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Eye-Gaze Direction Modulates Race-Related Amygdala Activity

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Although previous research has found greater activity in the human amygdala in response to Black male compared with White male targets, the basis of this effect remains unclear. For example, is it race alone that triggers amygdala activity, or do other stimulus cues, in conjunction with racial group membership, also play a critical role in this regard? To address this issue, we used functional magnetic resonance imaging to measure amygdala activity in response to Black and White male targets displaying different eye-gaze directions (i.e. direct or averted gaze), as gaze cues have been shown to influence the socio-emotional aspects of person construal. The results revealed that eye-gaze direction significantly moderates race-related amygdala activity. Specifically, Black targets only generated greater amygdala activity than White targets when the faces bore direct gaze. This finding is noteworthy as it demonstrates the importance of compound stimulus cues in the appraisal of social targets.

KEYWORDS amygdala activation, eye-gaze, face perception, race

Group membership is a fundamental characteristic of person perception. Indeed, in almost every facet of human cognition, affect, and behavior, members of groups to which we belong (ingroup members) are responded to differently than are individuals with whom we do not share meaningful group memberships (outgroup members; Tajfel, Tuner, Austin, & Worchel, 1971). Not only are ingroup members largely favored over outgroup members (Brewer, 1999), they are also individuated, recognized, and remembered more than outgroup members (Brewer, 1988; Brigham & Malpass, 1985; Fiske & Neuberg, 1990; Levin, 1996; Meissner & Brigham, 2001). Moreover, people tend to automatically associate ingroup members with positive concepts and outgroup members with negative concepts, even if only at low levels of conscious awareness (De Houwer & Eelen, 1998; Dovidio, Kawakami, Johnson, Johnson, & Howard, 1997; Fazio, Jackson, Dunton, & Williams, 1995; Greenwald, McGhee, & Schwartz, 1998).

Consistent with this research, a growing body of work is finding that people exhibit different

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patterns of neural activity in response to ingroup compared with outgroup individuals (Golby, Gabrieli, Chiao, & Eberhardt, 2001; Hart et al., 2000; Phelps et al., 2000; Richeson et al., 2003; for a review, see Eberhardt, 2005). Much of this work has found that racial ingroup and outgroup members differentially activate the amygdala (e.g. Hart et al., 2000; Phelps et al., 2000; Wheeler & Fiske, 2005). Specially, studies have shown that activity in the amygdala: (i) is greater following the presentation of outgroup than ingroup faces, at least when presented very briefly (Cunningham, Johnson et al., 2004); (ii) habituates more slowly following the presentation of outgroup than ingroup faces (Hart et al., 2000; see also Olsson, Ebert, Banaji, & Phelps, 2005); and (iii) correlates with an unobtrusive measure of racial prejudice (Cunningham, Johnson et al., 2004; Phelps et al., 2000).

Based on these and related findings, the amygdala has been implicated as being responsive to the potential threat that may be posed by members of other racial groups and, furthermore, that differential amygdalar activity might provide the impetus for intergroup bias. But why is the face of a racial outgroup member construed in a threatening manner? One possibility is that merely categorizing a target as 'not one of us' initiates the activation of the 'universal' outgroup stereotype, which includes traits such as *dishonest*, *competitive*, and *hostile* (Campbell, 1967). Another interesting possibility is that it is not outgroup status per se that triggers amygdala activation, but rather the presence of stimulus cues that signal threat, danger, or social importance. The current research examines this latter possibility. Specifically, we consider whether a cue that is particularly relevant to socio-emotional processing—namely, eye-gaze direction—modulates the extent to which racial outgroup, compared with ingroup, members activate the amygdala.

Amygdala and socio-emotional processing

The amygdala has consistently been identified as a structure that plays a critical role in emotional learning, memory, and the evaluative appraisal of social stimuli (Aggleton, 2000; LeDoux, 1996). Guiding behavioral generation, its primary function lies in linking perception and action by providing an emotional value or significance to stimulus inputs (Adolphs, 2001, 2003, 2006). This function is perhaps most apparent in the area of threat detection, an observation that is supported by both patient and brain imaging data. Damage to the amygdala has been shown to impair people's ability to recognize social emotions from facial expressions (Adolphs, Baron-Cohen, & Tranel, 2002). Compared to normal participants, patients with bilateral amygdala damage reliably overestimate the perceived trustworthiness and approachability of strangers (Adolphs, Tranel, Damasio, & Damasio, 1994). This is due in part to their failure to exhibit conditioned fear responses (Bechara et al., 1995) as well as their inability to utilize threat-relevant information communicated by the eyes of conspecifics (Adolphs et al., 2005).

Corroborating these findings, early neuroimaging investigations have demonstrated heightened amygdala activation when healthy participants view faces conveying negative emotions, most notably fear (Baird et al., 1999; Breiter et al., 1996; Morris et al., 1996) and, to a lesser extent, anger and surprise (Sato, Yoshikawa, Kochiyama, & Matsumura, et al., 2004; Wright, Martis, Shin, Fischer, Rauch, 2002; see also Whalen et al., 2001). More recently, however, research has demonstrated that it is not the valence of stimuli per se to which the amygdala responds, but rather their emotional intensity (i.e. arousability; Anderson et al., 2003; Cunningham, Raye, & Johnson, 2004) and, in some cases, the ambiguity of the stimuli (e.g. Adams, Gordon, Baird, Ambady, & Kleck, 2003; Whalen, 1998). Based on work of this ilk, the amygdala has been characterized as a structure that helps people to navigate their social worlds by facilitating the acquisition of emotional knowledge and the low-level, relatively automatic recognition of stimuli that pose a potential threat.

So, why then would racial outgroups trigger the amygdala more than racial ingroups? This finding could be due, at least in part, to the particular ingroup and outgroup targets that have been examined. To date, much of the aforementioned research on heightened amygdala activity to outgroup compared with ingroup members has considered the responses of White perceivers to Black (outgroup) relative to White (ingroup) targets (e.g. Cunningham, Johnson et al., 2004; Wheeler & Fiske, 2005). Although some work has found evidence for differential amygdala activity among Black perceivers to White, compared with Black, targets (Hart et al. 2000), this effect seems to be largely due to differential rates of habituation to ingroup versus outgroup targets, rather than differences in initial activation (see also Olsson et al., 2005). Furthermore, some work has found that at least under some processing conditions, Black perceivers also show heightened activity to Black male targets (i.e. racial ingroup members), compared with White male (i.e. racial outgroup members) targets (Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005), which suggests that the differential amygdala activity that is typically attributed to ingroup versus outgroup status may be better attributed to the particular race (and gender) of the targets that have been examined—Black males. It is possible, in other words, that these findings are driven in part by the differential threat signaled by an outgroup that is stereotypically associated with threat, namely young Black males.

Indeed, the prevailing stereotype of Black men is that they are dangerous and threatening (Cottrell & Neuberg, 2005; Devine & Elliott, 1995). Furthermore, Black men are strongly associated with violent crime (Correll, Park, Judd, & Wittenbrink, 2002; Eberhardt, Goff, Purdie, & Davies, 2004; Payne, 2001) and angry facial expressions of emotion (Ackerman et al., 2006; Hugenberg & Bodenhausen, 2004). It follows, therefore, that Black male targets are particularly potent threat signals for White perceivers, compared with White male (i.e. ingroup) targets. Consistent with this reasoning, White perceivers have been found to orient their attention to faces of Black male targets (Ito & Urland, 2003, 2005; Richeson & Trawalter, 2008; Trawalter, Todd, Richeson, & Baird, 2007), much like individuals selectively attend to cues and stimuli associated with physical threat and danger (e.g. snakes; Öhman, Flykt, & Esteves, 2001).

Taken together, this research suggests that for many White individuals, Black men are appraised as a particularly threatening racial outgroup and, thus, capture attention, presumably due to the need for heightened vigilance to the potential threat source. Consequently, this work suggests that the differential amygdala activity in response to Black, compared with White, men is largely due to the differential threat signal (and, thus, functional significance) associated with Black, compared with White, men (see also Kenrick, Delton, Robertson, Becker, & Neuberg, in press).

Threat and eye-gaze direction

Although this research indicates that the cultural stereotype of Black men makes them a particularly threatening outgroup for White perceivers, other cues that are more evolutionarily important should be able to attenuate, if not completely trump, this effect. For instance, eye-gaze direction is one of the most basic social cues that perceivers rely upon (e.g. Hood, Willen, & Driver, 1998). Almost without exception, the most important social targets are those with whom direct eye contact has been established (Baron-Cohen, 1995). Consistent with this idea, recent imaging investigations have found that a person's eye-gaze direction results in differential activity in the amygdala (George, Driver, & Dolan, 2001; Kawashima et al., 1999; Ochsner, 2004). Furthermore, patients with amygdala damage have impaired ability to use eye-gaze direction as a cue to direct attention (Akiyama, et al., in press), and they show a severe reduction in direct eye contact during actual interactions (Spezio, Huang, Castelli, & Adolphs, 2007). Taken together, this work suggests that the amygdala is particularly sensitive to eye-gaze direction, presumably because of its socio-emotional signal value.

Although direct eye-gaze signals that targets are motivated to approach, the meaning of direct gaze can differ significantly. Specifically, direct eye-gaze can signal both positive approach tendencies, such as romantic interest (Mason, Tatkow, & Macrae, 2005), as well as negative approach tendencies, such as hostility and impending peril (Argyle & Cook, 1976). Hence, direct eye-gaze may be especially significant to perceivers when communicated by a threatening outgroup member. In other words, social cues that are associated with threat, such as racial group membership, may combine with eye-gaze direction to communicate a target's threat potential and, thus, modulate amygdala activity accordingly. Furthermore, given that direct eye-gaze facilitates social categorization (Macrae, Hood, Milne, Rowe, & Mason, 2002), it is not surprising that exposure to Black male targets displaying direct gaze often results in heightened amygdala activity. Indeed, the race cues associated with threat are facilitated by the compatible signal value of the eye-gaze cues. If the Black male targets were displaying averted eye-gaze, however, the race and gaze cues would be in competition. That is, although the racial (and gender) group membership of the target is associated with threat, it may fail to elicit differential amygdala activity because the gaze information suggests that the target does not pose an immediate threat (cf. Hart et al., 2000; Phelps et al., 2000). In other words, averted gaze may attenuate the threat value associated with Black male targets relative to White male targets.

Overview of the present work

The present work examined explicit threat perceptions (Study 1) and implicit threat perceptions as revealed in neural activity in the amygdala (Study 2) in response to facial photographs of Black, compared with White, male targets who bore direct eye-gaze or indirect gaze (averted or closed eyes). Because of the shared signal value of threat, Black male targets with direct eye-gaze were expected to evoke greater threat perceptions and amygdala activity than White male targets with direct eye-gaze, and compared with Black male targets with either closed eyes or averted eye-gaze. In other words, averted eye-gaze, in particular, was expected to attenuate if not completely undermine the race difference in amygdala activity found in previous research, thus reiterating the role of the amygdala in monitoring for cues of particular socio-emotional relevance.

Study 1

Based on the research presented previously, we conducted a behavioral study in order to test whether Black and White male targets with direct versus indirect (averted, closed eyes) eye-gaze are perceived to differ in threat value. That is, can eye-gaze direction modulate the perception of threat communicated by Black male targets?

Method

Materials The stimulus materials for both Study 1 and Study 2 were facial photographs of 32 unfamiliar targets (16 Black faces and 16 White faces). Each target was photographed displaying direct eye-gaze. To create faces with averted gaze and closed eyes, the original faces were manipulated using Adobe Photoshop. In total, 96 stimulus faces were created: 16 Black/direct-gaze (BDG); 16 Black/averted-gaze (BAG); 16 Black/closed-eyes (BCE); 16 White/direct-gaze (WDG); 16 White/averted-gaze (WAG); and 16 White/closed-eyes (WCE). The faces were digitized color images of young adults in full-frontal pose. Each target conveyed a neutral facial expression. In Study 1, 10 faces of each type (Black or White; direct-gaze, averted-gaze, closed-eyes) were randomly selected to be rated, for a total of 60 faces.

Participants & procedure Twenty White undergraduate students attending a New England college came in to the lab individually to provide behavioral ratings of the faces. In addition to examining systematic differences in how threatening the faces were perceived to be, we also examined whether the manipulation of some of the photographs in Photoshop (i.e. those with averted gaze and closed-eyes) might also influence how they were perceived. In order to examine both of these issues, the 60 faces selected at random were rated on how threatening the face was, as well as on how odd or artificial the face appeared, both on 7-point Likert-type scales.

Results and discussion

Artificiality We first assessed how artificial the faces appeared, in order to ensure that any results of eye-gaze that emerge could not be attributed to the manipulation of some of the faces. The mean artificiality ratings for each face were calculated and then subjected to 2 (target race: Black, White) × 3 (eye-gaze: direct, averted, closed eyes) analysis of variance (ANOVA). Results revealed a main effect of race ($F(1,19) = 6.31$, $p < .05$). White faces ($M = 3.00$) were rated as being more artificial-looking than the Black faces ($M = 2.75$). Furthermore, the main effect of eye-gaze was also reliable ($F(2,38) = 8.49$, $p < .001$). Faces with closed eyes ($M = 3.14$) were rated as looking more artificial than either faces with averted eye-gaze ($M = 2.79$) or faces with direct eye-gaze ($M = 2.71$), which did not differ. The interaction between race and gaze was not statistically reliable ($F(2,38) = 1.92$, $p > .15$). Consequently, the results seem to be largely attributable to perceptions of White faces with closed eyes, rather than differences among the Black and White faces with direct or averted eye-gaze, the primary focus of the present work.

Threat perceptions To test our primary predictions, the mean threat ratings for each face were calculated and subjected to the same 2 (target race: Black, White) × 3 (eye-gaze: direct, averted, closed eyes) ANOVA. The means are presented in Table 1. Consistent with predictions, results revealed a main effect of race ($F(1,19) = 5.53$, $p < .03$), as well as a main effect of eye-gaze ($F(2,38) = 27.6$, $p < .0001$). Both of these effects, however, were moderated by a significant race by gaze interaction ($F(2,38) = 18.1$, $p < .0001$). Because we were most interested in the relative threat of faces with direct compared with averted eye-gaze, we conducted a second ANOVA, excluding the faces with closed eyes. Results revealed the same main effects of race ($F(1,19) = 7.18$, $p < .05$) and gaze ($F(1,19) = 21.4$, $p < .0002$), as well as the significant interaction ($F(1,19) = 35.5$, $p < .0001$). Examination of the means revealed that Black faces with direct gaze were rated as more threatening than Black faces with averted gaze (respective *Ms* = 3.43 & 2.54; $t(19) = 5.81$, $p < .0001$). By contrast, White faces with direct and averted gaze were perceived to be equally threatening (respective *Ms* = 2.58 & 2.63; $t(19) = .67$, $p = ns$). Furthermore, whereas Black faces with direct gaze were perceived as more threatening that White faces with direct gaze ($t(19) = 4.9$, $p < .0001$), Black and White faces with averted gaze were perceived to be equally (non)threatening ($t(19) = .60$, $p = ns$). These results suggest that, indeed, White perceivers are likely to find faces of Black male individuals with direct eye-gaze to be more threatening than Black male individuals with averted gaze, or compared to White male individuals irrespective of gaze. In other words, these behavioral ratings provide initial evidence for the claim that eye-gaze moderates the effect of race on perceptions of threat.

Study 2

Considered in tandem with the research reviewed previously, the results of Study 1 suggest that averted eye-gaze direction can attenuate the extent to which Black male targets are perceived to be more threatening than White male targets. Although the results of Study 1 are promising,

Table 1. Mean threat judgments for Black and White targets by eye-gaze direction

	Direct	Averted	Closed
Black targets	3.43 (0.91)	2.54 (0.86)	2.44 (0.88)
White targets	2.58 (0.99)	2.63 (0.82)	2.19 (0.93)

Note: Standard deviations are in parentheses.

they emerged from explicit judgments of threat, which are likely to be influenced by both low level activity in the amygdala and higher level cognitive processing in frontal areas (e.g. Cunningham, Johnson et al., 2004). Hence, a strong test of the extent to which eye-gaze direction moderates threat perception requires an examination of neural activity in the amygdala while participants are engaged in an unrelated task. Consequently, in Study 2 we examined the veracity of the hypothesis that eye-gaze direction moderates the effect of race on more implicit threat responses—neural activity in the amygdala.

Method

Participants Nine paid student volunteers from a New England college (6 female; 19–23 years of age) participated in the experiment. All participants were White, right-handed, native English speakers with no history of neurological problems. All gave informed written consent according to the procedures approved by the Committee for the Protection of Human Participants at the college.

Materials The stimulus materials were identical to those described in Study 1; however, the full set of 96 faces was used in Study 2. In the magnetic resonance imaging (MRI) scanner, stimuli were generated using an Apple G3 Laptop computer running PsyScope software. Stimuli were projected to participants with an Epson (model ELP-7000) LCD projector onto a screen positioned at the head end of the bore. Participants viewed the screen by use of a mirror placed at a 45° angle on top of the head coil. A fiber optic, light sensitive key press interfaced with the PsyScope Button Box (New Micros, Dallas, Texas) was used to record participants' behavioral responses.

Procedure Scanning involved a blocked-presentation of the stimuli, with the blocks alternating between Black and White faces. Stimulus presentation of the experimental blocks (12 blocks) alternated with baseline blocks, which comprised a blank screen with a central fixation cross. Both the presentation blocks and the baseline blocks were 20 s in duration. During each presentation block, 8 faces (e.g. Black targets displaying direct gaze) were presented to participants. Each face remained on the screen for 2.5 s and was located either to the right or left of the fixation cross. The location of the faces on the screen was counterbalanced across participants and the order of presentation of the faces was randomized. Participants were instructed to focus on the fixation cross. When a face appeared on the screen, they were requested to report, by means of a key press, whether the face appeared to the left or right of the fixation cross.

Gradient-echo echoplanar MR images were acquired using a 1.5 Tesla GE Signa System (General Electric, Milwaukee, WI, USA). A quadrature birdcage head coil was used for RF transmission and reception. In each of 25 non-contiguous planes parallel to the anterior-posterior commissure, 112 T2*-weighted MR images depicting BOLD contrast were acquired with TE 35 ms, TR 2500 ms, flip angle 90°, slice thickness 4.5 mm, and skip slice 1 mm. Head movement was limited by foam padding within the head coil. For each participant, 3-D MRI anatomical data were also obtained using the Spoiled Grass (SPGR) technique. T1-weighted images (TR 7.7 ms, TE 3 ms, flip angle 15°, slice thickness 1.2 mm) were obtained in the AC-PC orientation. BOLD images were realigned to correct for interscan movements and coregistered to the participant's anatomical image using SPM99 (Wellcome Department of Cognitive Neurology, London). The resulting matching brain images were spatially normalized with a cubic (3×3×3 mm) voxel size. BOLD images were further smoothed using an isotropic Gaussian filter of 6 mm FWHM and corrected for global activity by proportional scaling.

Data analysis first removed low-frequency drifts in the signal plus global changes in activity. The six different stimulation conditions (Black or White faces, direct-gaze, averted-gaze, or closed-eyes) were then modeled as boxcar functions, convolved with a hemodynamic response function. Based on previous findings, our hypothesis was that the combination of direct gaze and ingroup-outgroup status would modulate activation in the amygdala. Accordingly, region-of-interest (ROI) analyses were restricted to the right and left amygdala. We performed two types of ROI analyses on our data. The first relied on a functional definition, while the second relied on an anatomical definition.

A functional ROI was defined using the contrast most central to our hypotheses, that Black faces displaying direct gaze would produce increased amygdala activity relative to White faces displaying direct gaze. This methodology has been used widely as a means by which to discern functional regions of interest (see Kanwisher, McDermott & Chun, 1997). In order to identify specific amygdala regions showing significant BOLD changes, statistics were computed on a voxel-by-voxel basis using the general linear model. Specific effects were tested by applying appropriate linear contrasts for each condition, resulting in a t statistic for each ROI. These individual contrast images were then submitted to a second-level, random-effects analysis to create mean t images (thresholded at $P = 0.005$, uncorrected; minimal cluster size = 20 mm^3). An automated peak-search algorithm identified the location of peak activations and deactivations based on z value and cluster size.

A second ROI analysis was performed based on neuroanatomy. To ensure neuroanatomical specificity, coordinates from the Talairach and Tournoux (1988) atlas were used to place spherical regions of interest, with a 5 mm radius (524mm^3), in the right (center point: $x = 15$, $y = –6$, $z = –21$) and left amygdala (center point: $x = –15$, $y = –6$, $z = –21$). Data were extracted from this region on a subject-by-subject basis, and direct tests of our hypotheses were performed off line. Significance levels are reported for the critical comparisons within the right and left amygdala.

Results and Discussion

The behavioral data (response accuracy and latencies) were submitted to a 2 (race: Black or White) × 3 (eye-gaze: direct, averted, eyes closed) repeated-measures ANOVA. This revealed no effects of the experimental manipulations on either the accuracy or latency of participants' responses.

Our prediction was that the amygdala response to racial targets would be modulated by gaze direction. Results from our functional ROI revealed a region in the right amygdala ($x = 15$, $y = –6$, $z = 24$; extent = 12 voxels) for which BOLD signal intensities were significantly greater in response to Black faces than to White faces ($t(8) = 6.06$, corrected $p < .01$) for the direct gaze (BDG > WDG) condition only (see Figure 1). No significant effect of race was observed in the right or left amygdala when targets displayed averted gaze or had their eyes closed (BAG > WAG; BCE > WCE). No significant differences within either the right or left amygdala were observed with regard to the main effect of race (BDG+BAG+BCE > WDG+WAG+WCE) or gaze (BDG+WDG > BAG+WAG; BDG+WDG > BCE+WCE).

Table 2 displays the results of whole brain voxel-wise analyses for the two most relevant contrasts stemming from our hypotheses regarding the effects of eye-gaze direction: (1) BDG > BAG and (2) WDG > WAG. Because we were primarily interested in the relative *threat* of faces with direct compared with averted eye-gaze, however, we extracted individual data from the functionally derived ROI and conducted a 2 (race) × 2 (eye-gaze) ANOVA, excluding the faces with closed eyes. Results revealed neither main effects of race ($F(1,8) = .65$, $p = .44$) nor eye-gaze ($F(1,8) = .07$, $p = .80$); however, the

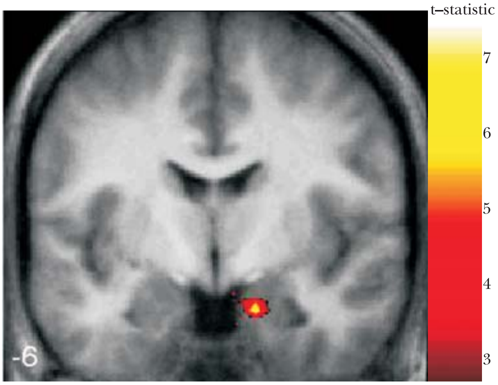

Figure 1. Coronal section through the right amygdala (15, –6, –24; 12 voxels), showing the functional region of interest derived from the contrast BDG >WDG

Table 2. Whole brain analysis for the comparisons of interest

		Coordinates				
Brain region	BA	X	Y	Z	Size	*t* value
Black direct > Black averted						
L Insula	na	–26	0	–15	17	7.76
R Amygdala	na	15	–6	24	12	6.06
R Insula	na	36	0	9	11	4.98
L Supramarginal gyrus	40	–33	–66	24	25	4.70
R Hippocampus	na	24	–27	–6	15	4.50
R Middle frontal gyrus	9/46	15	51	36	22	4.73
L Inferior occipital gyrus	18	–18	–96	6	10	4.09
R Precentral gyrus	4	30	–27	42	10	3.47
R Medial orbital gyrus	12	6	54	–21	14	3.23
White direct > White averted						
R Inferior occipital gyrus	17	15	–96	–15	21	5.75
L Superior temporal gyrus	22	–48	–54	24	73	4.41
L Middle frontal gyrus	9/46	–27	27	45	22	4.30

Notes: BA, approximate Broadmann's area location. L, left; R, right; Talairach coordinates of locations based on center of mass. Size, number of 3 × 3 × 3 mm voxels.

interaction between race and gaze was reliable ($F(1,8) = 4.98$, $p = .056$) Examination of the means revealed that Black faces with direct eye-gaze produced significantly greater amygdala activity than Black faces with averted eye-gaze (respective *M*s = 0.077 & –.041; $t(8) = 2.31$, $p = .05$). By contrast, White faces with direct and averted eye-gaze produced similar levels of amygdala activity (respective *Ms* = –.004 & .056; $t(8) = -1.08$, $p = .31$). Consistent with the results of the analyses reported previously, Black faces with direct eye-gaze produced significantly greater amygdala activity than White faces with direct eye-gaze (respective *M*s = .077 & –.004; $t(8) = 2.26$, $p = .05$), whereas the amygdala activity associated with Black and White faces with averted eye-gaze did not differ reliably(respective *Ms* = –.041 & .056; $t(8) = -1.58$, $p = .15$). In fact, the means were in the opposite direction; White faces with averted eye-gaze were associated with marginally *more* amygdala activity than Black faces with averted eye-gaze.

Our second set of analyses, based on anatomical localization, yielded results that converge quite nicely with those obtained from the functional ROI analyses presented previously. A 2 (race: Black, White) × 2 (eye-gaze: direct, averted) ANOVA on neural activity in the right amygdala anatomical ROI revealed neither main effects of race nor eye-gaze, but a significant interaction effect ($F(1,8) = 7.22$, $p < .05$). As depicted in Figure 2, Black faces with direct gaze produced greater amygdala activity than White faces with direct gaze ($t(8) = 3.25$, $p < .01$); but, the amygdala activity associated with exposure to Black and White faces with averted gaze did not differ ($t(8) = -1.36$, $p = ns$). Furthermore, Black faces with direct gaze produced significantly more amygdala activity than Black faces with averted gaze ($t(8) = 2.42$, $p < .05$). By contrast, White faces with direct gaze produced marginally *less* amygdala activity than White faces with averted gaze ($t(8) = -1.85$, $p = .10$).

Analyses of the mean percent signal change within the anatomically derived ROI placed in the left amygdala revealed similar effects for race and eye-gaze. Similar to the ANOVA results for the functional ROI and anatomically derived right amygdala ROI presented previously, only a significant interaction between race and gaze emerged from the 2 (race) × 2 (eye-gaze) ANOVA ($F(1,8) = 15.20$, $p < .01$). As shown in the right panel of Figure 2, Black faces with direct gaze produced more activity in the left amygdala than White faces with direct gaze ($t(8) = 2.74$, $p < .05$). Interestingly, neural activity in this region in response to White faces with averted eye-gaze was significantly greater than activity to Black faces with averted gaze ($t(8) = -2.47$, $p < .05$). Moreover, Black faces with direct gaze produced significantly more activity in this left amygdala ROI than Black faces with averted gaze ($t(8) = 2.65$, $p < .05$). By contrast, neural activity to White faces with direct and averted gaze did not differ significantly ($t(8) = -1.04$, $p =$ *ns).* Considered in tandem, these results are consistent with predictions, suggesting that eye-gaze direction moderates the effect of race on neural activity in the amygdala.

General discussion

The present findings corroborate previous research that has observed differential activity in the amygdala after exposure to Black, compared with, White faces (Cunningham, Johnson et al., 2004; Hart et al., 2000; Lieberman et al., 2005; Wheeler & Fiske, 2005). Extending previous research, however, race per se was not sufficient to trigger amygdala response; rather, race and eye-gaze cues worked in concert to modulate activity in this neural structure. Confirming our prediction, Black targets elicited greater amygdala activity compared with White targets (i.e. Black > White) *only* when the targets displayed direct gaze. When gaze was averted or the eyes were closed, no significant increase in

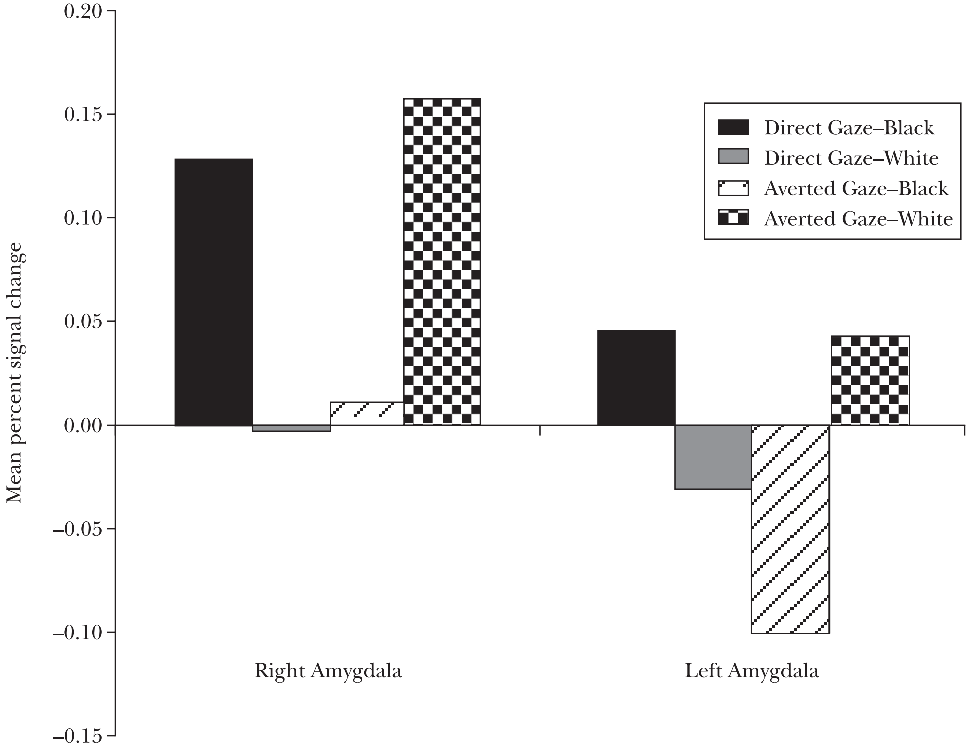

Figure 2. Mean percent signal change within the anatomically selected regions of interest placed in the right and left amygdala

amygdala activity was observed in response to Black targets, and, if anything, results suggested that averted eye-gaze might amplify the threat or uncertainty associated with ingroup (i.e. White) targets. These findings further demonstrate the importance of gaze cues in social cognition (Adams et al., 2003; Baron-Cohen, 1995; Emery, 2000; Macrae et al., 2002). Signaling the emotional status or behavioral intentions of conspecifics, gaze cues alert perceivers to possible threat or danger, particularly when the self is the object of others' attention.

But why do outgroup targets displaying direct gaze trigger an elevated amygdala response? One candidate explanation is that the amygdala is signaling the presence of an unfamiliar stimulus that has acquired additional emotional significance through prior learning or experience (e.g. Olsson et al., 2005). That is, the amygdala is tagging a potentially important emotional stimulus in the environment, a stimulus that is made salient through cultural forces that reflect the current status of intergroup relations. That eye-gaze cues should modulate amygdala activity in this way is consistent with evidence from a variety of sources. Neurophysiological investigations in monkeys have identified cells in the medial and lateral nuclei of the amygdala that are sensitive to eye-gaze direction (Brothers, Ring, & King, 1990). Similarly, human lesion studies have revealed impairments in the interpretation of gaze-related, emotional information following amygdalotomy (Adolphs et al., 1994; Young et al., 1995). In particular, recent research suggests that whereas normal individuals (i.e. those not suffering from amygdala damage) tend to spontaneously attend to the eye region of targets as a means of fear-relevant information gathering, those individuals suffering from amygdala damage fail to do so, leaving them unable to recognize fearful expressions (Adolphs et al., 2005). Interestingly, simply instructing these patients to focus on the eyes of targets is sufficient to reverse—albeit only temporarily—the previously obtained decrements in emotion recognition (Adolphs et al., 2005).

Of potential theoretical interest in the present study is the laterality of the observed effect; the functional analyses revealed differential activity to Black versus White faces with direct gaze, in the right, but not the left, amygdala and the anatomical analyses revealed greater reactivity overall in the right compared with the left amygdala. Whalen and colleagues (1998, 2001) have suggested that one function of the amygdala is to modulate the vigilance level of an organism. In pursuit of this objective, the right amygdala is thought to play a critical role in the detection of emotionally arousing or potentially threatening stimuli. Consistent with this perspective, Kawashima et al. (1999) found that the right, but not left, amygdala was sensitive to eye contact. Furthermore, a recent examination of neural activity as a function of skin tone revealed that the right amygdala was more active for light and darker skinned Black targets as well as for darker skinned White targets, relative to light-skinned White targets (Ronquillo et al., 2007). The present study, therefore, corroborates this work, finding that differential amygdala activity to outgroup, compared with ingroup, targets is more robust in the right amygdala.

The ability to negotiate a complex world may require neural systems that are specialized in the task of social information processing (Adolphs, 2001, 2003). As other people are some of the most important objects we encounter, social-cognitive functioning may recruit operations that are finely tuned to discerning the signal value of these targets (see Ochsner, 2004 for a similar argument). In recent years, researchers have begun to explore the neural processes that underlie social cognition, particularly the operations that support emotional appraisal, person perception, and the ability to discern the intentions of others (for a review, see Lieberman, 2007). In each of these tasks, eye-gaze cues have been shown to modulate the inferences that people make as they strive to understand other social agents (Baron-Cohen, 1995; Emery, 2000). Extending this line of inquiry, the present results revealed that eye-gaze cues also shape people's emotional reactions to members of different racial groups. In so doing, the current work highlights the importance of compound stimulus cues in the cognitive neuroscience of person perception.

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