

Neuroanatomical Correlates of Externally and Internally Generated Human Emotion

Eric M. Reiman, M.D., Richard D. Lane, M.D., Geoffrey L. Ahern, M.D., Ph.D., Gary E. Schwartz, Ph.D., Richard J. Davidson, Ph.D., Karl J. Friston, M.B.B.S., Lang-Sheng Yun, Ph.D., and Kewei Chen, Ph.D.

Objective: Positron emission tomography was used to investigate the neural substrates of normal human emotion and their dependence on the type of emotional stimulus. **Method:** Twelve healthy female subjects underwent 12 measurements of regional brain activity following the intravenous bolus administration of [^{15}O]H $_2\text{O}$ as they alternated between emotion-generating and control film and recall tasks. Automated image analysis techniques were used to characterize and compare the increases in regional brain activity associated with the emotional response to complex visual (film) and cognitive (recall) stimuli. **Results:** Film- and recall-generated emotion were each associated with significantly increased activity in the vicinity of the medial prefrontal cortex and thalamus, suggesting that these regions participate in aspects of emotion that do not depend on the nature of the emotional stimulus. Film-generated emotion was associated with significantly greater increases in activity bilaterally in the occipitotemporoparietal cortex, lateral cerebellum, hypothalamus, and a region that includes the anterior temporal cortex, amygdala, and hippocampal formation, suggesting that these regions participate in the emotional response to certain exteroceptive sensory stimuli. Recall-generated sadness was associated with significantly greater increases in activity in the vicinity of the anterior insular cortex, suggesting that this region participates in the emotional response to potentially distressing cognitive or interoceptive sensory stimuli. **Conclusions:** While this study should be considered preliminary, it identified brain regions that participate in externally and internally generated human emotion.

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While studies of laboratory animals have begun to characterize the brain regions and pathways that participate in dissectable components of fear (1), studies of human subjects are required for determining how they

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are related to the full range of emotions, experiential aspects of emotion, and the emotional response to different kinds of emotional stimuli (e.g., thoughts and memories). In this study we used positron emission tomography (PET) measurements of regional brain activity (2) to investigate the neuroanatomical correlates of internally and externally generated human emotion independent of emotional type or valence. In a separate report in this issue (3), we consider the neuroanatomical correlates of happiness, sadness, and disgust.

Several laboratories have used PET measurements of regional brain activity to investigate the neural substrates of normal human emotion. In the earliest study of an experimentally induced normal human emotion (4), anticipatory anxiety was associated with increased activity in the vicinity of the temporal poles. However, these findings could be partly attributable to the combined effects of increased blood flow in temporalis muscles, partial-volume averaging, and a thresholding procedure used to exclude data outside the brain (5, 6). In a study that controlled for these potential confounding factors and included a larger number of subjects (6), anticipatory anxiety was associated with increased ac-

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activity in anterior insular, anterior temporal, temporo-parietal, and lateral prefrontal regions, the caudate, thalamus, cerebellar vermis, midbrain, and a region that includes the anterior cingulate and medial prefrontal cortex. In a study that did not use an emotionally "neutral" task to control for recall memory and subvocalization (7), recall-generated sadness was associated with increased activity in the vicinity of the orbitofrontal cortex. In a study that used a complex emotion-generating task (i.e., recalling emotionally relevant situations while looking at emotionally congruent facial expressions) (8), sadness was associated with increased activity in anterior insular, medial prefrontal, and anterior cingulate regions and the thalamus, cerebellar vermis, and striatum. Additional studies are needed to investigate the neural substrates of emotion, how they are related to emotional type (3) and valence (9), and how they are related to different kinds of emotional stimuli, including simple and complex exteroceptive sensory stimuli, interoceptive sensory stimuli, and cognitive stimuli.

This study used PET to investigate the neural substrates of normal human emotion and their relation to the type of emotional stimulus. It was designed to generate intense target emotions (in this case, happiness, sadness, and disgust) in the laboratory setting, to control for potentially confounding features of the emotion-generating tasks (e.g., visual stimulation and recall memory), to obtain subjective and objective measurements of emotion, and to characterize and compare the increases in regional brain activity associated with the emotional response to complex visual (silent film) and cognitive (recall) stimuli.

METHOD

A screening procedure was used to identify 12 right-handed, neurologically and psychiatrically well, unmedicated female volunteers who were likely to have intense emotional responses in the PET laboratory. The study group was restricted to female subjects to maximize the homogeneity of emotion-dependent changes in regional brain activity and to increase the likelihood of intense self-reported emotional experiences (10). An advertisement was used to recruit female volunteers between the ages of 18 and 30 years who were "able to accurately describe [their] emotional reactions to daily events." Prospective subjects were initially screened with psychiatric and medical histories, the Structured Clinical Interview for DSM-III-R—Non-Patient Edition (11), the Edinburgh Handedness Inventory (12), and a neurological examination. They were included in the PET study if they reported separate experiences of happiness, sadness, and disgust during the previous 6 months; rated each of these experiences at least 6 on a 0–8 visual analog scale (in which 8 represented the most intense experience of the particular emotion in their lives); and rated each of an alternate screening set of three films targeting happiness, sadness, and disgust, respectively, at least 5 on an 8-point scale. The subjects provided written informed consent after the procedures had been fully explained, received compensation for their participation in the study, and were studied in accordance with institutional guidelines. One subject withdrew from the PET study before its completion because of back discomfort; her data are not included in this report. The 12 subjects who completed the PET protocol had a mean age of 23.3 years (SD=3.2), above average scores on the Vividness of Visual Imagery Questionnaire (13), a measure of imagery ability, and average scores compared with those of women of the same age on the

Affect Intensity Measure (14), an estimate of the tendency to experience emotions intensely.

Experimental Design

During the PET session, three empirically validated film clips from a silent color feature film (15) were used for the external generation of three subjectively, facially, and electrophysiologically well-characterized target emotions: happiness, sadness, and disgust. Three additional emotionally "neutral" film clips from a silent nature film were used to control for potentially confounding features of the emotion-generating film task, such as emotionally irrelevant visual stimulation and eye movement. Each emotion-generating and control film clip was approximately 2 minutes long, began before the radiotracer was administered, and continued throughout each PET scan. The 1-minute segment of each emotion-generating film clip that had been found to elicit the most intense emotional responses in the investigators was synchronized to the 1-minute scan.

During the PET session, autobiographical scripts of three recent experiences were used for the internal generation of the same three target emotions. These scripts were used to identify a time within the past 6 months in which the target emotion was experienced intensely and other emotions were experienced much less intensely. Three additional emotionally "neutral" autobiographical scripts of recent experiences were used to control for potentially confounding features of the emotion-generating recall task, such as emotionally irrelevant visual imagery, recall memory, and the recency of the recalled situation.

Immediately before each PET scan, subjects listened to a brief synopsis of a film clip or autobiographical script. For the emotion-generating tasks, subjects were asked to feel the relevant target emotion; for the control film and recall tasks, subjects were asked to feel emotionally "neutral." During each PET scan, subjects watched a film with their eyes fixed on the center of a ceiling-mounted 27-inch television monitor or contemplated the situation recalled in the previous reading of the autobiographical script with their eyes closed and directed forward. Immediately following each scan, subjects rated their experience of seven emotions (interest, amusement, happiness, sadness, fear, disgust, anger) on separate 0–8 visual analog scales.

To address potential order effects, the six film tasks and six recall tasks were performed in counterbalanced blocks; within each block, emotion-generating and control tasks were performed in alternating order and counterbalanced for which came first; within these constraints, the film clips and autobiographical scripts were presented in random order.

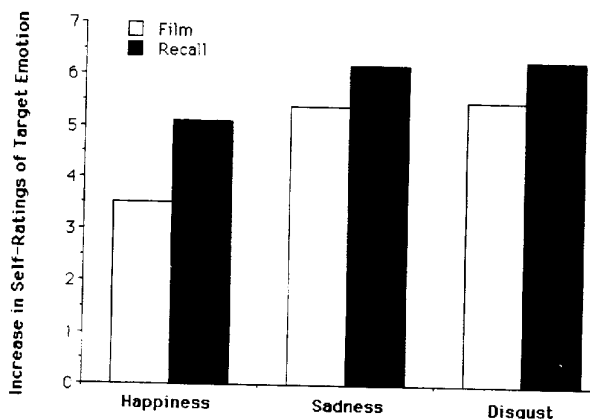
Imaging Procedures

Before the PET session, magnetic resonance imaging (MRI) was performed with a 1.5-T Signa system (General Electric, Milwaukee). T₁-weighted sagittal and coronal images of the brain were used to minimize tilt and optimize axial sampling in the PET scanner. A T₁-weighted, three-dimensional, volume spoiled-gradient recalled acquisition in the steady-state pulse sequence was used (TE=5 msec, TR=33 msec, angle=30°, number of excitations=1, field of view=24 cm, imaging matrix=256×192) to acquire 128 contiguous, 1.5-mm-thick horizontal slices of the brain to rule out gross anatomical abnormalities and facilitate comparisons between brain function and structure as described below.

Preparation of the subjects for psychophysiological measurements during the PET session included the placement of leads on the head, forearms, left leg, and fingers to record quantitative EEG, electro-oculographic, ECG, pulse wave, and electrodermal activity; placement of tonometers on the wrists for noninvasive blood pressure monitoring and a blood pressure cuff on the right arm for tonometer calibration; and placement of a hidden video camera in the ceiling-mounted television monitor to record facial expressions. (The quality of facial records was found to be unsatisfactory for blind ratings of facial expression with use of the Facial Action Coding System [16]; the other psychophysiological correlates of emotion will be described in a separate report.)

Preparation of the subjects for PET included the insertion of a

FIGURE 1. Increase in Subjective Ratings of Happiness, Sadness, and Disgust During Film and Recall Tasks^a



^aEach increase reflects the mean difference between ratings of the target emotion during the emotion-generating task and the average rating of the target emotion during the three control tasks on a 0-8 visual analog scale. There were significant increases in subjective ratings of each target emotion during the film and recall tasks.

TABLE 1. Significant Increases in Regional Brain Activity During Film-Generated Emotion^a

Region	Brodmann's Area	Atlas Coordinate			z Score	Mean Change in Activity (%)
		x	y	z		
Medial prefrontal cortex	9	0	+50	+28	2.93	1.4
		-6	-14	0	3.11	1.9
Thalamus		+10	-18	0	2.54	1.9
		-46	-52	+12	5.12	2.8
Occipitotemporoparietal cortex	19, 21, 22, 37, 39	+48	-42	+8	5.67	4.3
		-34	+4	-16	5.40	3.0
Anterior temporal cortex ^b	21, 28, 38	+42	+10	-20	7.06	6.1
		-24	-4	-12	4.18	1.8
Amygdala ^b		+16	-4	-12	4.06	1.8
Hypothalamus		0	-6	-12	4.03	2.4
Midbrain		+2	-20	-4	3.15	1.9
Lateral cerebellum		-38	-66	-16	3.51	3.1
		+34	-52	-20	4.14	3.4

^aThe locations of maximal z scores were defined according to the brain atlas of Talairach and Tournoux (19), such that x is the distance in millimeters to the right (+) or left (-) of the midline, y is the distance in millimeters anterior (+) or posterior (-) to the anterior commissure, and z is the distance in millimeters superior (+) or inferior (-) to a horizontal plane through the anterior and posterior commissures.

^bIncreases in activity in the anterior temporal cortex and amygdala could not be distinguished because of limitations in spatial resolution and the anatomical localization method used in this study.

catheter in the left antecubital vein to permit tracer administration; use of a head rest, foam, and tape to immobilize the head (since a fast-hardening foam mold would not permit quantitative EEG); and the performance of a transmission scan in which a germanium-68/gallium-68 ring source was used to correct subsequent emission images for radiation attenuation. During each scan, the subject rested quietly in the supine position without movement.

Twelve 31-slice PET images of regional brain activity (counts per pixel per minute) were obtained from each subject as she alternated between emotion-generating and control tasks. We used an ECAT 951/31 scanner (Siemens, Knoxville, Tenn.), 40-mCi intravenous bolus injections of [¹⁵O]H₂O, 60-second scans, and an interval of 10-15 minutes between scans. The radiotracer was administered at predetermined times shortly after the film and recall tasks began. PET im-

ages were reconstructed with an in-plane resolution of about 10 mm full width at half maximum and a slice thickness of 5 mm full width at half maximum. For data analysis, a Gaussian filter yielded an in-plane resolution of about 20 mm full width at half maximum and a slice thickness of about 10 mm full width at half maximum.

Image Analysis

Automated algorithms were used to align each subject's sequential PET images (17), to transform her PET images into the spatial coordinates of a standard brain atlas (18, 19), to investigate increases in regional brain activity independent of variations in whole brain measurements with the use of analysis of covariance (20), and to generate normalized t value (i.e., z score) maps of 1) increases in regional brain activity during externally generated emotion (i.e., an average of the three images acquired during the emotion-generating film tasks minus an average of the three images acquired during the control film tasks), 2) increases in regional brain activity during internally generated emotion (i.e., an average of the three images acquired during the emotion-generating recall tasks minus an average of the three images acquired during the control recall tasks), and 3) differences between the increases in regional brain activity during externally generated and internally generated emotion (18). To reduce type I errors, we used a critical z score of 2.58 (p<0.005, uncorrected for multiple comparisons) to characterize significant increases in regional brain activity. A critical z score of 1.65 (p<0.05, uncorrected for multiple comparisons) was used post hoc if the region was implicated in the independent comparison or the opposite

hemisphere. Automated algorithms were used to transform each subject's brain MRI into standard atlas coordinates (21), to compute an average of the 12 subjects' MRIs (21), and to superimpose each z score map onto the averaged MRI to permit visual inspection of the composite images.

A procedure developed and tested in our laboratory was used post hoc to address the combined effects of facial muscle activity and partial-volume averaging on measurements in anterior temporal and inferolateral prefrontal regions (6). Data from an independent study of jaw clenching in 14 subjects were used to identify these regions and exclude them from the statistical maps generated in this study; any remaining increases in activity were considered to arise in the brain. Another procedure developed and tested in our laboratory was used post hoc to address the combined effects of residual activity in ascending arteries (e.g., the internal carotid arteries) and partial-volume averaging on measurements in the anteromedial temporal lobes (22). For each subject, algorithms were used to coregister high-resolution PET and MRI images, to negate differences in activity in ascending arteries and other structures outside the brain, and to apply a Gaussian filter to blur the PET images to an in-plane resolution of 20 mm full width at half maximum.

RESULTS

In comparison with the average of the three control tasks, there were significant increases in ratings of the target emotion during each emotion-generating film task (repeated measures analysis of variance, F=226, df=1, 11, p<0.001) and each recall task (F=1041, df=1, 11, p<0.001) (figure 1) and minimal increases in nontarget emotions (3). In comparison with the film tasks, the recall tasks were associated with slightly greater increases in ratings of the target emotion (F=9.68, df=1, 11, p<0.01) (figure 1).

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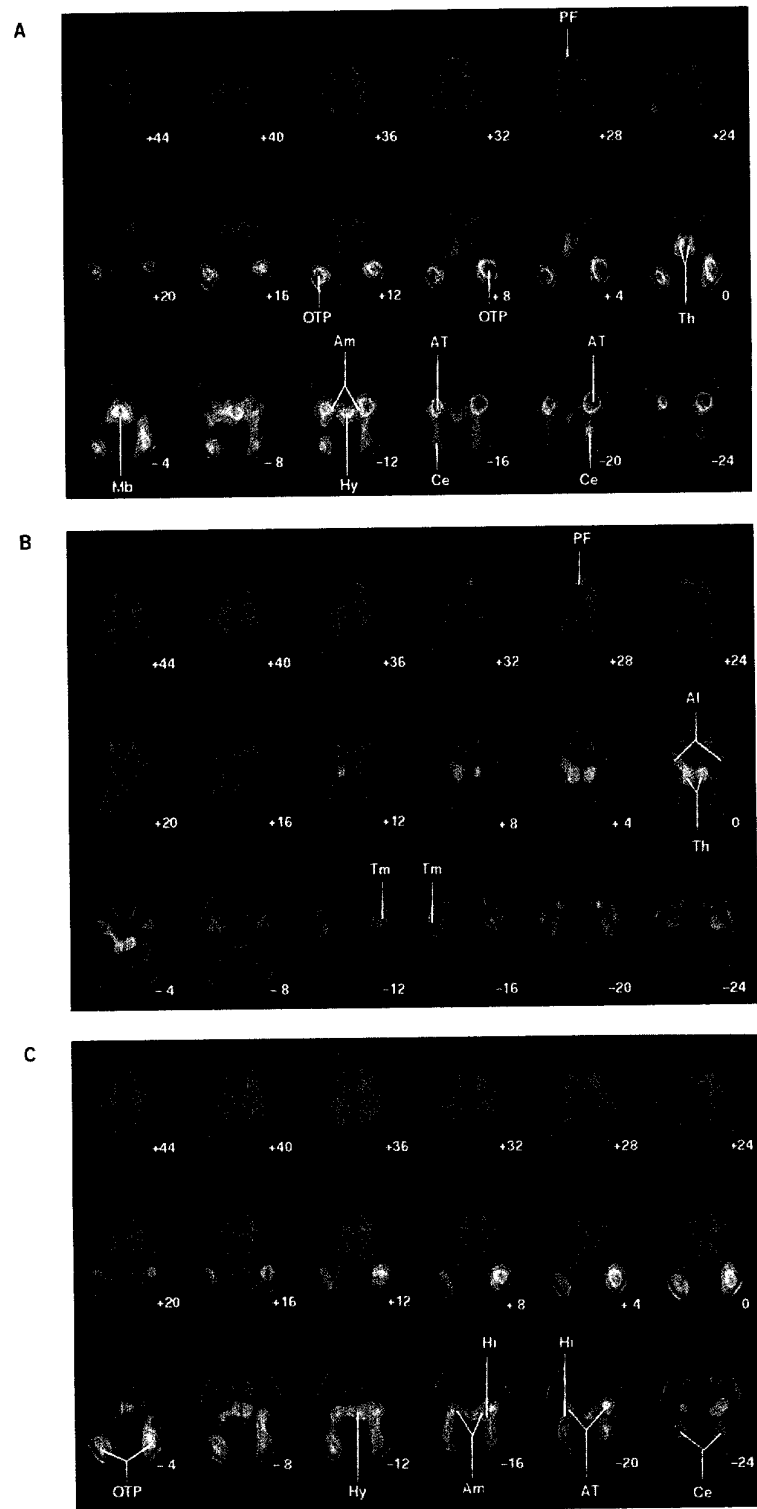
Film-generated emotion was associated with significant, symmetrical increases in brain activity in the medial prefrontal cortex, thalamus, occipitotemporoparietal cortex, lateral cerebellum, hypothalamus, midbrain, and a region that includes the anterior temporal cortex and amygdala (table 1; figure 2, part A). These increases were unrelated to the potentially confounding effects of ascending artery or temporalis muscle activity.

Like film-generated emotion, recall-generated emotion was associated with significantly increased activity in the thalamus and medial prefrontal cortex (table 2; figure 2, part B). Recall-generated emotion was also associated with significantly increased brain activity in the vicinity of the anterior insular cortex and the orbitofrontal and anterior temporal cortex (table 2; figure 2 part B). The increases in brain activity in the vicinity of the anterior insular cortex could reflect increases in the anterior insular cortex, claustrum, or lateral putamen. The increases in orbitofrontal and anterior temporal regions during recall-generated emotion appear to be related to the combined effect of increased blood flow in temporalis muscles and partial-volume averaging.

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^aAfter color-coded z score maps were computed, they were superimposed onto an average of the subjects' brain MRIs. Brain sections in each image correspond to the coordinates of a brain atlas (19); the number next to each section reflects the distance in millimeters superior (+) or inferior (-) to a horizontal plane between the anterior and posterior commissures; the right hemisphere in each section is on the reader's right. The images in parts A, B, and C, correspond to the data in tables 1, 2, and 3, respectively. As indicated in part A, film-generated emotion was associated with significant, symmetrical increases in activity in the vicinity of the medial prefrontal cortex (PF), thalamus (Th), occipitotemporoparietal cortex (OTP), lateral cerebellum (Ce), hypothalamus (Hy), midbrain (Mb), and a region that includes the anterior temporal cortex (AT) and the amygdala (Am). As indicated in part B, recall-generated emotion was associated with significant, symmetrical increases in activity in the vicinity of the medial prefrontal cortex (PF), thalamus (Th), anterior insular cortex (AI), and temporalis muscles (Tm). As indicated in part C, film-generated emotion was distinguished from recall-generated emotion by significantly greater, symmetrical increases in activity in the vicinity of the occipitotemporoparietal cortex (OTP), lateral cerebellum (Ce), hypothalamus (Hy), and a region that includes the anterior temporal cortex (AT), amygdala (Am), and hippocampal formation (Hi).

FIGURE 2. Images of Significant Increases in Regional Brain Activity During Film-Generated Emotion (A), of Significant Increases in Regional Brain Activity During Recall-Generated Emotion (B), and of Significantly Greater Increases in Regional Brain Activity During Film-Generated Emotion Compared With Those During Recall-Generated Emotion (C)^a



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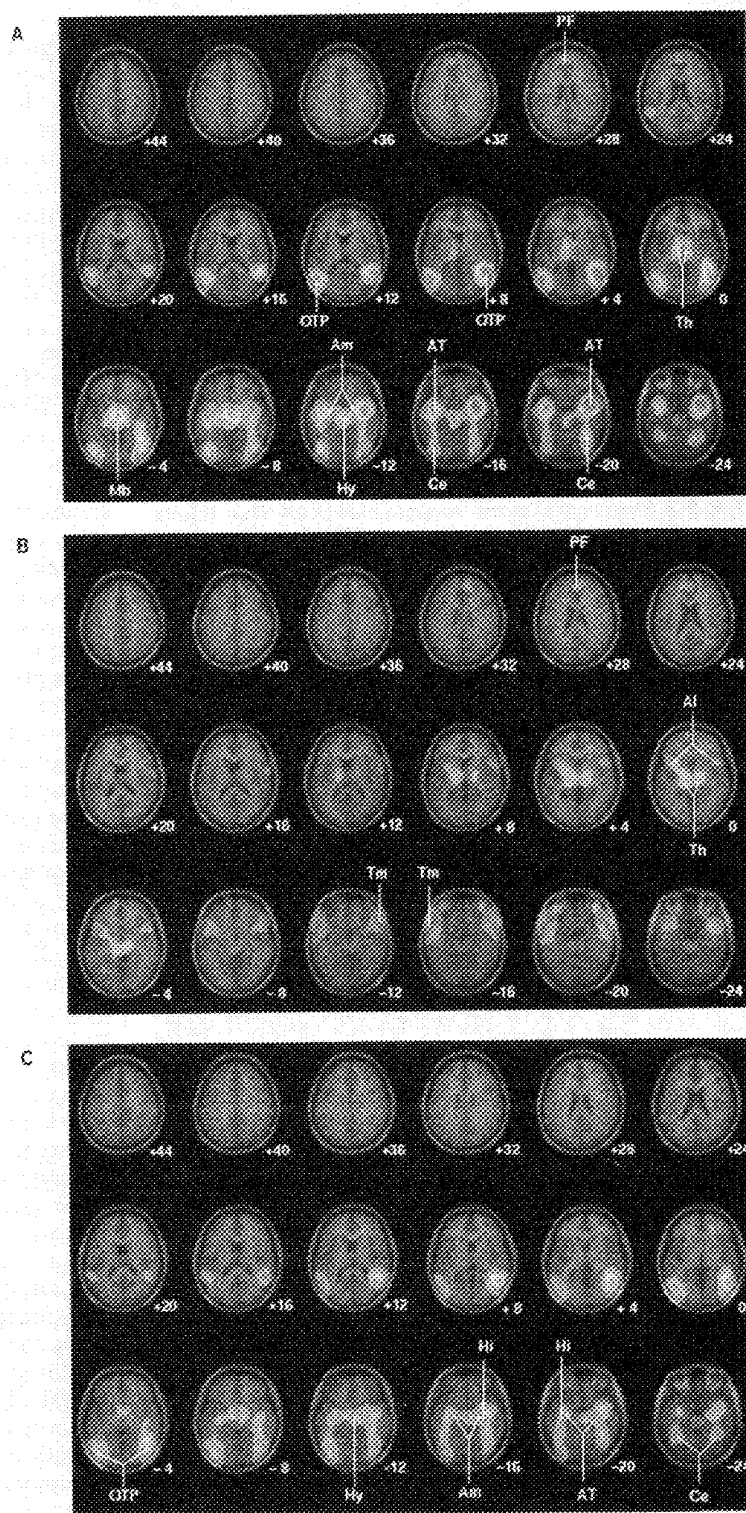
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ll-generated was significantly associated with recall-generated ($p < 0.005$, unpaired t-test).

Information correlates of their relationship. Since differences were not significant, the medial and lateral aspects of the type of stimulus-generated emotion recall were not significantly greater, especially in the left hemisphere, hypothalamic anterior cingulate formation aspects of the effect of an external subjective relationship to reflect recall-generated

involved in the monitoring of the expression of emotion. Operations making a difference between the two conditions were not identified within the prefrontal cortex. Prefrontal cortex is involved in conscious and unconscious processes. Prefrontal cortex participates in the initiation of emotion. Since the increase in the external from so-called emotion. The medial and lateral aspects of this relationship in order

limbic lobe thalamic nuclei

cus responsible for the observed increases in thalamic activity. The thalamus could participate in expressive or experiential aspects of emotion. Cannon and Bard's studies of "sham rage" suggest that the anterior thalamus participates in the integrated behavioral and autonomic expression of emotion (1). Researchers postulate that certain thalamic nuclei (e.g., intralaminar and reticular nuclei) participate in a network of structures that mediate consciousness (28). Auditory and visual relay stations in the thalamus (the medial and lateral geniculate, respectively) have been implicated in the evaluation process that invests modality-specific simple sensory stimuli with emotional significance (1). Since an increase in thalamic activity was observed in the absence of an exteroceptive sensory stimulus (i.e., during the recall-generated emotion), it does not appear to reflect this evaluative aspect of emotion.

This study supports involvement of the amygdala, hippocampal formation, and hypothalamus in the emotional response to a complex exteroceptive sensory (in this case, visual) stimulus; however, it raises the possibility that these structures are less relevant to emotions that are elicited in response to cognitive or interoceptive sensory stimuli. The amygdala, hippocampal formation, and hypothalamus have long been thought to be involved in the generation of emotion (1). The amygdala and hippocampal formation are supramodal sensory association areas that could participate in the evaluation process that invests exteroceptive sensory stimuli with emotional significance (1, 29). The hypothalamus could participate in autonomic or behavioral expressions of emotion (1).

This study, a recent study of picture-generated negative emotion (9), a recent study of picture-generated positive and negative emotion that controlled for emotional arousal (unpublished data of R.D. Lane et al.), and a study of film-generated fear (30) implicate posterior visual association areas in the emotional response to visual stimuli. While the occipitotemporo-parietal regions implicated in the present study are visual association areas that could participate in the evaluation of complex visual stimuli (31, 32) and the recognition of faces (33, 34), we postulate that modality-specific sensory association areas preferentially attend, evaluate, and prepare to respond to unpleasant or emotionally arousing sensory stimuli (9).

In this study, a region in the vicinity of the anterior insular cortex, claustrum, or lateral putamen was preferentially activated during recall-generated emotion. This increase in regional brain activity was significantly greater during recall-generated sadness than during either film-generated sadness or recall-generated happiness (3). Increased activity in the vicinity of the anterior insular cortex was also found during another study of recall-generated sadness (8) and studies of lactate-induced panic attacks (35), normal anticipatory anxiety (6), the perception of temperature and pain (36), taste (37), and the luteal phase of the menstrual cycle (38). These findings and others (39) lead us to postulate that this region is preferentially involved in the evaluative,

experiential, or expressive aspects of internally generated negative emotions. We propose that it participates in the evaluation procedure that invests potentially distressing cognitions, interoceptive sensory stimuli, or bodily sensations with emotional significance, perhaps serving to warn the individual about internal dangers.

In order to interpret PET findings, it is important to recognize limitations of this imaging technique. Limitations in the spatial resolution of our PET images, the contrast resolution of individual PET subtraction images, and the accuracy of the image deformation algorithm used to compute statistical maps make it difficult to specify the regions (e.g., specific thalamic nuclei; which structure in the vicinity of the insular cortex, claustrum, and lateral putamen; and which structures in the anterior temporal lobe) that are responsible for the observed increases in regional brain activity. Since increases in regional brain activity appear to reflect the activity of terminal neuronal fields (including those from local interneurons and afferent projections arising in other sites) (40), it is difficult to specify the neuronal projections that account for the observed increases in regional activity. Although this study provides information about the neuroanatomical correlates of emotion, lesion studies are required in order to determine whether the implicated regions are necessary or sufficient for the generation of emotion or its potentially dissectable components.

The use of a critical z score of 2.58 raises the possibility that some of the observed increases in regional brain activity could be attributable to the large number of regions compared in our statistical maps. On the basis of theoretical considerations alone, this criterion might seem too liberal, yielding an unacceptably high likelihood of statistical type I errors. However, it was chosen on the basis of a study in which we empirically evaluated the number of true signals and false signals associated with different critical values. Using the same radiotracer methods, imaging system, and brain-mapping algorithms used in this study, we analyzed PET images acquired in a separate group of normal volunteers during a well-characterized motor task and two baseline tasks to simulate true signals and false signals. We found that a critical z score of 2.58 was associated with 0-1 false signal in the entire statistical map (far fewer than one would expect considering the large number of resolution elements in the data set), that it improved the sensitivity for detecting true signals, and that it provided the best trade-off between type I and type II errors (unpublished data). Since most of the increases in regional brain activity were bilateral and the increases in midline structures have now been replicated in independent comparisons of film-generated emotion, recall-generated emotion, and picture-generated emotion (6, 9), we believe that they are unlikely to reflect statistical type I errors. Still, our results were not statistically corrected for the potential number of independent comparisons and, thus, should be considered preliminary. Additional studies are needed to replicate the observed increases in regional brain activity and

help characterize the potentially dissectable components of emotion to which they are related.

Although our direct comparison of the increases in regional brain activity during film- and recall-generated emotion indicates that certain regions are preferentially involved in the emotional response to certain exteroceptive sensory stimuli, this study cannot rule out their involvement in the emotional response to cognitive stimuli. Failure to detect significant increases in regional activity could reflect limitations in spatial resolution, statistical power, heterogeneity in the cognitive strategies used to perform the task, or a change in the pattern rather than the level of neuronal activity.

Finally, the combined effects of partial-volume averaging and either facial muscle activity or residual activity in ascending arteries can have potentially confounding effects on activity measurements in neighboring brain regions (5, 6). This study capitalized on techniques recently developed and tested in our laboratory to characterize these potential confounding factors and distinguish them from increases in activity in neighboring brain regions (6, 22).

Although the control tasks used in this study at least partially addressed the potentially confounding effects of visual stimulation and visual imagery (41), the emotionally "neutral" film clips did not control for several aspects of the visual stimulus, such as the recognition of faces (33, 34), facial emotions (34), and social interactions, and the emotionally "neutral" recall tasks did not control for the characters or setting of the recalled experiences. While this study and others (6) suggest that the observed increases in regional brain activity cannot be completely attributed to aspects of the tasks that are unrelated to emotion, additional studies are needed to consider this issue further. Additional studies are also needed to determine the extent to which modality-specific sensory association areas and anterior temporal lobe structures participate in the emotional response to other kinds of exteroceptive sensory stimuli, the extent to which anterior temporal lobe structures participate in internally generated fear (an emotion that is distinguished from the target emotions elicited in this study by consistent increases in autonomic activity [42, 43]), and the extent to which our findings can be generalized to males, different age groups, people who are not right-handed, individuals who vary in their ability to have intense emotions, and those who are not instructed to feel the target emotion.

Recently, we used PET and the International Affective Picture System (44) to investigate regions of the brain that are involved in picture-generated pleasant and unpleasant emotion (9). The study group was restricted to adult females but included a larger age range, was identified independent of the subjects' ability to have intense emotions, and received no instructions to experience emotion during the PET session. Picture-generated positive emotion and negative emotion were each distinguished from picture-generated "neutral" emotion by significantly increased activity in the same medial prefrontal and thalamic regions implicated in

the present study. In addition, picture-generated negative emotion was distinguished from both picture-generated positive emotion and neutral emotion by significantly increased activity in the occipitotemporal cortex, lateral cerebellum, and a region that includes the left amygdala, hippocampal formation, and parahippocampal gyrus.

This study demonstrates the ability to generate and measure normal human emotions in the PET laboratory. It identifies neuroanatomical correlates of internally and externally generated emotion, supports several long-held beliefs about the neural substrates of emotion, and challenges others. It underscores the importance of studying interactions between emotion and different types of emotional elicitors, including simple and complex exteroceptive sensory stimuli, interoceptive sensory stimuli, and sensory-independent cognitive stimuli. When used in conjunction with other neuroscientific methods (45), functional brain imaging techniques promise to help characterize how multiple mental operations and the spatially distributed processes that subserve them work in concert to produce normal human emotions—and how they conspire to produce emotional disorders.

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