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**AN ERP STUDY OF RESPONSES TO EMOTIONAL FACIAL EXPRESSIONS:
MORPHING EFFECTS ON EARLY-LATENCY VALENCE PROCESSING**

by

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**SUBMITTED TO SCRIPPS COLLEGE IN PARTIAL FULFILLMENT OF THE
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Abstract

Early-latency theories of emotional processing state that at least coarse monitoring of the emotional valence (a pleasure-displeasure continuum) of facial expressions should be both rapid and highly automated (LeDoux, 1995; Russell, 1980). Research has largely substantiated early-latency differential processing of emotional versus non-emotional facial expressions; however, the effect of valence on early-latency processing of emotional facial expression remains unclear. In an effort to delineate the effects of valence on early-latency emotional facial expression processing, the current investigation compared ERP responses to positive (happy and surprise), neutral, and negative (afraid and sad) basic facial expression photographs as well as to positive (happy-surprise), neutral (afraid-surprise, happy-afraid, happy-sad, sad-surprise), and negative (sad-afraid) morph facial expression photographs during a valence-rating task. Morphing manipulations have been shown to decrease the familiarity of facial patterns and thus preclude any overlearned responses to specific facial codes. Accordingly, it was proposed that morph stimuli would disrupt more detailed emotional identification to reveal a valence response independent of a specific identifiable emotion (Balconi & Lucchiari, 2005; Schweinberger, Burton & Kelly, 1999). ERP results revealed early-latency differentiation between positive, neutral, and negative morph facial expressions approximately 108 milliseconds post-stimulus (P1) within the right electrode cluster; negative morph facial expressions continued to elicit significantly smaller ERP amplitudes than other valence categories approximately 164 milliseconds post-stimulus (N170). Consistent with previous imaging research on emotional facial expression processing, source localization revealed substantial dipole activation within regions of the mesolimbic dopamine system. Thus, these findings confirm rapid valence processing of facial expressions and suggest that negative valence processing may continue to modulate subsequent structural facial processing.

Key words: valence processing, emotional facial expressions, P1, N170

**An ERP Study of Responses to Emotional Facial Expressions:
Morphing Effects on Early-Latency Valence Processing**

Adaptive behavior relies on the prompt discovery of emotionally salient environmental cues. Emotional facial expressions are particularly salient stimuli for conveying critical nonverbal messages to other individuals and thus serve as a critical, socially available index of affect (Adolphs, 2002b; Ashley, Vuilleumier & Swick, 2003; Batty & Taylor, 2003; Darwin, 1872). Hence, early-latency theories of emotional processing posit that at least coarse monitoring of the emotional valence (a pleasure-displeasure continuum) of facial expressions should be both rapid and highly automated (LeDoux, 1995; Russell, 1980).

Emotional Processing of Facial Expressions

Spatial Findings. Recent magnetic resonance imaging (MRI) studies have revealed a complex, interconnected neural network associated with emotional processing of facial expressions. This network encompasses face-processing regions of the inferior occipital cortices linked to initial perceptual analysis of faces, the middle fusiform gyri linked to structural processing of faces, and the superior temporal sulci linked to processing of dynamic aspects of faces along with the emotion-processing paralimbic and higher-cortical areas linked to conscious representations of emotional states (Adolphs, 2003; Allison, Puce & McCarthy, 2000; Haxby, Hoffman & Gobbini, 2000; Jehna et al., 2011; Kanwisher, McDermott & Chun, 1997; Lane et al., 1997). Perceptual representation and classification of emotional facial expressions has specifically been linked to the mesolimbic dopamine system (Posner, Russell & Peterson, 2005), which is composed of the amygdala, occipital cortices, orbitofrontal cortex (the orbital and rectal gyri), basal ganglia, and right parietal areas (Adolphs, 2002a; Adolphs, 2003; Adolphs, Damasio, Tranel & Damasio, 1996; Jehna et al., 2011; Lane et al., 1997; Whalen, Rauch, Etcoff, McInerney, Lee & Jenike, 1998). Furthermore, imaging studies on emotional facial expression processing have determined that neural correlates of positive

and negative facial expressions overlap considerably but are nonetheless distinguishable. For example, Adolphs, Damasio, Tranel and Damasio (1996) determined that lesions of the right inferior parietal cortex and anterior intracalcarine cortex impair recognition of negative facial expressions but not positive facial expressions. In sum, imaging and lesion evidence has established a set of brain regions consistently associated with the emotional processing of facial expressions along with subsets of brain regions that differentiate between positive and negative valence.

Temporal Findings. Whereas imaging evidence has identified neural systems underlying emotional processing of facial expression, spatial imaging methods sacrifice temporal resolution for spatial precision. As a result, scalp recordings of stimulus-driven brain electrical activity (e.g., event-related potentials, ERPs) have been used to determine the temporal aspects of emotional facial expression processing with a time resolution of milliseconds. According to LeDoux's (1995) dual facial processing model, more rudimentary differentiation of facial expression valence and arousal should occur before structural encoding (i.e., at an early latency) while fine-grained categorization of basic emotions should follow the encoding of structural facial components (i.e., at a later latency).

ERP findings have supported both early- and late-latency effects of emotion on facial expression processing. In support of early-latency emotional effects, Eimer and Holmes (2002) found significant differences between emotional and neutral facial expressions approximately 120 milliseconds after stimulus onset (other studies have similarly established early-latency differentiation between emotional and non-emotional facial expressions: Batty and Taylor (2003) found effects approximately 90 milliseconds post-stimulus, and Halgren, Raji, Marinkovic, Jousmaeki and Hari (2000) found effects 110 milliseconds post-stimulus). These early-latency ERP studies have demonstrated an influence of emotional versus neutral facial expressions on the P1 ERP, which has been established as a marker of affect processing (Keil, Bradley, Hauk, Rockstroh, Elbert & Lang, 2002). Facial processing studies have thus demonstrated the early onset of emotional facial

expression processing but have not yet addressed potential effects of valence on such processing. For instance, Eimer and Holmes (2002) used only fearful and neutral facial expressions in their study, precluding a more thorough exploration of positive, neutral, and negative valence effects on facial expression processing. In support of late-latency emotional effects, Ashley, Vuilleumier and Swick (2004) found enhanced ERP positivity for emotional as compared to neutral faces beginning approximately 180 milliseconds after stimulus onset; the P200 amplitude also distinguished between happy and fearful facial expressions, and an N300 amplitude later distinguished disgusted facial expressions from happy and fearful facial expressions (other studies have similarly established late-latency effects of emotional processing: Balconi and Lucchiari (2007), Balconi and Pozzoli (2008), Carretié and Iglesias (1995), Eimer, Holmes and McGlone (2003), and Krolak-Salmon, Fischer, Vighetto and Mauguière (2001) discovered differentiation between emotional and non-emotional facial expressions ranging from 220 to 250 milliseconds post-stimulus; Balconi and Pozzoli (2003) found differentiation between high-arousal facial expressions and low-arousal facial expressions approximately 230 milliseconds post-stimulus). Collectively, these findings point to early-latency neuronal processes that distinguish between broad emotional and non-emotional categories (with potential valence effects remaining purely speculative) and late-latency neuronal processing that distinguish among more refined emotional categories (Blau, Maurer, Tottenham & McCandliss, 2007).

Valence Processing of Emotional Facial Expressions

Research has largely substantiated the overarching existence of early- and late-latency emotional facial expression processing and has also demonstrated the fine-grained categorization of basic emotions at later latencies. However, the effect of valence on early-latency processing of emotional facial expression remains unclear. Only one study has specifically explored the effect of emotional valence on early-latency facial expression processing: Herrmann et al. (2002) used an indirect task in

which participants were asked to silently classify slides as a face (i.e., happy, neutral, and sad facial expression stimuli) or as a building; ERP amplitude and latency values for the three different valence facial expressions did not differ significantly. These null findings likely reflect critical methodological oversights, which appear prevalently throughout emotional processing research as well (Ashley, Vuilleumier & Swick, 2004; Balconi & Pozzoli, 2003; Herrmann et al., 2002; Pizzagalli, Lehmann, Hendrick, Regard, Pascual-Marqui & Davidson, 2002; Pizzagalli, Regard & Lehmann, 1999). A common denominator in the null findings of emotional facial expression processing research has been task type, particularly the use of indirect tasks (i.e., a task requiring explicit processing of non-emotional information or requiring the passive viewing of facial stimuli) as compared to direct tasks (i.e., a task requiring explicit processing of emotion). Holmes, Vuilleumier and Eimer (2003) found that when emotional information for face stimuli was directly attended, emotional effects were present. However, these emotional effects were completely eliminated on trials where face stimuli were presented but participants were not required to attend to the emotional information. Habel et al. (2007) also determined that bilateral amygdala activation was severely reduced when participants were required to discern age (indirect task) as opposed to emotion (direct task) (Batty & Taylor, 2003; Calder, Lawrence & Young, 2001). Thus, only tasks in which participants directly judged emotional expression reliably reveal early-latency effects of emotional processing (Eimer, Holmes & McGlone, 2003). These findings illustrate the importance of an explicit valence-processing task in studies exploring the effects of valence on facial expression processing and explain the absence of significant early-latency effects of valence in Herrmann et al.'s (2002) study. Other methodological limitations include the use of only a few facial expression photographs, shown repeatedly to subjects, without considering the effects of habituation (e.g., Herrmann et al.'s (2002) study only used 12 stimulus photographs); the use of a limited number of EEG channels during ERP recording, which restricts analysis to waveforms at select locations that

are reference-dependent and of limited sensitivity (e.g., Herrmann et al.'s (2002) study looked only at the Cz electrode); and the use of a narrow range of emotional facial expressions, which fails to exhaustively examine the emotional content of faces and its effect on ERPs (e.g., the facial expression photographs for Herrmann et al.'s (2002) study only depicted happy, sad, and neutral facial expressions). Accordingly, the effects of valence on emotional facial expression processing remain uncertain due to the paucity of research in this field as well as, in large part, to methodological limitations.

Objectives

In an effort to delineate the effects of valence on early-latency emotional facial expression processing, the current investigation compared behavioral and ERP responses to positive, neutral, and negative basic facial expression photographs (i.e., afraid, happy, neutral, sad, and surprise facial expressions) as well as to positive, neutral, and negative morph facial expression photographs (i.e., computer-generated morphs of the four prototypical facial expressions: afraid-surprise, happy-afraid, happy-sad, happy-surprise, sad-afraid and sad-surprise) during an explicit valence-rating task. The following section details the three primary objectives of the current study.

First Objective. This study attempted to establish and clarify the early-latency valence processing of emotional facial expressions through the use of a direct, valence-rating task and an emotional morphing manipulation. As noted, previous null findings of emotional facial expression processing studies have been linked to the use of indirect tasks to investigate particular components of facial expression processing (Balconi & Lucchiari, 2007; Hess, Philippot & Blairy, 1998; Krolak-Salmon, Fischer, Vighetto & Mauguière, 2001). In order to ensure that emotional information was attended, particularly valence, the current investigation employed a direct task in which participants were asked to provide valence ratings (from very negative to very positive) for the displayed facial expression photographs. As concerns the use of emotional morphing manipulations, previous

studies have used stimulus manipulation (e.g., facial inversion or morphing) in an effort to disturb and thus modulate the processing effects of facial identification as well as emotion recognition (Eimer & Holmes, 2007). Balconi and Lucchiari (2005) used morph structural facial expressions in order to disrupt facial patterns and to influence the structural processing of facial stimuli. Findings revealed that morph structural facial expressions elicited increased N170 peak amplitude compared to basic facial expressions. As the N170 ERP has largely been associated with the structural processing of facial expressions, the enhanced ERP for morph facial expressions may have reflected the increased difficulty in structural processing of unfamiliar or abstract structural patterns (Eimer & Holmes, 2007). Within the present investigation, emotional morph facial expressions were used in an effort to decrease the familiarity of the emotional patterns and thus preclude any overlearned responses to specific basic emotions. By disrupting more detailed emotional identification, it was proposed that morph stimuli would elicit a valence response independent of specific identifiable emotion, which has been absent in previous investigations of basic emotional facial expressions. In order to explore the potential valence-enhancing effects of morphing manipulations, amplitude values of the affect-sensitive P1 ERP were investigated with respect to valence category and stimulus manipulation.

Second Objective. Bruce and Young (1986, 1998) suggest that there are functional components called codes that underlie seven distinct types of facial information (i.e., pictorial, structural, semantic, identity, name, expression, and facial speech). The authors further propose that each facial code is processed independently, such that different brain regions involved in the distinct aspects of face processing should be topographically separated. In line with this model of face processing, previous ERP findings have established that structural and emotional features of the face are subserved by dissociable neural substrates (Balconi & Lucchiari, 2005; Bruce & Young, 1986; Cauquil, Edmonds & Taylor, 2000; Eimer & Holmes, 2002; Eimer, Holmes & McGlone, 2003;

Holmes, Vuilleumier & Eimer, 2003). In an effort to validate the functional model proposed by Bruce and Young (1998), the current study investigated N170, face-sensitive ERP amplitude values, which have primarily been associated with structural processing of facial expressions, as a function of valence category and morphing manipulations (Balconi & Lucchiari, 2005; Bruce & Young, 1986; Cauquil, Edmonds & Taylor, 2000; Eimer & Holmes, 2002; Eimer, Holmes & McGlone, 2003; Holmes, Vuilleumier & Eimer, 2003).

Third Objective. Dense-array ERP recordings provide both high temporal and spatial resolution, allowing for identification of the time course as well as the regions activated during early-latency, valence-dependent facial expression processing. Accordingly, following evaluation of peak ERP amplitude and latency for components associated with emotional processing (P1 ERP; 85-135 milliseconds post-stimulus) and facial expression processing (N170 ERP; 145-190 milliseconds post-stimulus), the current study used source localization to identify active gyri within these time points. Source localization employs an inversion formula in order to retroactively calculate dipole activations in the cortex (i.e., the sources of the ERP activity). Based on previous imaging research, the P1 and N170 activation intensities (nA) for the amygdala, fusiform gyri, inferior occipital gyri, lingual gyri, orbital gyri, parahippocampal gyri, posterior cingulate cortex, rectal gyri, subcallosal gyri, and uncus were extracted and analyzed (Blau, Maurer, Tottenham & McCandliss, 2007; Pizzagalli, REGARD & Lehmann, 1999; Posner, Russell & Peterson, 2005). The left- and right-hemisphere dipole strength values for each of these regions were also analyzed as imaging studies have found greater right-hemisphere activation during processing of emotional facial expressions (Adolphs, Damasio, Tranel & Damasio, 1996; Kesler/West et al., 2001).

Hypotheses

Valence Ratings and Response Times. The valence-rating task was used to validate the presumed valence categories of facial expression stimuli within the study. Accordingly, it was

hypothesized that positive, neutral, and negative facial expression stimuli would receive high (i.e., positive), moderate (i.e., neutral), and low (i.e., negative) valence ratings, respectively. Additionally, valence ratings and response times were used to confirm that morphing manipulations reduced the familiarity of the morph facial expression stimuli while maintaining the valence properties of their basic facial expression components. In order to confirm the morphing manipulation effect on familiarity, it was hypothesized that response times (RTs) for morph facial expressions would be slower than those for basic facial expressions; this prediction was in keeping with Schweinberger, Burton and Kelly's (1999) finding that emotion classification speed was slowed for ambiguous stimuli. In order to confirm that morphing manipulations did not alter valence properties, it was hypothesized that positive, neutral, and negative morph facial expression stimuli would receive identical valence ratings to the corresponding positive, neutral, and negative basic facial expression stimuli.

P1 ERP. Previous research on affective, non-facial images has established effects of valence approximately 90 to 120 milliseconds post-stimulus tied to the P1 ERP. It was hypothesized that valence processing of facial expression would influence this P1, affect-sensitive ERP too (Eger, Jedynek, Iwaki and Skrandies, 2003; Eimer & Holmes, 2002; Halgren, Raij, Marinkovic, Jousmaeki & Hari, 2000). Specifically, as morphing manipulations were used to modulate valence processing, it was predicted that effects of early-latency valence processing on peak amplitude would be more apparent in morph emotional facial expressions than basic emotional facial expressions (Batty & Taylor, 2003; Eger, Jedynek, Iwaki & Skrandies, 2003; Eimer & Holmes, 2007). Furthermore, as Dufey, Hurtado, Fernanández, Manes and Ibáñez (2010) determined that negative image stimuli presented a greater posterior P1 amplitude, followed closely by neutral image stimuli, and finally by the positive image stimuli with the lowest amplitude, a similar effect of valence on P1 amplitude was hypothesized within the current study (i.e., with negative morph facial expression photographs

eliciting the greatest P1 ERP activity, followed by neutral morph facial expressions, and then positive morph facial expressions). Based on previous imaging findings for emotional processing of facial expressions, it was predicted that neuronal activation during valence processing would occur primarily within the mesolimbic dopamine system (Adolphs, 2002a; Adolphs, 2003; Batty & Taylor, 2003; Lane et al., 1997; Whalen, Rauch, Etcoff, McInerney, Lee & Jenike, 1998). However, imaging research has yet to establish which brain regions elicit more or less activity in response to positive and negative facial expression stimuli; thus, no specific predictions were advanced as to whether positive or negative facial expressions would elicit stronger activity within the regions of interest.

N170 ERP. Based on previous theories and findings that structural and semantic features of the face are processed independently, it was hypothesized that facial structure and facial emotion would be processed separately and that valence processing of facial expressions would not influence the N170, face-sensitive ERP (Balconi & Lucchiari, 2005; Bruce & Young, 1986; Cauquil, Edmonds & Taylor, 2000; Eimer & Holmes, 2002; Eimer, Holmes & McGlone, 2003; Holmes, Vuilleumier & Eimer, 2003). This electrophysiological component reflects the encoding of facial structures and is not affected by face familiarity, facial expressions, or other identity factors (Eimer & Holmes, 2007). As the morphing procedure maintained basic structural properties of the valence of facial expressions, it was predicted that both basic and morphed emotional facial expressions would elicit similar N170 ERP responses across valence categories.

In sum, the purpose of the present study was to contribute to the understanding of temporal and spatial aspects of valence effects on early-latency emotional facial expression processing (the P1 ERP) and subsequent structural facial processing (the N170 ERP). In order to do so, ERP and source localization analyses were explored across the valence categories (positive, negative, and neutral) of both basic and morph facial expression photograph stimuli.

Method

Participants

Undergraduate student volunteers were recruited through an Introduction to Psychology course and through personal contacts. All participants gave informed consent and were compensated with extra course credit or a candy bar for their time. The sample comprised nineteen female participants between 18 to 22 years of age (mean: 19.16 years; SD 1.34 years). Out of nineteen initial participants, one was excluded due to technical problems that resulted in poor ERP data quality. Participation was entirely voluntary and in accordance with the Scripps College Institutional Review Board ethical guidelines.

Materials

Facial image stimuli were presented on a 27 cm x 34 cm Dell desktop computer monitor approximately 60 cm from the participant. A PC running E-Prime v2.0 (Psychology Software Tools, Inc., Sharpsburg, PA) experimental software controlled the presentation of the stimuli as well as the recording of behavioral responses. Electroencephalographic signals were recorded from 256 scalp sites using the Geodesic EEG Net Station v4.4.2 (Electrical Geodesics, Inc., Eugene, OR) and the 256-channel HydroCel Geodesic Sensor Net.

Affectively neutral, positive (happy and surprise), and negative (sad and afraid) facial expression stimuli were selected from the Karolinska Directed Emotional Faces inventory (KDEF; Lundqvist, Flykt, Öhman, 1998). The set contains 70 individuals, each displaying seven different emotional facial expressions, with each expression being color-photographed twice from five different angles. Of these, ten individuals with the most positive 'surprise' facial expression were selected on the basis of quantitative valence ratings from a pilot study (see Figure 1a). This was to ensure that the 'surprise' facial expression stimuli were positive and not negative in valence. Whereas happy, sad, and afraid belong to discrete valence categories, surprise can be positive or negative (Adolphs,

2002b; Kim, Somerville, Johnstone, Alexander & Whalen, 2003). Accordingly, within a preliminary study, the ‘surprise’ facial expressions were rated on a seven-point scale (1 = very negative, 2 = negative, 3 = slightly negative, 4 = neutral, 5 = slightly positive, 6 = positive, 7 = very positive). The photographs selected for the present study possessed a ‘surprise’ facial expression that fell between a positive and very positive valence rating (mean: 6.62; SD: 1.55), which ensured that ‘surprise’ facial expression stimuli were positive in valence. Originally, both male and female photographs were going to be included within this investigation. However, most of the ‘surprise’ facial expression photographs rated as being positive were of women, so men were excluded in order to preserve the positive valence of the surprise facial expression photographs. This should not have influenced results as Ito and Urland (2005) have demonstrated that the N170 component, which falls within the time segment of interest in this study, is not affected by gender of photographed faces.



Figure 1. a) The ‘surprise’ facial expression photographs of ten female KDEF photograph sets selected as stimuli within this study; b) A single set of basic facial expressions (top row; happy, surprise, neutral, afraid, and sad) and morph facial expressions (bottom row; happy-surprise, happy-afraid, happy-sad, sad-surprise, sad-afraid, and afraid-surprise).

In addition to five basic facial expressions (afraid, happy, neutral, sad and surprise), six morph facial expressions (afraid-surprise, happy-afraid, happy-sad, happy-surprise, sad-afraid and sad-surprise) were used in this study (see Figure 1b). The morphs were formed using a three part process of delineation, shape interpolation, and warping in Morpheus (Morpheus Software, LLC, Santa Barbara, CA) to blend between pairs of the afraid, happy, sad and surprise facial expression stimuli for each individual in a 50:50 proportion (i.e., halfway between a happy facial expression and a sad facial expression) (Young, Rowland, Calder, Etcoff, Seth & Perrett, 1996). All facial expression photographs were placed behind a black mask with an oval opening with hair, neck and background information occluded.

Behavioral Design and Procedure

Research was conducted in a single session lasting approximately 45 minutes to one hour. After written consent was obtained to participate in an experimental protocol approved by Scripps College, participants were prepared for ERP recording and given instructions on the valence-rating task. This task phase of the study comprised 275 trials, with each of the 11 emotion conditions (afraid, happy, sad, surprise, neutral, afraid-surprise, happy-afraid, happy-sad, happy-surprise, sad-afraid, and sad-surprise) presented exactly five times within each of five blocks; the photographed individual displaying the emotion was chosen at random on each trial from a set of 10 models. In each trial, a fixation cross appeared for 50 milliseconds, followed by a randomly selected facial expression photograph measuring 16 cm x 11 cm. This photograph remained on the screen until the participant had rated the valence of the facial expression on a visual seven-point scale (from left to right: very negative, negative, slightly negative, neutral, slightly positive, positive, very positive) (see Figure 2). Participant ratings were used after the fact to validate the presumed valence categories of facial expression stimuli within the study (e.g., happy facial expressions were categorized as having positive valence and, accordingly, should have received high valence ratings);

additionally, ratings and response times were used to confirm that morphing manipulations reduced the familiarity of the morph facial expression stimuli (e.g., participants should have responded more slowly to morph facial expressions than to basic facial expressions) while maintaining the structural and valence properties of their basic facial expression components (e.g., happy-surprise facial expressions should also have received high valence ratings because the morph is composed of two positive facial expressions).

Electrophysiological Procedure and Analysis

The EEG activity was sampled at 250 Hz with the vertex electrode as the online reference. Gain calibration was performed prior to the start of every recording and impedances for all channels were kept below 100 k Ω .

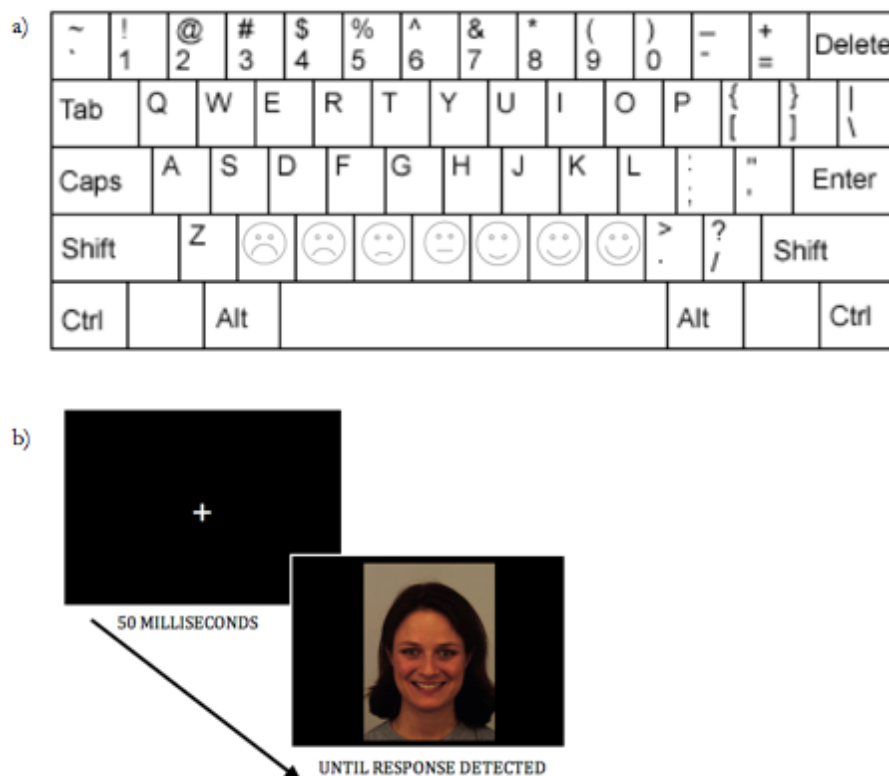


Figure 2. a) The seven-point visual valence scale (from left to right: very negative, negative, slightly negative, neutral, slightly positive, positive, very positive); b) In each trial, a fixation point appeared for 50 milliseconds, followed by a randomly chosen photograph, which remained on the screen until the participant had rated the valence of the emotional facial expression.

Initial off-line processing of the EEG data was performed using Net Station software v4.4.2 (Electrical Geodesics, Inc., Eugene, OR). A 40 Hz low pass filter and a 0.3 Hz high pass filter were applied in order to remove noise related to peripheral electrical equipment and the DC amplifier. Stimulus-locked ERP intervals were computed using a 600-millisecond epoch (200 milliseconds pre-stimulus and 400 milliseconds post-stimulus). Eleven event categories were used to segment the continuous data and compute single-subject averages: afraid, happy, sad, surprise, neutral, afraid-surprise, happy-afraid, happy-sad, happy-surprise, sad-afraid, and sad-surprise facial expression conditions.

Artifact detection criteria were defined with respect to the segment zero point, which included the entirety of the 600-millisecond epoch. A recording segment was marked for rejection if it contained more than 10 bad channels; channels were marked for rejection that contained more than 20% bad segments across the entire recording. A channel was marked bad when the differential average amplitude exceeded 200 μV , when the channel showed an eye blink ($>140 \mu\text{V}$ in electrodes above and below the eyes), or when the channel showed an eye movement (55 μV in electrodes lateral to the eyes). Data in bad channels were interpolated using spherical spline interpolation including all channels on the surface of the head, and ocular artifact removal (OAR) was applied in order to separate eye blinks from eye movements so that the proper correction factors could be applied. Following OAR, bad channel replacement was reapplied. ERP data were then averaged, corrected for a 200-millisecond baseline, and re-referenced to an average of all 256 electrodes.

Mean ERPs were computed for each subject. The emotion categories were then collapsed to form six categories: positive basic valence (happy and surprise); neutral basic valence; negative basic valence (sad and afraid); positive morph valence (happy-surprise morph); neutral morph valence (afraid-surprise, happy-afraid, happy-sad, and sad-surprise morphs); and negative morph valence

(sad-afraid morph). The ERPs for each valence and stimulus manipulation type were visualized topographically in Net Station.

Similar to prior facial expression research, extraction of peak amplitude measures was centered on the P1 maximum (84-134 milliseconds post-stimulus) as well as the N170 minimum (144-189 milliseconds post-stimulus). Average ERPs for each participant were extracted from both an electrode cluster close to the P3 site in the International 10-20 system (electrodes numbered 76, 77, 85, 86, 87, 97, 98) and an electrode cluster close to the P4 site (electrodes numbered 152, 153, 161, 162, 163, 171, 172). ERPs for parietal electrodes, particularly the P3 and P4 electrodes, have revealed early-latency valence processing effects in previous studies (Balconi & Pozzoli, 2003; Pizzagalli, Regard & Lehmann, 1999). Examination of grand averages indicated that they also did so here. Three-way, repeated measures Analysis of Variance (ANOVA) was carried out on the P1 and N170 peak amplitude values as a function of the within-subjects variables of valence (positive, neutral, and negative), stimulus manipulation (basic and morph), and side (left and right).

Source Localization Analysis

Source localization was performed on the pre-processed EEG data using GeoSource software, v2.0 (Electrical Geodesics, Inc., Eugene, OR). A standard, coregistered set of electrode positions was applied to a finite difference head model. Sources were then calculated under the sLORETA constraint with a Tikhonov regularization of 1×10^{-2} using a distributed inverse solving solution, which possesses a lower false error rate than minimum norm estimation (MNE). The source space was restricted to 2,447 cortical voxels that were each assigned to a gyrus on the basis of the Montreal Neurological Institute (MNI) probabilistic atlas. Based on previous findings, the P1 and N170 activation intensities (nA) for the amygdala, fusiform gyri, inferior occipital gyri, lingual gyri, orbital gyri, parahippocampal gyri, posterior cingulate cortex, rectal gyri, subcallosal gyri, and uncus were extracted (Blau, Maurer, Tottenham & McCandliss, 2007; Pizzagalli, Regard & Lehmann, 1999;

Posner, Russell & Peterson, 2005). Three-way, repeated measures ANOVA was carried out on the activation values of these regions as a function of the within-subjects variables of valence (positive, negative, and neutral), stimulus manipulation (basic and morph), and hemisphere (left and right).

Results

Subjective Valence Ratings and Response Times

ANOVA was carried out on participant's mean valence ratings as a function of the within-subjects variable of valence, which was computed by collapsing the eleven emotion facial expression categories into the six valence categories. There were significant differences in valence ratings among the six collapsed categories, $F(5,80) = 284.00$, $MSE = 0.12$, $p < .01$ (see Figure 3). Consistent with the research hypothesis, positive basic facial expressions ($M = 5.44$, $SD = 0.53$) and positive morph facial expressions ($M = 5.36$, $SD = 0.65$) did not differ significantly in their valence ratings, $t(16) = -1.15$, $p = .269$, and were rated as significantly more positive than other valence categories of facial expressions; neutral basic facial expressions ($M = 3.70$, $SD = 0.32$) and neutral morph facial expressions ($M = 3.6$, $SD = 0.52$) did not differ significantly in their valence ratings, $t(16) = 0.93$, $p = 0.37$, and were rated a significantly less positive than positive valence facial expressions but more positive than negative valence facial expressions; and both negative basic facial expressions ($M = 2.2$, $SD = 0.30$) and negative morph facial expressions ($M = 2.39$, $SD = 0.32$) were rated as significantly more negative than the other valence categories of facial expressions ($df = 16$, $p < .01$ for all t-tests). Though negative morph facial expressions were rated more positively than negative basic facial expressions, $t(16) = -3.60$, $p = .002$, the difference in ratings was very small (~ 0.19) and the ratings for both valence categories still fell within the "slightly negative" to "negative" range.

A paired-samples t-test was carried out on participant's mean response times for basic and morph facial expression stimuli. Consistent with the hypothesis, there was a significant difference in

response times as a function of stimulus manipulation, $t(1,17) = -3.315, p = .004$, such that participants responded more slowly to morph facial expressions ($M = 2066.81$ milliseconds, $SD = 751.35$ milliseconds) than to basic facial expressions ($M = 1875.41, SD = 653.56$).

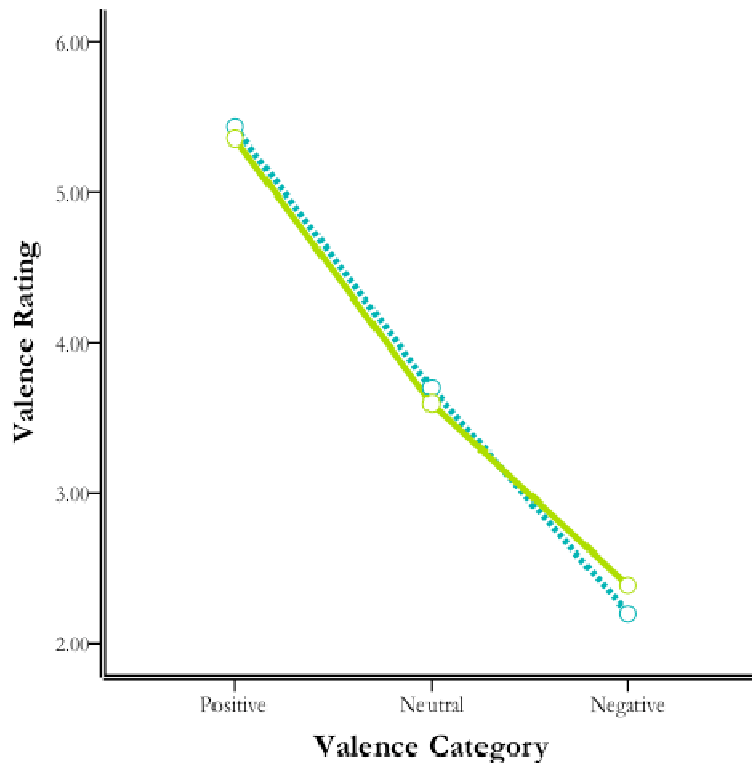


Figure 3. Mean valence ratings based on a seven-point scale (1 = very negative; 7 = very positive) for both basic facial expressions (blue dotted line) and morph facial expressions (green solid line) as a function of valence category (positive, neutral, and negative). Positive basic and positive morph (positive-positive) facial expressions received more positive ratings than the other valence categories; neutral basic and neutral morph (positive-negative) facial expressions received more negative ratings than positive valence categories and more positive ratings than negative valence categories; negative basic and negative morph (negative-negative) facial expressions received more negative ratings than the other valence categories.

Event-Related Potential Difference Waves

Three-way, repeated measures ANOVA was carried out on the P1 peak amplitude values (see Table 1) and N170 peak amplitude values (see Table 2) as a function of the within-subjects variables of valence (positive x neutral x negative), stimulus manipulation (basic x morph), and side (left x right). In order to rule out extraneous effects on peak amplitude values, three-way, repeated measures ANOVA was also carried out on P1 and N170 peak latencies.

P1 Amplitude. Consistent with the hypothesis that the P1 ERP reflects early-latency valence processing, there was a significant main effect of valence on P1 peak amplitude values, $F(2,34) = 5.81, MSE = 0.96, p = .007$, such that negative valence stimuli ($M = 1.35 \mu V, SD = 0.70 \mu V$) elicited

significantly higher peak amplitude values than positive valence stimuli ($M = 0.90 \mu\text{V}$, $SD = 0.74 \mu\text{V}$), $t(17) = -2.74$, $p = .014$. Additionally, neutral valence stimuli ($M = 1.13 \mu\text{V}$, $SD = 0.67 \mu\text{V}$) elicited marginally lower peak amplitude values than negative valence stimuli, $t(17) = -1.93$, $p = .070$, and marginally higher peak amplitude values than positive valence stimuli, $t(17) = -1.84$, $p = .083$. Peak P1 amplitude values revealed no other significant main effects or two-way interactions between within-subjects variables.

Consistent with the hypothesis that morphing manipulations would influence valence processing, the three-way interaction between valence, stimulus manipulation, and side was significant as well, $F(2,34) = 4.92$, $MSE = 1.40$, $p = .013$. Follow-up ANOVAs for left- and right-side P1 amplitude values as a function of valence and stimulus manipulation revealed no significant effects within the left electrode cluster and no significant main effect of stimulus manipulation within the right electrode cluster. In keeping with the significant main effect of valence on P1 peak amplitude values though, a follow-up ANOVA for right-side P1 amplitude values again revealed a significant effect of valence, $F(2,34) = 4.89$, $MSE = 1.18$, $p = .014$, such that negative valence stimuli ($M = 1.50 \mu\text{V}$, $SD = 1.29 \mu\text{V}$) elicited significantly higher peak amplitude values than positive valence stimuli ($M = 1.02 \mu\text{V}$, $SD = 1.29 \mu\text{V}$), $t(17) = -2.25$, $p = .038$. Neutral valence stimuli ($M = 1.27 \mu\text{V}$, $SD = 1.18 \mu\text{V}$), however, elicited peak amplitude values that did not differ from positive or negative peak amplitude values. There was also a significant interaction between valence and stimulus manipulation, $F = (2,34) = 4.60$, $MSE = 1.80$, $p = .017$ (see Figure 4). Post-hoc t-tests for the interaction effect revealed that positive morph facial expressions elicited significantly lower peak amplitude values than all other valence categories and that negative morph facial expressions elicited significantly higher peak amplitude values than the other two morph valence facial expressions. Accordingly, negative morph facial expressions elicited the highest right-side P1 peak amplitude values, followed by neutral morph facial expressions, and then by positive morph facial expressions.

While valence effects on P1 peak amplitude values appeared between morph facial expressions (as well as between basic and morph facial expressions), no valence effects appeared between basic facial expressions. The three-way interaction thus primarily reflected significant valence effects on the right-side P1 peak amplitude values for morph facial expressions.

Table 1

Mean P1 Amplitude Values (in μV) as a Function of Valence Category

| Valence Category | Left Side | | Right Side | | Both Sides | |
|------------------|-----------|------|------------|------|------------|------|
| | Mean | SD | Mean | SD | Mean | SD |
| Positive Basic | 0.62 | 0.68 | 1.31 | 1.28 | 0.96 | 0.70 |
| Positive Morph | 1.08 | 0.96 | 0.44 | 1.75 | 0.76 | 0.99 |
| Neutral Basic | 0.93 | 0.96 | 1.69 | 1.72 | 1.31 | 1.07 |
| Neutral Morph | 1.01 | 0.69 | 1.16 | 1.19 | 1.09 | 0.68 |
| Negative Basic | 1.24 | 0.72 | 1.19 | 1.26 | 1.22 | 0.73 |
| Negative Morph | 1.10 | 0.97 | 2.12 | 2.27 | 1.61 | 1.16 |

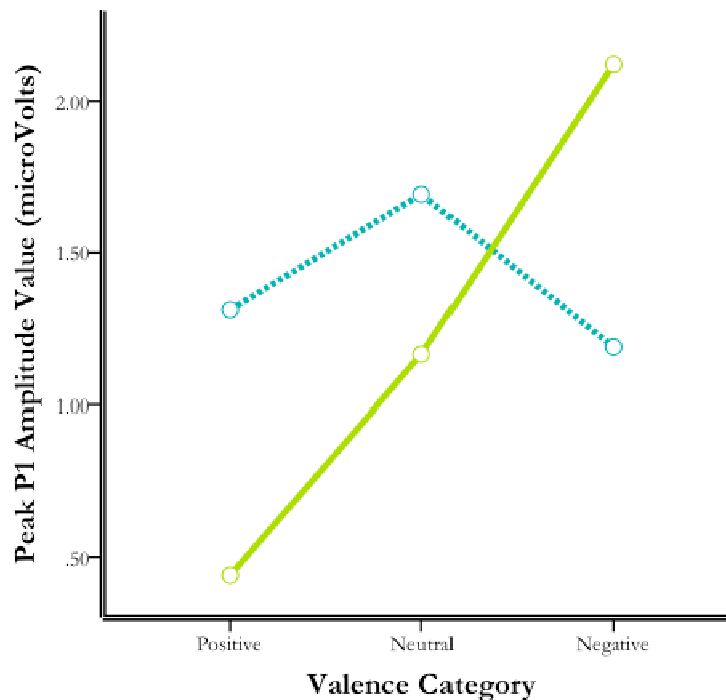


Figure 4. Averaged right-side P1 peak amplitude values for both basic facial expressions (blue dotted line) and morph facial expressions (green solid line) as a function of valence category (positive, neutral, and negative). The interaction between valence, stimulus manipulation, and side largely reflects significant valence effects on the right-side P1 peak amplitude values for morph facial expressions.

P1 Latency. Consistent with the findings from Balconi and Lucchiari's (2005) study on structural morphing of facial expressions, there were no significant main effects or interaction effects of valence, stimulus manipulation, and side on P1 latency values. The clustering of peak P1 latency values at approximately 108 milliseconds post-stimulus indicates that early-latency processing of emotional facial expressions follows a similar timeline across valence categories.

N170 Amplitude. Consistent with Bruce and Young's (1986, 1998) model of facial processing, there were no significant main effects (valence: $F(2,34) = 1.62$, $MSE = 1.26$, $p = .212$; stimulus manipulation: $F(1,17) = 0.21$, $MSE = 1.30$, $p = .652$; side: $F(1,17) = 0.31$, $MSE = 7.44$, $p = .582$) and no two-way interactions of valence and stimulus manipulation, $F(2,34) = 0.38$, $MSE = 0.89$, $p = .689$, or stimulus manipulation and side, $F(1,17) = 2.16$, $MSE = 0.45$, $p = .160$, on N170 peak amplitude values. There was a significant interaction between valence and side, $F(2,34) = 3.80$, $MSE = .924$, $p = .032$, but post-hoc t-tests revealed no significant effect of side on valence conditions; the absence of simple effects suggests that any differences resulting in an interaction were negligible. Inconsistent with the hypothesis that valence and structural processing are independent processes, though, the three-way interaction between valence, stimulus manipulation, and side was significant, $F(2,34) = 3.68$, $MSE = 1.16$, $p = .036$. Follow-up ANOVAs for left-side N170 amplitude values as a function of valence and stimulus manipulation revealed no significant main or interaction effects. For right-side N170 amplitude values, there also was no significant effect of stimulus manipulation and no significant interaction effect between valence and stimulus manipulation. A follow-up ANOVA for right-side N170 amplitude values, though, revealed a marginally significant effect of valence, $F(2,34) = 3.28$, $MSE = 1.64$, $p = .050$ (see Figure 5). Post-hoc t-tests for right-side N170 peak amplitude values showed that negative morph facial expressions elicited significantly lower peak amplitude values than all other valence categories. Similar to the valence, stimulus manipulation, and side interaction found for P1 peak amplitude values, the N170 interaction

predominantly reflected significant valence effects on the right-side peak amplitude values; however, whereas P1 valence effects were found for positive, neutral, and negative morph facial expressions, N170 valence effects were only found for negative morph facial expressions.

Table 2

Mean N170 Amplitude Values (in μV) as a Function of Valence Category

| Valence Category | <u>Left Side</u> | | <u>Right Side</u> | | <u>Both Sides</u> | |
|------------------|------------------|------|-------------------|------|-------------------|------|
| | Mean | SD | Mean | SD | Mean | SD |
| Positive Basic | -2.08 | 1.65 | -2.08 | 1.72 | -2.08 | 1.39 |
| Positive Morph | -1.68 | 2.03 | -2.49 | 2.11 | -2.08 | 1.67 |
| Neutral Basic | -1.64 | 1.78 | -2.41 | 2.13 | -2.03 | 1.46 |
| Neutral Morph | -1.91 | 1.75 | -2.17 | 1.59 | -2.02 | 1.45 |
| Negative Basic | -1.76 | 1.40 | -2.01 | 1.64 | -1.88 | 1.33 |
| Negative Morph | -2.08 | 2.28 | -1.23 | 1.98 | -1.65 | 1.97 |

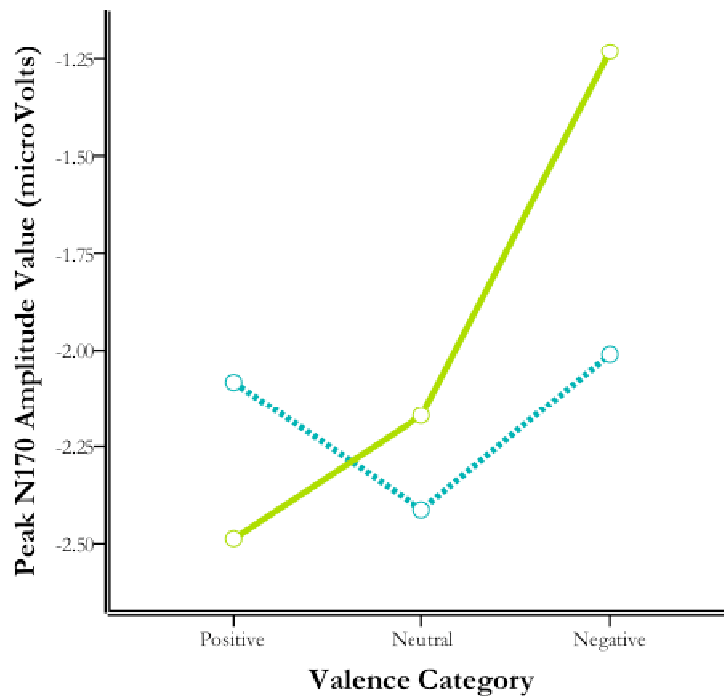


Figure 5. Averaged right-side N170 peak amplitude values for both basic facial expressions (blue dotted line) and morph facial expressions (green solid line) as a function of valence category (positive, neutral, and negative). The interaction between valence, stimulus manipulation, and side largely reflects significant valence effects on the right-side N170 peak amplitude values for negative morph facial expressions.

N170 Latency. Consistent with previous research, there were no significant main effects or interaction effects of valence, stimulus manipulation, and side on N170 latency values (Balconi and Lucchiari, 2005). The clustering of peak N170 latency values at approximately 164 milliseconds post-stimulus again demonstrates that processing of emotional facial expressions follows a similar timeline regardless of stimulus valence.

Source Localization

In order to localize the source of P1 and N170 activity, the average dipole strength was determined for all cortical gyri. Substantial gyral activation occurred within reported structural and emotional face processing neural networks. For both the P1 ERP at 108 milliseconds post-stimulus and the N170 ERP at 164 milliseconds post-stimulus, source localization revealed the greatest dipole activation within the limbic lobes (amygdala, parahippocampal gyri, posterior cingulate, and uncus), the frontal lobes (orbital gyri, rectal gyri, and subcallosal area), the occipital lobes (inferior occipital gyri and lingual gyri), and the fusiform gyri. Previous research has emphasized the role of the amygdala, fusiform gyri, inferior occipital gyri, orbital gyri, parahippocampal gyri, posterior cingulate, and uncus in emotional facial expression processing (Adolphs, 2002a; Adolphs, 2003; Adolphs, Damasio, Tranel & Damasio, 1996; Jehna et al., 2011; Lane et al., 1997; Whalen, Rauch, Etcoff, McInerney, Lee & Jenike, 1998). Subsequent analysis accordingly evaluated the P1 and N170 dipole strength values within these seven regions as a function of valence (positive, neutral, and negative), stimulus manipulation (basic and morph), and hemisphere (left and right).

P1 Regions of Activation. Consistent with evidence that the amygdala, fusiform gyri, parahippocampal gyri, and uncus are involved in processing of emotional facial expressions, dipole strength values within these regions revealed a significant main effect of valence approximately 108 milliseconds post-stimulus (amygdala: $F(2,34) = 3.67$, $MSE = 22.68$, $p = .036$; fusiform gyri: $F(2,34) = 4.09$, $MSE = 13.17$, $p = .026$; parahippocampal gyri: $F(2,34) = 4.42$, $MSE = 17.21$, $p = .020$;

uncus: $F(2,34) = 3.74$, $MSE = 27.16$, $p = .034$). Consistent with evidence that the amygdala and uncus are involved in the processing of fear, amygdala and uncus dipole strength values for negative facial expressions were significantly greater than those for positive facial expressions, $t(17) = -2.81$, $p = .012$ and $t(17) = -2.52$, $p = .022$, respectively. Similarly, dipole strength values within the fusiform gyri for negative facial expressions were significantly greater than those for positive facial expressions, $t(17) = 2.58$, $p = .019$. Dipole strength values for neutral facial expressions fell between did not differ from those for positive or negative facial expressions within the amygdala, fusiform gyri, and uncus, though. Within the parahippocampal gyri, dipole strength values for positive facial expressions were significantly lower than those for neutral facial expressions and negative facial expressions, $t(17) = -2.18$, $p = .044$ and $t(17) = -2.91$, $p = .010$, respectively. No other significant main effects or two-way interactions between valence, stimulus manipulation, and hemisphere were found within these regions.

Dipole strength values within the fusiform gyri and uncus did reveal three-way interactions between valence, stimulus manipulation, and hemisphere (fusiform gyri: $F(2,34) = 3.52$, $MSE = 4.85$, $p = .041$; uncus: $F(2,34) = 8.20$, $MSE = 9.81$, $p = .001$). Follow-up ANOVAs for left-and right-hemisphere dipole values as a function of valence and stimulus manipulation revealed a left-hemisphere main effect of valence within the fusiform gyri and uncus (fusiform gyri: $F(2,34) = 5.99$, $MSE = 6.23$, $p = .006$; uncus: $F(2,34) = 3.54$, $MSE = 20.21$, $p = .040$), such that dipole strength values for negative facial expressions were significantly greater than those for positive facial expressions, $t(17) = -3.62$, $p = .002$ and $t(17) = 2.40$, $p = .028$ respectively. Additionally, there was a significant right-hemisphere interaction between valence and stimulus manipulation within the uncus, $F(2,34) = 1.06$, $MSE = 17.85$, $p = .358$, such that dipole strength values were greatest for negative morph facial expressions, followed by positive morph facial expressions, and then neutral

morph facial expressions. There were no other significant main effects or interaction effects within the left- and right-hemispheres of the fusiform gyri and uncus.

The inferior occipital gyri, orbital gyri, and posterior cingulate revealed a significant main effect of hemisphere approximately 108 milliseconds post-stimulus (inferior occipital gyri: $F(1,17) = 4.54$, $MSE = 12.48$, $p = .048$; orbital gyri: $F(1,17) = 35.66$, $MSE = 6.32$, $p < .001$; posterior cingulate: $F(1,17) = 4.51$, $MSE = 7.13$, $p = .049$). Consistent with evidence that facial expression processing primarily occurs within the right hemisphere, post-hoc t-tests revealed greater dipole strengths within the right hemisphere as compared to the left hemisphere (inferior occipital gyri: $t(17) = -2.13$, $p = .048$; orbital gyri: $t(17) = -5.98$, $p < .001$; posterior cingulate: $t(17) = -2.12$, $p = .049$). No other significant main effects or interactions between valence, stimulus manipulation, and hemisphere were found within these regions.

N170 Regions of Activation. Consistent with the Bruce and Young's (1986, 1998) model of facial processing, there were no significant main effects or interaction effects of valence, stimulus manipulation, and hemisphere on the N170 dipole strength values within the amygdala, fusiform gyri, posterior cingulate, and uncus approximately 164 milliseconds post-stimulus. Consistent with evidence that facial expression processing primarily occurs within the right hemisphere, the inferior occipital gyri and orbital gyri revealed a significant main effect of hemisphere (inferior occipital gyri: $F(1,17) = 11.56$, $MSE = 8.06$, $p = .003$; orbital gyri: $F(1,17) = 6.12$, $MSE = 0.02$, $p = .024$), such that dipole strength was greater in the right hemisphere than in the left hemisphere for both regions, $t(17) = -3.40$, $p = .003$ and $t(17) = -2.48$, $p = .024$ respectively. There was also a significant main effect of stimulus manipulation within the parahippocampal gyri, $F(1,17) = 5.09$, $MSE = 11.09$, $p = .038$, such that dipole strength values were greater for morph facial expressions ($M = 5.48$ nA, $SD = 1.98$ nA) than for basic facial expressions ($M = 4.46$ nA, $SD = 1.72$ nA), $t(17) = -2.25$, $p = .038$. As N170 peak amplitude values revealed an effect of negative morph facial expressions that was

conspicuously absent within the current source localization results, an additional analysis was conducted in order to compare activation of the mesolimbic dopamine system with surrounding gyri. Dipole strength was significantly greater within mesolimbic dopamine system (i.e., amygdala, cingulate gyri, fusiform gyri, hippocampal gyri, orbitofrontal gyri, parahippocampal gyri; $M = 3.30$ nAmp meters, $SD = 0.82$ nAmp meters) than the surrounding gyri (i.e., angular gyri, cuneus, inferior frontal gyri, temporal and parietal gyri, lingual gyri; $M = 1.73$ nAmp meters, $SD = 0.58$ nAmp meters), $t(17) = 11.90, p < .001$.

Discussion

Methodological Findings

The present study's morphing manipulations appear to have disrupted overlearned, automatic responses to specific basic emotions while retaining more general processing of facial expression valence (Balconi & Lucchiari, 2005). Schweinberger, Burton and Kelly (1999) have established that emotion classification speed is slowed for ambiguous stimuli morphed midway between basic emotional categories supports this theory. As similar morphing manipulations were used in the present investigation, the slowed behavioral response times for morph facial expression stimuli compared to basic facial expression stimuli may reflect increased difficulty in processing the unfamiliar emotion patterns of the morph stimuli. At the same time, the similar P1 and N170 ERP latencies across valence categories suggest that morphing manipulations did not disrupt more general early-latency valence processing (i.e., valence and structural processing approximately 108 to 164 milliseconds post-stimulus) of morph facial expression stimuli as compared with basic facial expression stimuli. Thus, valence processing appears to have been maintained and discrete processing of emotions disrupted within morph emotional facial expression stimuli.

The morph facial expressions also appear to have successfully retained the structure and valence properties of basic facial expression stimuli. Basic and morph emotional facial expressions did not

differ in terms of valence ratings: positive basic and morph facial expressions were rated more positively than other valence categories; negative basic and morph facial expressions were rated more negatively than other valence categories; and neutral basic and morph facial expressions received valence ratings that fell between those for positive and negative facial stimuli. As concerns structural properties of the morph stimuli, coherence between the salient structures of basic and morph facial expression stimuli was established through digital editing of the morph emotional facial expression stimuli. Further, N170 ERP amplitude values, which have been associated with the structural processing of facial expressions, did not vary between basic and morph facial expression stimuli. An effect of stimulus manipulation was found for the N170 dipole strength values within the parahippocampal gyri, which are primarily associated with familiarity-based memory discrimination (Yonelinas et al., 2002). Thus, the effect of stimulus manipulation within this region likely reflects differential familiarity processing of basic and morph facial expressions and not differential structural processing. Taken collectively, these findings suggest that basic and morph facial expressions retained similar structural and valence properties but that morphing manipulations altered or delayed processing of discrete emotions (Balconi & Lucchiari, 2005; Balconi & Pozzoli, 2003).

ERP Findings

The familiarity of basic emotional facial expressions allows individuals to rapidly identify discrete emotions and categorize affect (LeDoux, 1995; Russell, 1980). Because morphing facial expressions renders them unfamiliar to participants, it was hypothesized that morph emotional stimuli would disrupt overlearned emotional identification to reveal a valence response independent of specific identifiable emotions for the affect-sensitive P1 ERP but not for the structural-sensitive N170 ERP.

Effects of Morphing and Valence on P1 Peak Amplitude. Consistent with this hypothesis, ERP findings within the current study revealed the presence of early-latency valence effects on

emotional facial expression processing (i.e., the P1 ERP) for morph stimuli but not for basic stimuli. Scalp-recorded ERPs approximately 108 milliseconds post-stimulus revealed a significant main effect of valence, such that negative valence stimuli elicited significantly higher P1 peak amplitude values than positive valence stimuli (see Figure 6). Findings further revealed significantly higher right-side peak amplitude values for negative morph facial expressions than other morph facial expressions as well as significantly lower right-side peak amplitude values for positive morph facial expressions than other morph facial expressions (see Figure 7; top row). As there were no simple main effects for basic facial expression stimuli, the significant main effect of valence and three-way interaction between valence, stimulus manipulation, and side likely reflect valence effects for the processing of morph emotional facial expressions. Thus, the processing of valence categories for morph but not basic facial expressions preceded previously established latencies for processing of other facial expression codes (i.e., the N170 ERP; Adolphs, 2002b). These results establish the early-latency processing of valence in emotional facial expressions as well as the valence-modulating effects of morphing manipulations.

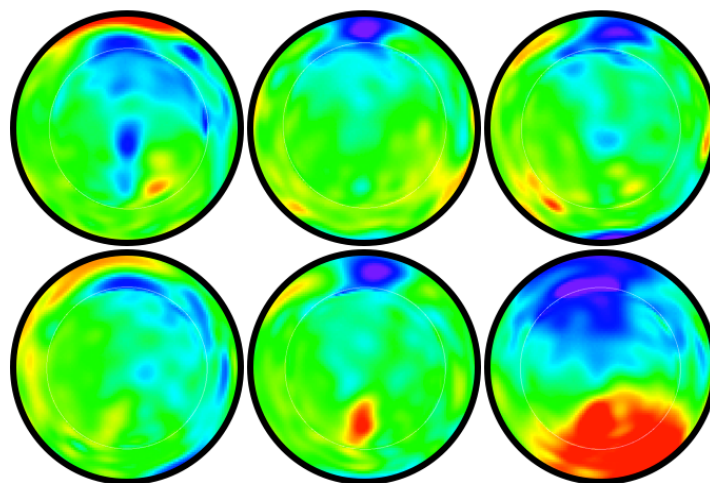


Figure 6. Topographic maps of basic emotional facial expression (top row) and morph emotional facial expression (bottom row) P1 ERPs for the three valence categories (from left to right: positive, neutral, and negative). Colors at the low end of the spectrum (i.e., purple and blue) represent low voltage values; colors at the high end of the spectrum (i.e., red, orange, and yellow) represent high voltage values; corresponding colors within the spectrum (i.e., green) represent intermediate values.

Emotional Modulation of N170 Peak Amplitude. Valence effects appear to have modulated subsequent processing of other facial expression codes as well. According to the two-stage model of face processing, the face-sensitive N170 ERP component reflects solely the structural encoding of facial expressions (Eimer, 2000; Eimer & Holmes, 2002; Liu, Harris & Kanwisher, 2002). Inconsistent with this model, scalp-recorded ERPs approximately 164 milliseconds post-stimulus revealed significantly lower right-side peak amplitude values for negative morph facial expressions than other morph facial expressions (see Figure 7). In keeping with the current finding, though, more recent evidence has suggested that the N170 may be modulated by emotional facial expressions (Batty & Taylor, 2003). For instance, Blau, Maurer, Tottenham and McCandliss (2007) found that N170 peak amplitude values for fear facial expressions significantly differed from peak amplitude values for neutral facial expressions. The present findings thus refute theories for discrete processing systems of facial codes and instead suggest a continuation of the negative valence effects from the P1 processing stage.

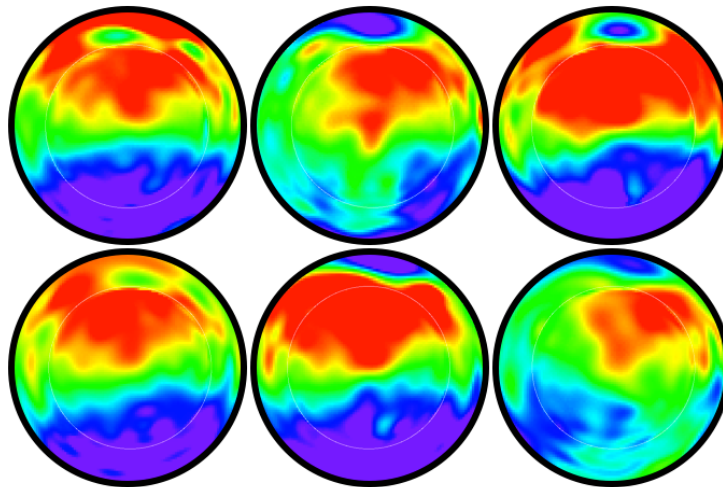


Figure 7. Topographic maps of basic emotional facial expression (top row) and morph emotional facial expression (bottom row) N170 ERPs for the three valence categories (from left to right: positive, neutral, and negative). Colors at the low end of the spectrum (i.e., purple and blue) represent low voltage values; colors at the high end of the spectrum (i.e., red, orange, and yellow) represent high voltage values; corresponding colors within the spectrum (i.e., green) represent intermediate values.

ERP Patterns for Basic Emotional Facial Expressions. Within the current study, the P1 and N170 ERPs revealed non-significant effects of valence for positive, neutral, and negative basic facial expressions. Inconsistent with these findings, recent ERP research has established early-latency differences between emotional and non-emotional facial expressions. These divergent results may have stemmed from methodological differences between the current investigation and past emotional facial expression processing studies. For instance, Eimer and Holmes (2002) determined that emotional facial expressions elicited greater P1 peak amplitude values than non-emotional facial expressions using two facial expressions (i.e., afraid and neutral). Accordingly, the absence of such an effect within the present investigation may have resulted from the use of several types of basic emotional facial expressions, which ranged in valence and arousal. The use of only one emotional facial expression in Eimer and Holmes's (2002) study may have resulted in sensitization to the discrete emotional properties of the fear stimuli. More specifically, sensitization may have reduced the processing of basic emotional facial expressions to produce an enhanced response to the negative valence of fear facial expressions. Within the current study, the inclusion of several types of basic emotional facial expressions may have prevented sensitization to specific basic emotional expressions, resulting in null valence effects. Previously collected ERP responses to discrete basic facial expressions should be further explored to test this hypothesis.

Enhanced Responses to Negative Morph Stimuli. Enhanced processing of negative stimuli has appeared consistently through the emotional processing literature (Ashley, Vuilleumier & Swick, 2003; Balconi & Pozzoli, 2003; Blau, Maurer, Tottenham & McCandliss, 2007; Batty & Taylor, 2003; Eimer & Holmes, 2002). It has been theorized that such an automatic and rapid response to emotionally salient, negative stimuli acts as a human safeguard, facilitating the survival of the human species through immediate and appropriate reaction to potential threats (Ellsworth & Scherer, 2003). The enhanced processing of negative morph facial expressions for both P1 and N170 ERPs within

the current study supports this theory that negative stimuli provoke adaptive and automatic responses. Further, the P1 response revealed a progressive decrease in right-side P1 peak amplitude values when shifting from negative to positive valence (i.e., negative morph facial expression stimuli elicited higher right-side P1 peak amplitude values than neutral morph facial expression stimuli, which elicited higher right-side P1 peak amplitude values than positive morph facial expression stimuli). Thus, the current P1 and N170 ERP results illustrate early-latency valence effects on emotional facial expression processing, particularly as concerns negative morph facial expressions, that modulate subsequent processing of other facial codes.

Source Localization Findings

Previous research has linked facial processing to the inferior occipital cortices and fusiform gyri and has linked emotional processing to the mesolimbic dopamine system (Adolphs, 2002a; Adolphs, 2003; Allison, Puce & McCarthy, 2000; Haxby, Hoffman & Gobbini, 2000; Jehna et al., 2011; Kanwisher, McDermott & Chun, 1997; Lane et al., 1997; Posner, Russell & Peterson, 2005; Whalen, Rauch, Etcoff, McInerney, Lee & Jenike, 1998). In keeping with these findings, substantial gyral activation occurred within the limbic lobes (amygdala, posterior cingulate cortex, parahippocampal gyri, and uncus), the frontal lobes (orbital gyri, rectal gyri, and subcallosal area), the occipital lobes (inferior occipital gyri and lingual gyri) and the fusiform gyri between 100-200 milliseconds post-stimulus presentation. Accordingly, activation of regions within the mesolimbic dopamine during this early-latency time frame were taken to illustrate that emotional properties of the facial expression stimuli were being encoded.

P1 Regions Involved in Valence Processing. Of the active P1 regions, the amygdala, fusiform gyri, parahippocampal gyri, and uncus revealed significant valence effects (see Figure 8). Specifically, dipole strength within the amygdala, parahippocampal gyri and uncus was significantly greater in response to negative facial expressions than positive facial expressions. Additionally, dipole strength

within the parahippocampal gyri was significantly greater in response to neutral facial expressions than positive facial expressions. These findings are consistent with the valence effects found for P1 peak amplitude values, which significantly distinguished between negative and positive valence stimuli and marginally distinguished between neutral and positive valence stimuli. Further, the amygdala as well as the adjacent parahippocampal gyri and uncus have been implicated in emotional facial expression processing, particularly in the recognition of threat-related stimuli and acquisition of fear-conditioned responses (Adolphs, 2002b; Anderson, Christoff, Panitz, De Rosa & Gabrieli, 2003; Armony & LeDoux, 2000; Morris, Ohman & Dolan, 1998; Morris, deBonis & Dolan, 2002; LeDoux, 1992; Vuilleumier, Armony, Driver & Dolan, 2001). Thus, the established roles of these three regions in processing threat-related stimuli correspond to the present activation patterns of valence processing within these three brain regions.

The fusiform gyri also revealed greater activation in response to negative facial expressions than positive facial expressions. Breiter et al. (1996) found that emotional expressions elicited increased fusiform activation in comparison with neutral faces, suggesting that fusiform activation may result from increased attention to emotional aspects of the stimuli via back projections from other regions, such as the amygdala and portions of the temporal lobe (Kesler/West et al., 2001). Similarly, within the current study, fusiform activation coincided temporally with activation of the amygdala and parahippocampal gyri, implicating the fusiform gyri in a nearly simultaneous feedback circuit with other valence processing regions. Further, dipole strength within the fusiform face area was greater for negative and positive morph facial expressions than for neutral facial expressions. The finding that emotional morphs elicited greater fusiform activity than neutral morphs is consistent with Breiter et al.'s (1996) proposal that activity within the fusiform gyri reflects increased attention to emotional aspects of the stimuli; these findings are also consistent with theories and evidence of enhanced processing for negative stimuli, as negative stimuli was consistently elicited greater activity

within the left and right fusiform gyri (Ashley, Vuilleumier & Swick, 2003; Balconi & Pozzoli, 2003; Blau, Maurer, Tottenham & McCandliss, 2007; Batty & Taylor, 2003; Eimer & Holmes, 2002).

Accordingly, the amygdala, fusiform gyri, parahippocampal gyri, and uncus – all found within the medial temporal lobe – were associated with rapid valence processing of emotional facial expressions, especially expressions of negative valence.

Dispersed N170 Activity. By contrast, source localization of the N170 ERPs revealed no effect of valence. The presence of a valence effect on N170 ERPs and the absence of such an effect with source localization suggests that the significant ERP findings reflected a widespread, enhanced response to negative facial expression stimuli that was dispersed throughout the mesolimbic dopamine system and fusiform gyri – as opposed to the P1 response, which was largely concentrated within the amygdala, fusiform gyri, and parahippocampal gyri. The enhanced dipole strength values for regions of the mesolimbic dopamine system as compared with gyral regions directly surrounding the mesolimbic dopamine system confirmed this widespread effect.

Right Hemisphere Lateralization. Hemispheric effects were found for P1 and N170 dipole strength values within the inferior occipital gyri, orbital gyri, and posterior cingulate. Consistent with previous ERP and imaging research, these regions elicited significantly greater activation in response to negative facial expressions as compared to positive facial expressions (Adolphs, Damasio, Tranel & Damasio, 1996; Batty & Taylor, 2003; Balconi & Lucchiari, 2007; Kesler/West et al., 2001; Pizzagalli, Regard & Lehmann, 1999). Thus, these lateralization findings add to evidence of a right-hemisphere advantage in the processing of facial expressions and, further, establish an early-latency right-hemisphere advantage during the valence processing of emotional facial expressions.

Source Localization Overview. In sum, source localization results converged with current ERP findings and previous imaging research. Early-latency processing peaking approximately 108 milliseconds post-stimulus within the amygdala, fusiform gyri, parahippocampal gyri, and uncus

appeared highly involved in valence processing. Those effects of early-latency valence processing then carried through and dispersed in subsequent processing of the facial expression stimuli throughout the mesolimbic dopamine system and fusiform gyri at approximately 164 milliseconds post-stimulus.

Conclusion

This investigation has demonstrated that early-latency processing of emotional facial expressions distinguishes between valence categories of morph facial expression stimuli but not between valence categories of basic facial expression stimuli. In particular, the valence effect is reflected in an early modulation of the P1 ERP, such that negative morph facial expressions enhance valence processing as compared to neutral and positive morph facial expressions. Additionally, contrary to the two-stage model of face processing, valence processing of negative morph facial expressions continued to modulate the later N170 ERP, which has previously been exclusively linked to structural processing of facial expressions. These findings are consistent with accounts that a rapid encoding system sensitive to the valence of emotional facial expressions modulates facial processing; and further, that this cannot be seen when the stimulus is a familiar specific emotion (i.e., a basic emotional facial expression).

Future Research

While the current investigation established early-latency effects of valence on emotional facial expression processing, future facial processing research should investigate early-latency emotional processing with respect to the 'functional model' (Smith & Lazarus, 1990), which includes the previously explored valence dimension as well as an arousal dimension. This model provides a more comprehensive picture of early-latency emotional processing of facial expressions because, within this model, "each emotional expression represents a subject's response to a particular kind of significant event – a particular kind of harm or benefit – that motivates coping activity" (Balconi &

Pozzoli, 2003, p. 69). While the valence dimension explains appetitive and aversive responses to positive and negative facial expressions, the dimension of arousal better explains the immediacy of viewers' responses to particularly alarming stimuli. For instance, negative high-arousal emotions (i.e., anger and fear) are expressions of a threatening situation requiring an active response, whereas negative low-arousal emotions (e.g., sadness) are expressions of a negative situation but do not require an active response. Accordingly, the hedonic value (valence) and power (arousal) of emotional facial expressions should influence both physiological and psychological early-latency emotional responses. The challenge in separating valence and arousal, though, will lie in finding positive facial expression stimuli that generate as much arousal as the strongest negative facial expression stimuli.

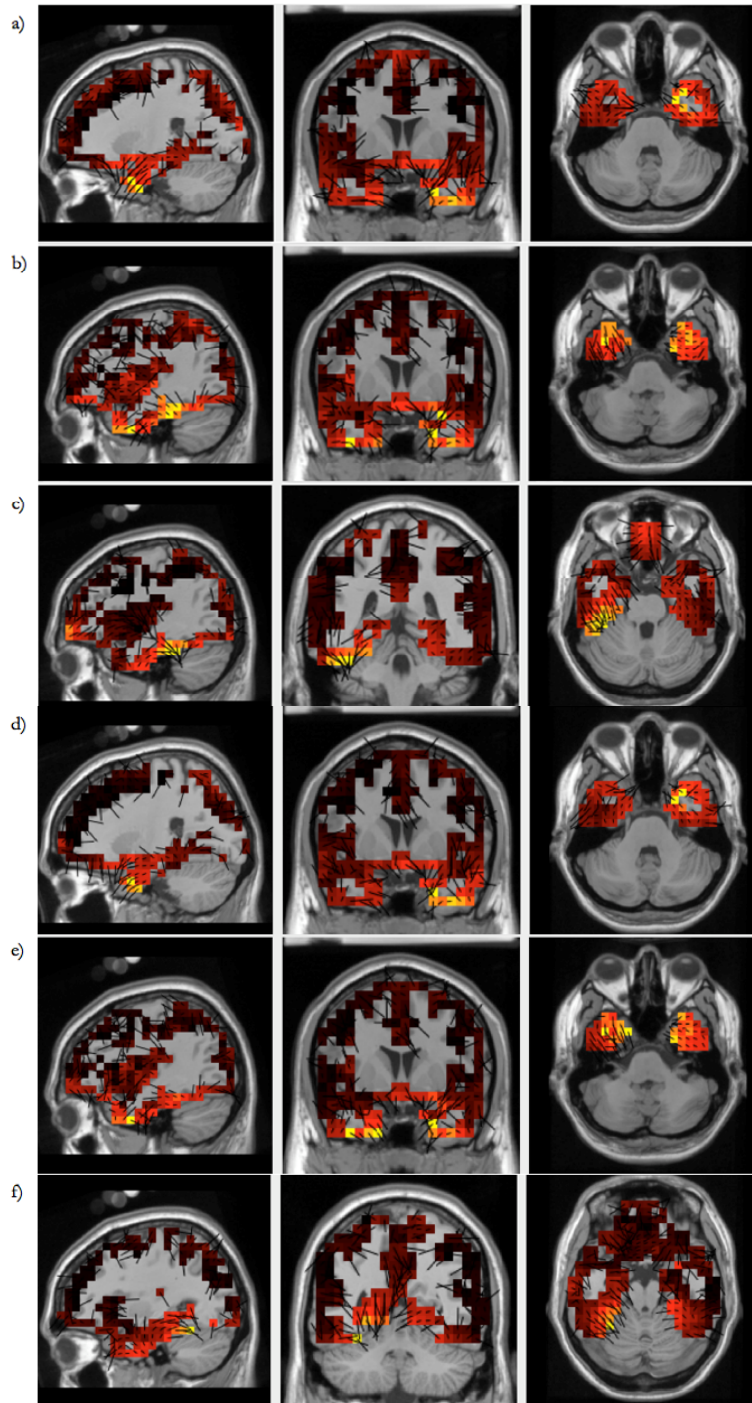


Figure 8. Clusters of substantial P1 activations (yellow > orange > red) for the following valence conditions (with dipole strength intensity and MNI coordinates): a) positive basic facial expressions revealed greatest activation within the left uncus (5.67 nA at -24x3x-34), b) positive morph facial expressions revealed greatest activation within the right middle temporal gyrus (5.00 nA at 39x3x-41), c) neutral basic facial expressions revealed greatest activation within the right fusiform gyrus (5.13 nA at 39x-39x-27), d) neutral morph facial expressions revealed greatest activation within the left uncus (8.17 nA at -24x3x-34), e) negative basic facial expressions revealed greatest activation within the right middle

temporal gyrus (8.46 nA at 39x3x-41), and f) negative morph facial expressions revealed greatest activation within the right fusiform gyrus (10.66 nA at 32x-53x-20).

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