Behavioral Neuroscience
2001, Vol. 115, No. 1, 33–42

0735-7044/01/$5.00 DOI: 10.1037//0735-7044.115.1.33

An fMRI Study of Personality Influences on Brain Reactivity to Emotional Stimuli

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Functional imaging studies have examined which brain regions respond to emotional stimuli, but they have not determined how stable personality traits moderate such brain activation. Two personality traits, extraversion and neuroticism, are strongly associated with emotional experience and may thus moderate brain reactivity to emotional stimuli. The present study used functional magnetic resonance imaging to directly test whether individual differences in brain reactivity to emotional stimuli are correlated with extraversion and neuroticism in healthy women. Extraversion was correlated with brain reactivity to positive stimuli in localized brain regions, and neuroticism was correlated with brain reactivity to negative stimuli in localized brain regions. This study provides direct evidence that personality is associated with brain reactivity to emotional stimuli and identifies both common and distinct brain regions where such modulation takes place.

Despite a strong scientific interest in the topic of emotions and the brain in the late 19th century (Darwin, 1872; James, 1884), a broad experimental effort to understand the neural basis of emotion did not commence until the last quarter of the 20th century. Inspired by animal studies investigating the role of the amygdala in fear (Cahill & McGaugh, 1990; Chapman, Kairiss, Keenan, & Brown, 1990; Davis, 1992; Davis, Rainnie, & Cassell, 1994; Gallagher & Holland, 1992; Kapp, Whalen, Supple, & Pascoe, 1992; LeDoux, 1993, 1995; Weisz, Harden, & Xiang, 1992; Whalen & Kapp, 1991; Zola-Morgan, Squire, Alvarez-Royo, & Clower, 1991), studies of patients with brain lesions have provided evidence about the brain organization of human emotions (Adolphs, Cahill, Schul, & Babinsky, 1997; Bechara et al., 1995; Cahill, Babinsky, Markowitsch, & McGaugh, 1995). Recent advances in functional brain imaging, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have permitted investigation of the neural correlates of emotion in healthy people.

A number of functional imaging studies have investigated brain activation patterns associated with emotional states. Using emotion induction based on either autobiographical memories or external stimuli, these studies have shown patterns of brain activation for pleasant and unpleasant emotion (Canli, Desmond, Zhao, Glover, & Gabrieli, 1998; Lane, Reiman, Bradley, et al., 1997), traumatic experience (Fischer, Wik, & Fredrikson, 1996), sadness, happiness, disgust (George et al., 1995; Lane, Reiman, Ahern, Schwartz, & Davidson, 1997), and fear and euphoria (Ketter et al., 1996). Data from these studies are not always consistent. One possible reason for this inconsistency is that although most studies assume that emotion-related activation patterns will be similar across people, there may be important individual differences in the biological basis of emotion.

Functional imaging studies of emotion have not yet explored potential determinants of individual variability, with the exception of gender (George, Ketter, Parekh, Herscovitch, & Post, 1996). However, some psychological determinants of individual variability in emotional responsiveness have been identified, such as specific personality traits. The personality traits of extraversion and neuroticism are strongly associated with positive and negative emotional experience, respectively (Costa & McCrae, 1980, 1991; Eysenck, 1990; John, 1990; Meyer & Shack, 1989). Individuals who exhibit a high degree of extraversion—the tendency to be upbeat, to be optimistic, and to enjoy social contact—report more positive emotions in everyday life than less extraverted individuals (Costa & McCrae, 1980). Individuals who exhibit a high degree of neuroticism—the tendency to worry, to be anxious, and to be apprehensive—report more negative emotions in everyday life than less neurotic individuals (Costa & McCrae, 1980). Experimental manipulations of affect have likewise documented strong personality–affect relations (Gross, Sutton, & Ketelaar, 1998).

We hypothesized that the similarity in the dimensional structure of personality and emotion is due to a common neural substrate where personality traits moderate the processing of emotional stimuli. Prior brain imaging studies have found personality-dependent variation in blood flow patterns at rest or during tasks unrelated to emotion (Ebmeier et al., 1994; Haier, Sokolski, Katz, & Buchsbaum, 1987; Johnson et al., 1999; Stenberg, Risberg, Warkentin, & Rosen, 1990; Stenberg, Wendt, & Risberg, 1993; Sugiura et al., 2000). No functional imaging studies, however, have investigated the relationship between emotional brain reactivity and personality.

The present study used fMRI to directly test whether individual differences in brain reactivity to emotional stimuli were correlated

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We thank W. Revelle for his comments on an earlier version of the article. This study was supported by the National Institutes of Health and by a National Research Service Award fellowship to Turhan Canli.

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with measures of extraversion and neuroticism. Participants watched alternating blocks of emotionally positive and negative pictures, and brain reactivity to these stimuli was correlated with individuals' scores on measures of extraversion and neuroticism. On the basis of data reviewed above, we hypothesized that extraversion is associated with greater brain reactivity to positive pictures and that neuroticism is associated with greater brain reactivity to negative pictures. We further hypothesized that these correlations would be most prominent in the prefrontal cortex, anterior cingulate, insula, and amygdala, all of which have been previously implicated in aspects of human emotion and personality (Bechara, Damasio, Tranel, & Damasio, 1997; Cahill et al., 1995; Fuster, 1989; Lane, Reiman, Ahern, et al., 1997; Pardo, Fox, & Raichle, 1991; Reiman et al., 1997; Vogt, Finch, & Olson, 1992).

Method

Participants

Fourteen right-handed healthy female volunteers (mean age = 25.6 years, range = 19–42 years) participated in this study. Data from these participants were previously analyzed with respect to the role of emotional arousal on brain activation patterns (Canli et al., 1998) and emotional memory (Canli, Zhao, Desmond, Glover, & Gabrieli, 1999) but not with respect to individual differences in personality. Women were chosen for this study because they are more likely to report intense emotional experiences (Shields, 1991) and because they show more physiological reactivity in concordance with valence judgments than men (Lang, Greenwald, Bradley, & Hamm, 1993).

Emotion Stimuli and Manipulation Check

Participants saw 20 negative and 20 positive pictures selected from a standardized set of pictures (International Affective Picture System; Lang & Greenwald, 1993). Negative pictures included images of angry or crying people, spiders, guns, and a cemetery. Positive pictures included images of a happy couple, puppies, foods like ice cream and brownies, and urban sunsets. Participants were instructed only "to pay attention to each picture as it's presented"; that is, they watched passively without an explicit task. Images were presented in five alternating blocks of four pictures each. The order of positive and negative blocks was alternated across participants. Each picture was presented for 7,500 ms, with an interstimulus interval of 1,125 ms. Total scan time was 345 s. As a manipulation check, participants were shown the same sequence of stimuli immediately after the scan and were asked to rate each picture on a visual scale (Lang & Greenwald, 1993) with regard to valence and arousal. For each individual, two paired *t* tests were performed to assess whether there was a significant difference between the negative and positive picture sets with respect to valence and arousal ratings.

Personality Measures

Personality scores were determined with the NEO Five-Factor Inventory (NEO-FFI), a 60-item questionnaire that measures the five personality dimensions (12 items for each dimension) of neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness (Costa & McCrae, 1991). Scores are summed totals and have a range of 0–48 in each of the five personality domains.

Magnetic Resonance Imaging

Data were acquired in a 1.5 T GE Signa MR imager (General Electric, Fairfield, CT), which was used to measure blood-oxygen level-dependent contrast (Ogawa, Lee, Nayak, & Glynn, 1990). For structural images, 16 coronal slices of 3-mm thickness were imaged with a T1-weighted flow-compensated spin-warp sequence (repetition time [TR] = 500 ms, minimum echo time [TE]). Functional images were obtained with a T2*-sensitive 3-D gradient echo spiral sequence with four interleaves (TR = 90 ms, TE = 40 ms, flip angle = 22°, field of view = 36 cm, in-plane resolution = 2.35 mm^2, acquisition time = 4.32 s per frame, number of frames = 80). Spiral methods differ from spin-warp techniques in that the *k*-space trajectory begins at the $k = 0$ origin and spirals outward to the desired maximum *k* radius. To allow operation with conventional scanners, the desired *k*-space coverage is obtained not with one acquisition but with a small number of interleaved trajectories. Improved spatial resolution can be achieved by increasing the number of interleaves at the expense of decreased temporal resolution or a decrease in the number of slices sampled (Glover & Song, 1998). The spiral technique also provides excellent motion immunity because, like projection reconstruction methods, the averaging from oversampling of the low spatial frequencies causes reduced pulsatility effects (Glover & Pauly, 1992). In addition, all moments of the gradients return periodically to zero, affording inherent moment compensation against motion-generated phase encoding. A whole-head coil was used for all participants. Head movement was minimized with a bite bar with each participant's dental impression. Standard algorithms for motion analysis (Friston, Williams, Howard, Frackowiak, & Turner, 1996) and correction (Woods, Cherry, & Mazziotta, 1992) were used. Functional activation (*z* score) maps were based on a correlation between the signal intensity of each pixel and a reference function that was computed by convolving a square wave at the task frequency (alternating blocks of negative and positive pictures) with a data-derived estimate of the hemodynamic response function (Friston, Jezzard, & Turner, 1994), and the maps were spatially smoothed at full-width-at-half-maximum = 4.8 mm.

Correlation Maps

For each participant, *z* scores for each slice were transformed into a common coordinate system by morphing the data onto a common template. Therefore, the exact same voxels were considered in all participants after they had been placed in normalized space. Then, for each voxel in the template, a correlation between the *z* score and personality score was computed. Thus, each voxel was represented by two columns: positive or negative *z* scores representing, for each participant, the degree of correlation between activation of that pixel in phase (positive pictures) or out of phase (negative pictures), respectively; and personality scores representing the degree of extraversion or neuroticism exhibited by each participant. To control for Type I errors, we performed a cluster analysis (Xiong, Gao, Lancaster, & Fox, 1995), with a $p < .05$ (two-tailed) intensity threshold and a spatial extent threshold that yielded a $p < .001$ significance level over the entire image. Significant clusters were color coded and displayed by projection onto an averaged T1-weighted anatomical image of each slice. Based on this methodology, functional activations emerged from the correlation maps in an unbiased fashion, as opposed to analyses based on anatomical interpretations of region-of-interest boundaries.

Results

Emotion Ratings

Participants experienced positive and negative picture sets as opposite in valence. On a scale from 1 (*unhappy*) to 9 (*happy*), positive pictures were rated 6.63 ± 0.68 (*M* ± *SD*) and negative pictures were rated 3.35 ± 0.42. These ratings were significantly different from each other, $t(13) = 13.33$, $p < .0001$. The two picture sets were also experienced as different in arousal. On a scale from 1 (*calm*) to 9 (*aroused*), positive pictures were rated 4.35 ± 1.32 and negative pictures were rated 5.33 ± 1.34.

These ratings were significantly different from each other, $t(13) = 3.33$, $p < .01$, indicating that the negative pictures were rated as more arousing than the positive pictures.

Personality Measures

Neuroticism scores ranged from 6 to 36 (M = 21.79, SD = 8.53), and extraversion scores from 21 to 42 (M = 31.57, SD = 6.82). There was a (statistically nonsignificant) negative correlation between participants' neuroticism and extraversion scores ($r = -.42$, $p = .14$). Participants' scores were also converted to T scores to compare this sample with the normative NEO-FFI population, which is standardized to have a T score mean (± SD) of 50 (± 10). This sample was within the average range of the normative sample (Costa & McCrae, 1991), with a mean of 53.36 (± 9.75) for neuroticism and 54.45 (± 11.67) for extraversion.

Correlation Maps: Extraversion and Neuroticism

There were multiple loci of significant correlations between participants' personality scores and brain activation in response to emotional pictures. Level of brain activation to positive (relative to negative) pictures correlated significantly with participants' extraversion scores in both cortical (frontal, temporal) and subcortical (e.g., amygdala, caudate, putamen) regions (see Table 1; Figure 1, top row). Brain activation to negative, relative to positive, pictures correlated significantly with participants' neuroticism scores in left frontal and temporal cortical regions (see Table 1; Figure 1, bottom row). Figures 2 and 3 show scatter plots from clusters in which levels of brain reactivity to positive pictures correlated with extraversion and in which brain reactivity to negative pictures correlated with neuroticism, respectively.

Discussion

Personality measures of extraversion and neuroticism were found to correlate significantly with highly localized changes in brain activation to positive and negative stimuli. Extraversion correlated with level of brain activation to positive (relative to negative) pictures in numerous cortical and subcortical brain locations. There were no correlations between extraversion and levels of brain activation to negative (relative to positive) pictures. These findings are consistent with behavioral evidence showing that extraversion is correlated with positive emotional reactivity but not with negative emotional reactivity (negatively correlated; Gross & John, 1995). In contrast, neuroticism correlated with level of brain activation to negative (relative to positive) pictures in the left temporal and frontal lobes. These data show that individual differences in brain reactivity to emotional stimuli are associated with specific personality traits.

We found differing patterns of personality-based correlations with emotional responsiveness in the frontal versus the temporal cortex. The frontal cortex, in the left middle frontal gyrus, was associated with significant correlations for both extraversion and neuroticism. The left middle frontal gyrus was the only location where neighboring clusters represented correlations of higher extraversion (but not neuroticism) scores with levels of brain activation to positive pictures, and higher neuroticism (but not extraversion) scores with levels of brain activation to negative pictures. This finding is consistent with earlier imaging studies of extraverted and depressed participants: Extraverts, relative to introverts, show elevated left-frontal blood flow even at rest (Stenberg et al., 1990), whereas depressed patients, whose condition has been linked to neuroticism across many studies (Clark, Watson, & Mineka, 1994), show reduced metabolism in the left frontal cortex (Baxter et al., 1989). The temporal cortex, on the other hand, was associated with significant correlations for extraversion in the right hemisphere and for neuroticism in the left hemisphere.

Table 1
Loci of Brain Reactivity to Emotional Stimuli Correlating With Personality

Location	x	y	z
Correlations of extraversion with increased brain activation to positive (relative to negative) pictures			
Left frontal lobe	−24	+10	+49
Left middle frontal gyrus	−37	+15	+43
	−27	−3	+46
Right inferior frontal gyrus	+44	+15	−10
Left precentral gyrus	−36	−5	+56
	−47	−6	+45
Right cingulate gyrus	+8	+15	+26
Right temporal lobe	+44	−4	−18
Right inferior temporal gyrus	+37	−4	−24
Left lateral globus pallidus	−21	−8	+5
Right amygdala	+23	−4	−19
Left putamen	−30	−7	−9
	−32	−5	−2
Left caudate	−17	+3	+16
	−24	+16	+15
Correlations of neuroticism with increased brain activation to negative (relative to positive) pictures			
Left middle temporal gyrus	−61	−4	−7
Left middle frontal gyrus	−33	+6	+49
Correlations of neuroticism with decreased brain activation to negative (relative to positive) pictures			
Right middle frontal gyrus	+29	+34	+38

Note. Listed are loci of significant brain correlation between measures of extraversion and neuroticism and brain activation in response to positive (relative to negative) or negative (relative to positive) emotional pictures. Three-dimensional clusters of significant correlations were determined by the methods of Xiong et al. (1995). Talairach coordinates of these clusters were determined by the methods of Desmond and Lim (1997). Regions are identified by name of location and coordinates in the brain atlas of Talairach and Tournoux (1988). All clusters in this table have mean correlation coefficients greater than .70. x = distance in millimeters to the right (+) or left (−) of midline; y = distance anterior (+) or posterior (−) to the anterior commissure; z = distance superior (+) or inferior (−) to a horizontal plane through the anterior and posterior commissures.

The correlation between extraversion and cingulate activation to positive emotional stimuli may be related to attentional bias or awareness of emotional signals. For example, the attentional bias for positive stimuli that has been reported for extraverted participants in an orienting task (Derryberry & Reed, 1994) may be related to anterior cingulate reactivity to positive stimuli, and greater emotional awareness has been correlated with greater cingulate activation (Lane et al., 1998). However, the relationship

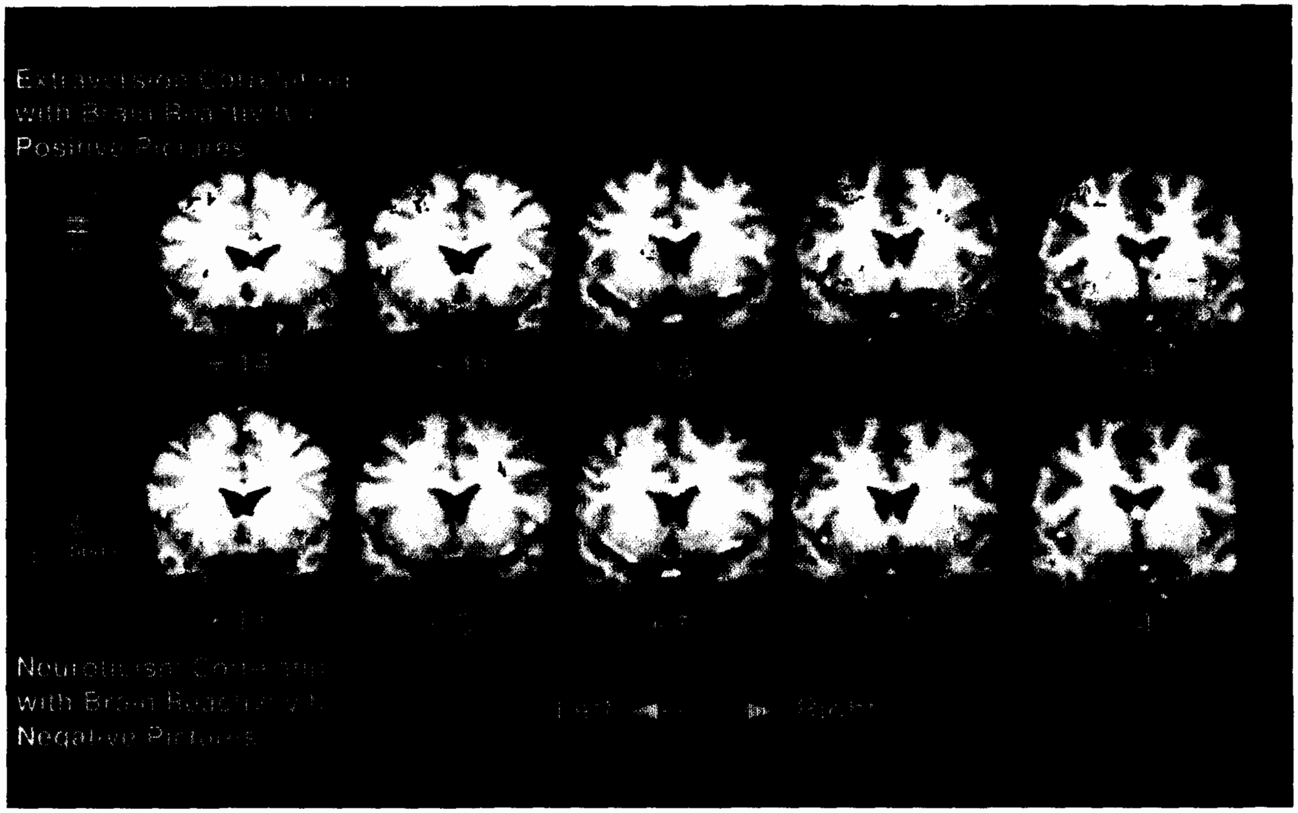

Figure 1. Loci of significant correlation between extraversion and neuroticism and emotional reactivity. Shown are coronal slices illustrating loci of significant ($p < .05$) correlations between personality measures and emotional reactivity. Loci colored in red represent regions of significant positive correlation between extraversion and reactivity to positive pictures. Loci colored in blue represent regions of significant positive correlation between neuroticism and reactivity to negative pictures.

between cingulate activation and extraversion extends beyond emotion-related processes, because earlier imaging studies noted a similar relationship in nonemotional tasks or at rest (Ebmeier et al., 1994; Haier et al., 1987; Johnson et al., 1999; Sugiura et al., 2000).

The correlation between extraversion and amygdala activation to positive emotional stimuli is consistent with a PET study that reported a significant correlation between extraversion and regional cerebral blood flow in the amygdala at rest (Johnson et al., 1999). Johnson and colleagues reported this correlation for the left hemisphere, whereas the current study noted a significant correlation for the right. This may be due to a gender difference, because Johnson et al. used both male and female participants(10 male, 8 female), whereas our study used female participants only.

The correlation between extraversion and amygdala reactivity to positive stimuli may explain some inconsistencies in the literature on the role of the amygdala in emotional processing. Whereas there is consensus that the amygdala plays a significant role in emotional memory (Adolphs et al., 1997; Bechara et al., 1995; Cahill et al., 1995, 1996; Cahill & McGaugh, 1998; Canli & Brown, 1996; Canli et al., 1999; Chapman et al., 1990; Davis, 1992; Davis et al., 1994; Gallagher & Holland, 1992; Hamann, Ely, Grafton, & Kilts, 1999; Kapp et al., 1992; LaBar, LeDoux, Spencer, & Phelps, 1995; LeDoux, 1993, 1995; Muller, Corodimas, Fridel, & LeDoux, 1997; Rogan, Staubli, & LeDoux, 1997; Weisz et al., 1992; Whalen & Kapp, 1991; Zola-Morgan et al., 1991) and in the processing of emotional facial expressions (Adolphs, Tranel, Damasio, & Damasio, 1994, 1995; Breiter et al., 1996; Calder et al., 1996; Morris et al., 1996; Phillips et al., 1997; Whalen et al., 1998), there is also considerable variability in amygdala activation across a number of different studies and paradigms. For instance, emotional face recognition in patients (other than Urbach-Wiethe patients) with bilateral amygdala damage was reported to be impaired in some studies (Calder et al., 1996; Scott et al., 1997) but not in others (Hamann et al., 1996). Imaging studies of amygdala responses to fearful faces reported bilateral (Whalen et al., 1998) or unilateral activation patterns (Breiter et al., 1996; Morris et al., 1996) or a lateralization pattern that depends on stimulus intensity (Phillips et al., 1997). Happy facial expressions were found to activate the amygdala in one study (Breiter et al., 1996) but not in two others (Morris et al., 1996; Whalen et al., 1998). Negative visual stimuli activated the amygdala in some imaging studies (Irwin et al., 1996; Lane, Reiman, Ahern, et al., 1997) but not in others (Cahill et al., 1996; Canli et al., 1998; Fischer et al., 1996).

There is also considerable variability in amygdala activation with respect to the experience of emotions. For instance, imaging studies have reported amygdala activation during the experience of intense emotions such as euphoria, fear, and posttraumatic stress

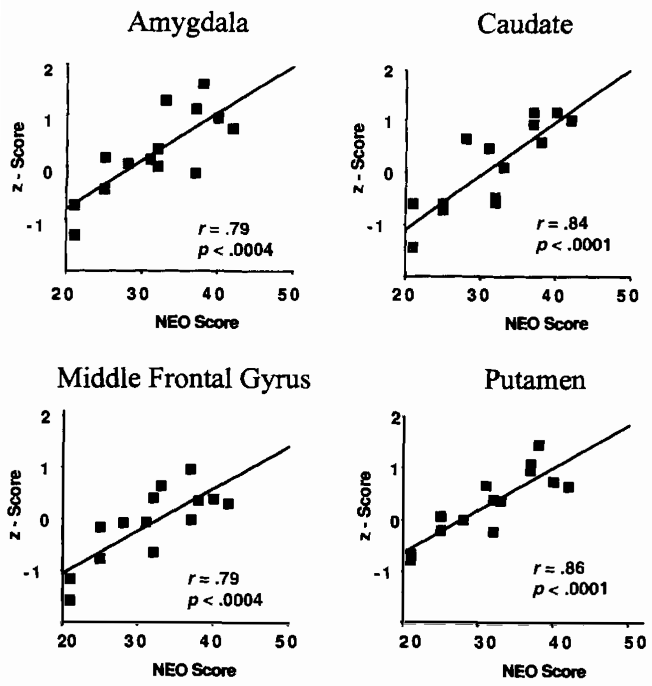

Figure 2. Correlations between extraversion and brain activation to positive pictures. Shown are scatter plots from four clusters where brain reactivity to positive pictures correlated with extraversion. The regions depicted in these scatter plots are amygdala (Slice −1 in Figure 1 [top row]), caudate (Slice +5 in Figure 1), putamen (not shown in Figure 1), and middle frontal gyrus (Slice +14 in Figure 1). Positive correlations signify greater reactivity to positive pictures (represented by positive *z* scores) with higher extraversion scores.

(Ketter et al., 1996; Rauch et al., 1996), but not phobia (Fredrikson, Wik, Annas, Ericson, & Stone-Elander, 1995; Rauch et al., 1995). Electrical stimulation of the amygdala induces negative emotions, including fear, in humans (Halgren, 1992) and may thus be sufficient to trigger emotional states. However, the amygdala may not be necessary for the experience of emotion, because patients with bilateral amygdala damage report emotional responses to negative emotional material (Adolphs et al., 1997), rate the experienced valence and arousal of emotional pictures similar to controls (Hamann, Cahill, & Squire, 1997; Hamann, Cahill, McGaugh, & Squire, 1997), and report experiencing happiness or sadness (Young et al., 1995; Young, Hellawell, Van de Wal, & Johnson, 1996).

The present findings raise the possibility that at least some of these inconsistencies may be due to variation in participants' extraversion. For instance, null results in amygdala activation to negative emotional stimuli (Cahill et al., 1996; Fischer et al., 1996) may be due to the presence of highly extraverted participants in the sample, who may respond more strongly to positive than negative stimuli, relative to less extraverted participants. Individual differences in the effects of procaine, which may produce intense fear or euphoria (Ketter et al., 1996), may also be personality dependent. Participants high in extraversion (but not neuroticism) may be more likely to react to procaine with euphoria, and participants high in neuroticism (but not extraversion) may be more likely to react with fear. Null results in amygdala activation to facial expressions of happiness (Morris et al., 1996; Whalen et al., 1998) may be due to the absence of highly extraverted participants in the sample, because amygdala reactivity to positive stimuli, including happy faces, may only be observed in highly extraverted participants. These explanations do not invalidate or exclude other explanations that have been put forth to account for experimental discrepancies. For example, differences in amygdala responsiveness to happy faces may be explained by careful anatomical considerations, as made by Whalen et al. (1998). They found that voxels in the amygdaloid region showed decreased activation to happy faces in the amygdala proper (similar to Morris et al., 1996) but increased activation in the amygdala–sublenticular substantia innominata region (similar to Breiter et al., 1996). It should also be noted that these studies (Breiter et al., 1996; Morris et al., 1996; Whalen et al., 1998) used mostly male participants, whereas the present study used only female participants. It is currently unknown whether the correlations observed in our sample will generalize to male participants.

This study provides evidence that the processing of emotional stimuli in the caudate nucleus is associated with personality. This finding can explain why previous work found caudate activation to pleasant pictures only in contrast to neutral, but not negative,

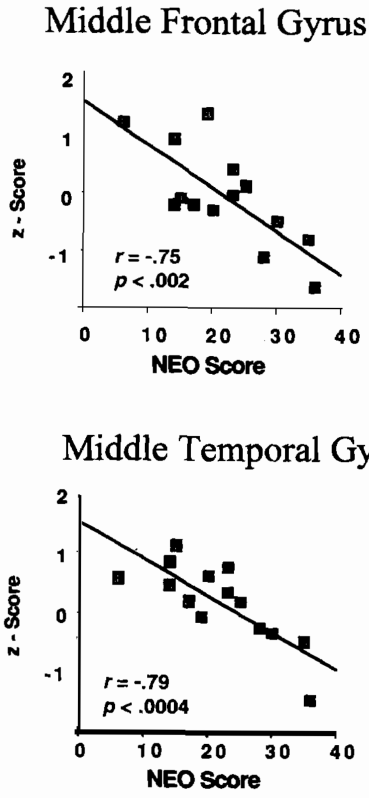

Figure 3. Correlations between neuroticism and brain activation to negative pictures. Shown are scatter plots from two clusters where brain reactivity to negative pictures correlated with neuroticism. The regions depicted in these scatter plots are middle frontal and middle temporal gyrus (Slices +5 and −4 in Figure 1 [bottom row], respectively). Negative correlations signify greater reactivity to negative pictures (represented by negative *z* scores) with higher neuroticism scores.

control conditions (Lane, Reiman, Bradley, et al., 1997). Our data show that for different individuals, the caudate may respond more strongly to either negative or positive stimuli and that the variable that correlates with caudate activation to positive stimuli is the degree of extraversion. In the absence of participant selection for extraversion, there would be no consistent caudate reactivity to positive, relative to negative, emotional stimuli.

The strength of correlations between neural activation and personality dimensions was strong, especially compared with behavioral data one might encounter in other studies of personality and emotion. It is not yet clear why the fMRI correlations were so strong, but one possibility is that behavioral data represent the sum of activation in all brain systems whereas our study focused on brain activation in individual brain structures. The signal derived from individual brain structures that show a strong correlation between activation and a personality trait may well be obscured at the behavioral level by the totality of all other active brain systems that govern emotional behavior. One would therefore expect that correlations between behavior and individual brain structures would be much stronger than between two behavioral measures, each of which represent the complex interactions of processes mediated by a number of brain structures.

The present study enhances knowledge about the neuropsychological interaction between personality and emotion in two major ways. First, the use of an emotion-relevant task reveals personality influences on emotional responsiveness. Prior imaging studies of personality-dependent blood flow patterns were performed at rest or during tasks unrelated to emotion (Ebmeier et al., 1994; Haier et al., 1987; Johnson et al., 1999; Stenberg et al., 1990, 1993; Sugiura et al., 2000). Second, fMRI, due to its superior spatial resolution, provides a more precise localization of where personality interacts with emotion. Some earlier studies, for example, used methods that were unable to differentiate cortical from subcortical activity (Stenberg et al., 1990, 1993). In contrast, we identified several subcortical areas of interest, most notably the amygdala, caudate, and putamen, where extraversion correlated with an increase in activation to positive (relative to negative) pictures. This is the first demonstration that the processing of emotional stimuli in subcortical regions, such as amygdala, may be moderated by a specific personality trait. Future work will further take advantage of fMRI by developing event-related designs to reveal interactions between personality and trial-specific task performance.

The data presented here lead to a conceptualization of brain reactivity to emotional stimuli in terms of individual differences. Our study clearly shows that some structures, such as the amygdala, exhibit considerable variance in their responsiveness to one or the other valence across participants and that this variance is related to individual differences in extraversion or neuroticism. Thus, it is the degree of extraversion or neuroticism that is associated with whether a specific brain structure will exhibit relatively greater reactivity to positive or negative stimuli, respectively. Although we interpret the data to represent a linear relationship between personality scores and brain reactivity, other interpretations that assume more complex relationships between personality and brain reactivity cannot be excluded. Future studies will need to test larger numbers of participants across the spectrum of personality scores (low, medium, high) to determine whether the relationship between personality and brain reactivity is linear.

The data presented in this study are limited to women. It is possible that men may show different activation patterns. Indeed, previous PET imaging studies reported gender differences even at rest (Gur et al., 1995) and differential activation patterns in some emotion-related tasks (George et al., 1996; Pardo, Pardo, & Raichle, 1993). It remains to be determined whether males show similar patterns of brain reactivity as women in response to emotional stimuli as a function of extraversion or neuroticism.

The lack of a neutral baseline condition complicates the interpretation of the data somewhat, because an increase in activation to negative stimuli is equivalent to a decrease in activation to positive stimuli. If a particular structure is believed to react to negative stimuli with increased activation, but not to positive stimuli with decreased activation, then this structure should also show more activity in a contrast between the negative versus neutral, but not the positive versus neutral, condition. Our interpretation of the data presented here is that positive emotional stimuli are associated with increased activation in particular brain regions in extraverted participants. In the absence of a neutral comparison, an alternative interpretation is that extraversion is related to decreased neural processing for negative stimuli. This alternative interpretation is not parsimonious because it has been shown that extraversion is positively correlated with positive emotional reactivity and is not negatively correlated with negative emotional reactivity (Gross & John, 1995). However, the inclusion of a neutral baseline condition in future studies would allow for the testing of such alternative explanations more directly.

Another issue that will need to be resolved is whether the observed correlations between brain reactivity to emotional stimuli and personality dimensions were driven by valence, emotional arousal, or a combination of both. This is because negative pictures are typically more arousing than positive pictures. Regions that are sensitive to either arousal or valence could both show similar correlations with extraversion or neuroticism. The findings reported in this study for the amygdala, putamen and caudate, and inferior temporal gyrus (i.e., reactivity to positive stimuli correlated significantly with extraversion) held up with a subset of participants ($n = 7$) who experienced the two emotion conditions as different in valence but not in arousal (data not shown). This suggests that the correlations between personality scores and brain reactivity in these structures were driven primarily by valence, not arousal. However, the small number of participants makes it inappropriate to make that determination with certainty. Future work needs to collect data from a larger number of participants for which valence and arousal are systematically manipulated to ascertain which structures are reactive to which dimension of emotional experience.

There were many more locations where brain reactivity to emotional stimuli correlated with extraversion than with neuroticism. One possible reason for this is that the strong valence characteristics of the negative stimuli left less opportunity for individual variability (the standard deviation is almost 50% less for negative than for positive valence ratings). A stimulus set that had a wider range of valence characteristics may have been more effective in identifying locations where reactivity to negative pictures correlates with neuroticism. Future work will need to test this hypothesis with a larger, more varied set of emotional stimuli.

We conceptualize individual differences in brain reactivity to emotional stimuli in terms of "processing biases" that represent the neural signature of extraversion or neuroticism. The brain of a highly extraverted person may be more biased to respond to positive, relative to negative, stimuli in specific frontal and temporal cortical regions, as well as specific subcortical loci such as the amygdala. The brain of a highly neurotic person may be more biased to respond to negative, relative to positive, stimuli in left frontal and temporal cortical regions. This processing bias may be based on prior experience and/or genetic determinants. Evidence for genetic influences on personality comes from studies that reported genetic contributions to extraversion or novelty seeking (Benjamin et al., 1996; Ebstein et al., 1996) and neuroticism (Lesch et al., 1996). One challenge for future studies will be to elucidate the path by which genetic contributions to personality manifest themselves in brain activation patterns to emotional stimuli.

Influential conceptualizations of brain reactivity to emotional stimuli have been put forth by Gray, Eysenck, and Davidson. Gray's (1987) model conceptualizes two motivational systems that regulate aversive and appetitive motivation, referred to as the *behavioral inhibition system* (BIS) and the *behavioral approach system* (BAS), respectively. The BIS is sensitive to punishment and nonreward, whereas the BAS is sensitive to reward and escape from punishment. Because Gray's model is organized around the concepts of reward seeking and punishment avoidance, and because it grew out of the pharmacological animal literature, it does not relate directly to our investigation of brain reactivity to emotional stimuli.

Eysenck's work (1967, 1990; Eysenck & Eysenck, 1985) focused on the personality domains of extraversion and neuroticism (and a third domain, psychoticism). He related extraversion to arousal and neuroticism to strong emotional states. Thus, his model predicts a relationship between emotion and neuroticism but not between emotion and extraversion (Matthews & Gilliland, 1999). In contrast, our data show that both extraversion and neuroticism (the former more prominently than the latter) correlate with emotional brain reactivity and support the view that emotion processing may represent a domain of human behavior moderated by personality.

Davidson's (1995) model is focused on approach and withdrawal, and it postulates that the anterior left and right hemispheres are lateralized for approach-related (positive) and withdrawal-related (negative) processes, respectively. Our data are consistent with Davidson's model in the case of brain reactivity to positive stimuli: We found more clusters in the left than the right hemisphere where extraversion correlates with reactivity to positive stimuli. Our data are inconsistent with Davidson's model for negative stimuli: Clusters where neuroticism correlates with reactivity to negative stimuli were not lateralized toward the right hemisphere. This lack of evidence for lateralized processing may be due to the relatively small number of observable clusters (see above), individual differences in the experience of emotional arousal (Canli et al., 1998), or other factors such as experimental design or methodology (Canli, 1999).

The fact that personality is a significant factor in brain reactivity to emotional stimuli highlights the importance of individual differences in the study of the biological basis of emotion. Other imaging studies (Cahill et al., 1996; Hamann et al., 1999; Kosslyn, Thompson, Kim, Rauch, & Alpert, 1996; Nyberg, McIntosh, Houle, Nilsson, & Tulving, 1996) have also relied on correlational analyses to illustrate the role of individual differences in emotion, memory, and visuospatial processing. This shift from grouped to single-participant data underscores the power of brain imaging technology to visualize not only brain functions that are common across people but also brain functions that are at the root of individuality.

The present findings suggest a neural mechanism for the relations between extraversion and positive emotions and between neuroticism and negative emotions in everyday life that have been found by many researchers (Costa & McCrae, 1980, 1991; Eysenck, 1990; Gross et al., 1998; John, 1990; Meyer & Shack, 1989). Participants in our study had the identical objective experience of seeing alternating sets of positive and negative pictures. However, the different brain activation patterns that these pictures produce across individuals may result in two different subjective interpretations of the identical objective experience—an emotionally positive interpretation biased by brain responses to the positive elements of experience and an emotionally negative interpretation biased by brain responses to the negative elements of experience.

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Received February 17, 2000
Revision received July 11, 2000
Accepted July 31, 2000 ■

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