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Association between trait emotional awareness and dorsal anterior cingulate activity during emotion is arousal-dependent

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The dorsal anterior cingulate cortex (dACC) is commonly thought to subserve primarily cognitive functions, but has been strongly implicated in the allocation of attention to emotional information. In a previous positron emission tomography (PET) study, we observed that women with higher emotional awareness as measured by the Levels of Emotional Awareness Scale (LEAS) showed greater changes in regional cerebral blood flow (rCBF) in dACC induced by emotional films and recall. In the current study, we tested whether these effects were due to the processing of any non-neutral stimulus, or were specific to conditions of high emotional arousal. Our results extend the previous finding by demonstrating a positive correlation between emotional awareness and dACC activity only in the context of viewing highly arousing pictures. No such relationship was observed when comparing pleasant or unpleasant pictures to neutral or to each other. We also observed that the relationship between LEAS and dACC activity was present in both sexes but stronger in women than men. These results reinforce the concept that greater trait awareness of one's own emotional experiences is associated with greater engagement of the dACC during emotional arousal, which we suggest may reflect greater attentional processing of emotional information.

Introduction

A leading model of ACC function holds that the rostral ACC (including subgenual ACC) is preferentially engaged during emotional tasks and that the dACC is preferentially engaged during cognitive processing (Bush et al., 2000; Devinsky et al., 1995; Mohanty et al., 2007). Regarding the latter, several neuroimaging studies highlight the role of the dACC in directing (Weissman et al., 2005) and capturing (Corbetta et al., 1991; Pardo et al., 1990) attention, error detection (Fassbender et al., 2004), conflict monitoring (Botvinick et al., 2004), mental effort (Mulert et al., 2005) and many other cognitive functions. Contrary to this model, lesions in the dACC are known to alter emotional experience (Cohen et al., 2001) and may leave cognitive functions intact (Fellows and Farah, 2005). In addition, meta-analytic data demonstrate activation of the dACC in several functional imaging studies of emotion (Phan et al., 2002). More specifically, the dACC is activated when attention is directed to the feeling of sadness (Drevets and Raichle, 1998), when the unpleasantness of pain is amplified by post-hypnotic suggestion (Rainville et al., 1999), during the experience of social rejection (Eisenberger et al., 2003) and during awareness and monitoring of one's own emotional experiences (Hutcherson et al., 2005; Ochsner et al., 2002; Taylor et al., 2003). These observations suggest that the dACC participates in emotional as well as cognitive processing, and raise questions (Lane and McRae, 2004) about the validity of a dichotomy between cognitive (dACC) and affective (rostral ACC) divisions of the ACC (Bush et al., 2000; Mohanty et al., 2007).

Although it is clear that the dACC plays a role in emotional as well as cognitive processing, few studies have investigated individual differences that affect dACC activity during emotional tasks. We previously observed a positive correlation between emotion-induced rCBF in the dACC and scores on the LEAS (Lane et al., 1998), a measure of differentiation and complexity of emotion information processing (Lane and Schwartz, 1987). The LEAS was designed to measure individual differences in the capacity to experience emotional feelings in a differentiated and complex way and to detect such feelings in others (Lane et al., 1990). This previous PET study in 12 women involved emotion induction through the use of film clips and instructed recall of past experiences. A conjunction analysis revealed that the correlation between LEAS and rCBF attributable to emotion during the two induction methods overlapped significantly in the right dACC (BA 24) with its maximum value at [14 6 30]. The authors interpreted this finding as reflecting greater allocation of attention to one's own emotional state in those with greater emotional awareness.

In the previous study, all of the emotion-inducing scripts and films were selected to maximize their arousal value. Since arousal level was not systematically varied, and since happy, sad and disgust stimuli were

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aggregated, the degree to which previous results were due to the high arousal level or simply the emotional nature of the stimuli is unknown. Therefore, it is unknown whether the relationship between dACC activity and emotional awareness holds during the processing of emotional, but less arousing, stimuli. The dACC is part of an arousal system (Paus, 2000), including a likely effect on skin conductance responses (Fredrikson et al., 1998; Tranel and Damasio, 1994). In addition, because highly arousing stimuli engage attention more readily than less arousing stimuli (Anderson and Phelps, 2001; Öhman and Mineka, 2001), the relationship between dACC and LEAS may primarily be a function of the arousal level of the emotional stimuli. To address this, the present study included both pleasant and unpleasant stimuli that are normatively rated as high and low on arousal.

Arousal may be defined as a state of behavioral activation that varies in intensity from calm, relaxed and sleepy to excited, stimulated and alert that is associated both with activation of the sympathetic nervous system and heightened intensity of subjective emotional experiences (Lane et al., 2000). The construct of arousal can be assessed in several ways. The first is self-report. The standardized stimulus set used in the present study provides normative self-report ratings for two fundamental dimensions of emotion, valence (pleasant-unpleasant) and arousal (low-high) (Bradley and Lang, 1994). Second, arousal can be measured using one of several peripheral psychophysiological measures. Skin conductance response (SCR) or electrodermal activity measures the production of sweat (typically on the palmar surface of the hand) and is a measure of sympathetic activation (Shields et al., 1987). SCR has been shown to be elicited by both pleasant and unpleasant arousing emotional stimuli (Lang et al., 1993a,b). Because the dimension of arousal was not addressed in the previous study, the current study included subjective (ratings on an arousal scale) and objective (skin conductance responses to each picture) measures of arousal.

A secondary issue raised by the previous study was whether the relationship between emotional awareness and dACC activity also applies to men. There are several reasons to hypothesize that there may be differences between the sexes. On average, women score higher than men on the LEAS (Feldman Barrett et al., 2000), in addition to superior performance on tasks involving categorization of emotional stimuli (Hall and Matsumoto, 2004) and verbal and non-verbal judgments of emotion (Fischer, 2000; Hampson et al., 2006). Volumetric studies have shown that women have greater amounts of grey matter in the ACC than men (Good et al., 2001) and neuroimaging studies have reported greater activation of dACC in response to emotional stimuli (especially negative stimuli) in women than men (Wrase et al., 2003). Given the evidence that emotion processing and dACC function may differ in men and women, we investigated the possibility that the relationship between dACC activity and LEAS differs between the sexes.

The present study was designed to explore the relationship between LEAS and dACC activity while individuals were processing less arousing and highly arousing positive and negative emotional stimuli. In addition, we included both men and women in the present sample to test for sex differences in the relationship between dACC activity and emotional awareness. In doing so, we hoped to clarify the effect of stimulus and individual characteristics on dACC activation during emotion processing.

Materials and methods

Participants

Forty-four healthy participants (22 women) completed the entire experimental procedure. Prospective subjects were screened by phone and excluded if they reported a history of neurological abnormalities, head injury, learning disabilities, current psychoactive medication use, current drug or alcohol abuse, current major depressive episode, or lifetime prevalence of bipolar or other psychotic disorder. Subjects were also excluded if they reported that they were non-native English speakers (to ensure that LEAS performance reflected their true ability) or reported homosexual orientation (to ensure a pleasant response to heterosexual erotic stimuli). Participants ranged in age from 19 to 30 (mean = 24.75, standard deviation (SD) = 3.35). Socioeconomic status (SES) was calculated from reported occupation (Nam and Boyd, 2004) in 36 participants who reported an occupation other than ‘student’ (mean = 63.84, SD = 20.05). Men and women did not differ in terms of age ($t(42) = 1.13$, $p = 0.27$) or SES ($t(30) = 0.08$, $p = 0.94$). Women were studied during days 5–11 (follicular phase) of their menstrual cycles. Participants completed a 5-h session at the Banner Good Samaritan PET Center in Phoenix, Arizona. Participants gave written informed consent and were compensated for their participation.

Brain imaging

T_1-weighted, volumetric magnetic resonance imaging (MRI) was performed with a 1.5-T Signa system (General Electric, Milwaukee) to rule out gross anatomical abnormalities and for subsequent coregistration with PET data. MRI acquisition sequence parameters were 192×256 matrix, TR = 33 ms, TE = 5 ms, $a = 30^0$, FOV = 24 cm which resulted in 1.5 mm thick contiguous images.

Positron emission tomography imaging

Functional images were acquired on an Exact HR+ PET scanner (Siemens, Knoxville, TN) operating in 3D mode, which simultaneously records data for 63 horizontal sections with a center-to-center separation of 2.46 mm, a FOV of 15.5 cm, in-plane resolution of 4.2 to 5.1 mm full width at half maximum, and an axial resolution of 4.6 to 6.0 mm full width at half maximum. All emission images were reconstructed using a filtered back-projection method using a Hanning filter resulting in a final in-plane resolution of 9.5 mm full width at half maximum. Attenuation was corrected using 2 Ge-68/Ga-68 external rod sources. Intravenous bolus injections of 15 mCi ^{15}O water were administered and 60-s static scans were automatically initiated when the tracer arrived at the brain and exceeded a 15% over baseline threshold. Serial scans 10–15 min apart were obtained as the participant was scanned during six picture viewing conditions (described below) and two visual fixation conditions.

Skin conductance responses

During imaging, skin conductance responses (SCRs) were collected in response to each picture to provide a measure independent of self-report to ensure that participants responded as planned to experimental conditions. In particular, we expected the high arousal pleasant and unpleasant conditions to elicit greater SCR amplitude than the corresponding low arousal conditions (Bradley et al., 1993; Lang et al., 1993a). SCRs were recorded with two Ag/Cl electrodes on the left palm. Electrodermal activity was recorded at 500 samples/s using a Biopac systems amplifier, with a gain of 20, a high-pass filter of 0.5 Hz and a low-pass filter of 1 Hz.

Task

In an 8-condition scanning session, the first and fifth conditions were always visual fixation, and six blocks of picture viewing conditions were counterbalanced around the two blocks of visual fixation. Each of the six picture-viewing conditions consisted of 14 International Affective Picture System (IAPS) pictures (Lang et al., 2001) shown for 6 s each, separated by a 1-s period of visual fixation. During the visual fixation conditions a cross-hair appeared on the screen in place of a picture followed by a blank screen for 1 s. Normative ratings of IAPS pictures were used to create blocks of highly arousing pleasant, highly arousing unpleasant, less arousing pleasant, and less arousing unpleasant pictures. Because the normative ratings of arousal and valence given by men and women diverge for the highly arousing pictures, the high arousal pleasant and high arousal unpleasant pictures were different for men and women, but were selected to maximize normative ratings of arousal in each group. The two neutral conditions consisted of one that contained human faces in each picture and one that did not contain any human faces (mostly scenes and everyday objects). The low arousal pleasant and low arousal unpleasant conditions as well as both sets of neutral pictures were the same for men and women.

Subjects were given the following instruction before each scan: "Please look at the screen and allow yourself to feel whatever each picture evokes in you." Immediately after each scan the pictures just shown were replayed in the same order and ratings of valence and arousal for each picture were obtained on a 9-point scale (Bradley and Lang, 1994) based on how the subject recalled experiencing the picture during the first viewing several minutes before. These ratings were taken primarily as a "manipulation check" to validate the placement of pictures into the conditions using normative valence and arousal ratings.

Psychometric measures

The Levels of Emotional Awareness Scale (LEAS)

The LEAS was the first of several psychometric measures administered during a 1-h psychometric testing session on the same day just prior to imaging. The LEAS is a written performance measure that asks the subject to describe his or her anticipated feelings and those of another person in each of 20 scenes (vignettes) described in two to four sentences. Highly reliable structural scoring criteria are used to evaluate the degree of differentiation and integration of the words denoting emotion attributed to self and other. Higher scores reflect greater differentiation in emotion and greater awareness of emotional complexity in self and other.

One scene is presented per page, followed by two questions, "How would you feel?" and "How would the other person feel?" at the top of each page. Subjects are instructed to use as much or as little of the remainder of each page as needed to answer the two questions. Each scene is scored separately and receives a score of 0 to 5 corresponding to the underlying cognitive-developmental theory of five levels of emotional awareness, resulting in a maximum total score of 100. Each reply receives separate scores for the emotion described for the "self" and for the "other." The lowest score (level 0) is for non-emotion responses in which the word "feel" is used to describe a thought rather than a feeling. Level 1 reflects awareness of physiological cues (e.g., "I'd feel tired"). Level 2 consists of words that are typically used in other contexts but are frequently used to convey relatively undifferentiated emotion (e.g., "I'd feel bad") or use of the word "feel" to convey an action tendency, "I'd feel like punching the wall." Level 3 responses involve use of one word conveying typical, differentiated emotion (e.g., happy, sad, angry). A glossary of words at each level was created prior to this study to guide scoring. The highest score for the "self" and "other," Level 4, is given when two or more Level 3 words are used that convey greater emotional differentiation than either word alone. Each scene thus receives a separate score for the self response and for the other response from 0 to 4. In addition, a third "total" score is given to each scene, equal to the higher of these two (self and other) scores, except when both self and other receive Level 4 scores. Under these circumstances, a total score of Level 5 is given for the scene if the emotions for self and other can be differentiated from one another. Only results using the total score are reported here. The ratings are based entirely on structure, involve virtually no inference regarding the meaning of words, and do not require any rating for appropriateness of the response. All protocols were scored by one expert rater.

Skin conductance responses

SCR amplitude was measured as the change in electrodermal activity from baseline to peak with onset between 1 and 4 s after stimulus onset. Trials in which SCR did not rise (above 0.02 Seimens), steadily declined, or began outside the onset window specified above were assigned a value of zero and included in all subsequent analyses. Two participants (both women) were missing SCR data due to equipment malfunction during data collection.

Functional data analysis

Image pre-processing and voxel-based analyses were performed using SPM2 (http://www.fil.ion.ucl.ac.uk/spm/). Images were realigned to the first visual fixation scan. Realigned images were then co-registered to the high-resolution anatomical T1 weighted MRI scan for each subject. The subjects' anatomical scans were then normalized to the Montreal Neurological Institute template image, and normalization parameters were applied to the co-registered functional scans. The images were then smoothed with a 12-mm FWHM Gaussian kernel. Fixed effects statistical models were used to create contrasts between conditions of interest for each subject. These contrasts were entered into a second-level, random-effects analysis along with each subjects' score on the LEAS measure as a covariate (simple regression) at the group level. Whole-brain group level regressions for all 44 subjects were performed using LEAS and contrasts of emotion with neutral picture viewing conditions (pleasant vs. neutral, unpleasant vs. neutral), as well as with contrasts of high and low arousal picture viewing conditions (high arousal vs. low arousal). Unless otherwise noted, the threshold for whole-brain contrasts at the second level analysis was set at $p < 0.001$, uncorrected, with an extent threshold of 10 voxels. To investigate sex differences, we examined the correlation with LEAS separately for men and women. Direct tests of sex differences were performed with a multiple regression analysis in SPSS using contrast values from the dACC ROI extracted from the high

Table 1
Means (and standard deviations) of self-reported ratings of valence, self-reported ratings of arousal, and skin conductance responses (SCR) by condition

		Pleasant	Unpleasant	Neutral
High Arousal	Valence	3.19 (0.80)	7.39 (1.05)	4.95 (1.66)
	Arousal	4.95 (1.66)	4.52 (2.07)	8.15 (1.04)
	SCR	0.67 (1.04)	0.76 (1.14)	0.22 (0.38)
Low Arousal	Valence	3.24 (0.84)	6.42 (0.82)	4.90 (0.59)
	Arousal	7.62 (1.28)	7.12 (1.22)	8.68 (0.48)
	SCR	0.15 (0.24)	0.27 (0.64)	0.15 (0.25)

For normatively neutral stimuli, those that contained human faces were considered more highly arousing, those without human faces were considered less arousing. SCR units are in microSiemens.

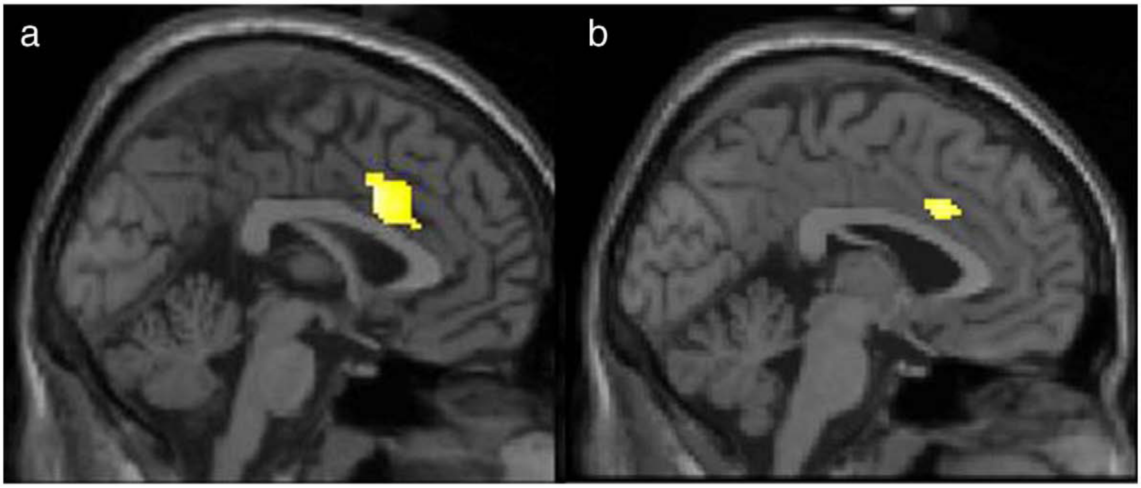

Fig. 1. Correlation between scores on the LEAS and rCBF from the contrast of high arousal (pleasant and unpleasant) vs. low arousal (pleasant and unpleasant) conditions in all 44 subjects (a) and in women only (b). The figure illustrates the local maximum in dACC ([0 12 32] $p<0.001$, uncorrected, $Z=4.04$ (a); and [−4 22 34] $p<0.001$, uncorrected, $Z=3.16$ (b)).

arousal minus low arousal contrast (Brett et al., 2002). In addition, these contrast values were used to determine whether self-reported valence and arousal and SCR were mediators of the relationship between dACC activity and LEAS.

Results

Manipulation check

Self-reported valence and arousal

In accordance with normative ratings, the repeated measures GLM in SPSS and post-hoc tests revealed that each condition was validated by self-reports from this sample. Pleasant conditions were more pleasant than neutral ($t(43)=14.74$, $p<0.001$), unpleasant conditions were more unpleasant than neutral ($t(41)=14.45$, $p<0.001$), and arousal ratings were higher for high than low arousal conditions for both pleasant ($t(41)=12.81$, $p<0.001$) and unpleasant ($t(41)=11.33$, $p<0.001$) pictures. Means and standard deviations for self-reported valence and arousal can be found in Table 1.

Skin conductance response

In accordance with previous findings, the repeated measures GLM in SPSS revealed that greater SCR value were observed for each emotion condition relative to neutral (pleasant: $t(41)=4.90$, $p<0.001$); unpleasant: $t(40)=3.79$, $p<0.001$) and for the high relative to the low arousal pleasant ($t(41)=4.02$, $p<0.001$) and unpleasant ($t(40)=3.49$, $p<0.005$) pictures. Means and standard deviations for SCR can be found in Table 1.

Psychometric data

LEAS

Total LEAS scores did not differ between men and women in this sample (men, mean=65.7, SD=9.57; women, mean=66.95, SD=8.61, $t(42)=0.465$, $p=0.65$). This finding contrasts with normative evidence that women on average score higher than men (Feldman Barrett et al., 2000).

Imaging data

Emotion and LEAS

Whole-brain analyses using a simple correlation to relate LEAS to the change in rCBF during viewing of all emotional pictures relative to neutral did not reveal a correlation in the dACC, even at low statistical thresholds ($p<0.01$ uncorrected). In addition, contrasts that related LEAS to pleasant and unpleasant conditions compared with each other or to neutral conditions separately did not reveal activation in the dACC ($p<0.01$, uncorrected).

Arousal and LEAS

Whole-brain analyses using a simple correlation to relate LEAS with the contrast of high arousal (pleasant and unpleasant) vs. low arousal (pleasant and unpleasant) conditions for all 44 subjects revealed an area of dACC with the local maximum at coordinates [0 12 32] ($Z=4.04$, $p<0.001$, uncorrected; Fig. 1a). A list of all significant activations for this comparison can be found in Table 2.

Arousal, LEAS and Sex

To investigate sex differences, we executed the correlation between dACC and LEAS separately for men and women. We observed a positive correlation between dACC activity in women (Fig. 1b) but no such activity in men, even at a lowered statistical threshold ($p<0.01$). A scatterplot depicting these correlations in men and women is displayed in Fig. 2. Direct tests of these sex differences were performed using a stepwise multiple regression analysis in SPSS using contrast values from the dACC ROI extracted from the high arousal minus low arousal comparison. This analysis revealed a small but significant main effect of sex with women showing greater dACC activity than men (Rsq=0.115, $p<0.025$). Next, significantly more variance was accounted for by adding LEAS to the model (Rsq=0.363, $p<0.001$). Lastly, the examination of the interaction between LEAS and sex revealed that even more variance in dACC was explained by LEAS in women than in men (Rsq=0.408, $p<0.05$)[1].

[1] This significance value was derived from the F value (3.026) converted to a t value (1.74) and was considered as a 1-tailed test.

Table 2
Brain areas where there is a significant ($p<0.001$, uncorrected) correlation between LEAS and the contrast high arousal (pleasant and unpleasant) minus low arousal (pleasant and unpleasant) conditions for all participants (N=44)

Region	Hemisphere	B.A.	*X* (mm)	*Y* (mm)	*Z* (mm)	*Z* score	Cluster size
Middle Frontal Gyrus	Right	8	30	12	40	4.46	14
Anterior Cingulate		24	0	12	32	4.04	272
Middle Frontal Gyrus	Left	6	−30	8	48	4.34	266
Postcentral Gyrus	Right	40	38	−32	48	3.93	208
Middle Frontal Gyrus	Right	9	30	36	28	3.3	38
Superior Frontal Sulcus	Right	6	18	2	60	3.49	31
Insula	Left		−38	−6	−4	3.3	22
Inferior Frontal Gyrus	Right	46	44	34	12	3.34	20
Midbrain	Right		12	−18	−8	3.22	11

P values shown are cluster-level corrected values. XYZ coordinates are in MNI space, B.A. = Brodmann Area.

Mediation analyses

Using contrast values from the dACC ROI extracted from the high minus low arousal contrast (Fig. 1a) we conducted separate mediation analyses (Baron and Kenny, 1986) to see if changes in self-reported valence or arousal or SCR mediated the relationship between dACC activity and LEAS. These analyses were performed to determine whether subjective (valence and arousal ratings) and objective (skin conductance) indices of emotional responsivity are each associated with dACC and LEAS such that they explain the main finding of the association between LEAS and dACC in the context of high relative to low arousal picture stimuli.

Self-reported valence and arousal

Neither self-reported valence nor arousal were significantly related to our predictor (LEAS, all p's>0.1) or our outcome measure (activity in the dACC; all p's>0.2). Thus, the requirements for a mediating relationship were not met.

Skin conductance response

SCRs were significantly related to both our predictor (LEAS; $R=0.313$, $p<0.046$) and our outcome variable (dACC activity, $R=0.418$, $p<0.007$). The mediation test indicated that SCR did not completely account for the relationship between dACC activity and SCR ($p=0.88$), which is consistent with the observation that the relationship between dACC activity and the LEAS still holds after variance due to SCR is removed ($R=0.313$, $p=0.046$).

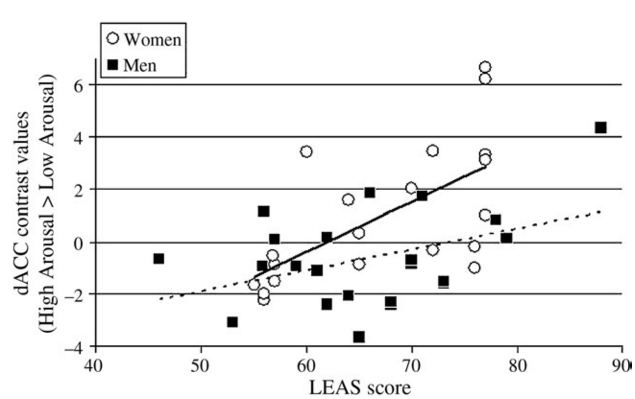

Fig. 2. Scatterplot of LEAS in relation to contrast values (high arousal vs. low arousal) extracted from the region of dACC observed in Fig. 1b. Women are plotted as open circles with the linear trend indicated with the solid line and men are plotted as filled squares with the linear trend indicated with the dotted line.

Discussion

This study investigated the role of arousal in the relationship between trait emotional awareness and dACC activity. We replicated a previous finding that women with greater trait emotional awareness show greater dACC activity when processing highly arousing positive and negative emotion-evoking stimuli. We also extended that finding by demonstrating that the relationship between dACC and emotional awareness is *specific* to highly arousing emotional stimuli. In addition, we observed that women had greater activity in the dACC than men, and that in women compared to men a stronger relationship exists between dACC activity and trait emotional awareness. Together these findings advance the understanding of the role of dACC in emotion information processing and highlight the need to examine the degree to which the dACC participates in mediating the inter-relationships of arousal, attention and the complexity of emotional experience.

Paus (2000) has demonstrated that the dACC is activated by stimulus-driven arousal and Critchley and colleagues (2003) have shown that the sympathetic component of heart rate variability correlates with dACC activity during mental stress. dACC activity is thus related to the arousal state of the organism and it receives arousal-related dopaminergic inputs as well as norepinephrinergic inputs from brainstem nuclei. These inputs are unique to the more dorsal areas of the ACC, with connections to the ventral areas of the ACC routed mostly through limbic structures such as the amygdala and ventral striatum (Paus, 2000). Thus, the specificity of the current finding to highly arousing stimuli is entirely consistent with the known characteristics of the dACC and is consistent with our observation that the relationship between dACC and LEAS is partially but not exclusively mediated by skin conductance responses.

It is reasonable that a region involved in the allocation of attentional resources would be responsive to conditions associated with high emotional arousal. From an evolutionary standpoint, organisms benefit from having a mechanism by which highly arousing stimuli can capture attention (Öhman and Mineka, 2001). Indeed, studies that employ emotional stimuli often show an interaction between attention and emotion in the dACC (Carlsson et al., 2004; Fichtenholtz et al., 2004) and experimental tasks that explicitly manipulate attention towards emotion robustly engage the dACC (Hutcherson et al., 2005; Lane et al., 1997a; Taylor et al., 2003).

In our previous study subjects were instructed to focus their attention on feeling the specific emotion targeted by the film and recall stimuli (happiness, sadness or disgust). That task instruction determined in advance how attention would be allocated and also constrained what subjects would likely experience by asking subjects to focus on feeling a single emotion. The present study broke new ground in demonstrating that the relationship between dACC and trait emotional awareness is still observed in the context of highly arousing stimuli when subjects can allocate their attention as they wish. Given the lack of constraints on feeling associated with the current task instruction to "allow yourself to feel whatever each picture evokes in you," and the nature of the emotional awareness construct as an index of the complexity of emotion information processing, the possibility exists that in the present context dACC activity is an indicator of complexity of emotion information processing. This conclusion is supported by our observation that simple self- ratings of pleasantness-unpleasantness (valence) and degree of arousal induced by the stimuli did not explain the association between LEAS and dACC activity.

A possible role of the dACC in processing complex emotion information is consistent with emerging evidence about the role of the dACC in cognitive tasks. Growing evidence from studies of inhibition and interference tasks using non-emotional stimuli implicate the dACC in several aspects of attentional control (Botvinick et al., 2001; Crottaz-Herbette and Menon, 2006; Fan et al., 2003; Posner and Dahaene, 1994). Specifically, the dACC appears to be more active during attentional tasks that involve the navigation of competing stimuli, such as conflict monitoring (Botvinick et al., 2004; Egner et al., in press), error monitoring (Fassbender et al., 2004), and response inhibition (Weissman et al., 2003). Recent attempts to distinguish between these processes have highlighted the dACC's role in conflict monitoring more specifically. That is, the dACC appears to be monitoring the presence of cognitive conflict and recruiting other prefrontal regions (such as DLPFC) to resolve this conflict when necessary (Botvinick et al., 2004; Fan et al., 2003).

Given that the attentional function that the dACC performs is often specifically related to the monitoring of conflict, it is relevant to note that the LEAS is a measure of the degree to which complexity can be appreciated in one's own and others' emotional responses. Conflict involves multiple signals that compete for resolution for the purpose of behavioral action. Greater scores on the LEAS are assigned when an individual demonstrates an appreciation of multiple emotional signals, which may be conflicting, and which may require some resolution for the purpose of behavioral action.

The question then arises why differential engagement of dACC as a function of trait emotional awareness would occur in the context of highly arousing stimuli rather than simply emotional compared to neutral conditions. Individuals who are more emotionally aware are better able to tolerate and consciously process intense emotions than those who are less aware (Kano et al., 2003; Lane et al., 1997b; Thayer and Lane, 2000). Conversely, individuals functioning at a lower level are more likely to behave impulsively and be less aware of what they are feeling in the context of highly arousing emotions (Lane, 2000). This may be understood as a greater ability among more highly aware individuals to be cognizant of their own emotional reactions in the context of high arousal and to anticipate and evaluate the consequences of their actions in advance of their behavioral expression. This greater ability may be mediated at least in part by the dACC, consistent with Paus' view that the dorsal ACC is fundamentally involved in translating intentions into actions in the context of emotional arousal (Paus, 2000), and is consistent with the role of the dACC in mediating regulated rather than automatic, prepotent responses (Procyk et al., 2000). According to this view, the differences between high and low awareness individuals in the processing of emotional information, which may be particularly evident in the context of high arousal, could be related at least in part to their relative success or failure in recruiting the dACC (Lane et al., 1997b).

These considerations regarding arousal, attention and complexity may help to explain the sex differences that we observed. Many neuroimaging studies that report dACC activation during emotional tasks included only women in an attempt to minimize heterogeneity of response to emotional stimuli (for examples, see Hutcherson et al., 2005; Ochsner et al., 2002). The justification for the inclusion of women rather than men is that women report experiencing greater emotional intensity than men (Diener et al., 1985; Fujita et al., 1991; Grossman and Wood, 1993) and are more physiologically aroused in response to emotional stimuli, even when self-reported emotion differences are not found (Grossman and Wood, 1993). Consistent with these previous observations, we observed that dACC activation during the processing of high arousal pictures is significantly greater in women than in men. Combining these previous findings with evidence that women typically score higher on the LEAS than men, we predicted a greater association between dACC and LEAS in women than in men.

Our observation of a stronger dACC–LEAS relationship in women than men after controlling for sex differences in dACC activity extends the literature on sex differences in the neural substrates of emotion information processing. Our findings are consistent with the hypothesis that women who have greater trait emotional awareness are more likely to pay attention to their own emotional responses (Gohm and Clore, 2000; Thayer et al., 2003), not only when asked to focus their attention on their emotional state (as in the previous study), but also when allowed to freely attend as they wish (as in the current study). This hypothesis is supported by the fact that self-focus and negative affect are more strongly related in women than men (Mor and Winquist, 2002) and may relate to the observation that women often direct attention towards their own emotions via rumination (Nolen-Hoeksema and Jackson, 2001). In addition, the sex difference in the association between trait emotional awareness and dACC activity is consistent with evidence that women tend to process emotional information in a more complex way than men, as indicated by a tendency for women to manifest greater complexity in emotional experience (Feldman-Barrett et al., 2000), greater ability to differentiate between exteroceptive emotional stimuli (Hall and Matsumoto, 2004; Fischer, 2000; Hampson et al., 2006) and greater complexity in the recall of autobiographical memories that involve emotion (Cahill 2003).

Several issues remain to be clarified in future research. First, as noted above, we hypothesized that recruitment of dACC as a function of emotional awareness constitutes a neural substrate of greater complexity of emotional experience. In this study, however, we were not able to determine whether LEAS scores were associated with individual differences in the complexity of momentary experiences. The self-report measures that we used in this study were designed to validate the experimental conditions. A more unstructured response format (comparable to the LEAS itself) would have been needed to detect such individual differences in complexity of self-report, and insufficient time was available between scans to obtain such data. Therefore, only future work can determine whether the online processing that distinguishes high and low LEAS individuals is associated with greater complexity of emotional experience.

Secondly, the nature of the hypothesized alteration in attentional processes remains to be determined. The dACC has a documented role in the effortful allocation of attention towards emotion (Hutcherson et al., 2005; Taylor et al., 2003) but may also play a role in the bottom-up capture of attention by highly arousing stimuli (Meriau et al., 2006). It is unknown whether the hypothesized greater attention to one's own emotional experiences in those with higher LEAS was a result of or a cause of greater peripheral physiological responding. In addition, it is not known whether attention was altered by the mind-set of openness to feelings specified in the task instructions or whether attention was altered in relation to the stimuli themselves (e.g. wholistic vs. detail-oriented perception), the subject's own subjective responses (e.g., bodily sensation, action tendencies, one feeling or multiple feelings), or the associated cognitions triggered by the stimuli (e.g. autobiographical memories). In addition, the sex difference in the LEAS-dACC relationship raises the question of whether the nature of the alteration in attentional processes differs between men and women.

Conclusion

We have demonstrated that it is only in the context of highly arousing stimuli that dACC activity varies as a function of trait emotional awareness. We have also demonstrated that women show greater dACC activation than men, and that the relationship between LEAS and dACC activity is stronger in women than men. This study has therefore clarified that the relationship between dACC activity and LEAS is more specific than previously known along the dimensions of arousal and sex. We have also demonstrated that activity in the dACC correlates with emotional awareness when subjects are free to direct their attention as they wish, indicating that the attentional context of the relationship between dACC activity and LEAS is more general than was previously known. These new findings may help to explain why the dACC is activated in some but by no means all functional imaging studies involving activation of emotion, and argue against a strict dichotomy between the so-called cognitive and affective divisions of the ACC. Future work will be needed to more fully characterize the nature of the differential processing in those with greater trait emotional awareness, with special emphasis on how attention is deployed and on whether engagement of the dACC during conditions of high emotional arousal is associated with greater complexity of emotional experience.

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References

Anderson, A.K., Phelps, E.A., 2001. Lesions of the human amygdala impair enhanced perception of emotionally salient events. Nature 411, 305–309.

Baron, R.M., Kenny, D.A., 1986. The moderator-mediator variable distinction in social psychological research: Conceptual, strategic and statistical considerations. J. Pers. Soc. Psychol. 51, 1173–1182.

Botvinick, M.M., Braver, T.S., Barch, D.M., Carter, C.S., Cohen, J.D., 2001. Conflict monitoring and cognitive control. Psychol. Rev. 108, 624–652.

Botvinick, M.M., Cohen, J.D., Carter, C.S., 2004. Conflict monitoring and anterior cingulate cortex: An update. Trends Cogn. Sci. 8, 539–546.

Bradley, M.M., Cuthbert, B.N., Lang, P.J., 1993. Pictures as prepulse: Attention and emotion in startle modification. Psychophysiology 30, 541–545.

Bradley, M.M., Lang, P.J., 1994. Measuring emotion: The self-assessment manikin and the semantic differential. J. Behav. Ther. and Exp. Psychiatry 25, 49–59.

Brett, M., Anton, J.L., Valabregue, R., Poline, J.B., 2002. Region of interest analysis using an SPM toolbox. Paper presented at the Conference on Functional Mapping of the Human Brain, Sendai, Japan.

Bush, G., Luu, P., Posner, M.I., 2000. Cognitive and emotional influences in anterior cingulate cortex. Trends Cogn. Sci. 4, 215–222.

Cahill, L., 2003. Sex-related influences on the neurobiology of emotionally influenced memory. Ann.N. Y. Acad. Sci. 985, 163–173.

Carlsson, K., Petersson, K.M., Lundqvist, D., Karlsson, A., Ingvar, M., Öhman, A., 2004. Fear and the amygdala: Manipulation of awareness generates differential cerebral responses to phobic and fear-relevant (but nonfeared) stimuli. Emotion 4, 340–353.

Cohen, R.A., Paul, R., Zawacki, T.M., Moser, D.J., Sweet, L., Wilkinson, H., 2001. Emotional and personality changes following cingulotomy. Emotion 1, 38–50.

Corbetta, M., Miezin, F., Dobmeyer, S., Shulman, G., Petersen, S., 1991. Selective and divided attention during visual discriminations of shape, color, and speed: Functional anatomy by positron emission tomography. J. Neurosci. 11, 2383–2402.

Critchley, H.D., Mathias, C.J., Josephs, O., O'Doherty, J., Zanini, S., Dewar, B.K., Cipolotti, L., Shallice, T., Dolan, R.J., 2003. Human cingulate cortex and autonomic control: Converging neuroimaging and clinical evidence. Brain 126, 2139–2152.

Crottaz-Herbette, S., Menon, V., 2006. Where and when the anterior cingulate cortex modulates attentional response: Combined fMRI and ERP evidence. J. Cogn. Neurosci. 18, 766–780.

Devinsky, O., Morrell, M.J., Vogt, B.A., 1995. Contributions of anterior cingulate cortex to behaviour. Brain 118, 279–306.

Diener, E., Sandvik, E., Larsen, R.J., 1985. Age and sex effects for emotional intensity. Dev. Psychol. 542–546.

Drevets, W.C., Raichle, M.E., 1998. Reciprocal suppression of regional cerebral blood flow during emotional versus higher cognitive processes: Implications for interactions between emotion and cognition. Cogn. Emot. 12, 353–385.

Egner, T., Etkin, A., Gale, S., Hirsch, J., in press. Dissociable neural systems resolve conflict from emotional versus nonemotional distracters. Cereb. Cortex. Available online at: http://cercor.oxfordjournals.org/cgi/content/full/bhm179v1.

Eisenberger, N.I., Lieberman, M.D., Williams, K.D., 2003. Does rejection hurt? An fMRI study of social exclusion. Science 302, 290–292.

Fan, J., Flombaum, J.I., McCandliss, B.D., Thomas, K.M., Posner, M.I., 2003. Cognitive and brain consequences of conflict. NeuroImage 18, 42–57.

Fassbender, C., Murphy, K., Foxe, J.J., Wylie, G.R., Javitt, D.C., Robertson, I.H., Garavan, H., 2004. A topography of executive functions and their interactions revealed by functional magnetic resonance imaging. Brain Res. Cogn. Brain Res. 20, 132–143.

Feldman Barrett, L., Lane, R.D., Sechrest, L., Schwartz, G.E., 2000. Sex differences in emotional awareness. Pers. Soc. Psychol. Bull. 26, 1027–1035.

Fellows, L.K., Farah, M.J., 2005. Is anterior cingulate cortex necessary for cognitive control? Brain 128, 788–796.

Fichtenholtz, H.M., Dean, H.L., Dillon, D.G., Yamasaki, H., McCarthy, G., LaBar, K.S., 2004. Emotion-attention network interactions during a visual oddball task. Cogn. Brain Res. 20, 67–80.

Fischer, A.H. (Ed.), 2000. Gender and emotion: Social psychological perspectives. Cambridge University Press, New York, NY.

Fredrikson, M., Furmark, T., Olsson, M.T., Fischer, H., Andersson, J., Langstrom, B., 1998. Functional neuroanatomical correlates of electrodermal activity: A positron emission tomographic study. Psychophysiology 35, 179–185.

Fujita, F., Diener, E., Sandvik, E., 1991. Gender differences in negative affect and well-being: The case for emotional intensity. J. Pers. Soc. Psychol. 61, 427–434.

Gohm, C.L., Clore, G.L., 2000. Individual differences in emotional experience: Mapping available scales to processes. Pers. Soc. Psychol. Bull. 26, 679–697.

Good, C.D., Johnsrude, I., Ashburner, J., Henson, R.N.A., Friston, K.J., Frackowiak, R.S.J., 2001. Cerebral asymmetry and the effects of sex and

handedness on brain structure: A voxel-based morphometric analysis of 465 normal adult human brains. NeuroImage 14, 685–700.
Grossman, M., Wood, W., 1993. Sex differences in intensity of emotional experience: A social role interpretation. J. Pers. Soc. Psychol. 65, 1010–1022.
Hall, J.A., Matsumoto, D., 2004. Gender differences in judgments of multiple emotions from facial expressions. Emotion 4, 201–206.
Hampson, E., van Anders, S.M., Mullin, L.I., 2006. A female advantage in the recognition of emotional facial expressions: Test of an evolutionary hypothesis. Evol. Hum. Behav. 27, 401–416.
Hutcherson, C.A., Goldin, P.R., Ochsner, K.N., Gabrieli, J.D.E., Feldman Barrett, L., Gross, J.J., 2005. Attention and emotion: Does rating emotion alter neural responses to amusing and sad films? NeuroImage 27, 656–668.
Kano, M., Fukudo, S., Gyoba, J., Kamachi, M., Tagawa, M., Mochizuki, H., Itoh, M., Hongo, M., Yanai, K., 2003. Specific brain processing of facial expressions in people with alexithymia: An $H_2^{15}O$-PET study. Brain 126, 1474–1484.
Lane, R.D., 2000. Levels of emotional awareness: Neurological, psychological and social perspectives. In: Parker, J., Bar-On, R. (Eds.), Handbook of emotional intelligence. Jossey Bass, San Francisco, pp. 171–191.
Lane, R.D., McRae, K., 2004. Neural substrates of conscious emotional experience: A cognitive-neuroscientific perspective. In: Beauregard, M. (Ed.), Consciousness, emotional self-regulation and the brain. John Benjamins, Amsterdam, pp. 87–122.
Lane, R.D., Schwartz, G.E., 1987. Levels of emotional awareness: A cognitive-developmental theory and its application to psychopathology. Am. J. Psychiatr. 144, 133–143.
Lane, R.D., Quinlan, D.M., Schwartz, G.E., Walker, P.A., Zeitlin, S.B., 1990. The levels of emotional awareness scale: A cognitive-developmental measure of emotion. J. Pers. Assess. 55, 124–134.
Lane, R.D., Fink, G.R., Chua, P.M.L., Dolan, R.J., 1997a. Neural activation during selective attention to subjective emotional responses. NeuroReport 8, 3969–3972.
Lane, R.D., Reiman, E.M., Bradley, M.M., Lang, P.J., Ahern, G.L., Davidson, R.J., Schwartz, G.E., 1997b. Neuroanatomical correlates of pleasant and unpleasant emotion. Neuropsychologia 35, 1437–1444.
Lane, R.D., Reiman, E.M., Axelrod, B., Yun, L.S., Holmes, A., Schwartz, G.E., 1998. Neural correlates of levels of emotional awareness: Evidence of an interaction between emotion and attention in the anterior cingulate cortex. J. Cogn. Neurosci. 10, 525–535.
Lane, R., Nadel, L., Ahern, G., Allen, J., Kaszniak, A., Rapcsak, S., Schwartz, G. (Eds.), 2000. Cognitive Neuroscience of Emotion. New York, Oxford University Press.
Lang, P.J., Greenwald, M.K., Bradley, M.M., Hamm, A.O., 1993a. Looking at pictures: Affective, facial, visceral and behavioral reactions. Psychophysiology 30, 261–273.
Lang, P.J., Greenwald, M.K., Bradley, M.M., Hamm, A.O., 1993b. Looking at pictures: Affective, facial, visceral, and behavioral reactions. Psychophysiology 30, 261–273.
Lang, P.J., Bradley, M.M., Cuthbert, B.N., 2001. International affective picture system (IAPS). Instruction manual and affective ratings. Technical report. The University of Florida: The Center for Research in Psychophysiology.
Meriau, K., Wartenburger, I., Kazzer, P., Prehn, K., Lammers, C.H., van der Meer, E., Villringer, A., Heekeren, H.R., 2006. A neural network reflecting individual differences in cognitive processing of emotions during perceptual decision making. NeuroImage 33, 1016–1027.
Mohanty, A., Engels, A.S., Herrington, J.D., Heller, W., Ringo Ho, M.H., Banich, M.T., Webb, A.G., Warren, S.L., Miller, G.A., 2007. Differential engagement of anterior cingulate cortex subdivisions for cognitive and emotional function. Psychophysiology 44, 343–351.
Mor, N., Winquist, J., 2002. Self-focused attention and negative affect: A meta-analysis. Psychol. Bull. 128, 638–662.
Mulert, C., Menzinger, E., Leicht, G., Pogarell, O., Hegerl, U., 2005. Evidence for a close relationship between conscious effort and anterior cingulate cortex activity. Int. J. Psychophysiol. 56, 65–80.
Nam, C.B., Boyd, M., 2004. Occupational status in 2000: Over a century of census-based measurement. Popul. Res. Policy Rev. 23, 327–358.
Nolen-Hoeksema, S., Jackson, B., 2001. Mediators of the gender difference in rumination. Psychol. Women Q. 25, 37–47.
Ochsner, K.N., Bunge, S.A., Gross, J.J., Gabrieli, J.D.E., 2002. Rethinking feelings: An fMRI study of the cognitive regulation of emotion. J. Cogn. Neurosci. 14, 1215–1229.
Öhman, A., Mineka, S., 2001. Fears, phobias, and preparedness: Toward an evolved module of fear and fear learning. Psychol. Rev. 108, 483–522.
Pardo, J., Pardo, P., Janer, K., Raichle, M., 1990. The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. Proc. Natl. Acad. Sci. 87, 256–259.
Paus, T., 2000. Functional anatomy of arousal and attention systems in the human brain. Prog. Brain Res. 126, 65–77.
Phan, K.L., Wager, T., Taylor, S.F., Liberzon, I., 2002. Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. NeuroImage 16, 331–348.
Posner, M.I., Dahaene, S., 1994. Attentional networks. Trends Neurosci. 17, 75–79.
Procyk, E., Tanaka, Y.L., Joseph, J.P., 2000. Anterior cingulate activity during routine and non-routine sequential behaviors in macaques. Nat. Neurosci. 3, 502–508.
Rainville, P., Carrier, B., Hofbauer, R.K., Bushnell, M.C., Duncan, G.H., 1999. Dissociation of sensory and affective dimensions of pain using hypnotic modulation. Pain 82, 159–171.
Shields, S.A., MacDowell, K.A., Fairchild, S.B., Campbell, M.L., 1987. Is mediation of sweating cholinergic, adrenergic, or both? A comment on the literature. Psychophysiology 24, 312–319.
Taylor, S.F., Phan, K.L., Decker, L.R., Liberzon, I., 2003. Subjective rating of emotionally salient stimuli modulates neural activity. NeuroImage 18, 650–659.
Thayer, J.F., Lane, R.D., 2000. A model of neurovisceral integration in emotion regulation and dysregulation. J. Affect. Disor. 61, 201–216.
Thayer, J.F., Rossy, L.A., Ruiz-Padial, E., Johnsen, B.H., 2003. Gender differences in the relationship between emotional regulation and depressive symptoms. Cogn. Ther. Res. 27, 349–364.
Tranel, D., Damasio, H., 1994. Neuroanatomical correlates of electrodermal skin conductance responses. Psychophysiology 31, 427–438.
Weissman, D.H., Giesbrecht, B., Song, A.W., Mangun, G.R., Woldorff, M.G., 2003. Conflict monitoring in the human anterior cingulate cortex during selective attention to global and local object features. NeuroImage 19, 1361–1368.
Weissman, D.H., Gopalakrishnan, A., Hazlett, C.J., Woldorff, M.G., 2005. Dorsal anterior cingulate cortex resolves conflict from distracting stimuli by boosting attention toward relevant events. Cereb. Cortex 229–237.
Wrase, J., Klein, S., Gruesser, S.M., Hermann, D., Flor, H., Mann, K., Braus, D.F., Heinz, A., 2003. Gender differences in the processing of standardized emotional visual stimuli in humans: A functional magnetic resonance imaging study. Neurosci. Lett. 348, 41–45.