; Morris, Debones, & Dolan, 2002). Control points were placed on other areas of the face as well, to smooth out all facial features. An average of 149.8 control points was used for each face. The average number of control points for the angry-neutral morphs (148.3) was comparable to that used for the happy-neutral morphs (151.4; $t(7) = .90$, $p > .05$). For each of the original images, the sets of control points resulted in the formation of grids over each of the faces, which meshed during morphing to create the composite images (see Steyvers for a more detailed description of mesh warping). The final product was a set of 21 images for each model (210 total images; 105 male and 105 female) varying on a continuum from happy to neutral to angry in 10% gradients of emotion. See Figure 1 for an example of the series of images.

Task and Experimental Procedures

After participants received a general description of the experiment and provided informed consent, EEG/EOG sensor electrodes were attached and participants were given detailed task instructions. Each participant was seated approximately 65 cm directly in front of a 17-inch computer monitor with each face stimulus occupying 14.6 degrees of visual angle vertically and 9.7 degrees of visual angle horizontally. A facial affect categorization task was administered on a Pentium class computer, using Presentation software (Neurobehavioral Systems, Albany, CA), to control the presentation and timing of all stimuli, the determination of response accuracy, and the measurement of reaction times. The primary purpose of the facial affect categorization task was to focus participants' attention on the facial stimuli. The task required participants to categorize each face as negative, positive, or neutral. Prior to the task, all participants were given detailed instructions and 10 practice trials that included stimuli randomly selected from the larger set of 210 images. During the task, the 210 face images were presented in random order two times each across 10 blocks of 42 trials. To control for repetition effects, each image was presented once during the first half of the study (blocks 1–5) and then a second time during the second half of the study (blocks 6–10). A fixation mark (+) was always presented at the center of the screen during the interstimulus interval (ISI) to help participants remain focused throughout the task. Each face replaced the fixation cross in the center of the computer screen for 1,000 ms against a black background with an ISI of 1,500 ms. Participants were instructed

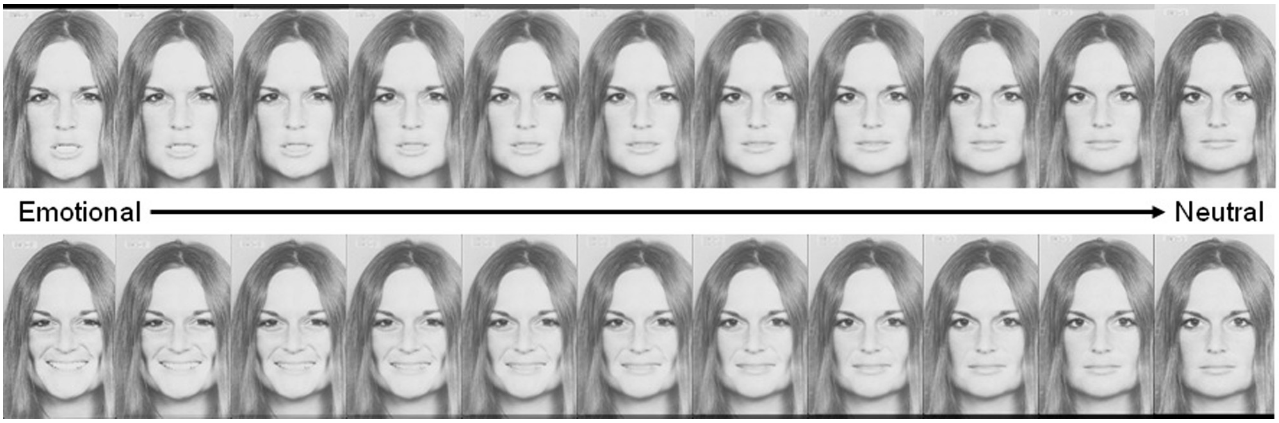

Figure 1. A series of morphs used for the current study. They range from prototypically angry to prototypically neutral (top) and prototypically happy to prototypically neutral (bottom). Face stimuli were from Ekman and Friesen's (1976) Pictures of facial affect.

to categorize the emotion of the face as positive, neutral, or negative by pressing the left, down, or right arrow keys with the right index, middle, and ring fingers, respectively, on a standard keyboard as quickly and as accurately as possible. The response window was 2,000 ms following face onset. Responses made outside this window were discarded. At the completion of the facial affect categorization task, participants rated the facial affect pictures using the SAM.

Psychophysiological Recording, Data Reduction, and Analysis

The electroencephalogram (EEG) was recorded from the frontal (Fz), fronto-central (FCz), central (Cz), and parietal (Pz) recording sites using an ECI electrocap. In addition, tin disk electrodes were placed on the left and right mastoids (M1 and M2, respectively). During the recording, all activity was referenced to Cz. The electrooculogram (EOG) generated from blinks and vertical eye movements was recorded using Med-Associates miniature electrodes placed approximately 1 cm above and below the participant's right eye. The right earlobe served as a ground site. All EEG/EOG electrode impedances were kept below 10 KΩ and the data from all channels were recorded by a Grass Model 78D polygraph with Grass Model 7P511J preamplifiers (bandpass = 0.1–100 Hz).

All bioelectric signals were digitized on a laboratory microcomputer using VPM software (Cook, 1999). The EEG was sampled at 200 Hz. Data collection began 500 ms prior to the onset of the imperative stimulus and continued for 1,500 ms. Off-line, the EEG for each trial was corrected for vertical EOG artifacts using the method developed by Gratton, Coles, and Donchin (1983; Miller, Gratton, & Yee, 1988) and then re-referenced to the average activity of the mastoid electrodes. In line with previous face studies from our laboratory (e.g., Moser, Huppert, Duval, & Simons, 2008), trials were rejected and not counted in subsequent analyses if: the record contained 25 ms of invariant (i.e., flat) analog data on any channel or the signal deviated by 200 μV above or below the pre-stimulus baseline. Single trial EEG data were lowpass filtered at 20 Hz with a 51-weight FIR digital filter as per Cook and Miller (1992). Finally, the EEG for each trial was time-locked to stimulus onset and averaged across all levels (21) of morphed faces ranging from prototypically angry to prototypically neutral to prototypically happy. This yielded ERPs for each electrode site. After artifact rejection, the mean number of averages used to calculate grand averages for each condition per participant was 19.86 (range = 16–20). A 2 (Facial Affect) × 11 (Morph Level) ANOVA revealed no significant main or interaction effects, verifying that after artifact rejection, there were no differences in the number of participant averages used to calculate ERP grand averages across conditions, *F*s < 1.2, *p*s > .32. Furthermore, trials were excluded from all analyses if the subject made an inaccurate response on the categorization task, resulting in an average of 13.5 trials used to calculate ERP averages for each condition.

Average activity in the 100 ms pre-stimulus window served as the baseline for all stimulus-locked ERPs. We were particularly interested in examining positive shifts occurring across time and location. Specifically, we homed analyses on early frontally-maximal positive shifts (Eimer & Holmes, 2002), as well as later parietally-maximal positive shifts, referred to collectively as the LPP (Cuthbert et al., 2000; Moser et al., 2008; Olofsson, Nordin, Sequeira, & Polich, 2008; Schupp et al., 2004). We defined three early time windows occurring 80–300 ms following stimulus onset, based on Eimer and Holmes (2002) and the pattern of our waveforms. In addition, the LPP was examined in three parts, as previous studies have suggested that different time windows of the LPP indicate different processes related to attention and memory (Olofsson et al., 2008). These previous studies have suggested that earlier LPP windows index attention and initial memory storage, whereas later windows index task demands and are sensitive to arousing, and motivationally salient, stimuli. Consistent with previous studies, we examined the LPP at three time windows (Early-LPP: 310–420, Mid-LPP: 450–650, and Late-LPP: 650–1,000 ms).

Each portion of the waveform falling within the areas of interest was then scored using data from the electrode site where it reached maximum amplitude. This was done to minimize contamination by component overlap (Luck, 2005) and to reflect the shift from early frontal positivity to late centro-parietal positivity (Eimer & Holmes, 2007).

Repeated-measures analyses of variance (ANOVAs) were performed on ERP, SAM, and behavioral (accuracy and reaction time; RT) measures using SPSS (v. 17.0; IBM software) general linear model analysis software. ERP, SAM, and RT were calculated for correct trials only.[2] For all ERP scoring windows, as well as SAM ratings, Accuracy, and RT, a 2 (Facial Affect: Happy, Angry) × 9 (Morph Level: 100%, 90%, 80%, 70%, 60%, 40%, 30%, 20%, 10% affect) repeated-measures ANOVA was conducted, where 100% affect represents the prototypical happy and angry faces. RT data were not normally distributed for all conditions, so square root transformations were applied to all RT data, resulting in normal distributions. Accuracy was defined as a response (positive, negative, neutral) that corresponded with the predominant expression depicted in the morphed faces. For example, a correct response on a trial with a morph that was 60% happy and 40% neutral was "positive." Since there is no predominant expression, and thus no one correct response, on trials with morphs depicting 50% affect (e.g., a 50% happy morph could be categorized as "happy" or "neutral"), they were not considered in these analyses. Although these conditions were excluded from analyses, figures include all levels of facial affect expression for illustrative purposes.

When significant ANOVA effects were detected, we report follow-up polynomial contrasts on the first two trends – linear and quadratic – to more thoroughly describe the nature of effects. Greenhouse-Geisser corrections were used for all multiple df effects, and alpha was set at .025 for these follow-up contrasts to correct for multiple comparisons ($p = .05/2 = .025$). Percentage of variance accounted for by each polynomial contrast was calculated as an indicator of effect size. Finally, in order to further examine associations between measures, averages were computed across subjects to obtain one value for each measure for each morph level. Morph level was treated as a continuous variable ranging from prototypically angry to neutral to prototypically happy. Pearson's correlations between measures were then computed to examine whether ERP, SAM, and behavioral measures covaried across morph levels. An alpha level cutoff of .001 was used to correct for multiple comparisons.

Results

Early ERP Windows (80–310 ms Following Stimulus Onset)

Stimulus-locked ERPs for prototypical angry, neutral, and happy faces are presented in Figure 2 across the four recording sites to illustrate the typical look of the waveforms. The early ERP windows were maximal at electrode site Fz, so this recording site was used for the early ERP analyses. The 2 (Facial Affect: Happy, Angry) × 9 (Morph Level) ANOVA did not reveal any significant main effects or interactions for any of the early time windows examined (Fs < 1, ps > .44).[3]

LPP Windows

All LPPs were maximal at electrode site Pz, so this recording site was used for all LPP analyses.

Early LPP (310–420 ms)

The 2 (Facial Affect: Happy, Angry) × 9 (Morph Level) ANOVA revealed a significant main effect of Facial Affect in the 310–345 window, $F(1, 28) = 5.58$, $p < .03$, indicating that angry faces elicited greater LPP positivity compared to happy faces overall. No other main effects or interactions were significant (Fs < 1.4, ps > .21).

Mid-LPP (450–650 ms)

Figure 3 shows LPP amplitude across all morph levels (except the 50% affect condition) at site Pz for the 450–650 ms window. There was a main effect of Facial Affect, $F(1, 28) = 11.80$, $p < .01$, and a main effect of Morph Level, $F(8, 224) = 6.54$, $p < .001$. The main effect of Facial Affect indicated that angry faces elicited greater LPP positivity compared to happy faces overall. There was a significant linear trend for the effect of Morph Level, $F_{\text{lin}}(1, 28) = 31.58$, $p < .001$, accounting for 58% of the variance. Faces depicting more affect elicited more LPP positivity than faces depicting less amounts of affect. The quadratic trend for Morph Level was not significant. The Facial Affect by Morph Level interaction was not significant, $F < 1$.

2 All significant main effects and interactions reported using the correct trial dataset were also significant when all (correct and incorrect) trials were included for analysis.

3 Based on impressions gleaned from Figure 2, a three-level repeated-measures ANOVA was conducted to examine differences in ERP amplitude for prototypical angry, neutral, and happy expressions at each of the early time windows. There were no significant main effects (Fs < 3.2, ps > .05), however.

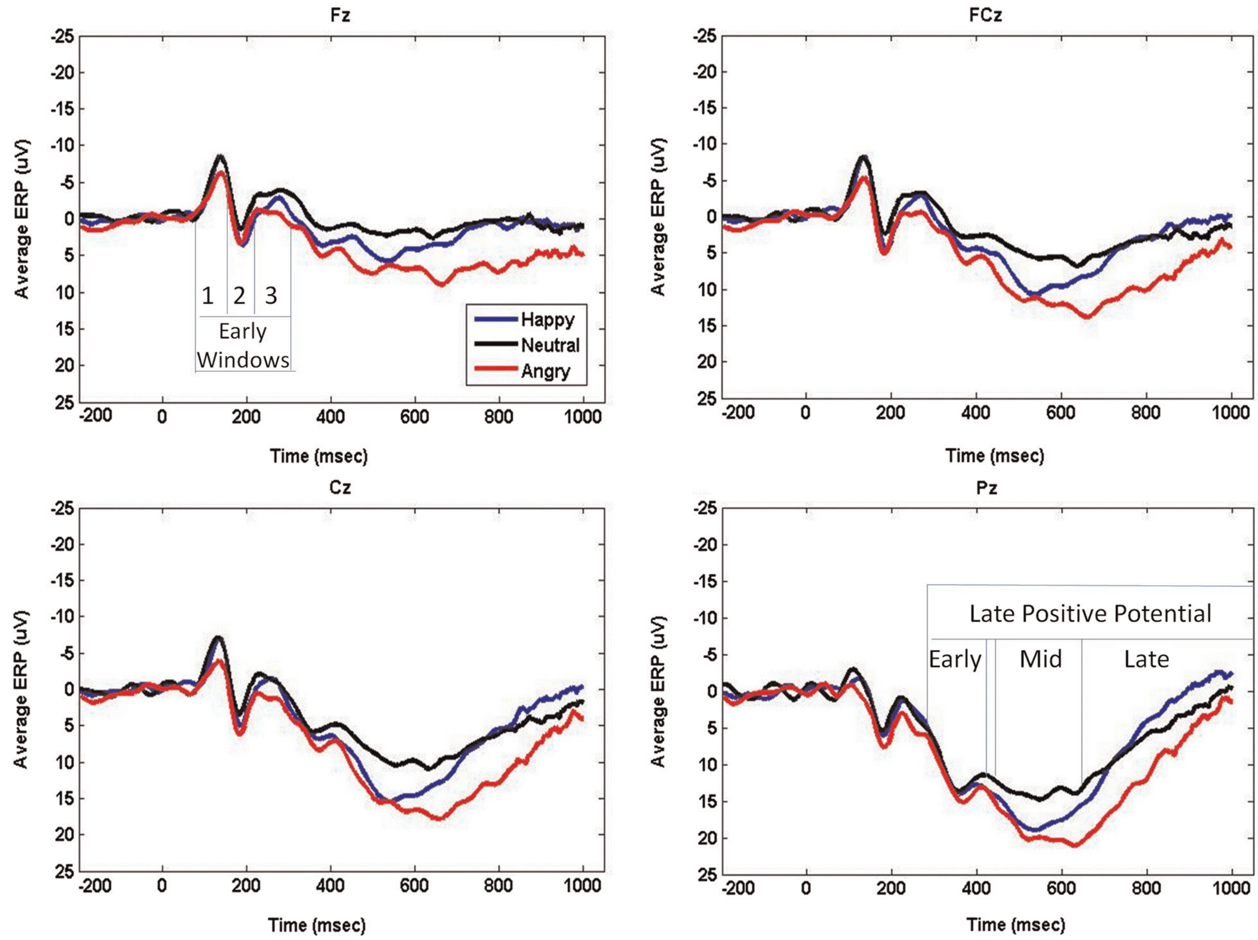

Figure 2. Stimulus-locked grand average ERP waveforms at each recording site (Fz, FCz, Cz, Pz) for prototypically angry (red line), neutral (black line), and happy (blue line) faces.

Late-LPP (650–1,000 ms)

For the Late-LPP window, there was a main effect of Facial Affect, $F(1, 28) = 20.81$, $p < .001$, indicating that angry faces elicited greater LPP positivity compared to happy faces overall (see Figure 4). The main effect of Morph Level and the Facial Affect by Morph Level interaction were not significant, ps > .05.

SAM Ratings

SAM ratings for the morphed faces ranging from prototypical happy to prototypical neutral and prototypical angry to prototypical neutral are presented in Figure 5, showing valence and arousal ratings. The 2 (Facial Affect: Happy, Angry) × 9 (Morph Level) ANOVA conducted on the valence ratings revealed a main effect of Facial Affect, $F(1, 28) = 434.94$, $p < .001$, a main effect of Morph Level, $F(8, 224) = 11.65$, $p < .001$, and a Facial Affect × Morph Level interaction, $F(8, 224) = 289.56$, $p < .001$. The main effect of Facial Affect indicated that happy faces were rated as more pleasant than angry faces overall. For the effect of Morph Level, the linear trend was significant, $F_{lin}(1, 28) = 36.67$, $p < .001$, accounting for 83% of the variance. This linear effect of Morph Level indicated that as faces morphed from neutral and approached the emotion prototypes, they were rated as happier or angrier as we expected. The significant Facial Affect × Linear Morph Level interaction, $F(1, 28) = 667.37$, $p < .001$, accounted for 94% of the variance, indicating that the amount of affective expression displayed by the angry faces was more strongly related to differences in valence ratings than the amount of affective expression displayed by the happy faces (see Figure 5). The Facial Affect × Quadratic Morph Level interaction was also significant, $F(1, 28) = 18.28$, $p < .001$, but only accounted for 1% of the variance.

The same analysis conducted on arousal ratings again revealed a main effect of Morph Level, $F(8, 224) = 67.97$, $p < .001$, with a significant linear trend, $F_{lin}(1, 28) = 88.02$, $p < .001$, accounting for 96% of the variance. Faces depicting more affect were rated as more arousing than faces depicting less affect (see Figure 5). The main effect of Facial

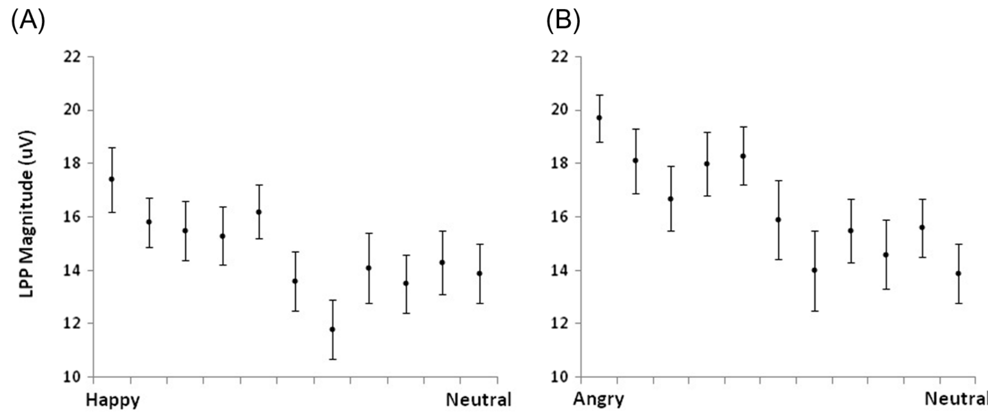

Figure 3. LPP magnitude for the Mid-LPP (450–650 ms) window at Pz for all gradients in facial expression ranging from (A) prototypically happy to prototypically neutral and (B) prototypically angry to prototypically neutral. Error bars indicate standard error of the mean (*SEM*).

Affect and the Facial Affect by Morph Level interaction were not significant, *F*s < 1.

Behavioral Data

Accuracy

Results revealed a main effect of Facial Affect, $F(1, 28) = 8.28$, $p < .01$, a main effect of Morph Level, $F(8, 224) = 30.87$, $p < .001$, and a Facial Affect × Morph Level interaction, $F(8, 224) = 31.41$, $p < .001$. The main effect of Facial Affect indicated that, overall, participants were more accurate when categorizing happy facial expressions ($M = .80$, $SD = 0.11$) compared to angry facial expressions ($M = .76$, $SD = 0.15$). For the main effect of Morph Level, the linear trend was not significant ($p > .10$), but the quadratic trend was, $F_{quad}(1, 28) = 308.34$, $p < .001$, and accounted for 59% of the variance. This quadratic effect indicated that accuracy was best for faces falling closer to the prototypes – that is, 100% happy, angry, or neutral – and was poorer for intermediate levels of affect. The Facial Affect × Linear Morph Level interaction was significant, $F(1, 28) = 34.65$, $p < .001$, and accounted for 28% of the variance. This interaction effect reveals that participants categorized all faces depicting greater than 50% happy affect with roughly equal accuracy. However, when categorizing faces along the angry continuum, participants were more accurate as faces depicted increasing levels of angry affect. This suggests that participants had more difficulty distinguishing ambiguous angry expressions from the other expressions (happy, neutral) compared to happy faces, which were identified with equal accuracy across levels of affect above 50% (see Figure 6). The Facial Affect × Quadratic Morph Level trend was not significant, $F < 1$.

Reaction Time

For RT, there was a main effect of Facial Affect, $F(1, 28) = 479.66$, $p < .001$, a main effect of Morph Level, $F(8, 224) = 10.96$, $p < .001$, and a Facial Affect × Morph

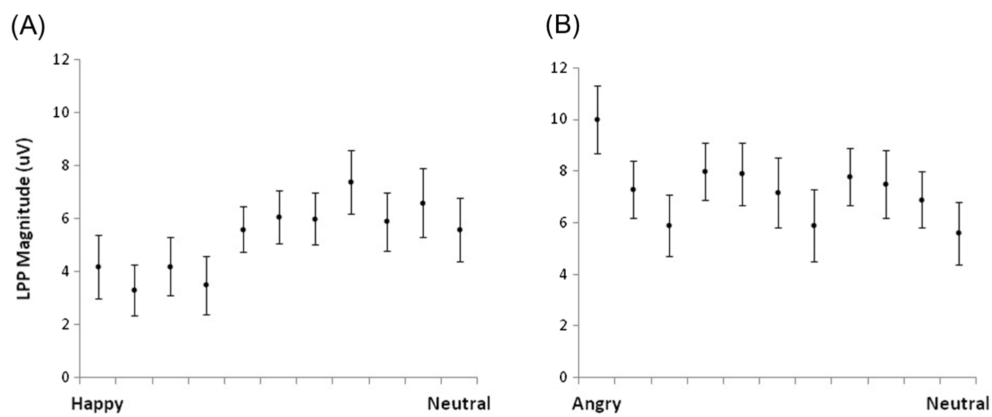

Figure 4. LPP magnitude for the Late-LPP (650–1,000 ms) window at Pz for all gradients in facial expression ranging from (A) prototypically happy to prototypically neutral and (B) prototypically angry to prototypically neutral. Error bars indicate *SEM*.

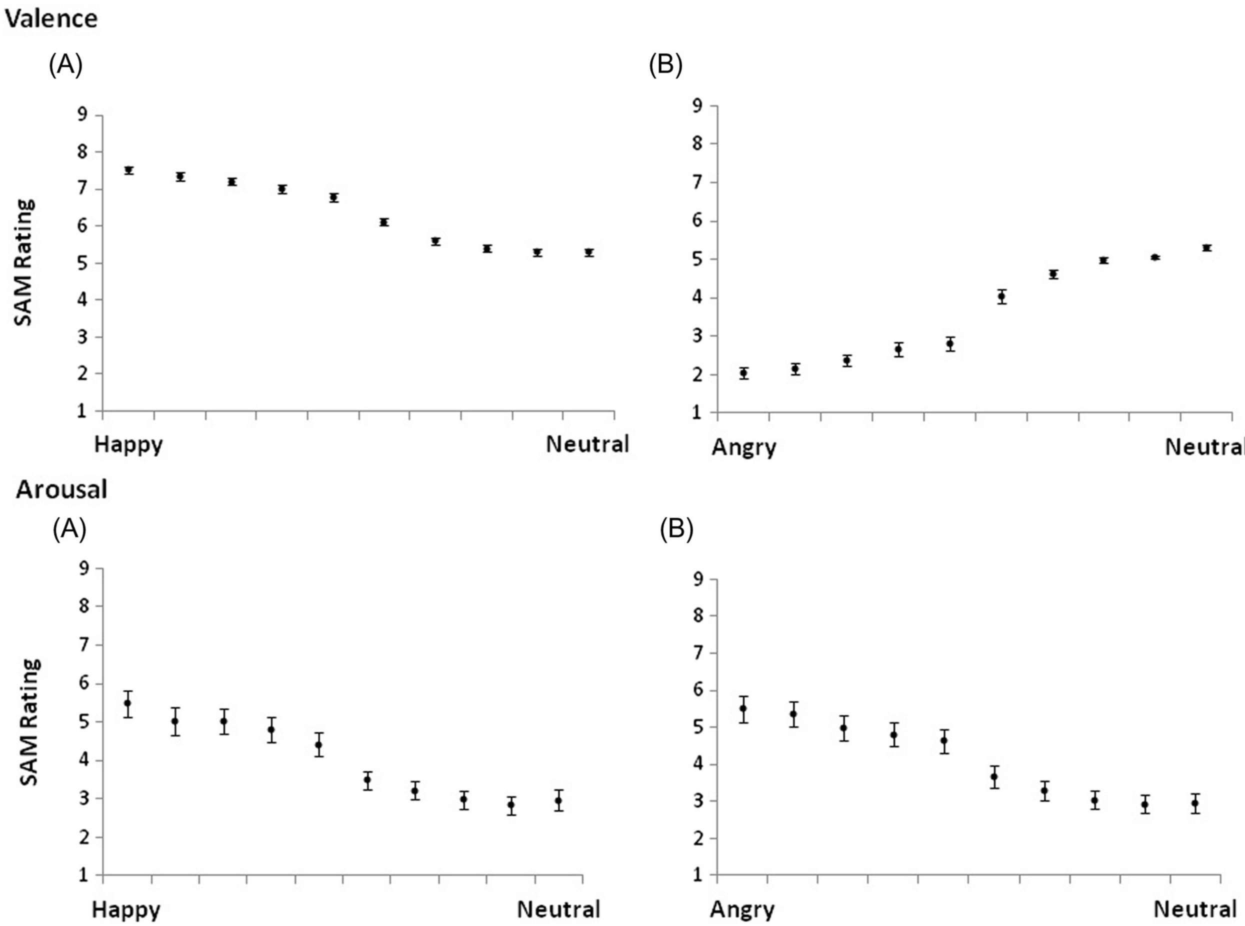

Figure 5. SAM valence and arousal ratings for all gradients in facial expression ranging from (A) prototypically happy to prototypically neutral and (B) prototypically angry to prototypically neutral. Error bars indicate *SEM*.

Level interaction, $F(8, 224) = 109.05$, $p < .001$. The main effect of Facial Affect indicated that, overall, participants were faster at categorizing happy facial expressions ($M = 35.13$; $SD = 0.73$) compared to angry facial expressions ($M = 36.34$; $SD = 0.67$). For the main effect of Morph Level, the linear trend was significant, $F_{lin}(1, 28) = 12.92$, $p = .001$ and accounted for 45% of the variance. Participants were fastest to categorize the prototypical faces, and were slower to categorize faces as they became more ambiguous. The quadratic trend was also significant, $F_{quad}(1, 28) = 37.09$, $p < .001$, but only accounted for 22% of the variance. The Facial Affect × Linear Morph Level interaction was significant, $F(1, 28) = 531.57$, $p < .001$, and accounted for 81% of the variance. The Facial Affect × Quadratic Morph Level trend was also significant, $F(1, 28) = 5.97$, $p < .025$, but only accounted for less than 1% of the variance. This pattern of effects suggests that when categorizing faces along the happy continuum, participants were faster for faces depicting high degrees of happiness. When categorizing faces along the angry continuum, however, participants were faster for faces depicting less anger and more neutral expressions. In addition, individuals were faster at categorizing happy faces compared to angry faces, but this effect was most pronounced for the faces depicting greater levels of affect – that is, faces containing 60% or more of the happy or angry expression (see Figure 6).[4]

Correlations

The Mid-LPP was positively correlated with SAM arousal ratings ($r = .75$, $p < .001$), suggesting an arousal effect in the Mid-LPP. The Mid-LPP followed the same pattern as SAM

[4] In line with the RT data, more timeouts (RTs > 2,000 ms) occurred on trials when more angry expressions were depicted. Specifically, more timeouts occurred as expressions moved from prototypically angry to neutral, and timeouts decreased as expressions moved from prototypically neutral to happy. This suggests that participants were so slow to respond to the most angry expressions that they were less able to make a response within the allotted time window of 2,000 ms.

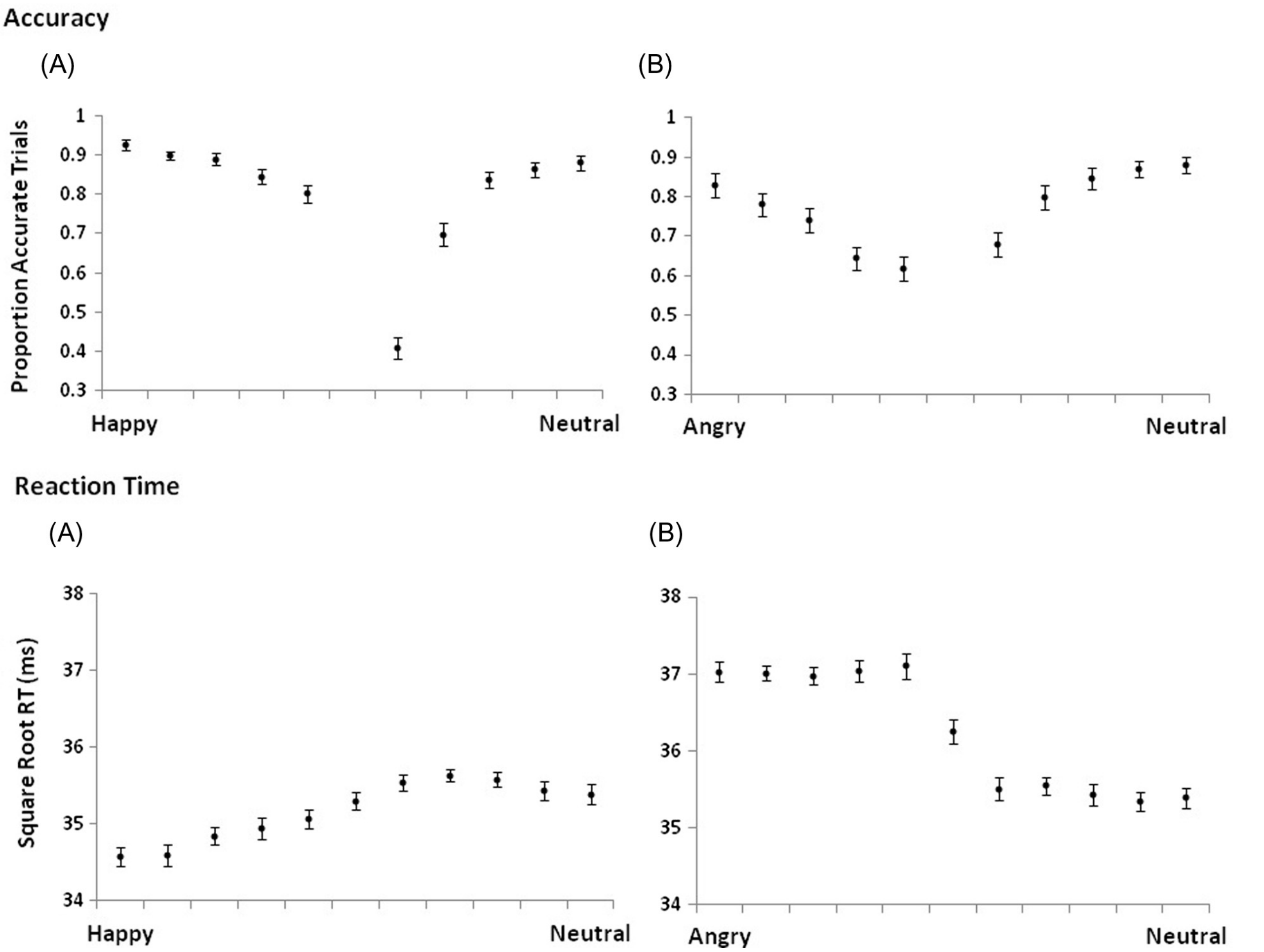

Figure 6. Proportion of accurate responses and RT for all gradients in facial expression ranging from (A) prototypically happy to prototypically neutral and (B) prototypically angry to prototypically neutral. Error bars indicate *SEM*.

arousal ratings, with greater LPP activation and higher arousal ratings as faces increased in their level of affective expression from neutral toward both ends of the continuum (happy and angry). The Late-LPP was negatively correlated with SAM valence ratings ($r = -.83, p < .001$) and positively correlated with RT ($r = .74$, $p < .001$). RT and SAM valence ratings were also negatively correlated with each other ($r = -.91$, $p < .001$). These correlations suggest a valence effect for both the Late-LP and RT. As faces increased across the continuum from happy to neutral to angry:
(1) the Late-LPP increased,
(2) faces were rated as less positive, and
(3) RT increased.

A partial correlation was conducted to follow up the three-way correlation between Late-LPP, SAM valence, and RT. When controlling for SAM valence ratings, the correlation between Late-LPP and RT was no longer significant ($r = .03$, $p = .90$), suggesting that perceived pleasantness mediated the relationship between the Late-LPP and behavioral performance.

Discussion

The primary aim of the current study was to investigate the sensitivity of early and late positive shifts of the ERP to degrees of facial affect expression. Results revealed that the LPP and behavioral measures were modulated by small differences in the level of facial affect expression. As the amount of affective expression of both happy and angry faces increased, so did their motivational relevance, as indexed by enhanced LPP magnitude between 450 and 650 ms post-stimulus onset, more extreme SAM ratings consistent with level of affect expressed, and changes in RT and Accuracy. Correlations between measures further suggested that ERP and behavioral data covaried across levels of facial affect expression. Specifically, two processes were observed: the Mid-LPP showed an arousal effect, whereas the Late-LPP showed a valence effect. In addition, angry faces elicited larger positive amplitudes across all three of the LPP time windows (i.e., 310–345, 450–650, and 650–1,000 ms).

The current finding that the LPP varied as a function of the level of affective expression is consistent with previous findings that the LPP is larger to emotional compared to neutral faces (Eimer & Holmes, 2002), and is tightly coupled to increases in the level of activation (i.e., arousal) elicited by emotional scenes (Olofsson et al., 2008). Our SAM findings are consistent with the LPP results and previous reports that healthy participants are sensitive to the affective expression portrayed by prototypical (e.g., Stenberg, Wiking, & Dahl, 1998) and ambiguous (Thomas et al., 2007) emotional expressions. Given that previous studies focused mainly on how prototypical faces modulate the LPP (e.g., Eimer & Holmes, 2002), the current LPP and SAM arousal results extend the literature to suggest that the brain is tuned to make fine discriminations between faces depicting slight differences in the level of facial affect among more ambiguous, ecologically valid faces, as early as 450 ms.

In addition to the main finding that ERP and behavioral measures were sensitive to slight changes in facial affect, our results also support the negativity bias hypothesis. Consistent with previous research (Balconi & Lucchiari, 2005; Balconi & Pizzoli, 2003; Dennis & Chen, 2007; Eger, Jedynak, Iwaki, & Skrandies, 2003; Eimer et al., 2003; Leppanen, Moulson, Vogel-Farley, & Nelson, 2007; Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004; Schupp et al., 2004), the LPP was enhanced in all time windows (310–1,000 ms) during the processing of angry compared to happy faces across all levels of expression. Angrier faces were also associated with impaired behavioral performance, as indicated by slower RTs and lower accuracy than happier faces. Although happy faces tended to be perceived as equally happy across levels of affect intensity, participants provided more graded responses to angry faces, relative to the amount of affect expressed.

Together with the behavioral findings, one might argue that angry faces may have elicited larger LPP amplitude because they were more difficult to categorize than happy faces. However, if difficulty was driving this effect, we would expect the more ambiguous angry faces to have the largest LPP, as they would be the most challenging to categorize. Given that the largest LPP values were observed for angry faces displaying the greatest amounts of affective expression, we can thus disassociate difficulty from emotion, and conclude that these effects were a function of the motivational salience/emotional qualities of the stimuli. That the happy and angry faces in the current study did not differ on overall SAM-reported arousal levels rules out the possibility of an arousal level confound. We have strong support, then, that angry faces were both harder to classify than happy faces, and attracted more attentional resources during the LPP time windows than did happy faces.

The current findings are consistent with reports that negative stimuli attract more attentional resources (Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001) and are processed more thoroughly than other types of stimuli (see Ohman & Mineka, 2001 for a review). However, these findings are inconsistent with previous findings that negative faces are detected more efficiently during visual search tasks compared to positive faces (e.g., Fox et al., 2000; Horstmann & Bauland, 2006). Although seemingly inconsistent with the visual search findings (Fox et al., 2000; Horstmann & Bauland, 2006), the tendency to allocate more attentional resources to angry faces may be contributing to slower and less accurate task performance on the timed categorization task, as more extensive cognitive evaluation is required before a response can be made (Baumeister et al., 2001). This notion is consistent with a number of studies suggesting that negative stimuli engage more attentional resources than other types of stimuli, subsequently interfering with performance on cognitive and behavioral tasks (e.g., Stroop Task; McKenna & Sharma, 1995; Go/No-Go task; De Houwer & Tibboel, 2010; a facial feature counting task; Eastwood, Smilek, & Merikle, 2003; and categorization/recognition tasks; Leppanen & Hietanen, 2003; Leppanen, Tenhunen, & Hietanen, 2003; Moser et al., 2008). Although some have suggested that this behavioral advantage for happy faces is the result of distinctive physical features (e.g., a smiling mouth; Adolphs, 2002), others suggest that it is the result of emotional and cognitive processing differences per se (e.g., Leppanen & Hietanen, 2003).

Our findings and previous literature suggest a two-process model for affective face processing. Initially, the Mid-LPP was correlated with SAM arousal ratings, demonstrating an arousal effect, such that more attentional resources were directed toward the most activating or arousing stimuli, as they were the most motivationally salient (Pratto & John, 1991). Then, the Late-LPP was correlated with SAM valence ratings, demonstrating a valence effect, such that negative faces, but not positive faces, continued to engage attentional resources (Fox et al., 2000) and were processed more thoroughly (Baumeister et al., 2001). The correlation between Late-LPP and RT was mediated by SAM valence ratings, suggesting that perceived pleasantness was related to behavioral performance, such that as more attentional resources were allocated to the more negatively perceived faces, the system slowed down and behavioral performance was impaired.

Our results did not replicate previous reports that affective faces result in a frontal positive shift in early ERP windows. The lack of enhanced positivity to affective faces across earlier components is consistent with Schupp et al. (2004), who however, demonstrated no reliable modulation of any ERP components in response to affective faces prior to 200 ms following face onset. Previous research investigating modulations of early ERP positivity by affective expressions embedded the face stimuli among other objects (e.g., houses) and showed generic positivity enhancements across several different expressions (Eimer & Holmes, 2007). Therefore, the lack of early ERP modulation in the current study is not surprising given that all of our stimuli were faces – as was also the case in Schupp et al. Together with the LPP results, these findings suggest that components reflecting later, more complex, processes of the visual system play the biggest role in affective discrimination.

This is especially evident given that the LPP, originating in parietal, inferotemporal, and occipital regions (Sabatinelli, Lang, Keil, & Bradley, 2007; Schupp et al., 2000), showed the greatest sensitivity to changes in facial affect expression. Given the interplay between frontal, visual, and subcortical regions during affective face processing (Eimer & Holmes, 2007), future studies using dense electrode montages as well as functional magnetic resonance imaging (fMRI) are warranted in order to further elucidate these interactive and dynamic mechanisms.

To extend the current findings, future research could also examine the effects of individual differences, particularly those characterized by an oversensitivity to social threat (i.e., social anxiety and depression), on ERPs and behavioral performance during morphed face processing. Prototypically negative facial expressions are typically used in studies investigating face processing in social anxiety (e.g., Moser et al., 2008). However, given that people with social anxiety tend to interpret ambiguous faces as negative (Franklin, Huppert, Langner, Leiberg, & Foa, 2005; Hirsch & Clark, 2004), future studies could extend this research to examine group differences in the processing of a variety of levels of facial affect. The preliminary study by Cavanagh and Geisler (2006) in depressed undergraduates provides initial support for examining ERP responses to morphed faces in groups showing sensitivity to social signals.

Overall, the findings described in the present study lead to two main conclusions regarding how healthy participants respond to facial affect expression. First, healthy participants discriminate between slight differences in the level of facial affect. An arousal effect was demonstrated in the Mid-LPP, such that faces depicting greater levels of affective expression elicited enhanced Mid-LPP magnitude and greater arousal ratings, while LPP magnitude and arousal ratings decreased as faces became more neutral. Second, a valence effect was observed in the Late-LPP, suggesting that angry faces continue to engage more processing resources than happy faces. This continued attention allocation toward angry faces was related to poorer response accuracy and slower RT. Together, the current findings highlight the brain's sensitivity to the salience of social signals and suggest a two-process model of affective face processing.

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References

Achaibou, A., Pourtois, G., Schwartz, S., & Vuilleumier, P. (2008). Simultaneous recording of EEG and facial muscle reactions during spontaneous emotional mimicry. *Neuropsychologia, 46*, 1104–1113.

Adolphs, R. (2002). Recognizing emotion from facial expressions. Psychological and neurological mechanisms. *Behavioral and Cognitive Neuroscience Reviews, 1*, 21–62.

Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature, 433*, 68–72.

Balconi, M., & Lucchiari, C. (2005). Event-related potentials related to normal and morphed emotional faces. *The Journal of Psychology, 139*, 176–192.

Balconi, M., & Pizzoli, U. (2003). Face-selective processing and the effect of pleasant and unpleasant emotional expressions on ERP correlates. *International Journal of Psychophysiology, 49*, 67–74.

Baumeister, R. F., Bratslavsky, E., Finkenauer, C., & Vohs, K. D. (2001). Bad is stronger than good. *Review of General Psychology, 5*, 323–370.

Bradley, M. M. (2009). Natural selective attention: Orienting and emotion. *Psychophysiology, 46*, 1–11.

Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The self-assessment manikin and the semantic differential. *Journal of Behavioral Therapy and Experimental Psychiatry, 25*, 49–59.

Campanella, S., Quinet, P., Bruyer, R., Crommelinck, M., & Guerit, J. M. (2002). Categorical perception of happiness and fear facial expressions: An ERP study. *Journal of Cognitive Neuroscience, 14*, 210–227.

Cavanagh, J., & Geisler, M. W. (2006). Mood effects on the ERP processing of emotional intensity in faces: A P3 investigation with depressed students. *International Journal of Psychophysiology, 60*, 27–33.

Cook, E. W. III (1999). *VPM reference manual*. Birmingham, AL: Author.

Cook, E. W. III, & Miller, G. A. (1992). Digital filtering: Background and tutorial for psychophysiologists. *Psychophysiology, 29*, 350–367.

Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: Covariation with autonomic arousal and affective report. *Biological Psychology, 52*, 95–111.

De Houwer, J., & Tibboel, H. (2010). Stop what you are doing! Emotional pictures interfere with the task not to respond. *Psychonomic Bulletin and Review, 17*, 699–703.

Dennis, T. A., & Chen, C. C. (2007). Emotional face processing and attention performance in three domains: Neurophysiological mechanisms and moderating effects of trait anxiety. *International Journal of Psychophysiology, 65*, 10–19.

Donchin, E. (1981). surprise! . . . Surprise? *Psychophysiology, 18*, 493–513.

Donchin, E., & Coles, M. G. H. (1988). Is the P300 component a manifestation of contextual updating? *Behavioral and Brain Sciences, 11*, 357–427.

Eastwood, J. D., Smilek, D., & Merikle, P. (2003). Negative facial expression captures attention and disrupts performance. *Attention, Perception, and Psychophysics, 65*, 852–858.

Eger, E., Jedynak, A., Iwaki, T., & Skrandies, W. (2003). Rapid extraction of emotional expression: Evidence from evoked potential fields during brief presentation of face stimuli. *Neuropsychologia, 41*, 808–817.

Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport, 13*, 4959–4965.

Eimer, M., & Holmes, A. (2007). Event-related brain potential correlates of emotional face processing. *Neuropsychologia, 45*, 15–31.

Eimer, M., Holmes, A., & McGlone, F. P. (2003). The role of spatial attention in the processing of facial expression: An ERP study of rapid brain responses to six basic

emotions. *Cognitive, Affective, & Behavioral Neuroscience, 3*, 97–110.
Ekman, P., & Friesen, W. V. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.
Fox, E., Lester, V., Russo, R., Bowles, R. J., Pichler, A., & Dutton, K. (2000). Facial expressions of emotions: Are angry faces detected more efficiently? *Cognition and Emotion, 14*, 61–92.
Franklin, M. E., Huppert, J. D., Langner, R., Leiberg, S., & Foa, E. B. (2005). Interpretation bias: A comparison of treated social phobics, untreated social phobics, and controls. *Cognitive Therapy and Research, 29*, 289–300.
Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology, 55*, 468–484.
Hirsch, C. R., & Clark, D. M. (2004). Information-processing bias in social phobia. *Clinical Psychology Review, 24*, 799–825.
Horstmann, G., & Bauland, A. (2006). Search asymmetries with real faces: Testing the anger superiority effect. *Emotion, 6*, 193–207.
Ito, T. A., Larsen, J. T., Smith, N. K., & Cacioppo, J. T. (1998). Negative information weighs more heavily on the brain: The negativity bias in evaluative categorizations. *Journal of Personality and Social Psychology, 75*, 887–900.
Kanouse, D. E., & Hansen, L. R., Jr. (1971). Negativity in evaluations. In E. E. Jones, D. E. Kanouse, H. H. Kelley, R. E. Nisbett, S. Valin, & B. Weiber (Eds.), *Attribution: Perceiving the causes of behavior* (pp. 47–62). Morristown, NJ: General Learning Press.
Leppanen, J. M., & Hietanen, J. K. (2003). Affect and face perception: Odors modulate the recognition advantage of happy faces. *Emotion, 3*, 315–326.
Leppanen, J. M., Moulson, M. C., Vogel-Farley, V. K., & Nelson, C. A. (2007). An ERP study of emotional face processing in the adult and infant brain. *Child Development, 78*, 232–245.
Leppanen, J. M., Tenhunen, M., & Hietanen, J. K. (2003). Faster choice-reaction times to positive than to negative facial expressions. *Journal of Psychophysiology, 17*, 113–123.
Liddell, B. J., Williams, L. M., Rathjen, J., Shevrin, H., & Gordon, E. (2004). A temporal dissociation of subliminal versus supraliminal fear perception: An event-related potential study. *Journal of Cognitive Neuroscience, 16*, 479–486.
Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge, MA: MIT Press.
Miller, G. A., Gratton, G., & Yee, C. M. (1988). Generalized implementation of an eye movement correction procedure. *Psychophysiology, 25*, 241–243.
McKenna, F. P., & Sharma, D. (1995). Intrusive cognitions: An investigation of the emotional Stroop Task. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 21*, 1595–1607.
Morris, J. S., Debones, M., & Dolan, R. J. (2002). Human amygdala responses to fearful eyes. *NeuroImage, 17*, 214–222.
Moser, J. S., Huppert, J. D., Duval, E., & Simons, R. F. (2008). Face processing biases in social anxiety: An electrophysiological study. *Biological Psychology, 78*, 93–103.
Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3, and the locus coeruleus norepinephrine system. *Psychological Bulletin, 131*, 510–532.
Ohman, A., Lundqvist, D., & Esteves, F. (2001). The face in the crowd revisited: A threat advantage with schematic stimuli. *Journal of Personality and Social Psychology, 80*, 381–396.
Ohman, A., & Mineka, S. (2001). Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review, 108*, 483–522.
Olofsson, J. K., Nordin, S., Sequeira, H., & Polich, J. (2008). Affective picture processing: An integrative review. *Biological Psychology, 77*, 247–265.
Peeters, G., & Czapinski, J. (1990). Positive-negative asymmetry in evaluations: The distinction between affective and informational negativity effects. In W. Stroebe & M. Hewstone (Eds.), *European review of social psychology* (Vol. 1, pp. 33–60). Chichester, UK: Wiley.
Posner, J., Russell, J. A., & Peterson, B. S. (2005). The circumflex model of affect: An integrative approach to affective neuroscience, cognitive development, and psychopathology. *Development and Psychopathology, 17*, 715–734.
Pratto, F., & John, O. P. (1991). Automatic vigilance: The attention-grabbing power of negative social information. *Journal of Personality and Social Psychology, 61*, 380–391.
Russell, J. A. (1980). A circumflex model of affect. *Journal of Personality and Social Psychology, 39*, 1161–1178.
Sabatinelli, D., Lang, P. J., Keil, A., & Bradley, M. M. (2007). Emotional perception: Correlation of functional MRI and event related potentials. *Cerebral Cortex, 17*, 1085–1091.
Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Cacioppo, J. T., Ito, T., & Lang, P. J. (2000). Affective picture processing: The late positive potential is modulated by motivational relevance. *Psychophysiology, 37*, 257–261.
Schupp, H. T., Ohman, A., Junghofer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: An ERP analysis. *Emotion, 4*, 189–200.
Skowronski, J. J., & Carlston, D. E. (1989). Negativity and extremity biases in impression formation: A review of explanations. *Psychological Bulletin, 105*, 131–142.
Sprengelmeyer, R., & Jentzsch, I. (2006). Event related potentials and the perception of intensity in facial expressions. *Neuropsychologia, 44*, 2899–2906.
Stenberg, G., Wiking, S., & Dahl, M. (1998). Judging words at face value: Interference in a word processing task reveals automatic processing of affective facial expressions. *Cognition and Emotion, 12*, 755–782.
Steyvers, M. (1999). Morphing techniques for manipulating face images. *Behavior, Research Methods, Instruments and Computers, 31*, 359–369.
Thomas, L. A., De Bellis, M. D., Graham, R., & LaBar, K. S. (2007). Development of emotional facial recognition in late childhood and adolescence. *Developmental Science, 10*, 547–558.
Tipples, J., Atkinson, A. P., & Young, A. W. (2002). The eyebrow frown: A salient social signal. *Emotion, 2*, 288–296.

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