Social context modulates neural response to human faces

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Abstract

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The ability to rapidly process and interpret the information contained in the human face is a crucial social ability, and its behavioral and neurobiological underpinnings have been well-studied throughout human development. Extensive research indicates that a particular region of the inferotemporal cortex, the fusiform gyrus, subserves early stages of face processing[1]. Functional magnetic resonance imaging (fMRI) research has robustly demonstrated selective activation in this cortical region during face perception. Studies of event-related potentials (ERPs) recorded from scalp regions corresponding to occipitotemporal cortex show a negative-going electrical deflection occurring at approximately 170 milliseconds after perceiving a face[2] (N170). While the N170 has been observed in children as young as 4 years of age, development of the N170 response to faces continues into adulthood, suggesting slow maturation of face processing throughout development[3-4].

The N170 reflects structural encoding, an early stage of face processing preceding higher-order processes like recognition of identity or emotion[5-6]. Evidence demonstrating that the N170 is enhanced by face inversion[7] and elicited by both intrinsic facial features (especially eyes) and the holistic composite of face features[2,8], suggests that the N170 is associated with a perceptual process responsible for structural encoding of faces. Despite its reflection of basic stages of face perception and its extremely short[9] latency, recent studies suggest that the N170 can be modulated by top-down influences, such as context-based expectations. For example, N170 amplitude is attenuated when faces are presented within an emotional scene, suggesting that early stages of structural encoding, indexed by the N170, are influenced by the presence of context at encoding[10-11]. Studies have also examined how contextual influences serve to disambiguate initially meaningless stimuli, an important ability that facilitates perception and recognition[12]. Bentin and colleagues[13-14] presented subjects with scrambled schematic faces that did not elicit an N170 effect. After exposure to normally configured versions of the schematic faces, and in so doing revealing that the ambiguous patterns represented faces, the same scrambled schematic face stimuli elicited an N170, suggesting that the N170 is modulated by the interaction of context and perceptual information. The stimuli in the aforementioned studies all contained intrinsic, albeit sometimes disarranged, facial features (the pattern of eyes, nose, and mouth). It is not yet known whether face-sensitive ERP responses can be elicited by contextual cues in the absence of intrinsic facial information. This topic has been investigated using other brain imaging methods. A seminal study using functional magnetic resonance imaging (fMRI) reported that the fusiform gyrus responded to contextual cues associated with faces in the absence of intrinsic facial features (a significantly degraded face in the presence of a body)[15]. However, the limited temporal resolution of fMRI prevents conclusions regarding the stage of face processing at which these effects were elicited. For example, given the likelihood of re-entrant feedback to the fusiform gyrus, it is possible that these effects signify upregulation of fusiform gyrus at later stages, due to cognitive or affective phenomena rather than perceptual processing, per se. Because the fusiform gyrus has also been shown to activate in the absence of any face-related stimuli, for example, when individuals cogitate on social phenomena[16], it is unclear whether these results are attributable to priming of a face encoding system or involvement in face-related regions in a broader social cognitive processing network.

The current study sought to elucidate the role of context in the earliest stages of face perception by investigating electrophysiological brain activity, the N170, in response to contextual cues in the absence of intrinsic face information, using a paradigm adapted from Cox, Meyers, & Sinha[15] in 8- to 16-year-old typically-developing children. The aims of the study are threefold: 1) to examine the influence of contextual visual experience: whether the N170 can be elicited in response to an initially ambiguous stimuli (a degraded face) subsequent to exposure to stimuli (a degraded face in the context of a human body) revealing what the initially ambiguous stimulus represented; 2) to examine the influence of the immediate visual context: whether N170 responses can be elicited in the absence of intrinsic facial information (the pattern of eyes, nose, and mouth) when a face is implied by the context of a human body; and 3) to investigate whether contextual cues (contextual visual experience and the immediate visual context) modulate the N170 throughout development. It is predicted, consistent with studies indicating the role of context in face processing, N170 will be enhanced to ambiguous stimuli after visual experience with cues indicating the identity of the ambiguous stimuli, and when the ambiguous stimuli are presented in social context. In addition, given the continuing development of the N170 throughout childhood and adolescence, we predict a positive correlation between the degree of modulation of N170 by social context and age. This study will be the first to investigate whether face-specific N170 responses can be elicited by contextual cues in the absence of intrinsic facial features, shedding light on the neural correlates of contextual face processing and the role of context in the development of face processing.

Methods

Participants

Twenty-one typically-developing children were recruited from ongoing research protocols at the Yale Child Study Center. Exclusionary criteria included seizures, neurological disease, history of serious head injury, sensory or motor impairment that would impede completion of the study protocol, active psychiatric disorder (screened with the Child Symptom Inventory: Fourth Edition[17]), medication known to affect brain electrophysiology, learning/language disability, and family history of Autism Spectrum Disorder. Six participants completed the protocol but were excluded from the analysis due to too few artifact-free trials (5) or corrupted data files (1). The final sample included fifteen children (12 male, 3 female) with a mean chronological age of 12.75 (SD = 2.44). Average full-scale IQ, measured by the Wechsler Abbreviated Scale of Intelligence[18] was 112.36 (SD = 14.61). The Edinburgh Handedness Inventory[19] identified two subjects as being left handed. All procedures were approved by the Human Investigation Committee at Yale School of Medicine and were carried out in accordance with the Declaration of Helsinki (1975/1983).

EEG recording procedure

Stimuli. Stimuli consisted of color digital images obtained from Adobe Stock Photos (Adobe Systems Incorporated) presented on a computer monitor. Images were standardized in terms of size and background color (white). Stimuli were presented randomly in blocks of the following stimuli classes: degraded faces alone, clear faces on bodies, clear faces alone, bodies with degraded faces, bodies alone, and scenes. Blocks were presented in pseudo-random order such that the first and last block always consisted of degraded faces alone; the order of all other blocks was random. Within each block, 50 unique stimuli were repeated two times for a total of 100 stimulus presentations from each category. Ten additional images in each stimulus class, shaded in red, were interspersed as target stimuli. To control for attention, participants were instructed to push a button when a red image appeared. Participants whose accuracy fell below 90% were excluded from the analysis. Examples of the stimuli used and the experimental design are presented in Figure 1.

Data collection. EEG was recorded in an electrically shielded, sound-attenuated, darkened room. Stimuli were presented on a Pentium-IV computer controlling a 51 cm color monitor (75-Hz, 1024x768 resolution) running Eprime 2.0 software. Displays were viewed at a distance of 90 cm. A large curtain obscured the rest of the room from the participant's view. An Electrical Geodesics 256-channel sensor net (Electrical Geodesics Incorporated) was dampened with potassium-chloride electrolyte solution, placed on the participant's head, and fitted according to the manufacturer's specifications[20]. The electrodes were evenly spaced and symmetrically covered the scalp from nasion to inion and from left to right ears. Impedances were kept below 40 kΩ.

ERP was recorded continuously throughout each stimulus presentation trial, consisting of a fixation cross (randomly varying from 250-750 milliseconds), stimulus (500 milliseconds), and blank screen (500 milliseconds). Total testing time was approximately 18 minutes.

The ERP signal was amplified (x1000) and filtered (0.1 Hz high-pass filter and 100 Hz elliptical low-pass filter) via a preamplifier system (Electrical Geodesics Incorporated). The conditioned signal was multiplexed and digitized at 250 Hz using an analog-to-digital converter (National Instruments PCI-1200) and a dedicated Macintosh computer. All 256 channels were recorded continuously using Netstation 4.3 software. The vertex electrode was used as a reference, and data were re-referenced to an average reference after collection.

Data editing and reduction. Data were averaged for each subject by stimulus type across trials. Averaged data were transformed to correct for baseline shifts and digitally filtered with a 30 Hz low-pass filter to reduce environmental noise artifacts. The window for segmentation of the ERP was set from 100 ms before and 700 ms after stimulus onset. NetStation artifact detection settings were set to 150 microvolts for bad channels, 150 microvolts for eye-blinks, and 150 microvolts for eye movements. Channels with artifacts on more than 25 percent of trials were marked as bad channels and replaced through spline interpolation. Segments that contained eye-blinks, eye movement, and those with more than 20 bad channels were also excluded. Participants with less than 40 good trials for any stimulus category were excluded from analysis.

Electrodes of interest were selected on both hemispheres to conform to T5 and T6 and were empirically validated by inspecting N170 magnitude and sensitivity to the clear face only condition compared with the scene condition in grand averages and individual data. Six electrodes over the left lateral posterior scalp (106, 107, 108, 109, 115, 116) and six electrodes over the right lateral posterior scalp (141, 152, 161, 170, 160, 169) were selected. The layout of the Geodesic Sensor net and the electrodes of interest are shown in Figure 2. Time windows ranged from 127 to 297 milliseconds post-stimulus onset, and were customized for each individual participant by visual inspection of the data. Peak and latency to peak were averaged across the specified electrodes within the specified time window, and these values were extracted for each participant.

Behavioral testing. Face perception ability was assessed using the Benton Test of Face Recognition[21].

Results

ERP analyses

Two separate analyses of the ERP variables were conducted to examine: (1) the influence of contextual visual experience by comparing degraded faces presented in the first block of the experiment (hereafter referred to as 'degraded 1') versus degraded faces presented in the last block of the experiment (hereafter referred to as 'degraded 2') and (2) the influence of immediate visual context by comparing degraded faces presented in the context of a human form versus degraded 1, clear faces on bodies, clear faces alone, and bodies alone. For each comparison, separate repeated measures analyses of variance (ANOVA) were conducted for N170 amplitude and N170 latency to peak. For each analysis, condition and hemisphere (left, right) were within-subject factors.

The Influence of Contextual Visual Experience

N170 Amplitude. Table 1 shows N170 amplitude for degraded 1 and degraded 2 in both hemispheres. ANOVA comparing N170 amplitude to degraded 1 versus degraded 2 revealed a significant main effect of condition, $F(1,14) = 14.95$, $p < .01$. In both the left and right hemispheres N170 amplitude was greater to degraded 2 than to degraded 1 ($t(14) = 4.8$, $p < .001$; $t(14) = 2.12$, $p = .05$) (see Figure 3).

N170 Latency. Table 2 shows N170 latency for degraded 1 and degraded 2 in both hemispheres. ANOVA comparing N170 latency to degraded 1 versus degraded 2 revealed a significant main effect of hemisphere, $F(1,14) = 5.47$, $p < .05$). N170 latency was shorter in the right hemisphere (mean = 178.69, SD = 32.3) than in the left hemisphere (mean = 183.59, SD = 37.19) ($t(33) = -2.1$, $p < .05$). No significant main effect of condition, or interaction of condition and hemisphere were observed.

The Influence of Immediate Visual Context

N170 Amplitude. Table 1 shows N170 amplitude in both hemispheres for the following conditions: degraded 1, clear faces alone, bodies with clear faces, bodies with no faces, and bodies with degraded faces. ANOVA comparing N170 amplitude to degraded 1, clear faces alone, bodies with clear faces, bodies with no faces, and bodies with degraded faces revealed a significant main effect of condition ($F(1,14) = 4.9$, $p < .01$). In both the left and right hemispheres N170 amplitude was greater to clear faces alone than to any other condition (all p's $< .05$). There was no significant difference in N170 amplitude to any of the other conditions (see Figure 4).

N170 Latency. Table 2 shows N170 latency in both hemispheres for the following conditions: degraded 1, clear faces alone, bodies with clear faces, bodies with no faces, and bodies with degraded faces. ANOVA comparing N170 latency to degraded 1, clear faces alone, bodies with clear faces, bodies with no faces, and bodies with degraded faces revealed no significant main effect of condition ($F(1,14) = 1.16$, $p > .05$), hemisphere ($F(1,14) = .18$, $p > .05$), and no significant condition by hemisphere interaction ($F(1,14) = .61$, $p > .05$).

Behavioral measures

Chronological age and score on the Benton Test of Face Recognition[21] were correlated with N170 amplitude and latency to 1) conditions testing the influence of contextual visual experience (degraded 2), 2) conditions testing the influence of immediate visual context (degraded faces on bodies), and 3) standard face perception (clear faces alone). A significant negative correlation was found between age and N170 latency to the clear faces alone condition in both the left ($r = -.54$, $p < .05$) and right hemispheres ($r = -.65$, $p < .01$) (see Figure 5). No other significant correlations were observed (all p's $> .05$).

Discussion

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Figure Captions

Figure 1. Sample stimuli used in our experiment. Stimuli were designed to allow us to examine the influence of contextual cues on the perception of ambiguous stimuli (degraded faces, A). We investigated whether: 1) the influence of contextual visual experience alters the N170 response to ambiguous stimuli (degraded faces, A) by comparing responses to the block of degraded faces presented at the beginning of the experiment with responses to the block of degraded faces presented at the end of the experiment; and 2) the immediate visual context (degrade faces in presence of a human form, C) changes N170 response relative to the ambiguous stimulus (A) and clear faces (D, E). We also examine responses to control conditions (B, F).

Figure 2. Schematic indicating electrode layout for the 256 channel Geodesic Sensor Net. Shaded regions indicate electrode groups over which data were averaged for N170 in each hemisphere.

Figure 3. Amplitude of the N170 component (in microvolts) elicited by degraded 1 and degraded 2 in both hemispheres. Error bars represent +/- 1 S.E. Significance at the $p < .05$ level is indicated by *.

Figure 4. Amplitude of the N170 component (in microvolts) elicited by clear faces alone, clear faces on bodies, degraded faces on bodies, bodies alone, and degraded 1 in both hemispheres. Error bars represent +/- 1 S.E. Significance at the $p < .05$ level is indicated by *.

Figure 5. Correlations between N170 latency to clear faces alone and age in both hemispheres.

Tables

Table 1

N170 Amplitude

Hemisphere	Condition	*M* (microVolts)	*SD*
Left	Degraded 1	0.50	2.7
	Bodies alone	.58	2.4
	Degraded faces on bodies	0.19	2.8
	Clear faces alone	- 1.0	2.1
	Clear faces on bodies	.08	2.6
	Degraded 2	- 1.5	2.6
Right	Degraded 1	- 0.35	2.5
	Bodies alone	.41	2.0
	Degraded faces on bodies	.82	2.5
	Clear faces alone	- 1.8	2.6
	Clear faces on bodies	- .29	3.2
	Degraded 2	- 1.2	2.6

Table 2

N170 Latency

Hemisphere	Condition	*M* (milliseconds)	*SD*
Left	Degraded 1	179.73	36.38
	Bodies alone	194.62	44.81
	Degraded faces on bodies	173.42	36.52
	Clear faces alone	180.18	36.15
	Clear faces on bodies	173.78	37.42
	Degraded 2	195.69	38.41
Right	Degraded 1	175.38	33.77
	Bodies alone	195.51	40.71
	Degraded faces on bodies	172.76	34.05
	Clear faces alone	179.47	36.52
	Clear faces on bodies	173.64	37.27
	Degraded 2	186.84	33.20

FIGURE 1 TOP

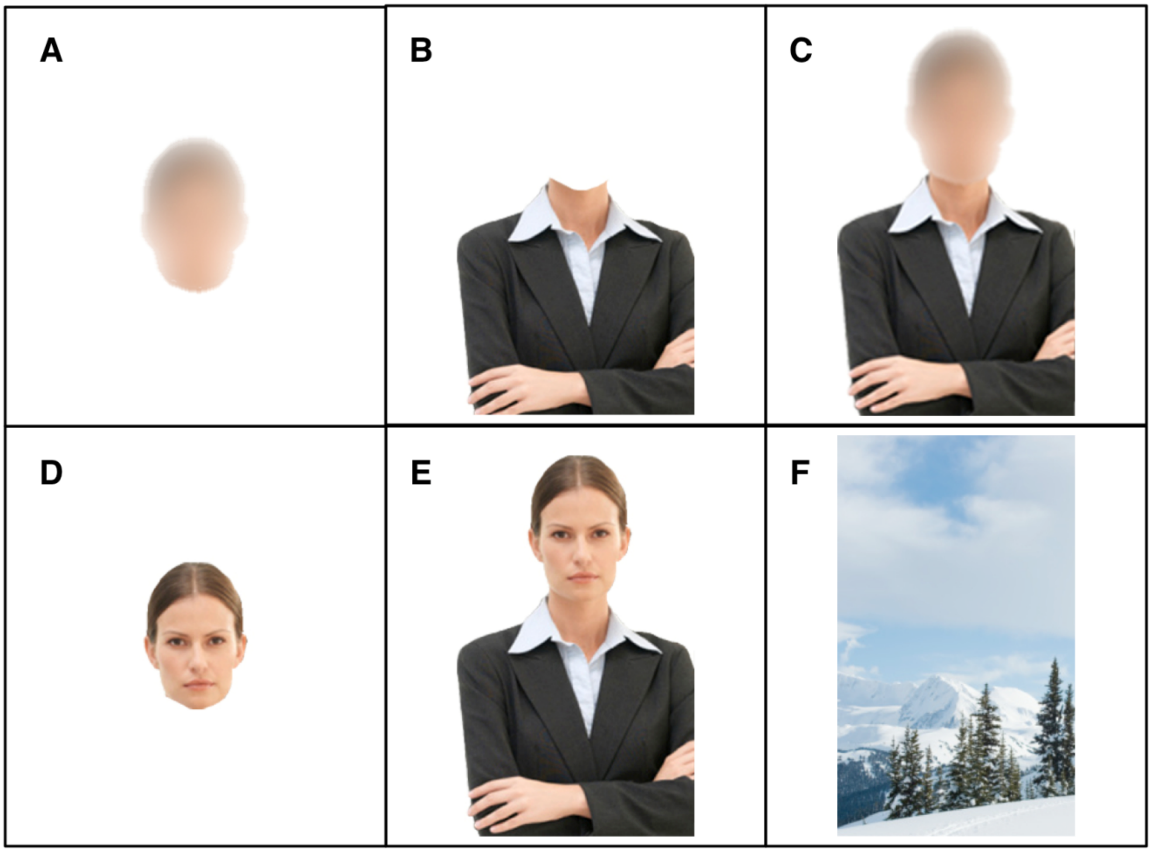


FIGURE 2 TOP

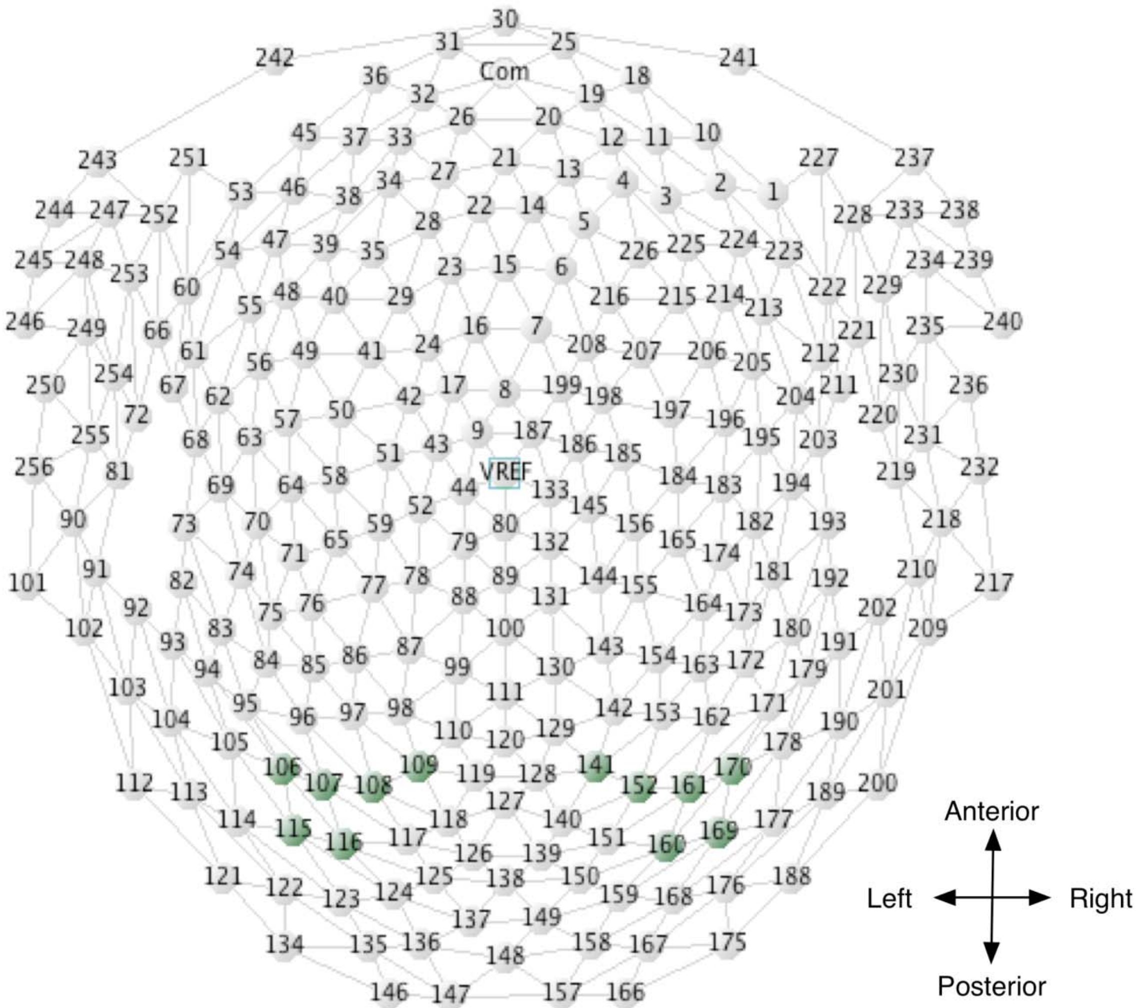


FIGURE 3 TOP

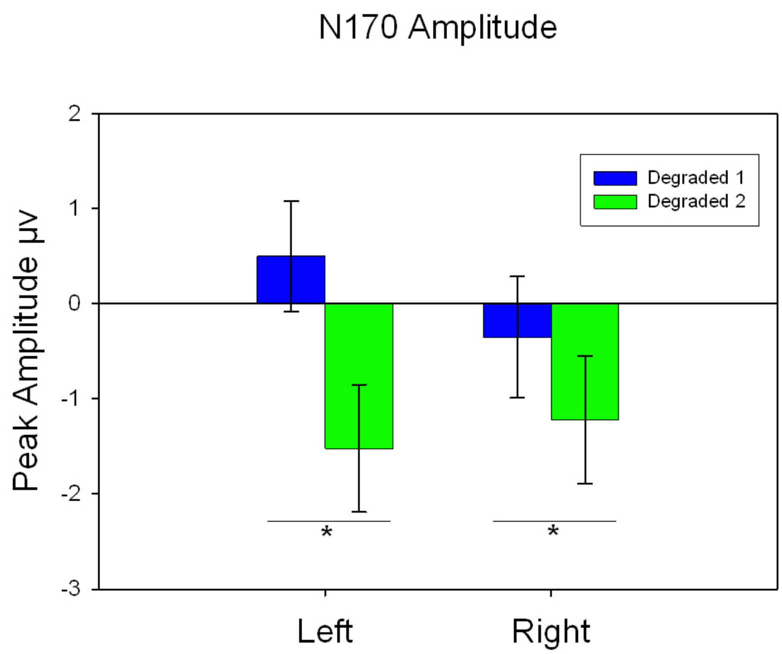

N170 Amplitude
Degraded 1
Degraded 2
Peak Amplitude µv
2
1
0
-1
-2
-3
*
*
Left
Right

FIGURE 4 TOP

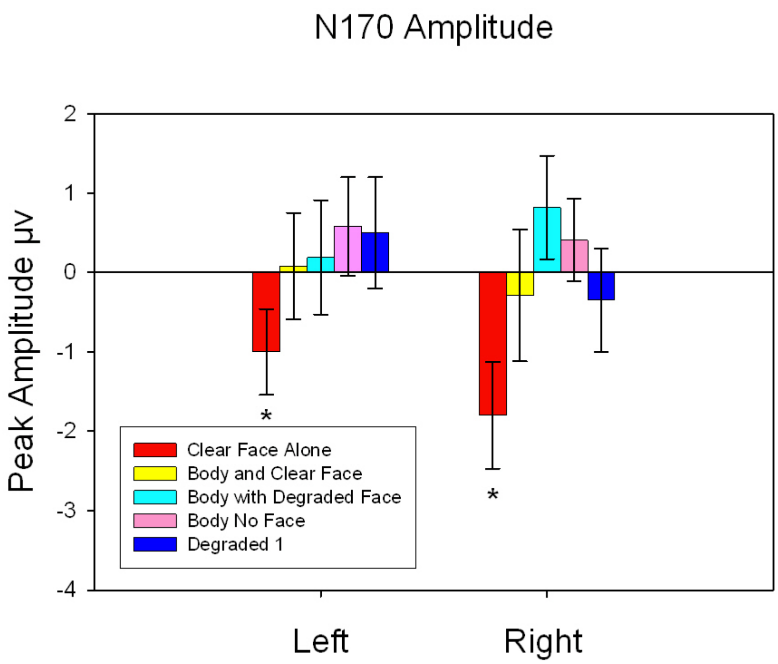
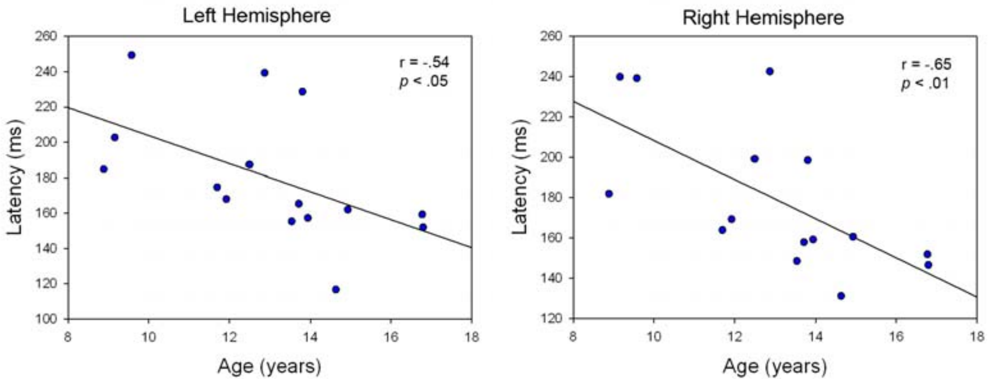

N170 Amplitude
Peak Amplitude µv
2
1
0
-1
-2
-3
-4
*
*
Clear Face Alone
Body and Clear Face
Body with Degraded Face
Body No Face
Degraded 1
Left
Right

FIGURE 5 TOP


Left Hemisphere
r = -.54
p < .05
Latency (ms)
Age (years)
Right Hemisphere
r = -.65
p < .01
Latency (ms)
Age (years)