

Individual differences in neural activity during a facial expression vs. identity working memory task

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ABSTRACT

Facial expressions of emotion constitute a critical portion of our non-verbal social interactions. In addition, the identity of the individual displaying this expression is critical to these interactions as they embody the context in which these expressions will be interpreted. To identify any overlapping and/or unique brain circuitry involved in the processing of these two information streams in a laboratory setting, participants performed a working memory (WM) task (i.e., *n*-back) in which they were instructed to monitor either the expression (EMO) or the identity (ID) of the same set of face stimuli. Consistent with previous work, during both the EMO and ID tasks, we found a significant increase in activity in dorsolateral prefrontal cortex (DLPFC) supporting its generalized role in WM. Further, individuals that showed greater DLPFC activity during both tasks also showed increased amygdala activity during the EMO task and increased lateral fusiform gyrus activity during the ID task. Importantly, the level of activity in these regions significantly correlated with performance on the respective tasks. These findings provide support for two separate neural circuitries, both involving the DLPFC, supporting working memory for the faces and expressions of others.

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Introduction

One of the most highly developed human visual skills is our ability to detect and process facial information. We prefer to look at faces (Morton and Johnson, 1991), and spend more time looking at faces than other visual stimuli (Valenza et al., 1996), making us experts at navigating our social environments. Up until recently, much of the research on face processing focused on our ability to perceive the unique identity of a seemingly unlimited number of faces (Ellis and Rolls, 1992; Sergent et al., 1992). In recent years, however, extant research on face processing has led to the development of models of face perception that distinguish between neural circuitries that support the perception of changeable facial features (e.g., emotional expression, eye gaze), and invariant facial features (e.g., face structure, identity; Haxby et al., 2000; Calder and Young, 2005). For example, within a core system for face processing, it has been shown that changeable features produce greater activity in the superior temporal

sulcus (STS), while invariant features produce greater activity in the lateral fusiform gyrus (Haxby et al., 2000). Moreover, this core system recruits assistance from other regions that extract relevant meaning from the faces (e.g., amygdala/insula for emotional information, intraparietal sulcus for spatial attention, auditory cortex for speech).

One way to assess the neural substrates of face processing is to have subjects maintain facial information in working memory (WM) during neuroimaging. WM is an integral component of many cognitive operations, from complex decision making to selective attention (Baddeley, 1986). Neuroimaging studies have consistently demonstrated that WM tasks activate a bilateral region of dorsolateral PFC (DLPFC; BA 46/9; Cohen et al., 1994; Barch et al., 1997; Braver et al., 1997; Courtney et al., 1997; Kelley et al., 1998; Smith et al., 1998; Levy and Goldman-Rakic, 2000; Braver et al., 2001; Curtis and D'Esposito, 2003). One commonly utilized WM task is the *n*-back task, which requires participants to decide whether the current stimulus matches the one presented *n* trials earlier. Specifically, this task has been used in a series of studies on face processing (Hoffman and Haxby, 2000; Gobbini et al., 2004; Leibenluft et al., 2004; Weiner and Grill-Spector, 2010) because, as in the present study, the primary goal of this work was to elicit attention to certain stimuli (or features of stimuli), and to focus less on the memory performance, per se. Moreover, the *n*-back has been used to demonstrate that the DLPFC is implicated in numerous cognitive functions relevant to WM, including holding to-be-remembered information on-line (Goldman-Rakic, 1994; Jonides et al., 1993), monitoring and manipulating the to-be-remembered information (Petrides, 1994), response selection (Rowe

Abbreviations: STS, superior temporal sulcus; WM, working memory; EMO, emotional facial expression; ID, facial identity; DLPFC, dorsolateral prefrontal cortex; LDLPFC, left DLPFC; RDLPFC, right DLPFC; ACC, anterior cingulate cortex; OFC, orbitofrontal cortex; RT, reaction time; RACC, rostral anterior cingulate cortex; TPJ, temporoparietal junction; dAmyg/SI, dorsal amygdala/substantia innominata.

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et al., 2000), implementation of strategies to facilitate memory (Bor et al., 2003; 2004), organization of material before encoding (Fletcher et al., 1998), and verification and evaluation of representations that have been retrieved from long-term memory (Dobbs et al., 2002; Rugg et al., 1998). While many of these studies have examined WM for words and objects, similar findings have been found for WM for faces (e.g., Kelley et al., 1998; Druzgal and D'Esposito, 2006) with some specifically using the *n*-back task (Braver et al., 2001; Wager and Smith, 2003; Owen et al., 2005). Notably, these *n*-back studies have largely focused on invariant facial features (e.g., face identity).

These WM tasks have also shown that other brain regions might support the role of the DLPFC during WM. Specifically, a posterior region within anterior cingulate cortex (ACC) has been found to increase in activity during WM tasks, purportedly due to increased demands on cognitive control when WM load is high (Gray and Braver, 2002). Also, the amygdala, a region than can function to increase vigilance levels to specific categories of stimuli in order to facilitate adaptive learning and responding (Whalen, 1998; Davis and Whalen, 2001) has been shown to contribute to performance in WM tasks. For example, in both rats (Peinado-Manzano, 1990; McIntyre et al., 2003) and humans, variance in amygdala activity predicted behavioral performance in a WM task (Schaefer et al., 2006). Specifically, during a high WM load, as amygdala activity increased, response time decreased. These results are consistent with models of amygdala function that emphasize its involvement not only in emotion, but also in support of higher cognition (for a review, see Phelps, 2006).

More recently, WM tasks have been used to identify separable neuroanatomical networks for changeable (e.g., expression) vs. invariant (e.g., identity) facial features consistent with previous theories and data (e.g., Haxby et al., 2000; Calder and Young, 2005). LoPresti et al. (2008), using a delayed match to sample task, observed sustained activity in the left orbitofrontal cortex (OFC) that was larger for an emotional version of this task compared to an identity version. Moreover, they found transient responses in temporal and occipital cortices, including the right inferior occipital cortex that were larger during the identity task, while right STS and posterior parahippocampal cortex showed larger responses during the emotion task.

In the present study, we used the *n*-back task to compare neural responses during an emotional expression WM task compared to a face identity WM task. We also planned to relate these neural activations to behavioral performance. Indeed, neural responses during WM tasks are associated with memory performance (Engle et al., 1999; Cowan, 2001; Vogel & Machizawa, 2004, see also Kane and Engle, 2002, for a review). We predicted that participants would show increased activity in the bilateral DLPFC for both tasks, consistent with previous research (Kelley et al., 1998; Braver et al., 2001). Moreover, we predicted a significant increase in activity in regions shown to be particularly responsive to emotional expressions (STS, amygdala, OFC) during the emotion task, whereas other regions responsible for processing identity (lateral fusiform) would respond during the identity task. Indeed, previous research has demonstrated correlated activity between the fusiform and DLPFC (Rissman et al., 2004). While there are no direct connections between the DLPFC and the amygdala, communication between these regions has been demonstrated via direct connections with the orbital prefrontal cortex (OFC) as well as via both thalamic and striatal circuits (Hariri et al., 2003). Critically, the findings of Schaefer et al. (2006) noted above, revealed that amygdala-DLPFC connectivity correlated with WM performance for neutral and positively valenced stimuli. However, an open question is whether this effect is maintained under situations of WM load when participants are required to ignore one aspect of a stimulus (facial identity) and attend to another (emotional expression).

Methods

Participants

Twenty healthy Dartmouth undergraduates (9 female; 18–23 years old, mean age = 19.2) volunteered to participate. All participants had normal or corrected-to-normal vision, used no psychoactive medication, and reported no significant neurological or psychiatric history. None were aware of the purpose of the experiment, and they were all compensated for their participation through monetary payment or course credit. Written informed consent was obtained from each participant before the session, and all procedures were approved by Dartmouth College Committee for the Protection of Human Subjects. Two participants were removed from the sample due to noise and movement artifacts. As a result, the final sample contained 18 participants (9 females).

Procedure

All tasks were performed while participants were in the scanner. Participants performed a standard version of a task that has been used in many previous studies of WM, the 2-back task. However, participants viewed blocks of trials in which they were asked to perform the task according to the emotional expression (EMO) of the faces, and other blocks of trials in which the same stimuli were presented and participants were asked to perform the task according to the identity (ID) of the faces presented. Pilot data in which 15 participants performed a 2-back and another 15 participants performed a 3-back revealed that performance was more similar between the EMO and ID tasks for the 2-back (mean accuracy difference = 7%) than the 3-back (mean accuracy difference = 11%), and that performance was higher overall across participants in the 2-back (mean accuracy = 77%) than in the 3-back (mean accuracy = 70%). For these reasons, we chose to use the 2-back in our final version of the experiment. Each participant had two runs of 16 practice trials in which four shapes (triangle, square, circle, diamond) appeared on the screen in four different colors (red, yellow, green, and blue). In the first practice run, participants were asked to perform a 2-back based on the shape of the image, and in the second practice run, they performed the task based on the color of the image. This was constructed so participants were familiarized with performing the 2-back task based on only one aspect of the image and ignoring another. After the practice, four runs of experimental trials followed, each run containing four alternating blocks of EMO and ID trials. Order was counterbalanced such that half of the subjects saw the EMO block first and the other half saw the ID block first. Each block consisted of 21 total trials (16 faces and 5 intermixed fixation trials, according to the Methods of Schaefer et al., 2006), followed by 16 fixation trials. One face at a time was presented at the center of the computer screen, on a black background. Before the start of a new block, the word "EMOTION" or "IDENTITY" appeared in the center of the screen to indicate to the subject which task they should prepare to perform.

We selected images of four identities (2 females, 2 males) from the NimStim standardized facial expression stimulus set (Tottenham et al., 2009), each posing four emotional expressions (angry, happy, fearful, and neutral), for a total of 16 faces. The stimuli were randomly presented, and each was presented once per block for 2000 ms, followed by a fixation cross that appeared for 500 ms (Fig. 1). For each face presented, participants made a two alternative forced-choice decision about whether the emotion/identity was the same or different from the face presented two trials prior.

Behavioral data analysis

As has been previously described (Wilcox, 1992; Bush et al., 1993), trimming is an effective technique for dealing with outliers. Therefore,

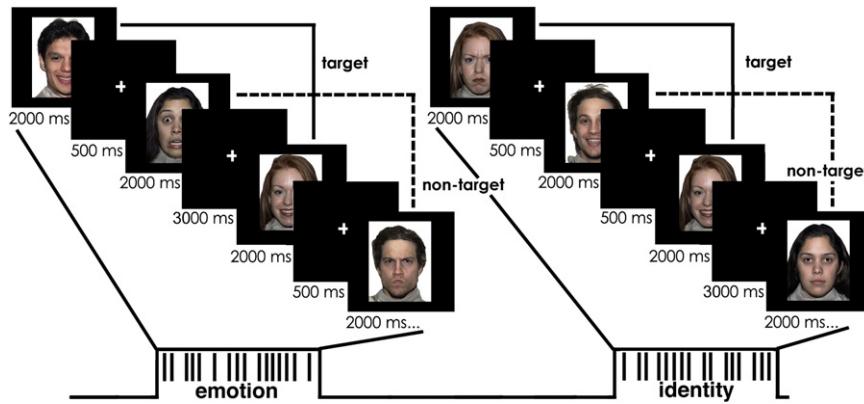


Fig. 1. A depiction of the experimental design. Happy, fearful, angry and neutral faces were presented for 2000 ms followed by a fixation cross for 500 ms. Sixteen faces appeared in each block, along with five fixation cross trials for 3000 ms. The task for each face was to decide whether the expression/identity was the same or different as the face presented two trials prior. Target trials were trials on which the current image was the same as the one that appeared two trials prior, and non-target trials were trials on which the current image was not the same as the one that appeared two trials prior.

we chose to trim trials for each subject according to a typical trimming threshold of the top 10% and bottom 10% reaction time (RT) values.

Image acquisition

All subjects were scanned on a 3.0 Tesla Philips Intera Achieva Scanner (Philips Medical Systems, Bothell, WA) equipped with a SENSE birdcage head coil. Visual stimuli were generated with a Dell laptop computer running E-Prime software (Schneider et al., 2002). They were projected onto a screen positioned at the head end of the bore by an Epson (Model ELP-7000) LCD projector. Participants viewed the screen through a mirror mounted on top of the head coil. A fiber-optic, light-sensitive key press that interfaced with the E-Prime button box was used to record participants' behavioral responses. Cushions minimized head movement.

Anatomical T1-weighted images were collected using a high-resolution 3D magnetization-prepared rapid gradient echo sequence, with 160 contiguous 1-mm thick sagittal slices (echo time [TE] = 4.6 ms, repetition time [TR] = 9.8 ms, field of view [FOV] = 240 mm, flip angle = 8°, voxel size = 1 × 0.94 × 0.94 mm). Functional images were acquired using echo-planar T2*-weighted imaging sequence sensitive to blood-oxygenation-level-dependent (BOLD) contrast. Each volume consisted of 36 interleaved 3-mm thick slices, AC-PC aligned, with 0.5 mm interslice gap (TE = 35 ms, TR = 2500 ms, FOV = 240 mm, flip angle = 90°, voxel size = 3 × 3 × 3 mm).

Imaging data analysis

Preprocessing and the general linear model

The fMRI data were analyzed using Statistical Parametric Mapping software (SPM2, Wellcome Department of Imaging Neuroscience, London, UK). Raw functional data were preprocessed following standard procedures, starting with correcting for head movement. None of the subjects had head movement more than 1.5 mm in any direction. Functional images were then normalized to standard space using the Montreal Neurological Institute (MNI)-152 template. Spatial smoothing was applied to the normalized functional images using a Gaussian kernel of 6 mm full width at half maximum.

For each participant, a general linear model incorporating task effects and covariates of no interest (a session mean, a linear trend for each run, and six movement parameters derived from realignment corrections) was used to compute parameter estimates (β) and t -contrast images (containing weighted parameter estimates) for linear contrast maps for EMO versus ID, ID versus EMO, EMO versus fixation, and ID versus fixation. Contrast maps were then entered into a second-level, random effects model to create mean t images

(threshold at $p < 0.001$, uncorrected, with an extent threshold of 10 contiguous voxels), which accounts for inter-subject variability and allows population based inferences to be drawn. An automated search algorithm identified the location of peak activations and deactivations on the basis of z values and cluster sizes. Importantly, given the difference in RTs between tasks, RT differences are regressed out of all analyses of imaging data to show regions that were differentially active for each task without the confound of time on task.

Regions of interest

ROI analyses were conducted using the MarsBaR tool within SPM2 (Wellcome Department of Imaging Neuroscience, London, United Kingdom). Spherical regions (6 mm radius) were defined around each of these peak activations, and all significant voxels ($p < 0.001$) were included. Signal intensities (beta weights) from significantly activated voxels for each ROI were then calculated separately for each task comparison (i.e., EMO vs. fixation, ID vs. fixation) and examined statistically using repeated measures analysis of variance (ANOVA).

Between subjects correlations

We predicted that dorsolateral prefrontal cortex (DLPFC) activity would correlate with amygdala during the EMO task, but not the ID task, and with invariant processing regions (lateral fusiform) during the ID task, but not the EMO task.

In order to test these hypotheses, we first aimed to isolate a region of the DLPFC that was active for both working memory tasks by conducting a conjunction analysis. Conjunction analyses can be applied between conditions (Price and Friston, 1997), between sessions, and between subjects (Friston et al., 1999). In this study, we utilized a between-conditions conjunction, using an SPM of the minimum t statistic over the two contrasts specified in EMO vs. fixation and ID vs. fixation. This approach preserves only those voxels that are significant (thresholded) in both the contributing SPM maps [$SPM(t) = 3.65$, $p < 0.001$, uncorrected]. A sphere of 6 mm was made around the peak voxel in the right DLPFC (RDLPFC) and the left (LDLPC) for each individual participant, which was selected for use in this analysis. Two participants were removed from this analysis due to a lack of significant activity in these regions from which to extract a peak voxel. Then, we extracted the parameter estimates (beta weights) from the significantly activated voxels for each of the two regions (i.e., RDLPFC and LDLPC) from each participant and used this signal as a variable in subsequent voxelwise correlation analyses. In these analyses, we used activity in the bilateral DLPFC as a regressor to see, for participants where these regions are highly activated for both WM tasks, which other regions were also recruited for one of the two tasks (i.e., which regions correlated with DLPFC across subjects

for EMO WM and for ID WM). In order to examine whether there is a behavioral advantage to having greater activity in our predicted regions, we calculated z-scores for beta weights in left DLPFC, amygdala, and fusiform, and then used those to calculate the interaction score (the product of the z-scores) for left DLPFC * amygdala and left DLPFC * fusiform. This allowed us to extract a single factor that represents the amount of activity in left DLPFC * amygdala and left DLPFC * fusiform for each subject. These factors were used to correlate with both accuracy and RT in the EMO and ID task, respectively.

Results

Behavioral results

Accuracy

Performance (percentage of correct trials) was calculated separately for EMO and ID trials, as well as for target trials from each task. Target trials were trials on which the current image was the same as the one that appeared two trials prior, and non-target trials were trials on which the current image was not the same as the one that appeared two trials prior. A task (emotion, identity) \times trial (target, non-target) repeated measures ANOVA for accuracy revealed a significant main effect of task ($F(1,17) = 25.57$, $p < 0.001$), and corrected pairwise comparisons (Fisher's LSD) revealed that participants were significantly more accurate for the identity task than the emotion task ($p < 0.001$). There was also a significant task \times trial interaction ($F(1,17) = 5.08$, $p < 0.04$), such that participants were more accurate for the identity, as compared to the emotion task, on both target ($p < 0.001$) and non-target trials ($p < 0.01$), separately (mean \pm standard error: targets: EMO = 87.2% \pm 2.2, ID = 95.3% \pm 1.5; non-targets: EMO = 90.9% \pm 1.3,

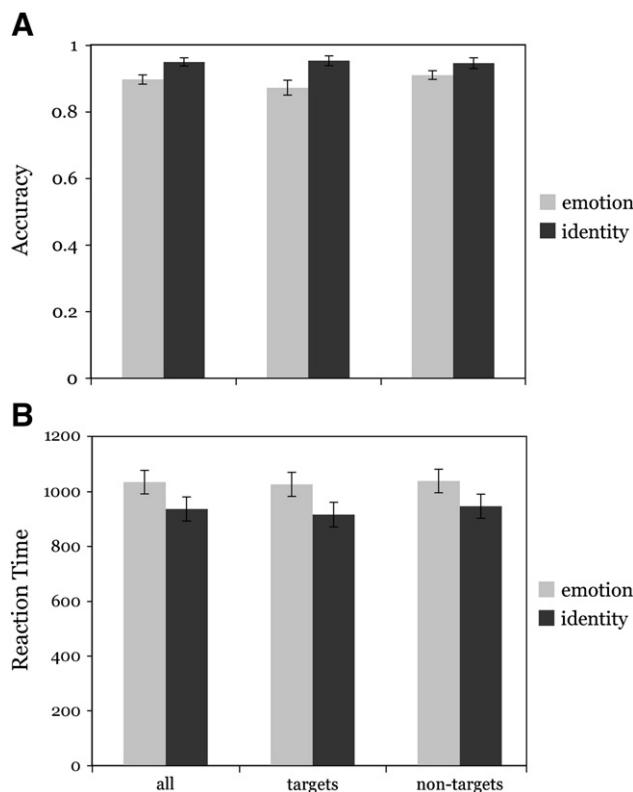


Fig. 2. Behavioral results. Behavioral performance (mean \pm standard error) on the emotion and identity 2-back tasks. Participants were significantly more accurate (A) and faster (B) on the ID task than the EMO task, for all trial types. There was no speed-accuracy tradeoff in performance between tasks.

ID = 94.4% \pm 1.6; Fig. 2A). There was no main effect of trial ($F(1,17) = 0.88$, $p > 0.3$).

Reaction time

RTs were also calculated separately for the two tasks. A task (emotion, identity) \times trial (target, non-target) repeated measures ANOVA for RTs revealed a significant main effect of task ($F(1,17) = 75.20$, $p < 0.001$), and pairwise comparisons (Fisher's LSD) revealed that RTs were significantly longer for the emotion task than the identity task ($p < 0.001$). There was also a significant main effect of trial ($F(1,17) = 5.70$, $p = 0.03$), and pairwise comparisons (Fisher's LSD) revealed that RTs were significantly longer for non-target trials than target trials ($p = 0.03$; mean \pm standard error: targets: EMO = 1025 ms \pm 44, ID = 915 ms \pm 45; non-targets: EMO = 1038 ms \pm 43, ID = 946 ms \pm 44; Fig. 2B). There was no interaction ($F(1,17) = 1.38$, $p > 0.2$). Finally, an analysis of RT data for only correct trials revealed the same effects.

fMRI results

Emotion versus identity

First, we identified neural activations that were greater during the EMO task than the ID task, and vice versa (see Table 1). Fig. 3 shows that for EMO>ID task, we observed significantly greater activity in the right posterior superior temporal sulcus (STS; $x, y, z = 60, -36, 3$), and the bilateral inferior frontal gyrus (right: 60, 30, -6; BA 46; left: -51, 30, -3). For the ID>EMO task, we observed greater activation in the rostral/ventral anterior cingulate cortex (rACC; 0, 42, -3), bilateral precuneus (right: 6, -57, 30; left: -9, -57, 36), and right temporoparietal (TPJ) junction (51, -57, 21).

Conjunction

Contrasts for both of the two tasks (EMO vs. fixation, ID vs. fixation) were overlapped, revealing regions that were active for both tasks. We found significant activity increases during both tasks in bilateral DLPFC (right: 54, 36, 27; left: -48, 30, 33; Fig. 4A). Other regions that were significantly active for both tasks included the dorsal anterior cingulate cortex (-9, 12, 42; BA 6), bilateral superior

Table 1
Brain regions identified during the emotion and identity working memory tasks.

x	y	z	F	Region
<i>Brain regions showing greater activity for the emotion task, as compared with the identity task (EMO>ID)</i>				
60	-36	3	3.94	right posterior superior temporal cortex
-57	-51	9	4.10	left posterior superior temporal cortex
60	30	-6	4.40	right inferior frontal gyrus
-51	30	-3	4.74	left inferior frontal gyrus
15	-72	12	4.69	right cuneus
-6	-81	3	4.31	left cuneus
<i>Brain regions showing greater activity for the identity task, as compared with the emotion task (ID>EMO)</i>				
0	42	-3	3.22	rostral anterior cingulate cortex
6	-57	30	4.64	right precuneus
-9	-57	36	3.62	left precuneus
51	-57	21	4.65	right temporoparietal junction
<i>Brain regions showing increased activity for both emotion and identity tasks (conjunction analysis)</i>				
54	36	27	10.48	right dorsolateral prefrontal cortex
-48	30	33	6.09	left dorsolateral prefrontal cortex
-9	12	42	7.96	left dorsal anterior cingulate cortex
33	-60	42	8.31	right superior parietal lobule
-30	-60	48	12.15	left superior parietal lobule
42	-42	-30	10.03	right fusiform gyrus
15	-99	-6	14.88	right visual areas
-24	-96	-3	10.52	left visual areas

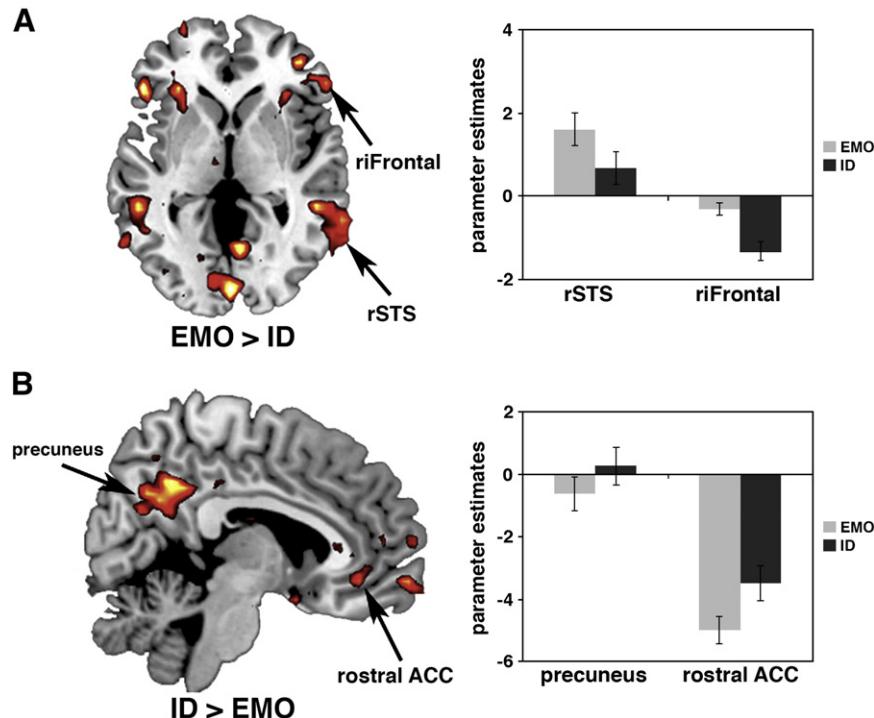


Fig. 3. Differential activity in response to the separate tasks. (A) Bilateral activity in the posterior superior temporal sulcus and inferior frontal gyrus was greater for the EMO task than for the ID task; (B) activity in the precuneus and rostral/ventral anterior cingulate was greater for the ID task than for the EMO task.

parietal lobule (right: 33, -60, 42; left: -30, -60, 48), the fusiform gyrus (42, -42, -30), and bilateral visual areas (right: 15, -99, -6; left: -24, -96, -3; Table 1).

Between subjects correlation with performance

We found that the left DLPFC correlated significantly with left dorsal amygdala/substantia innominata (dAmyg/SI) for EMO trials as compared to ID trials (peak at $x = -18, y = 0, z = -9$; Fig. 4B). Conversely, the same region in left DLPFC correlated significantly with left lateral fusiform gyrus for ID trials as compared to EMO trials (peak at $x = -36, y = -54, z = -12$; Fig. 4B). Due to the between subjects nature of this finding, we examined correlations between activity in these regions and behavioral performance (accuracy and RT) on the corresponding task. We found a significant negative correlation between the left DLPFC * dAmyg/SI and accuracy on the EMO target trials ($r(17) = -0.53, p = 0.02$; Fig. 4C), showing that greater DLPFC and dAmyg/SI activity was associated with poorer accuracy. There was also a significant negative correlation between left DLPFC * fusiform and RT on the ID task ($r(17) = -0.57, p = 0.01$) and for ID target trials ($r(17) = -0.60, p = 0.008$; Fig. 4C), where greater DLPFC and fusiform activity was associated with faster reaction times.

Discussion

We found a significant increase in activity in DLPFC during both the EMO and ID tasks supporting its generalized role in WM. Moreover, individuals that recruited greater DLPFC activity during both tasks also recruited greater amygdala activity during the EMO task and greater lateral fusiform during the ID task, as compared to individuals that recruited less DLPFC activity. Finally, the level of activity in these regions (i.e., DLPFC and amygdala/fusiform) was significantly correlated with performance on the respective tasks, such that greater activity in both the DLPFC and amygdala was negatively correlated with accuracy on the EMO target trials, and

greater activity in both the DLPFC and fusiform was negatively correlated with reaction time on the ID target trials. Here we discuss the implications of these findings, considering the experimental context in which they were observed compared to previous studies.

A differential set of brain regions have been shown to respond to changeable, as compared to invariant, features of facial information (Haxby et al., 2000; Calder and Young, 2005). Consistent with previous research, we found that differential brain regions increased in activity during tasks when proper WM performance depended on processing changeable vs. invariant facial features (LoPresti et al., 2008; Banko et al., 2009). Specifically, when performing the EMO task there was an increase in activity in the STS, and inferior frontal gyrus. Indeed, each of these regions has been linked to the recognition or judgment of emotional expressions (STS: Haxby et al., 2000; inferior frontal: Sprengelmeyer et al., 1998; Nakamura et al., 1999). In addition, we observed increased activity in a posterior region of the ACC (pACC) during the EMO task. Given that our RT data suggest that the EMO task was more challenging, this finding is consistent with studies showing pACC activity increases during WM tasks when there are increased demands on cognitive control (Gray and Braver, 2002).

When performing the ID WM task, we found significantly activated regions in the rostral anterior cingulate cortex (rACC) and precuneus, as well as the temporoparietal junction (TPJ). Perhaps the rACC, a region that is implicated in cognitive control, was active in response to the ID task because individuals must suppress their response to the emotional stimuli in order to better perform the task, particularly because emotional expressions have been shown to have a more automatic influence on memory for facial identity (D'Argembeau and Van der Linden, 2007). We note that emotional Stroop studies that require the suppression of emotional information activate a similar region of rACC (Whalen et al., 1998; see Bush et al., 2000). The precuneus has been shown to respond during mnemonic processing in support of working memory (McIntosh et al., 1996). Finally, the right TPJ has been shown to respond during processing

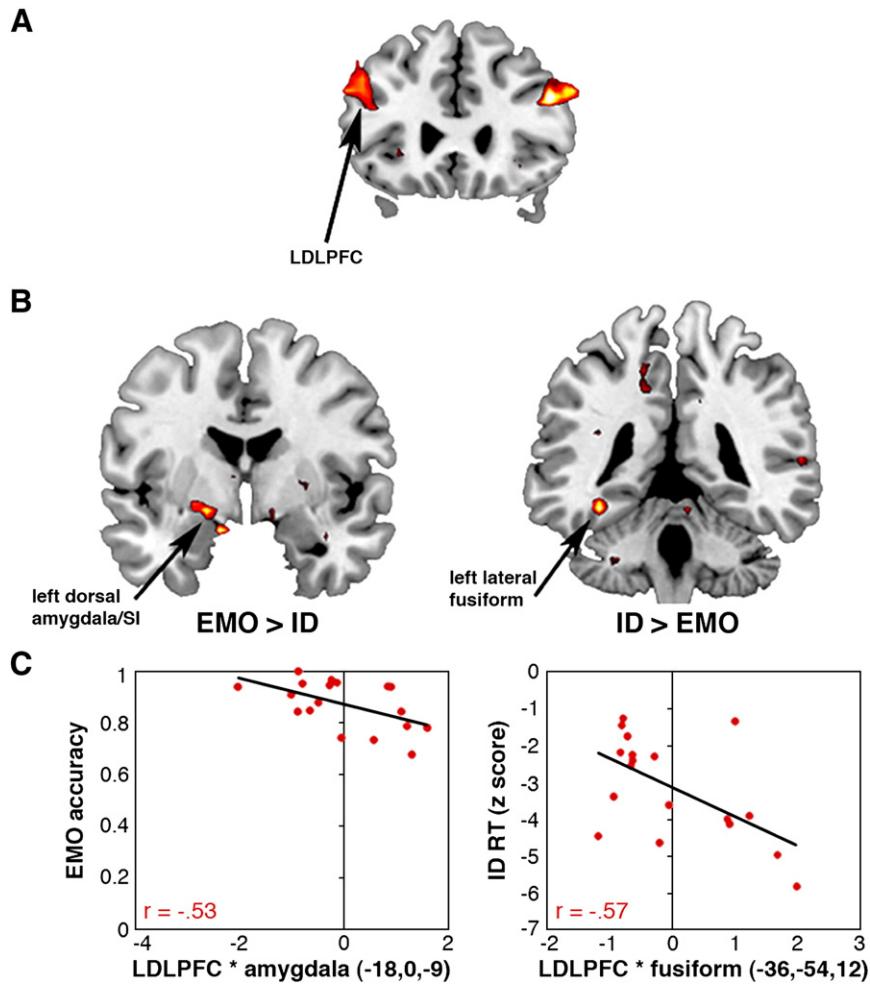


Fig. 4. Between subjects correlations with the dorsolateral prefrontal cortex and behavioral performance. (A) A conjunction analysis revealed that the bilateral DLPFC, along with dorsal anterior cingulate cortex, occipital cortex, and regions in the parietal and inferior temporal cortices (not shown) were active in response to both working memory tasks. The left dorsolateral prefrontal cortex (LDLPCF) was used as a seed region in subsequent analyses. (B) Across subjects, the level of activity in the LDLPCF correlated with the activity in the left dorsal amygdala/substantia innominata (dAmyg/SI) during the EMO 2-back and with the left fusiform during the ID 2-back; (C) the level of activity in the LDLPCF and dAmyg/SI negatively correlated with accuracy on the EMO task, and the level of activity in the LDLPCF and fusiform negatively correlated with reaction time on the ID task.

mental states and intentions of others (Saxe and Kanwisher, 2003; Apperly et al., 2004; Samson et al., 2004; Gobbini & Haxby, 2007), which could relate to the processing of different face identities.

Neural activity reflects performance

Individuals with a greater increase in activity in the DLPFC also had a greater increase in activity in the amygdala during the EMO WM task. These same individuals also had a greater increase in activity in the lateral fusiform cortex during the ID WM task. Both the amygdala and fusiform were left lateralized, likely because the seed region of this parametric analysis was also in the left hemisphere (LDLPCF). While the fusiform response to faces is more consistently found in the right hemisphere, it is indeed generally activated bilaterally (Haxby et al., 1994; Clark et al., 1996; Haxby et al., 1999; Halgren et al., 1999; Ishai et al., 1999; Hoffman and Haxby, 2000; Haxby et al., 2000; Pinsk et al., 2009; Weiner & Grill-Spector, 2010).

Due to the between subjects nature of this finding, we assessed behavioral effects associated with this differential level of activity. We found that the interaction of greater activity in the DLPFC and amygdala was negatively correlated with accuracy on the EMO target trials. This effect was not consistent with previous work by Schaefer et al. (2006) that showed increased amygdala response was correlated with faster RTs on a 3-back WM task. However, Schaefer

and colleagues used word (neutral) and face (neutral or smiling) stimuli, for which participants were instructed to simply respond as to whether the current stimulus matched the stimulus presented three trials back. In the present study, participants had the added difficulty of ignoring one aspect of the stimulus (identity) while monitoring another (emotional expression). Thus, it is possible that this extra layer of cognitive processing transitioned the amygdala response from facilitative (correlated with better behavioral performance, as in Schaefer et al., 2006) to deleterious in the present work. In other words, perhaps the amygdala activation indexed a greater level of global arousal in response to the stimuli, which may have distracted from the ability to monitor the expressions on a trial-by-trial basis.

Conversely, on target trials, greater DLPFC and fusiform activity predicted faster performance (i.e., negatively correlated with RT). This effect is consistent with previous work by Hoffman and Haxby (2000) that showed increased fusiform response to invariant facial features, and other work by Druzgal and D'Esposito (2006) that showed prefrontal and fusiform activity increased parametrically with memory load during encoding and maintenance of face stimuli.

Taken together, these findings suggest that activity in fusiform and amygdala that correlates with activity in WM regions (i.e., DLPFC) is associated with augmented or attenuated WM performance, respectively. It is not clear why amygdala activity would

affect accuracy while fusiform activity affects reaction time. Here we suggest several possible explanations for this discrepancy. First, this may be related solely to the sensitivity of these behavioral measures as executed in the present study, since Schaefer et al. (2006) demonstrated a similar effect for amygdala–DLPFC activity, but in relation to RT. Second, our region of fusiform activity is similar to a posterior region of fusiform gyrus (FFA-1: -38, -56, -13) identified in Pinsk et al. (2009) that was more active for upright and inverted faces, as compared to objects. Our region is also similar to the lateral fusiform, defined as part of the core system found in Haxby et al. (1999; -39 ± 2 , -55 ± 8 , -23 ± 6). Taken together, our fusiform activity likely represents a response in the core system, while the amygdala activity represents a response in the extended system, which could explain why fusiform activity correlates with RT, and amygdala activity correlates with accuracy.

One final explanation could be related to selection efficiency (i.e., individual's efficiency at excluding irrelevant items from being stored in memory). It has been that selection efficiency is improved in high memory capacity individuals, while low capacity individuals may store more information (including irrelevant information) in memory (Vogel et al., 2005). With relevance to our study, we found that participants with greater DLPFC activity for working memory (perhaps the high capacity individuals) also show greater activity in the amygdala (for the EMO task) and fusiform (for the ID task). Additionally, the greater DLPFC * amygdala response was correlated with lower accuracy, and the greater DLPFC * fusiform response was correlated with faster RTs. One possible explanation for this is that our low capacity participants show less neural recruitment (DLPFC, amygdala, fusiform) because they diffusely attend to both relevant (emotion for EMO task, identity for ID task) and irrelevant (identity for EMO task, emotion for ID task) facial information. This would also explain better performance during the more difficult EMO task (more practice attending to emotional information in all blocks of trials), and slower performance during the ID task (less able to ignore the irrelevant emotional information). However, the distinction between these two behavioral measures (accuracy/RT) was outside of the scope of this study, so future work will be needed in order to clarify this issue.

Comparing within and between subjects approaches

As previously stated, our within subjects analyses implementing a global contrast of the EMO and ID tasks is confounded somewhat by task difficulty (i.e., the EMO task was more difficult than the ID task). As such, more activation in the regions responsible for cognitive control (e.g., ACC) was found for the facial emotion task than the facial identity task. In contrast, more activation in regions of the default mode network (e.g., precuneus, angular gyrus), which has been found to consistently show relatively greater activity during simple tasks than during complex tasks, was found for the easier facial identity task than the facial emotion task.

Conversely, the between subjects analyses draw out individual differences by relating neural responses to behavioral performance. Specifically, there were differential responses in the fusiform and amygdala only in the between subjects analyses. It is interesting to note that we found activity in the core system for changeable features (pSTS) in the within subjects analysis (EMO>ID global contrast), but did not see a response in the core system for invariant features (fusiform) in this analysis (ID>EMO global contrast). One possible explanation for this is that the fusiform is recruited in both tasks in the within subjects analysis (see Conjunction analysis). Indeed, the fusiform could be recruited when processing emotional expressions because different individuals can have characteristic expressions, such as a crooked smile or a wry grin (Haxby et al., 2000).

Finally, we found an amygdala response in the between subjects, but not the within subjects (EMO>ID global contrast) analysis. Consistent with Haxby et al. (2000), we interpret this to be because this region, as part of an extended system, comes online only in order to assist the DLPFC (core system for WM) in the processing of emotional information.

Conclusions

The DLPFC has been consistently shown to be activated during WM tasks (Kelley et al., 1998; Braver et al., 2001), and other regions, particularly the cingulate cortex and the amygdala, are recruited with the DLPFC in situations of increased demand on WM (Gray and Braver, 2002; Schaefer et al., 2006). In this way, just as there is a core system for processing facial information (Haxby et al., 2000), the DLPFC may serve as part of a core system for working memory tasks, generally, and that it recruits assistance from other regions that can aid in face processing (i.e., fusiform gyrus, amygdala) in order to successfully meet specific task demands.

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