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Age-related differences in event-related potentials for early visual processing of emotional faces

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With advancing age, processing resources are shifted away from negative emotional stimuli and toward positive ones. Here, we explored this ‘positivity effect’ using event-related potentials (ERPs). Participants identified the presence or absence of a visual probe that appeared over photographs of emotional faces. The ERPs elicited by the onsets of angry, sad, happy and neutral faces were recorded. We examined the frontocentral emotional positivity (FcEP), which is defined as a positive deflection in the waveforms elicited by emotional expressions relative to neutral faces early on in the time course of the ERP. The FcEP is thought to reflect enhanced early processing of emotional expressions. The results show that within the first 130 ms young adults show an FcEP to negative emotional expressions, whereas older adults show an FcEP to positive emotional expressions. These findings provide additional evidence that the age-related positivity effect in emotion processing can be traced to automatic processes that are evident very early in the processing of emotional facial expressions.

Keywords: emotion; aging; event-related potentials; socioemotional selectivity theory; positivity effect

INTRODUCTION

Previous studies have indicated that there are age-related differences in how young and older adults process emotional facial expressions (Ruffman *et al.*, 2008). Typically, young adults show a preference for all emotional expressions, relative to neutral, with an added emphasis on negative emotional expressions (Compton, 2003; Carretié *et al.*, 2006; Rellecke *et al.*, 2012; for other affective stimuli, see Olofsson *et al.*, 2008). In contrast, older adults tend to show a preference for processing positive expressions, and may even suppress negative emotional expressions (Mather and Carstensen, 2005; Isaacowitz *et al.*, 2006; Mienaltowski *et al.*, 2011). Thus, with advancing age there is a shift away from processing negative facial expressions (e.g. angry) and toward processing positive facial expressions (e.g. happy). This age group by emotion interaction is known as the ‘positivity effect’ (Carstensen and Mikels, 2005; Langeslag and van Strien, 2009).

One account for age-related differences in emotional processing falls under the theoretical framework of socioemotional selectivity theory (SST; e.g. Carstensen, 2006). According to SST, as people age their perspective shifts from an expansive appraisal of future time to one that is more limited, which in turn leads to a subsequent shift in personal goals away from information gathering and toward the maintenance of emotionally meaningful experiences.

Research in support of SST suggests that cognitive control mechanisms are used to maintain a positive affective state by selectively processing positive information (Mather, 2012). Given that negative information is more potent than positive information (e.g. Rozin and Royzman, 2001; Isaacowitz *et al.*, 2009), older adults must

overcome a natural tendency toward automatically processing negative information (e.g. Kisley *et al.*, 2007) to avoid the impact of negative emotional stimuli. In other words, the cognitive control account holds that, despite well-documented degradation in control areas of the brain such as the prefrontal cortex that occurs with aging, older adults are motivated to use control processes to maintain positive well-being and this leads to the positivity effect.

A competing explanatory theoretical framework for the positivity effect is known as the aging-brain model (Cacioppo *et al.*, 2011). The aging-brain model states that the positivity effect is due to the degradation of the amygdala that occurs with advancing age. Because the amygdala is more reactive to negative than to positive emotional stimuli, degradation of the amygdala naturally leads to the shift toward positive stimuli observed in the literature. In support of the aging-brain model, persons with amygdala lesions show less reactivity to negative emotional stimuli, but spared reactivity to positive emotional stimuli (Berntson *et al.*, 2007). Cacioppo *et al.* (2011) suggest that these patients with amygdala lesions can serve as a model of healthy aging. In addition, some evidence shows that older adults have less functional amygdala activation to negative stimuli (Mather *et al.*, 2004).

In a recent review, Nashiro *et al.* (2012) suggest that the extant literature supports the cognitive control account of the positivity effect rather than the aging-brain model. First, they argue that the amygdala is relatively structurally intact in healthy aging. Second, they suggest that the reduced functional activation of the amygdala to negative stimuli in older adults can be accounted for by both the aging brain model and the cognitive control account because studies that rely on fMRI cannot provide a fine-grain analysis of the time course of amygdala activation. Therefore, it is difficult to determine if the amygdalae of older adults fail to show as strong of an initial activation to negative stimuli due to structural or functional changes associated with aging (aging-brain model), or if amygdala activity is downregulated via prefrontal influences after normal initial activation occurred (cognitive control account). Third, studies have shown that older adults have spared amygdala activation to positive emotional stimuli suggesting that the amygdala is still functioning, at least for positive stimuli (Mather *et al.*, 2004). Fourth, and in direct support of the cognitive control account, older adults engage the prefrontal cortex

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when passively viewing emotional stimuli more than do young adults. These prefrontal areas overlap with those that are activated by both younger and older adults when explicitly instructed to regulate their emotions (Wincoff *et al.*, 2011). In addition, older adults engage the rostral anterior cingulate cortex (rACC) when processing happy faces, but this rACC activation only occurs when their attentional resources are not engaged by a concurrent task (Brassen *et al.*, 2011). Moreover, this rACC activity is correlated with emotional well-being. Taken together, these studies suggest that when possible, older adults implement cognitive control processes via engagement of prefrontal cortex and rACC, and this gives rise to the positivity effect.

Isaacowitz *et al.* (2009) have suggested that the time course of preferential looking as recorded via eye tracking can also be used as evidence in support of the cognitive control account of the positivity effect. In their experiment, participants viewed pairs of faces—one emotional and one neutral—and the time spent looking at each face was recorded. They found that older adults looked more at happy than neutral faces, but this preference in gaze did not emerge until about 500 ms after the onset of the faces. In addition, older adults looked more at neutral than angry faces, but this preference did not emerge until 3 s after the onset of the faces. Isaacowitz *et al.* concluded that the positivity effect is not evident in the earliest stages of emotional processing, but rather, the positivity effect relies on slower cognitive control mechanisms that take time to implement.

When an individual maintains a particular goal state (e.g. avoid negativity) for a substantial period of time, then the reward mechanisms that underlie information processing and decision making favor this goal state and become the default (Bargh and Ferguson, 2000; Custers and Aarts, 2010). In social cognition, cues that are linked to stimuli that are relevant to a default goal become more salient (Di Russo *et al.*, 2006; Bayer *et al.*, 2009; Achziger *et al.*, 2012; or less salient if they are the target of emotion downregulation, Schweiger Gallo *et al.*, 2009). With respect to the positivity effect, Bannerman *et al.* (2011) have suggested that older adults' tendency to avoid negative emotional expressions can be seen in more automatic tasks that are typically unaffected by cognitive control mechanisms. In their experiment, young and older adults performed a faces/houses binocular rivalry task where the faces had happy, angry or neutral expressions. They found that older adults selectively suppressed angry faces. These results suggest that the positivity effect, especially as related to the suppression of anger, can be evident in automatic tasks, and that cognitive control may therefore not always be necessary for a positivity effect to emerge.

Here, we used event-related potentials (ERPs) to examine the neural temporal dynamics of the positivity effect to determine whether this age-related shift can emerge in the early, automatic stages of emotion processing. We compared ERPs elicited by emotional faces with those elicited by neutral faces in young and older adults. Eimer and colleagues have shown that ERPs elicited by emotional faces are relatively more positive in amplitude than ERPs elicited by neutral faces in young adults (Holmes *et al.*, 2006; Eimer and Holmes, 2007). This effect is typically evident at frontocentral electrode sites, and accordingly we term it the 'frontocentral emotional positivity' (FcEP). Eimer and Holmes (2007) suggest that the FcEP may reflect neural activity in prefrontal areas that are involved in the processing of emotional facial expressions.

The FcEP elicited by emotional faces may consist of two distinct phases. The early phase, approximately 100–150 ms after the onset of the emotional face, is thought to reflect the early, rapid and automatic processing of emotional expressions in prefrontal areas involved in emotion identification. The late phase, which begins approximately 200 ms after the onset of the emotional face, most likely reflects higher level processing such as a conscious evaluation of the emotional

context (Eimer and Holmes, 2007; similar to Olofsson *et al.*, 2008, for other types of affective stimuli). Therefore, if the positivity effect is evident in the early time window, this would provide support for the possibility that a neural mechanism of the positivity effect is active in the automatic phase of emotion processing, before cognitive control processes are implemented.

To examine the neural temporal dynamics of the positivity effect, we presented participants with faces exhibiting angry, happy, sad and neutral expressions. Participants pressed a button whenever a visual probe was presented over the face. We examined the FcEP in three time windows corresponding to the frontocentral N1/posterior P1 (110–130 ms), the frontocentral P1/posterior N170 (165–185 ms) and the late FcEP/early posterior negativity (225–350 ms). We expected to observe an age group by emotion interaction consistent with the positivity effect such that young adults would show an FcEP to negative emotional expressions, whereas older adults would show an FcEP to positive emotional expressions. Extending upon previous research, the results will shed light on whether the positivity effect can occur in the early, automatic stages of emotional processing.

METHODS

Participants

Data were collected from 31 adults: 16 young (eight women; age range = 18–31; mean = 19.94; s.d. = 3.17 years) and 15 older adults (seven women; age range = 61–77; mean = 69.53; s.d. = 4.14 years). Older adult participants were recruited from a southeastern metropolitan area and rewarded with an honorarium for participating. Young adults were college students who participated for course credit. The participants all had normal or corrected-to-normal vision. They each gave written, informed consent.

Stimuli and procedure

Testing occurred under dim lighting in a sound-attenuating chamber. Participants sat in front of a computer monitor, with a viewing distance of approximately 57 cm maintained using a chinrest. E-Prime (Psychology Software Tools, Pittsburgh, PA, USA) was used to control the experiment and collect responses. The stimuli were grayscale images adapted from the NimStim Face Stimulus Set (MacArthur Foundation Research Network on Early Experience and Brain Development, www.macbrain.org, Tottenham *et al.*, 2009). We used images of neutral, happy, angry and sad expressions from 30 different young actors. These actors included men and women and were ethnically diverse young adults. Only closed-mouth, medium-emotional-intensity expressions were used. The images were equated for overall luminance and scaled to fit into a bounding box subtending 9.4×12.1 of visual angle.

Participants performed a simple reaction time task in the presence of emotional or neutral faces. Trials began with a fixation cross ($0.4 \times 0.4^\circ$; 0.3 cd/m^2) positioned centrally on a white background (95.2 cd/m^2). After a random interval of 600–1000 ms, a face image was presented, centered on the fixation point. Following an interval of 400–800 ms, a black-and-white checkerboard probe ($5.7 \times 5.7^\circ$) flashed over the face for 100 ms. A 1400 ms response interval followed, during which participants were to respond to the onset of the probe as quickly as possible. After a block of 44 practice trials, participants completed four blocks of 192 experimental trials (768 total; 192 trials per emotion). Of these, 10% were catch trials in which a probe never appeared, and participants were instructed to withhold responses. Each face stimulus was randomly repeated no more than eight times. The participants' visual-evoked responses to the checkerboard probes have been described elsewhere (Mienaltowski *et al.*, 2011), as have the

participants' psychophysical responses to this task. For the benefit of the reader, the latter are reproduced in the 'Results' section herein.

EEG recording and signal processing

Electrophysiological data were recorded using a BioSemi Active-Two amplifier system. The scalp potentials were recorded from 32 standard electrode sites as described in our previous research (Mienaltowski *et al.*, 2011). Vertical electrooculogram (EOG) was calculated offline as the difference between electrodes positioned above and below the left eye. Horizontal EOG was calculated offline as the difference between electrodes positioned on the outer canthi of the left and right eyes. The EEG was digitized at 512 Hz. Data from the scalp sites were re-referenced offline to the average of all scalp electrodes. The continuous EEG data were digitally filtered (band pass 0.1–30 Hz) and segmented into 1000 ms epochs with a 100 ms prestimulus baseline time-locked to the onset of the face. Eye movements and blink artifacts were removed from individual segments following the procedure described by Gratton *et al.* (1983). Segments containing activity exceeding $\pm 100 \mu V$ were considered artifacts and excluded.

Analyses

Our main objective was to test for an FcEP in the ERPs to emotional faces compared with neutral faces. Given that the checkerboard probe randomly appeared 400–800 ms after the onset of each facial expression, waveform analysis was limited to a time frame that would avoid contamination by the probe-related visual evoked potential. We obtained the mean amplitude for three time windows after the onset of the faces: 110–130, 165–185 and 225–350 ms. These time windows were chosen based on the peaks present in the grand average waveform collapsed across both age groups and across all emotional faces. We obtained the mean amplitude measures at frontal (F3, Fz, F4), central (C3, Cz, C4), parietal (P3, Pz, P4) and occipital (O1, Oz, O2) scalp sites.

Next, we calculated difference scores by subtracting the activity elicited by neutral faces from the activity elicited by each emotional expression. We then used these difference scores as dependent measures in repeated measures analysis of variances (ANOVAs) (Greenhouse–Geisser corrected where appropriate). The repeated measures ANOVAs had Age Group (Young *vs* Older) as a between-subjects factor and Electrode (Frontal *vs* Central *vs* Parietal *vs* Occipital), Hemisphere (Left *vs* Central *vs* Right) and Emotion (Happy *vs* Angry *vs* Sad) as within-subjects factors.

The critical results involve an Age Group \times Emotion interaction which would indicate differential processing of the emotional expressions for young and older adults. Thus, we report the Age Group \times Electrode \times Hemisphere \times Emotion, Age Group \times Electrode \times Emotion, Age Group \times Hemisphere \times Emotion and Age Group \times Emotion interactions. Because only the Age Group \times Electrode \times Emotion interactions were statistically significant (see 'Results' section), we collapsed across hemisphere for the follow-up ANOVAs. Thus, we tested for an Age Group \times Emotion interaction separately for the Frontal (averaged across F3, Fz, F4), Central (averaged across C3, Cz, C4), Parietal (averaged across P3, Pz, P4) and Occipital electrodes (averaged across O1, Oz, O4).

Next, Helmert contrasts were used to follow up any significant Age Group \times Emotion interactions found at the Frontal, Central, Parietal or Occipital sites. In the first contrast, angry and sad were combined to form a 'negative' level of the emotion variable which was compared to happy. In other words, the first contrast examined whether Age Group interacted with Emotion for the comparison of happy *vs* negative expressions. The second contrast tested for an Age Group \times Emotion interaction due to differences between the two negative emotions.

Finally, to test the reliability of the emotion compared to neutral waveform differences within each age group, one-sample *t*-tests were used to compare the difference scores with $0 \mu V$. Thus, statistically significant results would indicate a reliable difference between the ERPs elicited by happy, angry or sad faces compared with the ERPs elicited by neutral faces. These results are reported in Figure 1—asterisks indicate any difference scores where the one-sample *t*-test yielded $P < 0.05$.

RESULTS

Behavioral results

Young adults (mean = 256 ms, s.e. = 12.3 ms) were faster than older adults (mean = 330 ms, s.e. = 11.3 ms) at detecting probes, $F(1,33) = 19.68$, $P < 0.05$. However, young (mean = 98.5%, s.e. = 0.8%) and older (mean = 96.6%, s.e. = 0.7%) adults were equally accurate in their responses, and emotion had no significant influence on probe RT or accuracy (Mienaltowski *et al.*, 2011).

Electrophysiological results

Figures 2 and 3 depict the ERP waveforms elicited by emotional and neutral facial expressions for young and older adults, respectively, at Frontal (averaged across F3, Fz, F4), Central (averaged across C3, Cz, C4), Parietal (averaged across P3, Pz, P4) and Occipital electrodes (averaged across O1, Oz, O4). Figure 1 depicts the difference scores in the two analysis windows (110–130 and 225–350 ms) that showed statistically significant Age Group by Emotion interactions. These difference scores were obtained by subtracting the activity elicited by neutral faces from the activity elicited by the emotional expressions for each age group separately. Only the electrode sites with statistically significant Age Group by Emotion interactions are plotted. The FcEP is indicated by a positive difference score at the Frontal electrode sites. This emotional enhancement for ERPs elicited by emotional expressions relative to neutral is indicated by negative difference scores at the Parietal or Occipital sites. Figure 4 shows the scalp distributions of these difference scores separately for the 110–130 and 225–350 ms windows as a function of Age Group and Emotion.

As seen in Figure 1 and demonstrated in the analyses that follow below, there is evidence for a positivity effect in the both the early (110–130 ms) and later (225–350 ms) time windows when comparing young and older adults electrophysiological reactions to the emotional facial expressions. Young adults show a stronger FcEP (i.e. positive difference score) for negative faces during the early time window (110–130 ms) at Frontal sites, whereas older adults show a stronger FcEP for happy faces in this time window. These results are reversed at Occipital sites such that young adults show a stronger negative difference score for negative faces, whereas older adults show a stronger negative difference score for happy faces. These patterns are repeated in the later time window (225–350 ms) at the Frontal and Parietal sites.

These patterns of results can also be seen in the scalp distributions shown in Figure 4. Especially in early (110–130 ms) time window, it can be seen that young adults have stronger frontal positivities and posterior negativities for angry and sad faces, whereas older adults have stronger frontal positivity and posterior negativity for happy faces. These patterns are seemingly reversed for the happy faces in the young adults (i.e. they have frontal negativity and posterior positivity), and for the angry and sad faces in the older adults (i.e. they have frontal negativities and posterior positivities). In other words, the scalp distributions of the difference waveforms for young adults viewing negative faces relative to neutral look similar to the scalp distributions for older adults viewing positive faces relative to neutral.

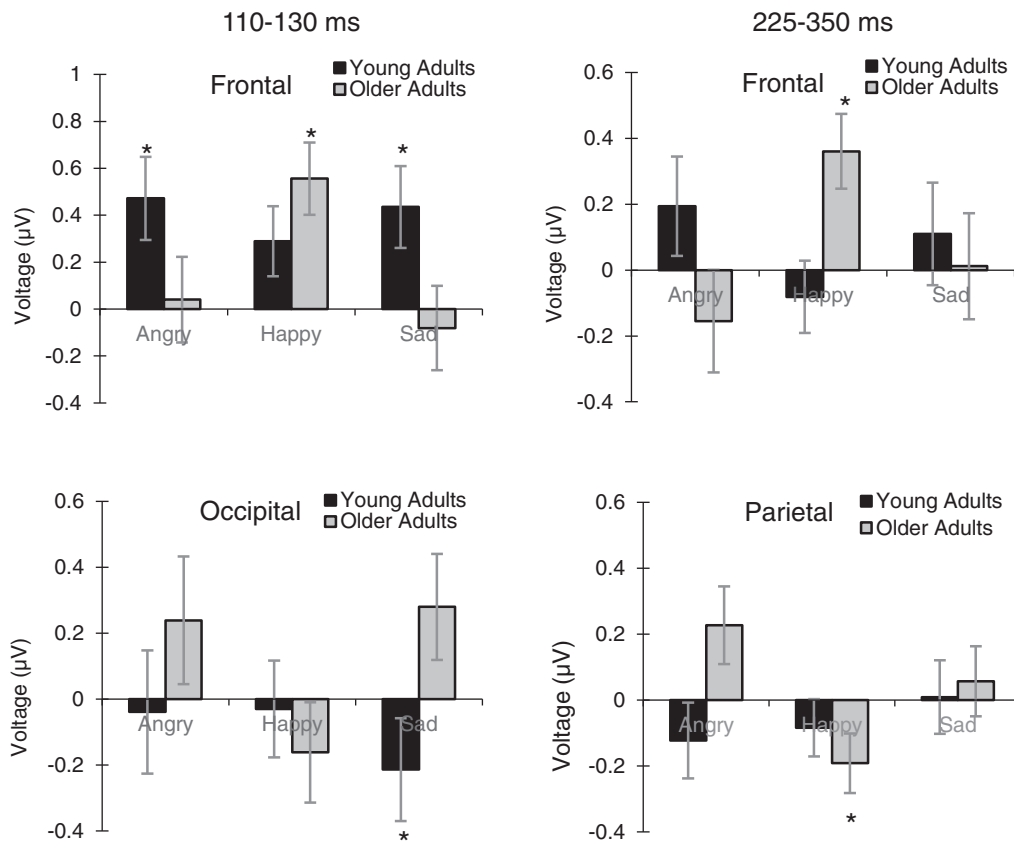


Fig. 1 Difference scores for young and older adults as a function of emotional expression at Frontal and Occipital electrodes for the 110–130 ms time window (left) and at Frontal and Parietal electrodes for the 225–350 ms time window (right). The difference scores were calculated by subtracting the ERP elicited by neutral faces from the ERP elicited by each emotional expression. An FcEP, indicated by positive difference scores at Frontal electrodes, indicates enhanced processing of that emotional expression. A negative difference score at Occipital and Parietal electrodes indicates enhanced processing of that expression. Error bars are standard error of the mean. Asterisks indicate that the difference score was statistically different from 0 μV at $P < 0.05$.

110–130 ms

Only the Age Group \times Electrode \times Emotion interaction was statistically significant, $F(6,174) = 4.794$, $P = 0.004$, $\eta_p^2 = 0.142$ and $\epsilon = 0.484$. The Age Group \times Electrode \times Hemisphere \times Emotion, $F(12,348) = 1.264$, $P = 0.267$, $\epsilon = 0.622$, Age Group \times Hemisphere \times Emotion, $F < 1$ and Age Group \times Emotion, $F < 1$, were not statistically reliable.

At the Frontal electrodes, the Age Group \times Emotion interaction was statistically significant, $F(2,58) = 6.012$, $P = 0.006$, $\eta_p^2 = 0.172$ and $\epsilon = 0.872$. The Helmert contrasts revealed that this Age Group \times Emotion interaction was due to differences between happy and negative faces across age groups, $F(1,29) = 9.095$, $P = 0.005$, $\eta_p^2 = 0.239$, but not between angry and sad faces, $F < 1$.

At the Central electrodes, the Age Group \times Emotion interaction was not statistically significant, $F < 1$.

At the Parietal electrodes, the Age Group \times Emotion interaction was only marginally reliable, $F(2,58) = 3.079$, $P = 0.057$, $\eta_p^2 = 0.096$, $\epsilon = 0.942$, and was not further explored.

At the Occipital electrodes, the Age Group \times Emotion interaction was statistically significant, $F(2,58) = 3.904$, $P = 0.030$, $\eta_p^2 = 0.119$, $\epsilon = 0.913$. The Helmert contrasts revealed that this Age Group \times Emotion interaction was due to differences between happy and negative faces across age groups, $F(1,29) = 9.403$, $P = 0.005$, $\eta_p^2 = 0.245$, but not between angry and sad faces, $F < 1$.

165–185 ms

None of the interactions that included Age Group \times Emotion were statistically significant (all $F_s \leq 2.088$, $P_s \geq 0.113$).

225–350 ms

Only the Age Group \times Electrode \times Emotion interaction was statistically significant, $F(6,174) = 4.412$, $P = 0.006$, $\eta_p^2 = 0.132$ and $\epsilon = 0.502$. The Age Group \times Electrode \times Hemisphere \times Emotion, $F(12,348) = 1.707$, $P = 0.121$, $\epsilon = 0.503$, Age Group \times Hemisphere \times Emotion, $F(4,116) = 1.423$, $P = 0.246$, $\epsilon = 0.619$ and Age Group \times Emotion, $F < 1$ were not statistically reliable.

At the Frontal electrodes, the Age Group \times Emotion interaction was statistically significant, $F(2,58) = 6.012$, $P = 0.005$, $\eta_p^2 = 0.172$, $\epsilon = 0.929$. The Helmert contrasts revealed that this Age Group \times Emotion interaction was due to differences between happy and negative faces across age groups, $F(1,29) = 8.533$, $P = 0.007$, $\eta_p^2 = 0.227$, but not between angry and sad faces, $F(1,29) = 1.598$, $P = 0.216$.

At the Central electrodes, the Age Group \times Emotion interaction was not statistically significant, $F < 1$.

At the Parietal electrodes, the Age Group \times Emotion interaction was statistically significant, $F(2,58) = 3.737$, $P = 0.034$, $\eta_p^2 = 0.114$ and $\epsilon = 0.915$. The Helmert contrasts revealed that this Age Group \times Emotion interaction was due to differences between happy and negative faces across age groups, $F(1,29) = 5.628$, $P = 0.025$, $\eta_p^2 = 0.163$, but not between angry and sad faces, $F(1,29) = 2.555$, $P = 0.121$.

At the Occipital electrodes, the Age Group \times Emotion interaction was not statistically significant, $F(2,58) = 2.291$, $P = 0.112$, $\epsilon = 0.963$.

DISCUSSION

Young and older adults were presented with faces displaying angry, happy, sad and neutral expressions, and responded to a probe that

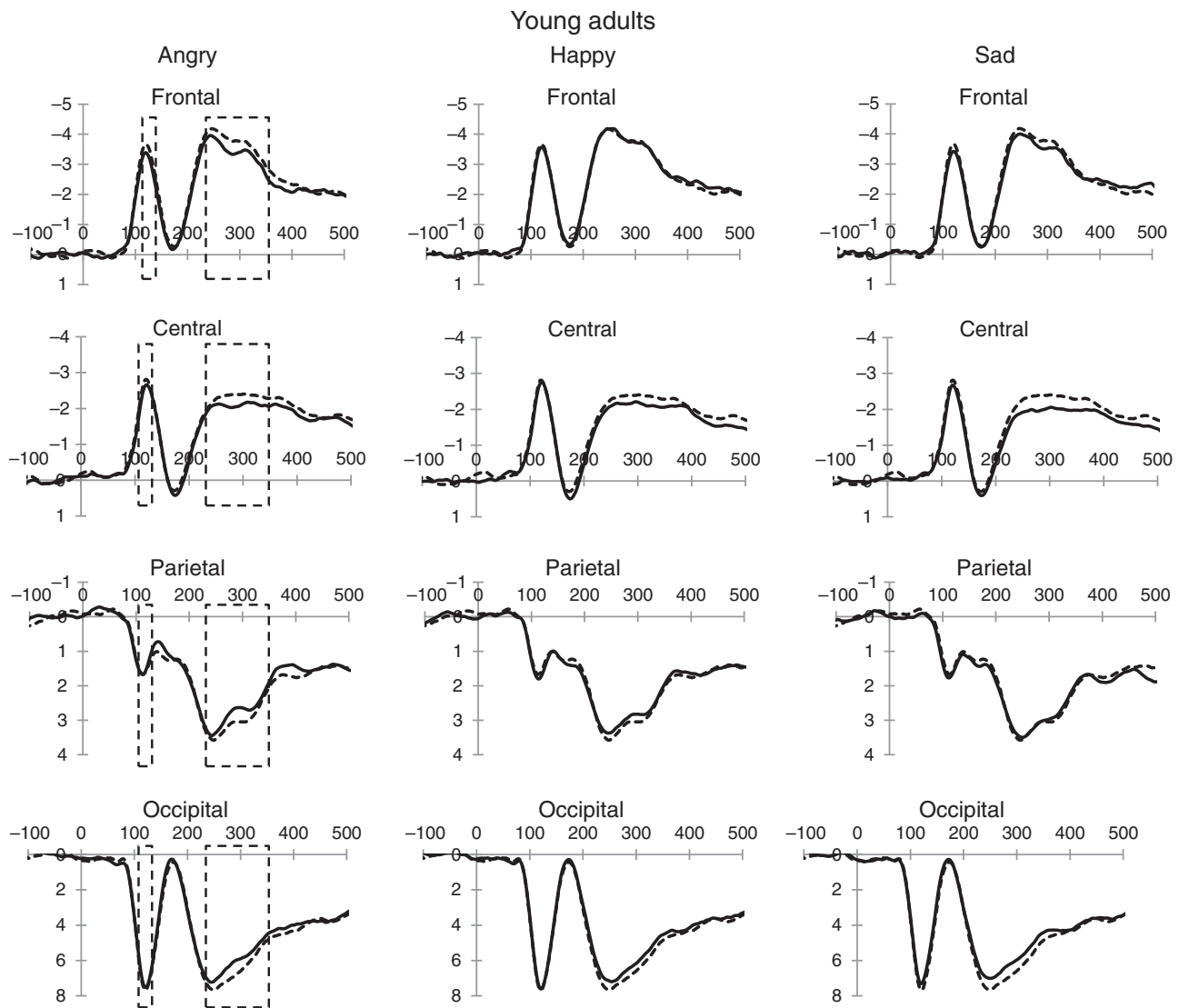


Fig. 2 ERPs for young adults at Frontal (averaged across F3, Fz, F4), Central (averaged across C3, Cz, C4), Parietal (averaged across P3, Pz, P4) and Occipital electrodes (averaged across O1, Oz, O4). Separate plots for angry, happy and sad facial expressions compare the ERPs elicited by the emotional faces (solid lines) with the ERP elicited by neutral faces (broken lines). Analysis windows (110–130 and 225–350 ms) where significant positivity effects were found are indicated on the plots for the angry faces. The horizontal axis is time in milliseconds, and the vertical axis is voltage in microvolts.

appeared over the faces in a go/no-go task. For this task, the emotions expressed on the facial stimuli were not directly relevant to the judgment being made. ERPs elicited by the neutral faces were subtracted from the ERPs elicited by the emotional expressions to examine the FcEP that is evident as a positive difference score with this subtraction.

In our analyses, age group by emotion interactions emerged that are consistent with the positivity effect. At frontal scalp sites, young adults showed a stronger FcEP for negative faces, whereas older adults had a stronger FcEP for happy faces. This neural manifestation of the positivity effect was observed within 110–130 ms of the onset of the emotional faces, the earliest interval that emotion-related ERP enhancements are typically observed (Eimer and Holmes, 2007). This age difference was again seen at a later interval (225–325 ms), but not in an intermediate interval (165–185 ms). At posterior scalp sites in both the early (110–130 ms) and later time intervals (225–325 ms), young adults showed greater negativity for negative faces. In contrast, older adults showed greater negativity for happy faces at these posterior scalp sites. Thus, it seems like these frontal and posterior brain activities are two sides of the same coin, although higher density

EEG recordings with subsequent source modeling would need to be performed to confirm if a single dipole can account for the emotion effects evident at both frontal and posterior sites. Overall, young adults enhanced neurophysiological reactions to negative faces and older adults enhanced neurophysiological reactions to happy expressions are consistent with a positivity effect interpretation (Mather and Carstensen, 2005; Langeslag and van Strien, 2009).

The findings for young adults converge with a recent study that manipulated the task relevance of emotional expressions. Rellecke *et al.* (2012) presented angry, happy, neutral faces to young adult participants under varying task conditions where the emotional expression was relevant (e.g. naming the emotional expression) or irrelevant (e.g. passive viewing). Their results, as interpreted from ERPs elicited by the emotional faces relative to the neutral faces, indicated that only angry expressions were afforded increased processing at early perceptual stages when they were task-irrelevant. On the other hand, happy expressions only received enhanced processing when the expressions were task-relevant. In our study, the expressions were task-irrelevant, and we similarly observed enhanced processing for only the

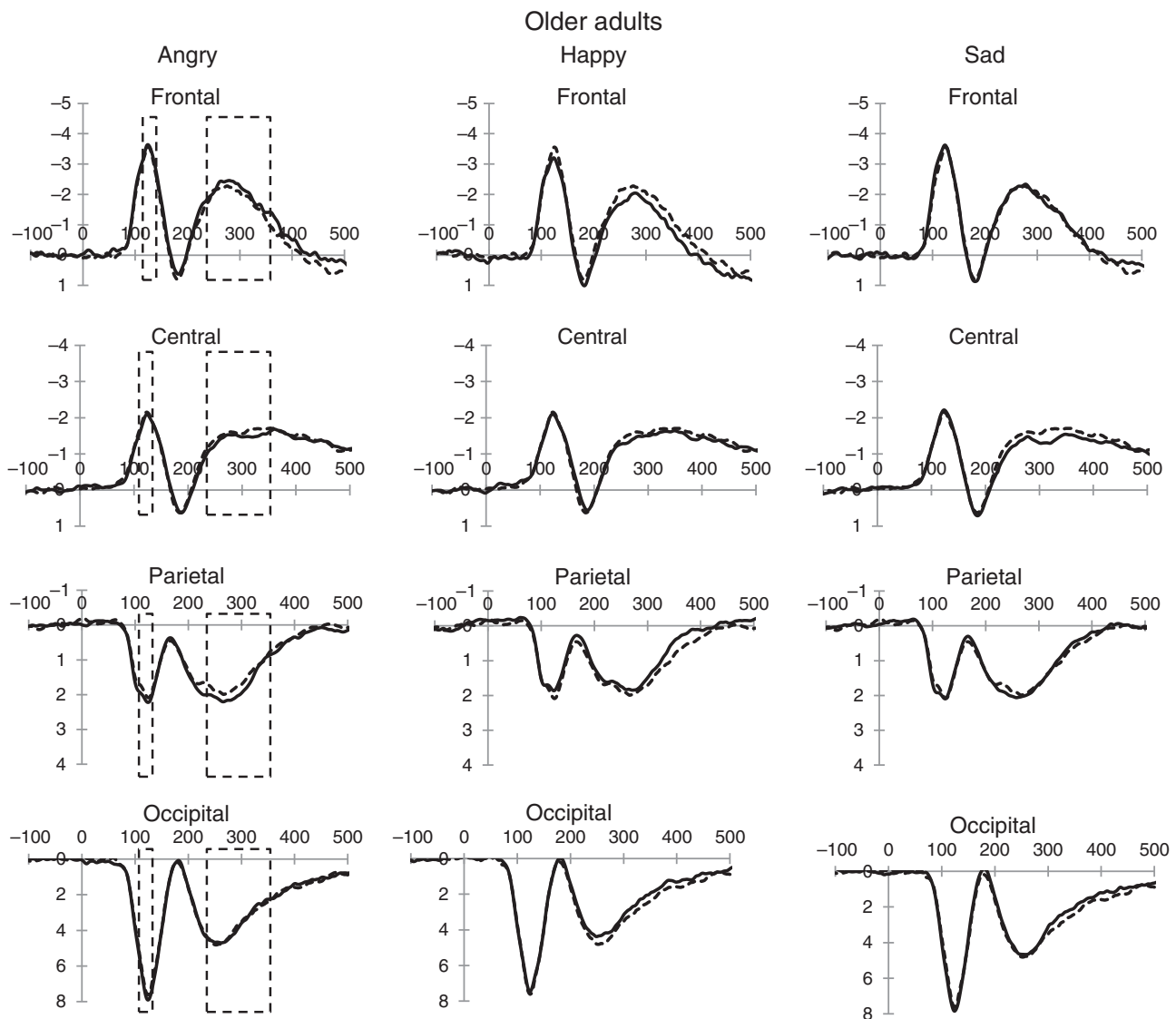


Fig. 3 ERPs for older adults at Frontal (averaged across F3, Fz, F4), Central (averaged across C3, Cz, C4), Parietal (averaged across P3, Pz, P4) and Occipital electrodes (averaged across O1, Oz, O4). Separate plots for angry, happy and sad facial expressions compare the ERPs elicited by the emotional faces (solid lines) with the ERP elicited by neutral faces (broken lines). Analysis windows (110–130 and 225–350 ms) where significant positivity effects were found are indicated on the plots for the angry faces. The horizontal axis is time in milliseconds, and the vertical axis is voltage in microvolts.

negative expressions in young adults. Interestingly, for older adults, we observed enhanced processing for happy expressions. This suggests that, for older adults, there is a shift away from automatically processing negative emotional stimuli toward automatically processing positive emotional stimuli. To further test this idea, it would be necessary to manipulate the task relevance of the emotional expressions to determine whether older adults demonstrate enhanced processing of negative expressions only when top-down, endogenous factors come in to play (i.e. only when the negative expressions are relevant to their current goals).

This experiment extends upon prior findings by demonstrating that the positivity effect emerged within 130 ms after the onset of the emotional facial expressions, the earliest time period during which emotional effects are evident in affective stimulus processing (e.g. Olofsson *et al.*, 2008). According to Eimer and Holmes (2007), this early activity most likely reflects the rapid, automatic processing of emotional expressions in prefrontal areas involved in emotion identification. In this study, the young and older adults divergent responses to positive and negative emotional expressions suggest that processing differences that

lead to a positivity effect may occur earlier than previously reported in the literature (cf. Isaacowitz *et al.*, 2009). This early emergence of the positivity effect is consistent with the study by Bannerman *et al.* (2011) who showed that the positivity effect is evident in a binocularly rivalry task. Given that their task was not expected to rely on voluntary control, Bannerman *et al.* recognized that the ‘... age-related positivity effect may not always require full cognitive control and may operate more automatically’ (p. 377).

It is possible that the positivity effect observed within 130 ms of the onset of the emotional expressions observed here is due to the fact that older adults have spared amygdala activation to positive stimuli but reduced amygdala activation to negative stimuli (cf. the aging-brain model; Cacioppo *et al.*, 2011). As noted in the introduction, fMRI evidence cannot determine whether this reduced activation to negative emotional stimuli is due to modulations via cognitive control mechanisms because of the technique’s limitations in the temporal domain. EEG, on the other hand, is well-suited to analyze the time course of neural activity. Unfortunately, the amygdala is deep within the brain and produces a closed electrical field, and thus, the amygdala is

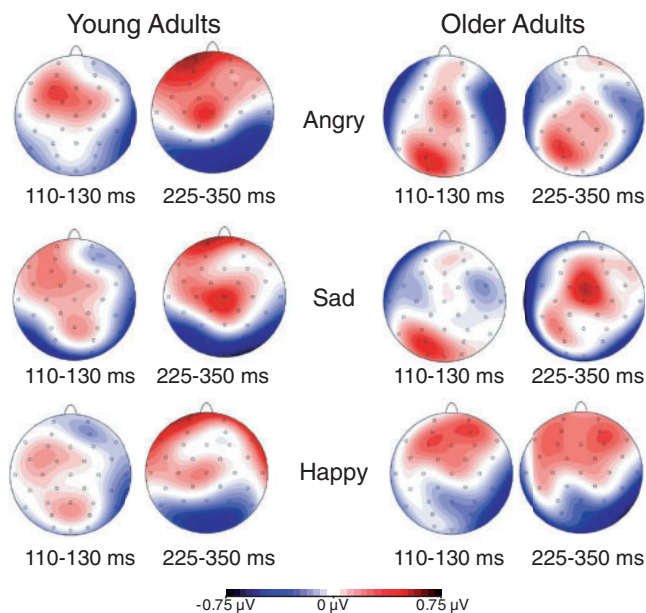


Fig. 4 Scalp distributions of the difference waveforms obtained by subtracting the ERPs elicited by the neutral faces from the ERPs elicited by the emotional faces for young (left) and older (right) adults. The scalp plots are shown for each emotion difference waveform (angry, happy and sad) and the two time windows (110–130 and 225–350 ms). Note that the scalp distributions for negative expressions (angry and sad) in young adults look similar to the scalp distributions for happy expressions in older adults. On the other hand, the scalp distributions for happy faces in young adults look similar to the scalp distributions for negative expressions in older adults.

generally thought to be invisible to EEG recordings at the scalp. Through a combination of neuropsychology and electrophysiology, Rotshtein *et al.* (2010) were able to test the influence of the amygdala on ERP measures of emotion by comparing patients with amygdala lesions due to medial temporal lobe epilepsy to healthy controls. Participants viewed fearful and neutral faces and were asked to detect any repetitions in the stimuli. They measured the ERPs elicited by the fearful compared with the neutral faces. The healthy controls showed the typical enhancement of the ERPs elicited by the fearful faces relative to neutral. In contrast, the patients with amygdala damage did not show as large of an enhancement in their ERPs elicited by the emotional expression in an early (100–150 ms) and late (500–600 ms) time window. However, amygdala lesions had no effect on emotion processing in an intermediate (150–250 ms) time window. Moreover, the reduction of the ERP emotion effect was related to the severity of the amygdala lesions. According to Rotshtein *et al.*, this evidence suggests that the emotion enhancement effects seen in the ERPs, especially in the early time window, are due to the rapid influence from the amygdala on cortical processing. Here, we showed that the positivity effect occurred in an early (110–130 ms) and late (225–350 ms), but not intermediate (165–185 ms), time windows. Thus, the positivity effect, especially in the early time window, might be explained by the fact that positive but not negative stimuli robustly activate the amygdala for older adults (Mather *et al.*, 2004), and in turn, the amygdala enhances cortical processing within the first 130 ms of processing emotional stimuli.

Limitations

This study is not without its limitations. First, the emotional stimuli used in this study only included young adult faces. This limitation is one that is shared with a number of studies that have demonstrated the positivity effect in older adult samples (Mather and Carstensen, 2003; Isaacowitz *et al.*, 2006, 2009; Mienaltowski *et al.*, 2011). One possible

consequence is that the results might be partially explained by in-group/out-group differences. A previous study of young adults has shown that they differentially process photographs of young adult faces compared with older adult faces as measured by ERPs at fronto-central scalp sites (Ebner *et al.*, 2011). Future studies should consider using stimuli depicting both young and older adults displaying emotional expressions to explicitly examine this alternative hypothesis. Second, we could not directly measure amygdala activity, thus our suggestion that the early manifestation of the positivity effect may be due to differential amygdala activation across age groups is tentative. Future research should utilize concurrent fMRI and EEG to determine whether amygdala activation is related to the positivity effect as measured by these early ERP effects. Intracerebral EEG recordings would also be able to directly assess amygdala contributions to the positivity effect with the temporal specificity necessary to disentangle the aging-brain model predictions from the cognitive control account. In addition, it is likely that aging alters the dynamic interplay amongst motivation, cognitive control, perception and automatic processes, resulting in the various manifestations of the positivity effect. Thus, any ultimate explanation will necessarily be nuanced and will need to consider the multiple influences on age-related changes in emotion processing.

CONCLUSION

In summary, our results are consistent with previous reports of a negativity bias in younger adults (for review, see Compton 2003; Olofsson *et al.*, 2008) and a shift toward preferentially processing positive information with advancing age (Mather, 2012). These findings extend prior research by demonstrating that age-related differences in the perception of emotional stimuli may begin earlier after their onset than has been supported in earlier work.

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