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Processing of affective faces varying in valence and intensity in shy adults: An event-related fMRI study

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Abstract

Recent behavioral and electrocortical studies have found that shy and socially anxious adults are hypersensitive to the processing of negative and ambiguous facial emotions. We attempted to extend these findings by examining the neural correlates of affective face processing in shy adults using an event-related fMRI design. We presented pairs of faces that varied in affective valence and intensity. The faces were morphed to alter the degree of intensity of the emotional expressive faces. Twenty-four (12 shy and 12 non-shy) young adult participants then made same/different judgments to these faces while in an MR scanner. We found that shy adults exhibited greater neural activation across a distinct range of brain regions to pairs of faces expressing negative emotions, moderate levels of emotional intensity, and emotional faces that were incongruent with one another. In contrast, non-shy individuals exhibited greater neural activation across a distinct range of brain regions to pairs of faces expressing positive emotions, low levels of emotional intensity, and emotional faces that were congruent with one another. Findings suggest that there are differences in neural responses between shy and non-shy adults when viewing affective faces that vary in valence, intensity, and discrepancy.
Keywords: shyness, fMRI, emotion, valence, intensity, discrepancy, adults.

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Shyness reflects an anxious preoccupation of the self in response to real or imagined social situations (Melchoir & Cheek, 1990). Although over 90% of the population has reported experiencing shyness at some point in their lives in different situations (Zimbardo, 1977), only a smaller percentage (10-15%) of individuals are characterized by temperamental shyness (Kagan, 1994). Temperamental shyness has its roots in infancy, reflects stable withdrawal and reticence in social situations across development, and is predictive of depression and anxiety disorders. The phenomenon is associated with a number of distinct psychophysiological correlates at rest and in response to social provocation, including greater relative right frontal EEG activity, high and stable heart rate, and high morning salivary cortisol responses in children and adults (for reviews, see Schmidt & Buss, 2010; Schmidt, Polak, & Spooner, 2005).

Current thinking suggests that origins and maintenance of individual differences in shyness may be linked to an inability to regulate fear (Schmidt et al., 2005). Indeed, individuals who are shy are known to exhibit distinct behavioral and psychophysiological correlates during emotion processing and are hypersensitive to negative emotions, particularly those associated with fear and threat (Theall-Honey & Schmidt, 2006).

In a series of studies with adults using a range of face processing tasks and behavioral and neural measures, we found that shyness is associated with a bias to negative emotions. For example, shy adults exhibit a bias to angry and ambiguous faces (morphed by 50%) as early as 100 ms after face presentation than their non-socially anxious counterparts (Miskovic & Schmidt, 2012) and a lower threshold to detect anger faces from other affective faces (Gao, Chiesa, Maurer, & Schmidt, 2012) on behavioral measures.

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These emotion face-processing biases are also known to have distinct electrocortical and neural correlates among shy individuals, particularly as they relate to the processing of negative emotions such as fear and threat. For example, we recently found that relative to their non-shy peers, adults who were classified as temperamentally shy exhibited a shorter latency to the onset of the P1 ERP component during the processing of fear, but not other emotions (Jetha, Zheng, Schmidt, & Segalowitz, 2012), suggesting a hypervigilance to fear early in visual processing using electrocortical measures. Shy adults also exhibited greater bilateral amygdala activation (Beaton et al., 2008) and reduced fusiform activity (Beaton et al., 2009) during the processing of familiar and unfamiliar faces as measured by fMRI. These patterns of neural responses suggest that shy individuals exhibit an initial hypervigilance for detecting negative emotions and threat cues as reflected in a short ERP latency to the processing of fear faces and increased bilateral amygdala activation, followed by avoidance of unfamiliar faces reflected in reduced fusiform activity. Together these findings are consistent with a vigilance–avoidance hypothesis of anxiety (e.g., Bogels & Mansell, 2004).

We attempted to extend our recent findings on the neural correlates of face processing in shy adults by examining the processing of affective faces that varied in affective valence (i.e., positive vs. negative) and intensity (i.e., moderate vs. low). We examined whether people who were shy would exhibit more sensitivity to lower versus higher intensities of faces varying in affective valence and whether there were distinct neural correlates associated with these processes. Valence and intensity are two fundamental characteristics of emotion.

There is evidence to suggest that affective valence and intensity are distinguishable on regional electrocortical and fMRI measures, suggesting possible different neural substrates that underlie these two affective dimensions. For example, Schmidt and Trainor (2001) found that young adults exhibited greater relative left frontal EEG activity during the processing of positive musical emotions and greater relative right frontal EEG activity during the processing of negative musical emotions. Adults also exhibited more overall frontal EEG alpha activity when emotions were of greater intensity. In addition, more recent studies have distinguished affective valence and intensity in adults using fMRI measures during the processing of olfactory and gustatory stimuli (Anderson et al., 2003; Small et al., 2003). The authors were able to double dissociate activation in the orbitofrontal cortex and amygdala with processing of stimuli that varied in valence and intensity, respectively.

In the current study we presented a sample of shy and non-shy adults with affective faces that varied in affective valence and intensity while in an MR scanner. We examined whether shy adults would be more sensitivity to positively versus negatively valenced affective faces and for detecting different levels of affective intensity than non-shy adults. We predicted that shy individuals, compared with their non-shy counterparts, would exhibit greater neural activity in anterior brain circuits during the processing of negative relative to positively valenced emotions and intense relative to lower affectively intense facial expressions.

Method

Participants

Participants included 152 (61 males, *M* age = 19.74 years; and 91 females, *M* age = 20.41 years) undergraduate students enrolled in psychology classes at McMaster University. The participants completed a series of questionnaires as part of a larger study on the neural correlates of social anxiety (Beaton et al., 2008, 2009, 2010). Participants received partial course credit for their voluntary participation in the initial screening procedure.

Participant Selection

Of the 152 participants, 30 were selected for high (*n* = 15; upper 25%) and low (*n* = 15; bottom 25%) shyness based on their responses to the Cheek and Buss Shyness Scale (Cheek, 1983). Of these 30 participants, 24 (12 shy: 5 female and 7 male; and 12 non-shy: 4 female and 8 male) agreed to participate. The selected groups did not differ in age, $t(22) = 0.67$ or gender composition, $\chi^2(1) = 1.50$, ns.

All participants were right-handed, healthy young adults with no current or history of mental illness or learning disability and had not used medications that act on the central nervous or adrenocortical systems within 2 weeks of participation. All selected participants were briefed about the procedures and signed a consent form prior to study initiation. All participants were reimbursed for travel and parking costs and received $100 remuneration for their time for participating in the fMRI component of the study. The McMaster University Health Sciences and St. Joseph's Healthcare Research Ethics Boards approved all procedures.

Affective Face Stimuli and Presentation

Face images varying in affective valence of angry, sad, and happy were obtained from Ekman and Friesen (1976) affective faces dataset. Digital images were converted to grayscale and further adjusted for size, contrast, and luminosity to match the parameters of a standardized set of male and female neutral face stimuli (Ekman & Friesen, 1976). The faces were then morphed to alter the intensity of the affective expressive faces (i.e., angry, sad, happy) on a scale from low (i.e., 10 to 30%) to moderate (i.e., 40 to 60%) to high (i.e., 70 to 100%) using Fantamorph software (www.fantamorph.com).

A total of 60 trials were presented to each participant while in the MR scanner.

In each trial, two adjacent faces were presented simultaneously that were either congruent or incongruent in their affective valence and intensity. A congruent trial presented two faces expressing identical affective valence and intensity. An incongruent trial always contained one neutral face and a face of varying affective valence and intensity. There were an approximately equal number of congruent and incongruent pairs of affective faces representing 36.6% (22/60) and 38.3% (23/60), respectively, of the total trials. Another 25% (15/60) of the trials were pairs of congruent neutral faces.

The participants indicated whether the two faces were the same or different with the use of a response box. Image presentation and response recordings were done with the use of E-prime v1.2 (Psychology Software Tools, Pittsburgh, PA). Reaction times (RT) and accuracy were computed for each trial. RT and accuracy data were not acquired for four participants (2 shy and 2 non-shy participants) due to technical error.

In order to eliminate participant burden and fatigue while in the MR scanner, we limited the number of trials and decided a priori which emotions and intensities to overrepresent. Trials expressing the angry emotion were overrepresented in our sample, with more trials expressing low and high intensities. It was expected that this emotion would be the most emotionally salient for people who are shy, given that it is presumed to elicit threats even at low intensities. For the sad and happy emotions, we overrepresented the moderate intensities in order to increase the level of ambiguity of the face. Analyses involved a two-step mixed model approach, which is relatively robust to the effects of first-level design heterogeneity and unequal first-level variances (Friston et al., 2005).

Trials with at least one angry face encompassed 41.6% (25/60) of the trials and were morphed in intensity to low (11/25 trials), moderate (4/25 trials) and high (10/25 trials) expression. Trials with at least one sad face included 16.6% (10/60) of the trials and were morphed in intensity to low (4/10 trials), moderate (5/10 trials) and high (1/10 trials) expression. Trials with at least one happy face encompassed 16.6% (10/60) of the trials and were morphed in intensity to low (4/10 trials) and moderate (6/10 trials) expression. Finally, pairs of neutral faces encompassed 25% (15/60) of the trials.

Due to the small number of trials for some emotions and intensities, and in order to increase statistical power, we collapsed angry and sad facial emotions into a negative valence category across all intensities for the valence analyses. In addition, the positive valence category represented happy facial emotions collapsed across all intensities. Incongruent and congruent pairs of faces were collapsed that were expressing 40–60% (i.e., moderate intensity) and 10–30% (i.e., low intensity) emotion for discrepancy analyses.

Image Acquisition and fMRI Analyses

Images were acquired using a General Electric 3-Tesla, whole-body short bore scanner with eight parallel receiver channels (General Electric, Milwaukee, WI). A three-dimensional volume spoiled gradient recalled (SPGR) pulse sequence with 124 slices (1.5-mm thick) was used to acquire anatomic images in the axial plane. Functional images were gathered with a gradient-echo EPI sequence and covered the whole brain in 32 to 37 axial slices (4-mm thick). Slices begin at the cerebral vertex and included the entire cerebrum and the greater part of the cerebellum (TR/TE = 2700/35 ms, FOV = 24 cm, matrix = 64 × 64, flip angle 90°).

Acquired images were transferred to a workstation to be processed and analyzed with the use of Brain Voyager QX version 2.3 (Brain Innovation B.V., Maastricht, The Netherlands). The functional data sets were temporally corrected for interleaved slice acquisition, 3D-motion corrected, realigned and smoothed using a Gaussian kernel at 6 mm and normalized to Talairach space (Talairach & Tournoux, 1988). High-resolution T1-weighted three-dimensional anatomic magnetic resonance imaging data sets were transformed into Talairach space used for co-registration and averaged to generate a composite image, which was created using all anatomic data sets.

The test period comprised of 60 trials presented for 2700 ms followed by a jittered fixation cross of varying duration (2700–10,800 ms). An event-related deconvolution model for each participant was used to examine blood oxygenation level dependent (BOLD) signal at each and every voxel. Activation maps were computed using a random effects model and determined clusters of activity associated with peak differences between the shy and non-shy groups and within group comparisons in valence (positive vs. negative), intensity (moderate vs. low), and discrepancy (congruent vs. incongruent faces) within an anatomically defined whole brain mask. Peak differences (as reported in the activation table) indicate the voxel eliciting the highest level of activation or deactivation within an activation cluster for the given comparison.

Contrasts were corrected for multiple comparisons using the standard false discovery rate (FDR, set at $p < 0.05$) (Genovese, Lazar, & Nichols, 2002). Each voxel was 3 mm^3 and clusters of significant activation were set at thresholds of 150 voxels or greater. Functional MR imaging data for 2 non-shy participants were lost due to technical error.

Results

We examined whether people who are shy would show greater sensitivity to lower versus higher intensities of faces varying in affective valence than non-shy adults and whether there were distinct neural correlates associated with these processes. We predicted that shy individuals would exhibit greater neural activity in anterior brain circuits during the processing of negatively valenced and more intense facial expressions compared with their non-shy counterparts. Within-group t-tests were computed to determine the condition driving between group differences.

Affective Valence

To examine if neural responses during detection were related to affective valence, we contrasted neural responses for shy and non-shy adults when they viewed faces categorized as positively valenced emotion (i.e., happy) with negatively valenced emotions (i.e., sad and angry). As predicted, shy individuals exhibited greater neural activation to faces expressing negative emotions, whereas non-shy individuals displayed heightened activity to faces expressing positive emotions. When considering specific brain regions, there was greater activation in the right inferior frontal gyrus [$x = 53$, $y = 28$, $z = 6$, $t(21) = 3.803$, voxels = 443, $p = 0.0002$, $d = 1.701$] and middle temporal gyrus [$x = 39$, $y = -78$, $z = 20$, $t(21) = 3.823$, voxels = 615, $p = 0.0002$, $d = 1.710$] by the shy adults relative to the non-shy adults when they viewed faces expressing negatively valenced emotions.

In contrast, non-shy individuals exhibited greater activation in the right middle frontal cortices [$x = 34$, $y = 49$, $z = 14$, $t(21) = -4.188$, voxels = 1692, $p = 0.00004$, $d = 1.873$] when viewing positively valenced emotions relative to shy individuals (see Table 1 and Figure 1).

Affective Intensity

We contrasted neural responses for shy and non-shy adults when they viewed faces categorized as moderate versus low affective intensity. Shy individuals exhibited greater activation in the rostral anterior cingulate cortex (ACC) [$x = 0$, $y = 39$, $z = 2$, $t(21) = 3.322$, voxels = 678, $p = 0.001$, $d = 1.486$], BA 32 while viewing moderate, relative to low intensity affective faces than non-shy individuals.

In contrast, non-shy individuals exhibited greater activation in the right amygdala [$x = 17$, $y = -4$, $z = -24$, $t(21) = 3.173$, voxel = 316, $p = 0.002$, $d = 1.419$], the ventromedial frontal gyrus [$x = 1$, $y = 50$, $z = -15$, $t(21) = -3.972$, voxels = 350, $p = 0.00009$, d = 1.776] and the dorsal ACC [$x = 0$, $y = 31$, $z = 17$, $t(21) = -3.694$, voxels = 916, $p = 0.0003$, 1.652], BA 24 while viewing low, relative to moderate, affective intensity faces than shy individuals (see Table 2 and Figures 2 and 3).

Table 1. *Affective Valence*: Between group differences for shy versus non-shy individuals contrasting neural activation to faces expressing negative (sad and angry) minus positive (happy) emotion

Affective valence								
		Coordinates						
Brain region	**BA**	**X**	**Y**	**Z**	**T-value**	***p* value**	**Cohen's d**	**# Voxels**
Shy> Non-shy								
Right inferior frontal gyrus	45	53	28	6	3.80302	0.00017	1.701	443
Right middle temporal gyrus	19	39	-78	20	3.82304	0.000157	1.710	615
Non-Shy>shy								
Right middle frontal gyrus	10	34	49	14	-4.18833	0.000036	1.873	1692

All data presented are corrected for multiple comparison at FDR = 0.05.

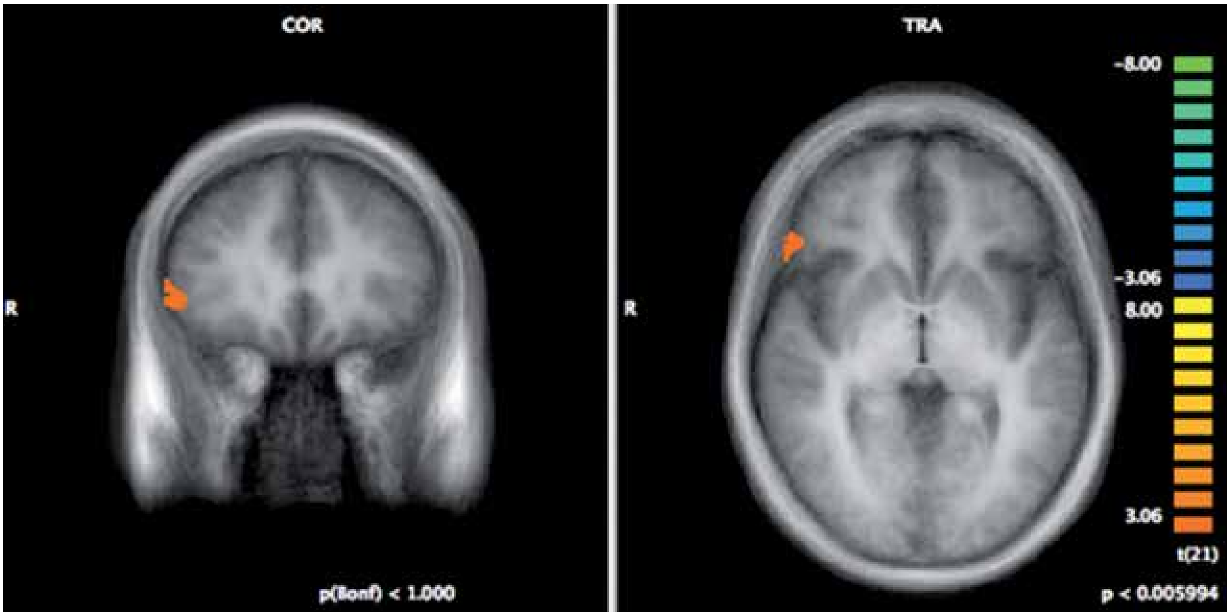


Figure 1. *Affective Valence*: Between-group activation differences in the right inferior frontal gyrus were elicited by the shy individuals to negative emotions relative to positive emotions, denoted in warm colors.

Table 2. *Affective Intensity*: Between-group differences for shy versus non-shy individuals contrasting neural activation to faces expressing moderate (40-60% emotional expression) minus low (10-30% emotional expression) emotion

Affective intensity								
		Coordinates						
Brain region	**BA**	**X**	**Y**	**Z**	**T-value**	***p* value**	**Cohen's d**	**# Voxels**
Shy>Non-shy								
Rostral anterior cingulate	32	0	39	2	3.32188	0.000993	1.486	678
Cerebellar tonsil		-5	-40	-36	-3.16192	0.00171	1.414	311
Non-shy>Shy								
Left superior frontal gyrus	10	-24	57	15	-3.86627	0.000133	1.729	599
Ventromedial frontal gyrus	11	1	50	-15	-3.97187	0.000087	1.776	350
Dorsal anterior cingulate	24	0	31	17	-3.69358	0.000258	1.652	916
Right amygdala/uncus	28	17	-4	-24	3.17323	0.001647	1.419	316
Cerebellum		-32	-43	-29	3.66712	0.000285	1.640	633

All data presented are corrected for multiple comparison at FDR = 0.05.

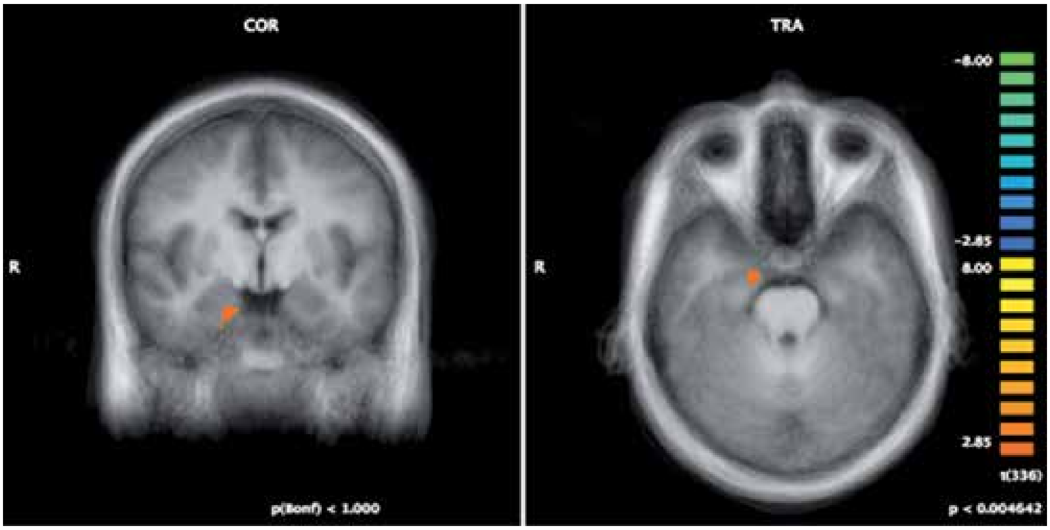


Figure 2. *Amygdala Activation to Affective Intensity:* Between-group activation differences in the right amygdala were elicited by non-shy individuals to moderate emotional expressions relative to low emotional expressions.

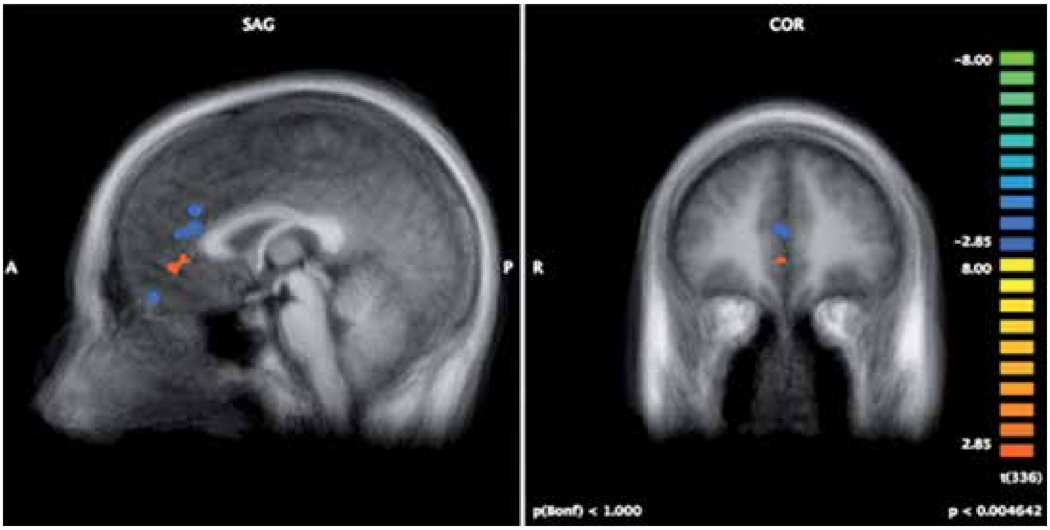


Figure 3. *Affective Intensity:* Between-group activation differences in the dorsal anterior cingulated cortex (ACC), BA 24, were elicited by the shy individuals to moderate emotional expressions relative to low emotional expressions, denoted in warm colors. Between group activation differences in the rostral ACC, BA 32, were elicited by the non-shy individuals to low emotional expressions relative to moderate emotional expressions, denoted in cool colors.

Discrepancy

We contrasted neural responses for shy versus non-shy adults while viewing congruent versus incongruent affective face stimuli. Shy individuals exhibited significantly greater activation across many brain regions when viewing incongruent relative to congruent affective face stimuli. When considering particular brain regions, shy individuals exhibited greater activation in the left superior temporal gyrus [$x = -55$, $y = -6$, $z = -8$, $t(21) = 4.378$, voxels = 1096, $p = 0.00002$, $d = 1.958$] and the inferior parietal lobule [$x = -49$, $y = -32$, $z = 42$, $t(21) = 4.621$, voxels = 5032, $p = 0.000005$, $d = 2.067$ and $x = 46$, $y = -60$, $z = 40$, $t(21) = 4.271$, voxels = 4663, $p = 0.00003$, $d = 1.910$] when viewing incongruent pairs of affective faces relative to congruent than non-shy individuals.

In contrast, non-shy individuals exhibited the opposite pattern, displaying increased neural responses to congruent relative to incongruent affective face stimuli. There was greater neural activation in the fusiform gyrus [$x = -37$, $y = -10$, $z = -27$, $t(21) = -3.881$, voxels = 588, $p = 0.0001$, $d = 1.736$], parahippocampal gyrus [$x = 33$, $y = -8$, $z = -23$, $t(21) = -4.916$, voxels = 4165, $p = 0.000001$, $d = 2.198$], superior parietal lobule [$x = 14$, $y = -71$, $z = 59$, $t(21) = -3.846$, voxels = 333, $p = 0.0001$, $d = 1.720$] and the inferior frontal gyrus near the ventral striatum [$x = 13$, $y = 10$, $z = -7$, $t(21) = -4.137$, voxels = 1513, $p = 0.00005$, $d = 1.850$] by non-shy individuals when viewing congruent pairs of affective faces, relative to incongruent, than shy individuals (see Table 3 and Figure 4).

Reaction Time and Performance Data

Shy and non-shy adults did not differ on reaction time for the same/different judgments, $t(18) = -1.76$, p

Table 3. *Discrepancy:* Between group differences for shy versus non-shy individuals contrasting neural activation to faces expressing incongruent minus congruent emotion

Discrepancy								
		Coordinates						
Brain region	BA	X	Y	Z	T-value	*p* value	Cohen's d	# Voxels
Shy>Non-shy								
Right middle frontal gyrus	46	41	36	17	3.50593	0.000517	1.568	525
Right middle frontal gyrus	9	45	17	32	3.47248	0.000583	1.553	334
Right middle frontal gyrus	6	18	14	62	3.99619	0.000079	1.787	479
Left superior temporal gyrus	22	-55	-6	-8	4.37805	0.000016	1.958	1096
Left inferior parietal lobule	40	-49	-32	42	4.62085	0.000005	2.067	5032
Right cingulate gyrus	31	3	-39	33	4.29206	0.000023	1.919	4100
Right inferior parietal lobule	40	46	-60	40	4.27127	0.000025	1.910	4663
Non-shy>Shy								
Right medial frontal gyrus	10	9	59	14	-4.10047	0.000052	1.834	461
Right medial frontal gyrus	10	10	45	14	-3.50638	0.000516	1.568	599
Right superior frontal gyrus	8	7	35	47	-3.69340	0.000258	1.652	419
Right inferior frontal gyrus	47	29	19	-11	-3.81989	0.000159	1.708	389
Ventral striatum	25	13	10	-7	-4.13651	0.000045	1.850	1513
Parahippocampal gyrus		33	-8	-23	-4.91595	0.000001	2.198	4165
Left fusiform gyrus	20	-37	-10	-27	-3.88076	0.000125	1.736	588
Left cingulate gyrus	31	-14	-25	42	-3.72410	0.00023	1.665	307
Brainstem/pons		-2	-35	-30	-3.68107	0.00027	1.646	1729
Cerebellum		-34	-44	-29	-3.65623	0.000297	1.635	360
Cerebellum		23	-50	-28	-3.86788	0.000132	1.730	318
Right middle occipital gyrus	37	41	-67	6	-4.20469	0.000034	1.880	1297
Right superior parietal lobule	7	14	-71	59	-3.84623	0.000144	1.720	333
Right cuneus	7	13	-72	33	-3.57756	0.000398	1.600	1379

All data presented are corrected for multiple comparison at FDR = 0.05.

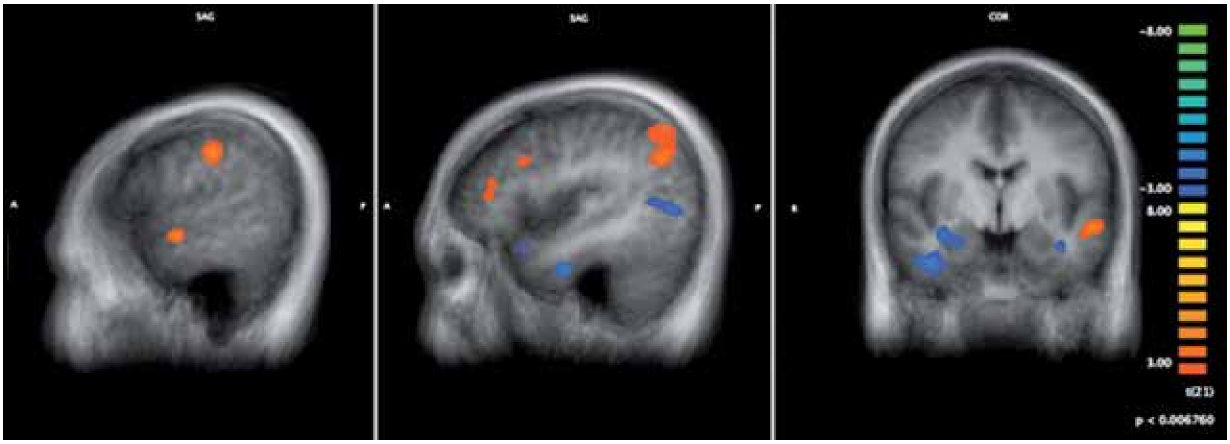


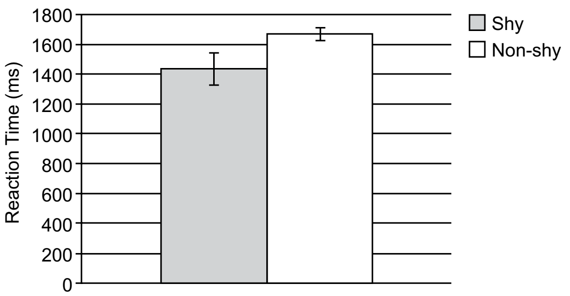
Figure 4. *Discrepancy:* Between-group activation differences in the middle frontal gyrus, superior temporal gyrus and inferior parietal lobule were elicited by shy individuals to incongruent stimuli relative to congruent stimuli denoted in warm colors. Between-group activation differences in the inferior frontal gyrus, parahippocampal gyrus, fusiform gyrus and superior parietal lobule were elicited by non-shy individuals to congruent stimuli relative to incongruent stimuli denoted in cool colors.

> 0.05, $d = 0.407$ [shy (mean ± SD): 1439.1 ± 577.6 ms, non-shy (mean ± SD): 1674.7 ± 446.9 ms] nor did the two groups differ on accuracy, $t(18) = 0.67$, $p > 0.05$, $d = 0.947$ [shy (mean ± SD): 19.1 ± 1.88%, non-shy (mean ± SD): 17.09 ± 2.43%] across all trials (Figure 5). As well, the two groups did not differ on speed or accuracy measures when making same/different judgments for positively versus negatively valenced stimuli or moderate versus low intensity affective face pairs (p's > .05).

Discussion

To assess the neural correlates underlying the processing of affective valence and intensity in shy and non-shy adults, we presented them with a discrepancy detection paradigm using faces that varied along these affective dimensions while in a MR scanner. As predicted, shy individuals showed heightened neural responses to negatively valenced emotions and faces expressing moderate levels of emotional expression. During the detection of affective discrepancy, shy individuals showed heightened activation of the inferior frontal and middle temporal cortices in response to negatively relative to positively valenced stimuli. These findings are consistent with previous studies identifying a key role for the lateral inferior frontal region in the processing of affective valence (Anders et al., 2004; Anderson et al., 2003; Lewis, Critchley, Rotshtein, Dolan, 2007; Small et al., 2003) and, in particular, greater engagement of this region by negative emotions such as anger and fear (for review, see Fusar-Poli et al., 2009). Such group differences suggest greater engagement of social and affective regions by the shy individuals in response to negative or threatening stimuli. Moreover, these findings are in keeping with observations that socially anxious individuals show an attention and memory bias towards negative/threatening stimuli (especially those social or punishing in nature) (Monk & Pine, 2004).

a) Reaction Time



b) Accuracy

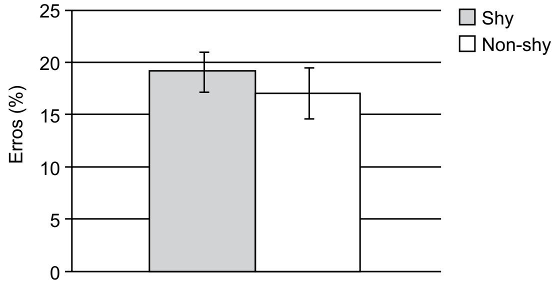


Figure 5. *Reaction Time and Performance Data:* Means (and error bars) for shy and non-shy individuals on (a) reaction time and (b) accuracy when making same different judgments across all trials.

The non-shy participants were distinguishable from their shy counterparts by greater engagement of the middle frontal cortices in response to positive emotions. This region has been shown to be particularly sensitive to positively valenced emotion (Dolcos, LaBar, & Cabeza, 2004), although previous studies have associated positive valence with the left rather than the right hemisphere. Middle frontal activation has been observed in studies involving emotional reappraisal (Ochsner, Bunge, Gross, & Gabrieli, 2002) and the cognitive control of emotion (Cunningham, Raye, & Johnson, 2004). It is possible, therefore, that the present findings reflect a processing bias by the non-shy individuals for positive rewarding stimuli. As a consequence, such individuals may experience social cues more positively and be more likely than shy individuals to engage in approach behaviors in social circumstances (Davidson, Jackson, & Kalin, 2000; Hardin et al., 2006).

Regarding affective intensity, shy participants showed a heightened neural response in the rostral ACC to face stimuli depicting moderate levels of emotional intensity compared to lower levels of emotional intensity. This region represents a functional subdivision of the ACC that is involved in the assessment of emotional salience and the regulation of emotional responses (Bush, Luu, & Posner, 2000). Consequently, engagement of this region in response to changes in stimulus intensity may suggest that the neural responses of shy individuals were dominated by the emotional stimulus characteristics of the displays. This is consistent with the idea that these individuals would show heightened sensitivity to emotional displays that were more intense.

In contrast, non-shy individuals showed heightened engagement of the right amygdala with the presentation of moderately intense stimuli and engagement of the ventromedial prefrontal cortex (VMPFC) and dorsal ACC to stimuli depicting lower levels of emotional intensity. Amygdala engagement has been reported in a number of studies examining emotional intensity (Anderson et al., 2003; Lewis et al., 2006; Small et al., 2003), and some have suggested that the amygdala is preferentially involved in the processing of intensity as opposed to valence aspects of emotion (Anderson et al., 2003; Colibazzi et al., 2010; Small et al., 2003). Others have similarly identified that VMPFC recruitment is driven by affective intensity irrespective of valence (Murphy, Nimmo-Smith, Lawrence, 2003; Phan, Wager, Taylor, Liberzon, 2002; Steele & Lawrie, 2004). Thus, whereas the non-shy response to affect intensity was typified by the engagement of intensity-preferential structures, it appears that the shy neural response was dominated by changes in stimulus affective value or salience.

Differential neural activation patterns also distinguished the shy from non-shy responses to stimulus discrepancy. We observed that shy individuals engaged face responsive regions including the superior temporal sulcus (STS) and the inferior parietal cortices when viewing sets of emotionally incongruent faces. According to Haxby, Hoffman, & Gobbini (2000), the STS is a component of a core system specialized for face perception and is distinctly involved in processing the changeable aspects of facial configuration. Previous research suggests that shy individuals are behaviorally more sensitive and reactive to discrepancy within stimuli (Kagan & Snidman, 1991). Therefore, heightened engagement of the STS may suggest that shy individuals are more attuned to changes in facial cues during the detection of discrepancy, consistent with ideas indicating greater vigilance for emotional threat detection in shyness.

For non-shy individuals the presentation of emotionally congruent stimuli as opposed to incongruent stimuli resulted in heightened activity in the inferior frontal gyrus and ventral striatum. This pattern suggests that, for non-shy individuals, paired emotionally congruent faces may have served as a strong socially rewarding signal (Beaton et al., 2008). Although speculative, these findings may reflect differences in processing style. As the task was to determine emotional congruency between pairs of faces, these results may suggest a greater processing emphasis on the discernment of featural facial information by shy individuals.

It is important to note that although clinical populations were not used in this study, the above findings indicate that the neural correlates of emotion processing for shy and non-shy individuals are significantly and meaningfully different. Large effects sizes were found for all statistically significant regions when comparing the shy and non-shy groups. Such strong group differences merit further investigation to provide a better understanding of the neural basis of shyness.

Limitations

There were a number of limitations to the present study. First, although we selected from a sample of 152 participants, we scanned a limited subset of 24 individuals. Second, our affective stimuli were also restricted to happy, sad, and angry and did not present the full range of standard emotions. Furthermore, the range of intensities across emotions was not balanced, with anger purposely overrepresented across a larger range of intensities, given its saliency in eliciting threat. Finally, further research is needed to determine whether neural activity associated with the discrepancy detection comparison was in response to stimuli discrepancy or the emotional expressive faces.

Conclusion

Across the dimensions of valence, intensity and stimulus discrepancy, we identified different neural responses between shy and non-shy individuals. We found that shy individuals engaged regions that were reflective of processing styles with a negative emotional bias, placed a heightened demand on emotional regulation with increases in affective intensity and emphasized change detection with stimulus incongruency. In contrast, the activation patterns in non-shy individuals were marked by an emphasis on positive emotional cues, the engagement of previously established intensity-preferential structures and engagement of social reward related regions with emotionally congruent stimuli. These results extend previous empirical work identifying different neural correlates in adults that may be demarcated along the dimensions of affective valence and intensity to individual differences in shyness. These findings are consistent with the hypothesis that people who are shy show a bias to negative emotions and that the maintenance of shyness may be due in part to an inability to regulate negative emotion.

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