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Affective ambiguity for a group recruits ventromedial prefrontal cortex

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Affective appraisal often involves processing complex and ambiguous stimuli, such as the mood of a group people. However, affective neuroimaging research often uses individual faces as stimuli when exploring the neural circuitry involved in social appraisal. Results from studies using single face paradigms may not generalize to settings where multiple faces are simultaneously processed. The goal of the current study was to use a novel task that presents groups of affective faces to probe the medial prefrontal cortex (PFC), a region that is critically involved in appraisal of ambiguous affective stimuli, in healthy volunteers. In the current study, 27 subjects performed the Wall of Faces (WOF) task in which multiple matrices of faces were briefly presented during functional MRI. Subjects were asked to decide whether there were more angry or happy faces (emotional decision) or whether there were more male or female faces (gender decision). In each condition, the array contained either an equal (ambiguous trials) or an unequal (unambiguous trials) distribution of one affect or gender. Ambiguous trials relative to unambiguous trials activated regions implicated in conflict monitoring and cognitive control, including the dorsal anterior cingulate cortex (ACC), dorsolateral PFC, and posterior parietal cortex. When comparing ambiguous affective decisions with ambiguous gender decisions, the ventromedial PFC (including the ventral ACC) was significantly more active. This supports the dissociation of the ACC into dorsal cognitive and ventral affective divisions, and suggests that the ventromedial PFC may play a critical role in appraising affective tone in a complex display of multiple human faces.

Keywords: Facial expression; Affect; Ambiguity; Fmri; Appraisal

Introduction

Affective facial expressions (e.g., happy, angry, and fearful faces; Matsumoto and Ekman, 1998) have been used extensively to measure behavioral and neural responses (Whalen et al., 1998b). These paradigms usually involve either implicit or explicit emotional judgments about individual faces. Recently, several neuroimaging studies have used morphed or composite faces (Nomura et al., 2003; Winston et al., 2003), which may be more representative of the type of emotions seen by humans on a daily basis (i.e., ambiguous facial expressions). These studies have shown that appraisal of emotional ambiguity relative to gender ambiguity in morphed face stimuli is associated with activation of the ventromedial prefrontal cortex (vMPFC), specifically the anterior aspect of the ventral anterior cingulate cortex (ACC) (Nomura et al., 2003; Winston et al., 2003). This "affective" division of the ACC (Bush et al., 2000) is anatomically and functionally connected to other structures within the limbic system including the amygdala, hypothalamus, ventral striatum, anterior insula, hippocampus, and orbitofrontal cortex. Lesion studies suggest that the vMPFC and the orbital frontal lobes are critical for social information processing (Pears et al., 2003). It appears that these neural substrates are central for integrating emotional and motivational information (Bush et al., 2000). However, findings based on individual face presentations may not generalize to affective processing in social or group settings where multiple faces with different emotional expressions are simultaneously encountered.

Recent studies using stimuli containing multiple faces have contributed to the understanding of the neural circuitry involved in social appraisal. For example, stimuli containing multiple facial expressions have been used to identify an exaggerated appraisal of risk and a limited expectation of reward in individuals with social anxiety disorder (Gilboa-Schechtman et al., 2005).

In the current study, we used a novel task, the Wall of Faces (WOF), to probe the neural circuitry underlying affective appraisal of multiple simultaneously presented faces. During each trial in the

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WOF, subjects briefly viewed a group of 32 emotionally expressive faces (see Fig. 1). The ratio of male to female faces and angry to happy faces was parametrically adjusted in each trial so that presentations could be either ambiguous (e.g., 16 angry and 16 happy) or unambiguous (e.g., 6 female and 26 male). Participants were asked to identify either the predominant gender or the predominant emotion within the set of faces. This investigation examined which brain regions were differentially activated by the degree of ambiguity (equal proportion of same emotion versus disproportionate) and the type of decision (emotion versus gender). Recently, a similar presentation was used to measure affective appraisal in patients with social anxiety disorder and found differences in response rate and response bias in response to ambiguous stimuli (Gilboa-Schechtman et al., 2005).

We hypothesized that processing ambiguous relative to unambiguous stimuli would elicit responses in brain regions involved in cognitive conflict (e.g., the dorsal anterior cingulate) (van and Carter, 2002). We further hypothesized that determining the affect versus the gender of a group of ambiguous faces would activate brain regions involved in linking the perception of an emotion to a somatic state (e.g., the vMPFC).

Methods

Subjects

27 healthy adult volunteers (16 females and 11 males), average age 25 (SD 11.1, range 18–56) years with an average education level of 13.3 (SD 1.1, range 12–16) years, participated in this study, which was approved by the University of California, San Diego Human Research Protection Program. All subjects gave their informed, written consent to participate. Individuals were excluded if they had a current and/or prior major psychiatric disorder using the Structured Clinical Interview for DSM-IV (First et al., 1995), or were taking any psychotropic medications.

Task

The WOF was programmed using Presentation® software (Version 0.70, http://www.neuro-bs.com) and presented faces from a standardized set (Matsumoto and Ekman, 1998). For each trial, an array of 32 faces (see Fig. 1) subtending an angle of approximately 6 degrees was presented against a black background for 3 s. The subject was cued 500 ms prior to the presentation of the faces by a centrally displayed word (either “gender” or “emotion”), that indicated whether the task would be to decide on gender or emotion. Specifically, the individuals had to determine whether (1) there were more male or female faces (gender decision) or (2) whether there were more happy or angry faces (affective decision). The entire trial lasted 5 s. The 32 faces were presented for 3 s along with the options “Angry–Happy” or “Female–Male”, which corresponded to the LEFT or RIGHT button, respectively. The options were displayed for an additional 1.5 s. Thus, for each trial, the subject had 4.5 s to make a decision. No feedback concerning a correct or incorrect response was given to the subject. To jitter the task, a baseline fixation cross was displayed in the center of the screen varying from 0 to 7 s in between each trial. In total, 36 affective decision trials and 36 gender decision trials were randomly presented. The affective trials were composed of 18 ambiguous trials (16 angry and 16 happy faces per trial) and 18 unambiguous trials (6 angry and 26 happy or 26 angry and 6 happy faces per trial). The gender trials were composed of 18 ambiguous trials (16 female and 16 male faces per trial) and 18 unambiguous trials (6 female and 26 male or 26 female and 6 male faces per trial). The distribution of these trials was counterbalanced. The ratio of male to female faces in the affective trials, and the ratio of happy to angry faces in gender trials were controlled and counterbalanced. Specific sets of faces were determined at random for each trial at runtime. The response (LEFT or RIGHT button) and the response latency were recorded for each trial. Summed scores were calculated for ambiguous and unambiguous conditions in affective and gender trials for response selection (as the proportion of angry decisions in affective trials or male decisions in gender trials) and latency (average response latency).

FMRI analysis pathway

The data were preprocessed and analyzed with the software AFNI (Cox, 1996). Data were normalized to Talairach coordinates. The echoplanar images were realigned to a central slice selected to minimize differentially acquired scans and time-corrected for slice acquisition order. To exclude the voxels showing an artifact-related signal drop, a combined threshold/cluster-growing algorithm was

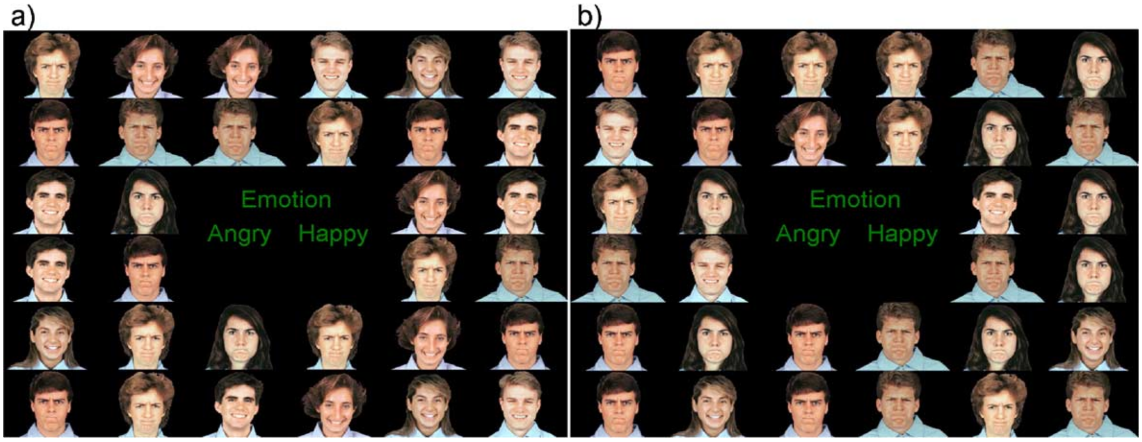

Fig. 1. The Wall of Faces paradigm. During each trial, the subject views the matrix of faces for approximately 3 s. In this trial, the subject is asked to judge whether there are more happy or angry faces in the crowd. An example of an (a) ambiguous and (b) unambiguous affective trial is shown below.

applied. This screened out nonbrain voxels and voxels falling within the artifact region by creation of an average mask of the population and removing voxels outside the mask. The preprocessed time series data for each individual were analyzed using a multiple regression model consisting of 11 regressors. There were 6 task-related regressors, which identified the time-series for the three ratios (6/26, 16/16, and 26/6) of gender (female–male) and emotion (angry–happy). Each regressor was created using a reference function corresponding to the 3 s during a trial during which subjects viewed the array of faces. These regressors were convolved with a prototypical hemodynamic response function prior to inclusion in the regression model. In addition, three regressors were used to account for residual motion (in the roll, pitch, and yaw direction), and a baseline regressor and linear trends regressor were used to eliminate slow signal drifts. The AFNI program 3dDeconvolve was used to calculate the estimated voxel-wise response amplitude. A 6 mm full-width half-maximum Gaussian filter was applied to the voxel-wise percent signal change data to account for individual variations of anatomical landmarks.

Statistical analyses

Our first analysis tested for differential blood oxygenation level dependent (BOLD) signal during gender and affective trials. The second analysis contrasted ambiguous and unambiguous trials, and the final analysis contrasted ambiguous gender and ambiguous affective trials. The third analysis was a conjunction analysis, i.e., each voxel had to satisfy simultaneously several threshold criteria. In particular, we examined voxels that showed significant activation during ambiguous relative to unambiguous trails during both affective and gender conditions. Finally, simple contrasts were examined between affective and gender ambiguous or unambiguous trials. Voxel-wise percent signal change data were entered into a mixed model ANOVA with trial type (gender versus affect; ambiguous versus unambiguous; ambiguous gender versus ambiguous affect) as a fixed factor and subjects as a random factor. A threshold adjustment method based on Monte-Carlo simulations was used to guard against identifying false positive areas of activation (Forman et al., 1995). Based on these simulations, it was determined that a voxel-wise a priori probability of 0.01 would result in a corrected cluster-wise activation probability of 0.01 if a minimum volume of 1024 μl and a connectivity radius of 4.0 mm were considered. For the interaction analysis, the probability was raised to 0.05 and the minimum volume was lowered to 512 μl as multiple comparisons were performed. Finally, the average percent signal difference was extracted from regions of activation that were found to survive this threshold/cluster method.

All analyses for the behavioral data were carried out with SPSS 10.0 (Norusis, 1990). A mixed model ANOVA (fixed factor: task conditions, random factor: subjects) was used to analyze the behavioral measures. The planned comparisons were evaluated using the Least Significant Difference post hoc analysis.

Results

Behavioral results

Subjects' response selection (i.e., the proportion of angry selections for affective decisions or male selections for gender decisions) and response latency (milliseconds) did not differ between gender and affective judgment trials ($t(26) = 0.763$, $P =$

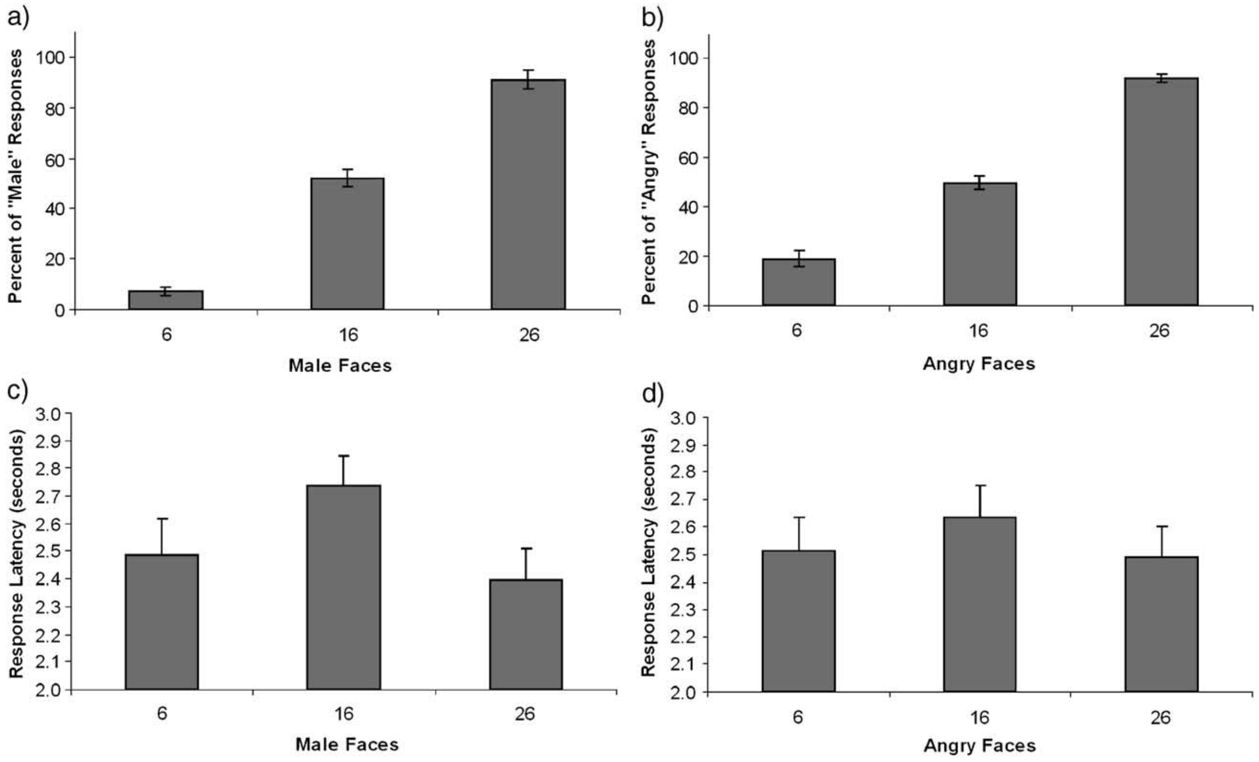

Fig. 2. Response selection for 6, 16, and 26 stimuli faces in an array of 32 faces for (a) male faces and (b) angry faces. Response latency for 6, 16, and 26 faces in an array of 32 faces for (c) male faces and (d) angry faces with standard errors.

Table 1
Areas of activation for ambiguous–unambiguous stimuli

Location (Brodmann Area)	Volume	*x*	*y*	*z*	*t* score
Bilateral lingual gyrus (18)	11712	−7	−75	−1	6.67
Left angular gyrus (39)	7744	−28	−53	36	5.25
Right dorsolateral prefrontal cortex (9)	4480	38	9	32	3.68
Right precuneus (7)	3072	25	−60	36	5.51
Right inferior parietal lobule (40)	2880	41	−52	57	2.01
Dorsal anterior cingulate Gyrus (32)	2624	2	19	37	1.59
Left dorsolateral prefrontal cortex (9)	2176	−47	8	34	2.38
Left postcentral gyrus (3)	1984	−44	−23	59	4.00
Right precentral gyrus (4)	1792	38	−15	61	3.68
Left superior parietal lobule (7)	1024	−13	−69	56	3.12

Note. $P < 0.01$, Interaction, $m^3 > 1024$.

Table 2
Areas of activation where the activation is greater in ambiguous than unambiguous stimuli for both the affective and gender contrasts

Location (Brodmann Area)	Volume	*x*	*y*	*z*
Left lingual gyrus (18)	2560	−31	−72	−4
Left superior parietal lobule (7)	1344	−29	−51	42
Bilateral lingual gyrus (18)	1088	5	−82	−1
Left precuneus (31)	896	−23	−70	28
Right lingual gyrus (18)	832	31	−69	−5
Right inferior frontal gyrus (9)	768	39	6	31
Bilateral cingulate gyrus (32)	704	0	19	40

(Affect Ambiguity > Affect Unambiguity) ∩ (Gender Ambiguity > Gender Unambiguity).
Note. $P < 0.05$, Interaction, $m^3 > 512$.

NS and $t(26) = 0.650$, P = NS, respectively). However, response latencies were significantly longer in ambiguous versus unambiguous conditions for both gender and affective trials ($t(26) = 8.754$, $P < 0.001$ and $t(26) = 3.841$, $P < 0.001$, respectively) and response selections in the unambiguous condition were significantly more biased than in the ambiguous condition ($t(26) = 12.85$, $P < 0.001$ and $t(26) = 13.70$, $P < 0.001$, respectively; see Fig. 2).

Functional neuroimaging results

Affect/gender contrast

No clusters survived thresholding when comparing all gender trials versus all affective judgment trials.

Ambiguous/unambiguous contrast

Areas in the posterior parietal cortex, dorsolateral prefrontal cortex (dLPFC), striate cortex, and the dorsal ACC were significantly more active during ambiguous trials relative to unambiguous trials (see Table 1 and Fig. 3).

Ambiguous gender/ambiguous affective trials conjunction analysis

The contrast of affective ambiguous-affective unambiguous trials resulted in a single significant cluster activation in the parietal lobe. However, it should be noted that the contrast for affective ambiguous-affective unambiguous does not produce a significant cluster in the ventral ACC at this threshold ($P < 0.01$). A slightly lower threshold produces activation in the ventral ACC. The contrast of gender ambiguous–gender unambiguous trials resulted in activation in the right temporal lobe, bilateral occipital lobe, right inferior frontal gyrus, left postcentral gyrus, and dorsal ACC (see Table 2 and Fig. 4).

Affect-gender in ambiguity

Four clusters displayed significantly more activity during ambiguous affective trials compared with ambiguous gender trials: (1) ventral ACC and ventral MPFC, (2) right middle and superior temporal gyrus, (3) right supramarginal gyrus, and (4) left superior frontal gyrus (see Table 3 and Fig. 5). Activations in these areas did not correlate with response latency.

Gender ambiguity

During gender trials, there was greater activation in the right superior temporal gyrus, bilateral occipital lobe, right precuneus, right inferior frontal gyrus, left postcentral gyrus, and dorsal cingulate gyrus during ambiguous versus unambiguous trials (see Table 4).

Affective ambiguity

For the contrast of affective ambiguous versus unambiguous trials, the only area that showed a significant difference at the predetermined thresholds was in the left inferior parietal lobule (see Table 5). However, at slightly lower t values, the ventral anterior cingulate activation becomes apparent.

Discussion

This study implemented an affective appraisal task to probe the neural circuitry underlying affective appraisal of multiple

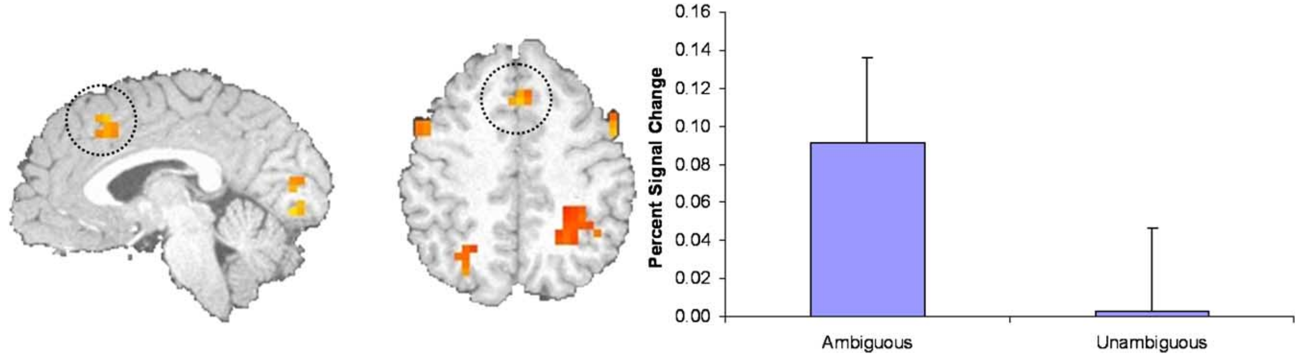

Fig. 3. Response difference in the dorsal anterior cingulate for the ambiguous versus unambiguous trials. The BOLD percent signal changes reflect the combined activation of affective and gender trials for both conditions.

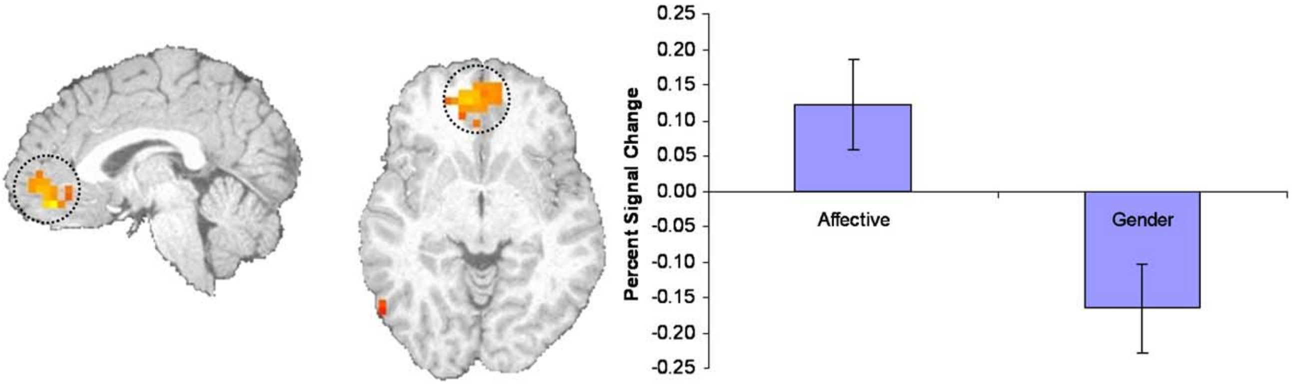

Fig. 4. Response difference in the medial prefrontal cortex for where the activation is greater for ambiguous stimuli than for unambiguous stimuli in both the affective and gender contrasts [(Affect Ambiguity > Affect Unambiguity) ∩ (Gender Ambiguity > Gender Unambiguity)]. The picture bellow displays areas that show greater activation in both conditions in red and areas that are greater in one condition in orange. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

simultaneously presented faces. There were two main findings. First, ambiguous trials (regardless of the type of judgment being made) activated a network of brain regions implicated in attention, working memory, and higher-order cognitive processes, including the dorsal ACC, dorsolateral PFC, and the posterior parietal cortex. Second, several brain regions, which are critically involved in processing the facial expression of individual faces, were active when processing the emotion of an ambiguous group of faces. Specifically, we found increased activity during ambiguous emotional judgments in the right supramarginal gyrus and right superior temporal gyrus, regions critical for emotion recognition (Adolphs et al., 1996). Emotional ambiguity also evoked activation in the ventromedial PFC (including the ventral ACC), an area which has been consistently shown to play a role in emotional processing (Phan et al., 2002).

The ACC/medial PFC was active in the contrast between all ambiguous and all unambiguous trials, as well as in the contrast between ambiguous affective and ambiguous gender trials. However, the sub-region of the ACC/medial PFC that was active was dependent on the specific task demands. The dorsal region was more active during ambiguous trials (irrespective of the type of judgment), while a ventral region was more active during ambiguous trials when subjects made an affective decision. The ACC has two primary functional subdivisions: the dorsal cognitive division and the ventral affective division (Vogt et al., 1992). The dorsal ACC is important for conflict monitoring (Botvinick et al., 1999) while the ventral ACC is involved in the integration of emotional information (Whalen et al., 1998b), and in resolving emotionally-laden conflict (Whalen et al., 1998a).

Table 3
Areas of activation for affective ambiguity–gender ambiguity

Location (Brodmann Area)	Volume	*x*	*y*	*z*	*t* score
Ventral anterior cingulate/medial prefrontal gyrus (32/10/11)	3136	2	47	−4	4.66
Right middle and superior temporal gyrus (39/21)	2240	56	−56	7	4.62
Right supramarginal gyrus (40/39)	1216	50	−54	31	4.04
Left superior frontal gyrus (9)	1088	−24	49	35	3.05

Note. $P < 0.01$, $\mathrm{m}^3 > 1024$.

The design of the WOF stimuli allowed for a comparison between the brain response during appraisal of ambiguous affective groups of faces and the brain response during appraisal of ambiguous gender groups of faces. This contrast revealed that the ventral ACC may be uniquely involved in the assessment of affective information in a complex display of multiple human faces. Tasks that activate this ventral subdivision of the ACC often present ambiguous stimuli, where the available information is inadequate for determining a “correct” response. For example, guessing games (Elliott et al., 1999) and tasks with stimuli containing morphed faces (Winston et al., 2003) have elicited activation in this region. Given the role of the ventral ACC in integrating emotional information, it is not surprising that tasks involving appraisal of complex affective stimuli, such as the WOF, activate this structure. This may be explained by considering that affective appraisal of ambiguous stimuli requires integration of complex somatic information (such as internal state and visceral reaction).

A similar region in the ventral ACC has been found to have increased relative activation at rest, a finding that has been attributed to the focus on one’s internal state that occurs during rest (Wicker et al., 2003). This difference in activation in contrast

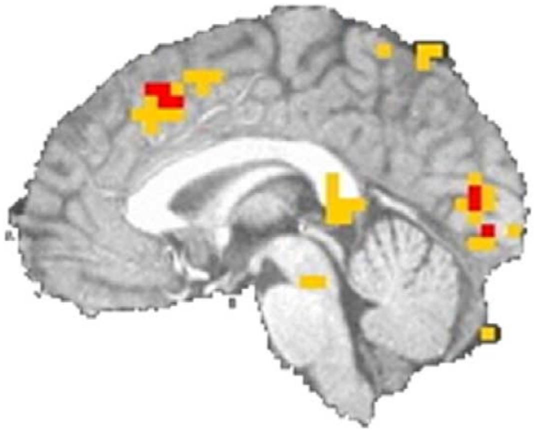

Fig. 5. Response difference in the ventromedial prefrontal cortex (including the ventral ACC) for affective ambiguity versus gender ambiguity trials. The BOLD percent signal changes reflect ambiguous minus unambiguous trials for both the affective and gender conditions (in red) and for either condition (in yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to rest may help explain the deactivation during calculation of ambiguous gender trials. Wicker et al. (2003) states that rest is "an ill-defined mental state because it may vary both from one subject to another and within the same subject," specifically in the medial prefrontal cortex when the "subject is in a state where he refers only to his own self". The activation during rest in the vMPFC has also been seen in other affective processing tasks. For example, in some situations, the affective task shows significant activation in contrast to the control task while still showing less activation than rest (Whalen et al., 1998a).

It appears that, during ambiguous situations, the contrasts between affective and gender judgments becomes amplified and can be more easily disambiguated using fMRI. This amplification could be due to the fact that there is insufficient external information to make an easy decision. The current imaging data are consistent with lesion studies suggesting that in primates the orbital frontal cortex may be more pertinent to social learning than the ventromedial PFC (Pears et al., 2003). However, the ventromedial PFC appears to play a larger role in social behavior in humans (Hornak et al., 2003) than in primates. One source of this increased ventromedial PFC involvement may relate to the development of a "theory of mind" (i.e., mentalizing others as having cognition) in the humans—a behavior that appears mediated by the ventromedial PFC as well as regions in the temporal gyrus (Berthoz et al., 2002).

Previous studies support the notion that processing ambiguous affective stimuli activates the medial PFC. For example, Nomura et al. (2003) investigated ambiguity processing using a morphed faces design and contrasted brain activation during the processing of ambiguous versus unambiguous emotion and gender stimuli. This study's results had some similarities to ours, but also several important differences. In both studies, the gender and affectively ambiguous processing conditions activated the dorsal ACC, while the ventral ACC was activated only for emotion ambiguity. The fundamental difference between the studies relates to the tasks that were used, particularly with the stimuli presented and with the ways in which the stimuli were perceived. By using a matrix of faces, the current study allows for modulation of the degree of ambiguity objectively for both gender and affective trials (group average = 52% and 50%, respectively). While using morphed faces, Nomura found that ambiguous gender was appraised as female 64% of the trials, while ambiguous emotion was appraised as negative 64% of the trials, indicating that the presentation of a matrix may be an especially useful way of parameterizing the study of affective ambiguity. The morphed faces paradigm is an effective way to modulate affective ambiguity when using a single facial stimulus. This provides a useful opportunity to parametrically control facial expressions. However, if accurately controlling the degree of ambiguity is of primary concern, then the WOF task may provide an informative alternative.

Table 4
Areas of activation for gender ambiguous–gender unambiguous trials

Location (Brodmann Area)	Volume	*x*	*y*	*z*	*t* score
Right superior temporal gyrus (39)	5056	51	−61	21	4.01
Left lingual gyrus (17)	4032	−21	−82	2	3.63
Right lingual gyrus (18)	2624	22	−74	−4	3.08
Right precuneus (31)	2368	24	−66	25	5.37
Right inferior frontal gyrus (9)	1600	36	8	30	4.53
Left postcentral gyrus (1)	1600	−44	−26	59	3.38
Bilateral cingulate gyrus (32)	1280	2	19	37	4.11

Note. $P < 0.01$, $\text{m}^3 > 1024$.

Table 5
Areas of activation for affective ambiguous–affective unambiguous trials

Location (Brodmann Area)	Volume	*x*	*y*	*z*	*t* score
Left inferior parietal lobule (40)	1792	−30	−45	40	4.486

Note. $P < 0.01$, $\text{m}^3 > 1024$.

One limitation of the current study was that the ambiguous stimuli were also more difficult (as reflected in the increased response latencies). Therefore, any subtraction of ambiguous and unambiguous stimuli is confounded by task difficulty. However, this does not affect the contrast of ambiguity conditions in the ventral ACC. Second, there was task switching, and this switching probably did recruit brain regions important for executive functioning. However, as the executive functioning component is presumably constant across the trials, this aspect should be removed by the subtraction of the task conditions. This does not address the possibility that there is an interaction effect between the task switching and the conditions of interest (i.e., ambiguity and affect). A third concern is that individuals may have realized that some sets of faces had equal amounts of male or happy faces. However, in posttask debriefing, people did not report realizing that some sets had no predominant face type and they did not appear to decrease response latency to these sets over time (indicating that they continued to give full effort to the set rather than dismissing it as impossible). The activation in the dorsal ACC related to conflict monitoring would occur due to differences in both ambiguity and difficulty. However, task-related activation did not correlate significantly with response latency in our study, which suggests that this activation is not due to increased effort. As affective and gender judgments do not appear to produce differential activation in the amygdala (Lange et al., 2003), the lack of amygdala activation in these contrasts in the current study was anticipated.

In conclusion, our results suggest that the ventromedial PFC (including the ventral ACC) is critically involved in appraising a complex display of multiple simultaneously presented faces. Likewise, the dorsal ACC and dorsolateral PFC play a more general role in making more analytical decisions in ambiguous environments.

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