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A Multimodal Investigation of Core Neural Responses Associated with Basic Emotion States

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A Multimodal Investigation of Core Neural Responses Associated with Basic Emotion States

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M.A., Emory University, 2007
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An abstract of
A dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
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Abstract

A Multimodal Investigation of Core Neural Responses Associated with Basic Emotion States
By Katherine E. Vytal

Although it is widely accepted that we experience basic emotion states (happiness, sadness, anger, fear, and disgust), the extent to which and level at which our minds and bodies differentiate such states is under debate. Previous research (e.g., Damasio et al., 2000; Ekman et al., 1983; Rainville et al., 2006) suggests that basic emotion states are associated with discrete patterns of neural and psychophysiological activity, yet these patterns have not been consistently demonstrated either between emotion states or across studies (Barrett & Wager, 2006). Additionally, most neuroimaging studies of emotion have explored only one or two emotions concurrently, typically using a single elicitation paradigm (e.g., viewing facial expressions or viewing emotional pictures), restricting generalizability of results and comparisons across emotion states. In an effort to determine whether or not there are discrete patterns of neural and autonomic nervous system (ANS) activity that characterize each basic emotion state, we conducted two studies: Study 1 is a meta-analysis of neuroimaging evidence in support of basic emotion states; Study 2 is a neuroimaging experiment investigating neural and psychophysiological activation patterns associated with basic emotion states. In Study 1 we used Activation Likelihood Estimation (ALE) to statistically compare results across neuroimaging studies of emotion. The results were consistent with basic emotion theory; Study 1 demonstrated that each of the emotion states was characterized by consistent neural correlates across studies. Further, these activations were discrete and overlapped substantially with established structure-function relationships in other domains. In Study 2 we used fMRI and physiological variables to explore activations associated with basic emotion states elicited by films and memories. The results of Study 2 demonstrated that basic emotions are associated with characteristic and differentiable neural correlates, and these findings converge with the results of the meta-analysis and previous research. In addition, we found that variability in these patterns was associated with elicitation method (films vs. memories) and with state and trait anxiety scores. Overall, these findings support basic emotion theory, and underscore the advantage of describing emotions on multiple levels (e.g., brain and ANS) and across different contexts in order to fully capture emotional experience.

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Chapter 1

General Introduction

1.1 Introduction

Philosophers and scientists alike have long sought to understand emotion and its role in thought and behavior. As early as 300 B.C. (Plato, The Republic), great thinkers have recorded their ideas regarding the ways in which emotions permeate our everyday life. Notwithstanding its lengthy presence in academic and empirical ventures, emotion is far from being a well-defined psychological concept. Universally accepted categories of emotion and ways in which people experience different emotions do not exist. Given the integral role of emotion in many psychological theories and clinical models, it is crucial for progress to be made toward a universally accepted definition of emotion, one that is substantiated and validated by scientific evidence. Emotions are arguably some of the most influential forces present in human interactions; they serve to motivate behavior, modify thought, and mediate action. They are also corollaries, both intentional and reflexive, to mental and physical events. Consequently, understanding emotion is central to understanding both normal and pathological functioning.

In parallel with subjective reports, theorists (e.g., Ekman, 1992) have proposed that emotions (e.g., happiness, sadness, anger, fear, and disgust) are recognized and interpreted as discrete categories. A large body of evidence from multiple domains (behavior, psychophysiology, and neuroscience) has been used to support this widely accepted claim (e.g., Ekman, 1992; Damasio, et al., 2000; Blair, Morris, Frith, Perrett, and Dolan, 1999). However, recently the evidence supporting these discrete emotion views has been challenged (e.g., Barrett and Russell, 1999). Reviews of the opposing evidence have highlighted current problems with identifying robust patterns of autonomic nervous system (ANS) and neural activity that differentiate among basic emotions,

suggesting that affective space may not be divisible into basic emotion categories (Cacioppo, Bernston, Larsen, Poehlmann, and Ito 2000; Phan, Wager, Taylor, and Liberzon, 2002). Specifically, reviews of psychophysiological evidence have concluded that it is not possible to discriminate among discrete emotion states on the basis of such measures (Barrett & Wager 2006; Cacioppo et al., 2000; Zajonc & McIntosh, 1992). Furthermore, meta-analyses of neuroimaging data (e.g., Phan et al., 2002; Murphy, Nimmo-Smith, and Lawrence, 2003) have presented mixed results in support of emotion-specific neural signatures, with some emotion states (e.g., fear uniquely and consistently activated amygdala) exhibiting more discrete patterns of neural activity than others (e.g., happiness and disgust both consistently activated basal ganglia). Critiques of these findings (e.g., Barrett et al., 2006) suggest that the neuroimaging data challenge the assumptions of the basic emotion view by failing to find reliable patterns of neural activity that can discriminate each of the basic emotions.

In addition to the equivocal support provided by meta-analytic reviews, no single neuroimaging study has examined whether there are differentiable patterns of neural and ANS activation associated with all five basic emotion states. The most analogous investigation to date, Damasio et al. (2000), used [^{15}O] positron emission tomography (PET) to examine the brain areas involved in the experience of four basic emotions: happiness, sadness, anger, and fear (excluding disgust and surprise for reasons not explicitly noted). However, their primary interest was in determining whether there were patterns of neural and ANS activity (HR, skin conductance) that indexed different internal states associated with each basic emotion (i.e., different levels of activation across somatovisceral brain regions), rather than the possibility that all 5 basic emotions

generate distinct neural signatures. As a result, they selected a series of a priori regions of interest (ROIs) to analyze their data, necessarily excluding brain regions that may play a critical role in differentiating basic emotion states. Their selected search volume identified regions that were active for all four emotion states, highlighting commonalities, rather than differences in regional activations involved in the experience of basic emotions. In addition, the use of PET (versus fMRI) limits the spatial and temporal resolution of the data (Weng, Ding & Volkow, 1999). This type of information is of particular importance in the study of spatial patterns, as is made clear by the equivocal results across previous meta-analyses of fMRI. Nevertheless, Damasio et al. found observable differences in brain activation across the basic emotion states they investigated, suggesting that there is at least some empirical grounding to the claim that people experience categorically separable basic emotion states. However, they did not statistically compare activation maps associated with each basic emotion state, so the question of differentiability can only be addressed at a qualitative, not quantitative level in their data.

In light of Damasio et al.'s (2000) findings and the results of recent meta-analyses (e.g., Murphy et al., 2003), the current investigation sought to determine whether or not robust patterns of neural and autonomic nervous system (ANS) activity characterize of each basic emotion state (happiness, sadness, anger, fear, disgust). Although surprise and contempt are typically considered basic emotion states, we did not include them in our investigation for several reasons. First, surprise can be both positively or negatively valenced, making it a less unified and potentially less stable basic emotion state. Second, in general, previous meta-analyses and studies of basic emotion have focused only on the

five basic emotion states listed above. Thus, the current investigation explored only those five states, facilitating correspondences between our findings and those of previous research. Third, the inclusion of two additional basic emotion states would have increased the number of stimuli (both subject-generated memories and experimenter-generated film clips), increasing the length of testing to an impractical level. As a consequence, we focused on determining biological patterns associated with happiness, sadness, anger, fear, and disgust. We approached this objective in two ways: first, through a quantitative meta-analysis of the current neuroimaging literature, and second, through a neuroimaging experiment that elicited basic emotion states using naturalistic stimuli.

In Study 1 we conducted a meta-analysis of neuroimaging evidence using activation likelihood estimation (ALE) (Laird et al., 2005), a technique that preserves additional spatial information present in the data over previously used methods. After compiling a large amount of data from studies published up until 2008, we analyzed the consistency and differentiability of patterns associated with basic emotion states. By taking advantage of a larger amount of data and a more sophisticated analysis technique than previous meta-analyses (e.g., Murphy et al., 2003; Phan et al., 2002) we were better equipped to detect potentially more subtle differences in activation elicited by basic emotion states. Quantitatively summarizing the support for basic emotion theory across a wide range of studies allowed us to draw more firm conclusions than we could from any single study (Kober & Wager, 2010).

In Study 2 we used functional magnetic resonance imaging (fMRI) and psychophysiological measures (i.e., heart rate [HR], electrocardiogram [ECG], respiration) to investigate how individuals respond to emotionally arousing stimuli within

two different paradigm modalities (viewing films clips and listening to autobiographical scripts). Subjects behaviorally rated each stimulus on multiple dimensions while they were in the scanner, and they completed several inventories indexing their state, trait, and five factor personality profiles. Study 2 served to clarify how our minds and bodies differentiate basic emotional states, and it explored individual differences in these patterns using personality variables. As suggested by Rainville et al. (2006), equivocal evidence in favor of differentiable basic emotion states could easily have resulted from inadequate elicitation of the emotion states and the incomplete characterization of physiological and neural patterns of activity. Consequently, this study also aimed to overcome previous ambiguities in the data by using two ecologically valid elicitation modalities and by analyzing the data using several different methods. Ultimately, this investigation provided valuable information about the parallels among neural, ANS, and behavioral responses to basic emotion states, critically informing the foundations of basic emotional and personality theory.

1.1.1 Psychophysiology of Basic Emotions

Psychophysiological and neuroscientific methods are the two primary approaches used to evaluate the differentiability of basic emotion states at the biological level. Historically, empirical support for the discrete emotion view has been evaluated using psychophysiological measures (e.g., heart rate, respiration, galvanic skin conductance (GSC), or electrocardiogram (ECG)) that reflect ANS activity. By combining these measures with multivariate computation techniques, changes in heart rate variability (HRV) can be used to accurately estimate the relative activations of the sympathetic and

parasympathetic systems (Rainville et al., 2006). Physiological variables can thus be used to characterize patterns in peripheral nervous system activity that are associated with basic emotion states.

Using psychophysiological measures, Ekman, Levenson, and Friesen (1983) were the first to demonstrate that emotions are differentiable on a biological level. Ekman et al. (1983) measured ANS activity (heart rate, skin temperature, GSC, and forearm flexor muscle tension) while subjects mimicked facial prototypes of emotion and recalled past emotional experiences that targeted six basic emotions (happiness, sadness, disgust, anger, fear, and surprise). Their results indicate that ANS activity differentiated not only between positive and negative emotions (supporting the dimensional view of emotions), but also more specifically among different negative emotions such as anger and fear (partially supporting the discrete view of emotions, and substantiating claims of autonomic specificity). Although the results did not reveal discrete ANS signatures for all basic emotions, they did indicate that certain emotions are differentiable beyond the valence and arousal dimensions.

Recent evidence from psychophysiology has replicated and extended this valuable finding to other discrete emotion states (happiness and sadness), a result of considering multiple component factors in addition to univariate analyses (Rainville, Bechara, Naqvi, & Damasio, 2006). The conclusions of a meta-analysis (Cacioppo, Bernston, Larsen, Poehlmann, & Ito, 2000) prompted Rainville et al. (2006) to measure ANS responses that would better assess the relative contributions of sympathetic and parasympathetic nervous system activity in a multivariate exploratory analysis. This analysis allowed Rainville et al. to develop a heuristic decision tree from the differentiable patterns of

cardiorespiratory activity observed while subjects experienced different basic emotions (happiness, sadness, anger, fear). By concurrently examining factors (HR, high frequency HRV, and respiratory variability) determined by a principal component analysis (PCA), Rainville et al. cleanly differentiated among emotion states. The results clearly demonstrated that, at least on the level of multivariate factors, physiological patterns could be used to differentiate certain emotion states.

Notwithstanding the evidence in favor of the discrete emotion view, evidence to the contrary has sparked debate over whether psychophysiological data can be used to differentiate among basic emotions. Meta-analyses have found that basic emotion categories cannot be consistently discriminated based solely on ANS activity (Cacioppo et al., 1997; 2000). Cacioppo et al. (1997) analyzed the results of 18 studies that used varying types of ANS measures and found some pattern reliability among emotions (e.g., anger was associated with higher diastolic blood pressure, smaller increases in cardiac output, and larger increases in peripheral resistance as compared with fear and sadness). However, the lack of overall consistency in somatovisceral patterns both within and between emotions led the authors to conclude that ANS activity alone could not differentiate among basic emotions. Cacioppo et al. stressed the fact that emotions may not reciprocally activate the sympathetic and parasympathetic branches of the ANS, and consequently, the majority of output measures (e.g., heart rate) are difficult to interpret when considered alone (because they do not differentiate between the two branches of the ANS). For example, the heart rate evoked by an aversive stimulus is a product of sympathetic and parasympathetic activation, and thus heart rate may decelerate or accelerate depending on the relative activation of each branch (Bernston, Cacioppo, &

Quigley, 1991). Additionally, different emotional elicitation paradigms tended to evoke different somatovisceral patterns for the same emotions (i.e., the results were not generalizable across stimulus type), adding unnecessary noise to the data (Zajonc & MacIntosh, 1992). Despite the fact that emotion states were not reliably differentiated, Cacioppo et al. claimed that the data appeared to differentiate between positive and negative evaluative systems, indicating physiological support for the dimensional view of emotions.

The results of a more recent meta-analysis (Cacioppo et al., 2000) paralleled those of their earlier review: although some emotion-specific somatovisceral signatures were identified, they found that most somatovisceral patterns were not unique or stable. The patterns that were identified reflected highly heterogeneous data, which suggests that unspecified moderating factors might be involved, challenging the idea of a direct relationship between discrete emotion states and ANS activity (Barrett, 2006). ANS activity is known to result from the physiological demands of activity or anticipated activity, and although some emotion states have characteristic behavioral responses associated with them, emotion states and reactive behaviors do not map directly on top of one another (Barrett, 2006). Consequently, the ANS response would be highly susceptible to paradigm differences and even qualitative differences in emotion states (e.g., happiness is less likely to elicit a specific behavior than fear), suggesting that monitoring ANS activity is perhaps not the best approach to examine the structure of affect space.

Despite the transparency of the debate, the controversy over whether or not psychophysiological evidence can and should be used to differentiate among basic

emotions is not necessarily all-or-nothing. Nyklíček, Thayer, and Van Doornen, (1997) was the first to approach ANS specificity with both the discrete and dimensional views using a hybrid model that incorporated the two views into one. In this hierarchical hybrid model, lower-order emotion categories are characterized by higher-order dimensions of arousal and valence. By conducting a multivariate pattern classification analysis on cardiorespiratory activity, Nyklíček et al. (1997) demonstrated that discrete emotions (elicited in this case by musical excerpts) represent specific locations in dimensional affective space.

Christie and Friedman (2004) also proposed a type of hybrid discrete-dimensional model to account for the inconsistencies in the psychophysiological literature and explain their own psychophysiological results (GSR, blood pressure, and ECG). Christie et al.'s (2004) multivariate approach explicitly acknowledged the co-existence of discrete and dimensional structuring of affective space, in which the type of underlying dimensional structure (valence-activation or approach-withdrawal) is dependent on the manner of assessment of the emotion state (self-reported or ANS-specific). Namely, the hybrid model is proposed to function in two ways: 1) self-reported discrete emotions are situated in an affective space that is structured by a positive-negative dimensional circumplex model, and 2) emotion-specific ANS activity is situated in an affective space that is structured by an approach-withdrawal dimensional circumplex model. By structuring the affective space based on the action associated with the emotive content, this interpretation supports Barrett's claim that ANS responses are related to behavior-oriented emotions.

Overall, psychophysiological evidence strongly suggests that at least some basic emotions are differentiable from others, particularly when multivariate analyses are used to analyze the data. The prevalence of heterogeneous data, despite significant findings, suggests that ANS specificity is partially reliant on paradigm and stimulus-type as well as the extent to which the emotion in question motivates a specific behavior. However, it is impossible to ignore the results (e.g., Rainville et al.) that demonstrate the differentiability of discrete emotions despite these caveats. Research that combines psychophysiological measures with other biological measures (e.g., PET and fMRI) can further clarify the differentiability of discrete emotions and the underlying structure of affective space.

1.1.2 Neuroimaging of Basic Emotions

The neural substrates of emotion were initially proposed to consist of general processing circuits, based on evidence from lesion studies in patients with midbrain and diencephalic damage (e.g., Bard, 1928; Papez, 1937). These relatively simplistic circuits were later expanded to a more complex network known as the limbic system (MacLean, 1952). Much like in the psychophysiological domain, recent evidence in neuroimaging suggests that distinct neural circuits involving both limbic and extra-limbic brain regions may support different emotion states. For example, studies in humans and animal models have strongly implicated the amygdala in the processing of fear (Davis, 1992). Using a classic fear-conditioning paradigm, where an unconditioned aversive stimulus like a shock is paired with a conditioned neutral stimulus such as a context, dozens of studies have demonstrated that the amygdala is critical for fear acquisition and expression.

Lesions to the amygdala have resulted in a failure to acquire a conditioned response (fear) to the conditioned stimulus (e.g., LeDoux, Iwata, Cicchetti, & Reis, 1988) and multiple cell recording has demonstrated that amygdala cell firing is modulated when the pairing of a neutral stimulus with an aversive stimulus results in the expression of fear (Applegate, Frysinger, Kapp, & Gallagher, 1982). However, studies have shown the amygdala is not exclusively involved in fear processing, and may also support positively-valenced emotion processing (Hamann et al., 1999; Breiter et al., 1996), limiting the claims that can be made as to the unique involvement of the amygdala in the experience of fear.

Discrete emotions such as sadness and happiness have also been proposed to engage distinct neural substrates. Neuroimaging studies that used autobiographical recall mood induction have implicated subcallosal cingulate cortex (SCC) in the experiences of sadness (e.g., Mayberg et al., 1999). Additionally, resting-state studies of patients with clinical depression, a mood disorder that can cause sustained periods of sadness, have shown hypometabolism of the SCC (Mayberg, Lewis, Regenold, & Wagner, 1994). Further implicating the SCC in the experience of sadness, SCC activity has been shown to return to normal when depressed individuals successfully respond to pharmacological treatment (Mayberg et al., 2000). This series of studies indicates a critical role for the SCC in sadness as well as an integral role for the SCC in understanding clinical mood disorders like depression.

In comparison to sadness, happiness induction has been associated with activity in the basal ganglia (e.g., Whalen et al., 1998). Viewing happy facial expressions (Whalen et al., 1998), recollecting happy events (Damasio et al., 2000), and viewing pictures

depicting happy scenes (Lane, Reiman, Ahern, Schwartz, & Davidson, 1997) have all been associated with increased activity in the basal ganglia. Yet just as the amygdala has exhibited a mixed association with fear and other emotion states, the basal ganglia have been implicated in the processing of withdrawal emotion states such as disgust (Philips et al., 1997), suggesting the basal ganglia is more generally involved in affective responses.

These inconsistent findings in the neuroimaging literature need to be addressed before any conclusions can be drawn as to whether or not there are patterns of neural activation that differentiate among discrete emotions. Although the idea of differentiable systems underlying different basic emotions has received support in qualitative and meta-analytic reviews, this support has been mixed, with some emotions having clearer associations with particular brain areas than others. Similar to the fact that psychophysiological literature exhibits mixed results regarding basic emotions, neuroimaging results appear to be equally as challenging to interpret, although several recent reviews have made this attempt.

In parallel with the findings from psychophysiology, meta-analyses (e.g., Phan et al., 2002; and Murphy et al., 2003) of neuroimaging data have reported mixed results in support of a discrete emotion view. Phan et al. found that both happiness and disgust consistently recruited the basal ganglia, suggesting a shared reliance on that region, and anger did not consistently recruit any region of the brain. Similarly, Murphy et al. found emotion-specific activation for some emotion states (characteristic neural activity in the amygdala, insula and globus pallidus, and lateral OFC was associated with fear, disgust, and anger, respectively), but not others (happiness and sadness were associated with

overlapping patterns of neural activity). A comparison of these meta-analyses indicates mixed support for the discrete emotion view.

Furthermore, although Phan et al. demonstrated a degree of emotion-related functional specificity in the brain (e.g., fear was associated with activity in the amygdala and sadness specifically engaged the SCC), regions most consistently activated by emotion states did not always differentiate them. It is theoretically important that regional activations unique to each emotion state should also be those that play a central role in differentiating one emotion state from another. Otherwise such differences in activation could be attributed to spurious effects such as statistical errors (e.g., Type II error resulting from uncorrected multiple comparisons) or other unrelated phenomena. The degree of correspondence between regions that reliably activate during the experience of an emotion, and regions that differentiate basic emotion states, should be explored further.

1.1.3 Emotion Elicitation Paradigms

The study of basic emotions has traditionally centered on the study of facial expressions. Darwin (1872) contended that all mammals reliably exhibit emotional facial expressions, implying that the expression of emotions is a selected trait. Ekman and Friesen (1986; 1969) pioneered the study of facial expressions in modern psychology, demonstrating that basic emotion categories (happiness, sadness, anger, fear, disgust, surprise) are universally recognized and expressed in the face. Although this conclusion has been met with strong opposition from some researchers (e.g., Jack, Blais, Scheepers,

Schyns, & Caldara, 1989) many researchers have adapted Ekman's paradigms and used facial expression stimuli developed by Ekman to study emotion.

Over a quarter of the current neuroimaging studies of basic emotions to date have used facial expressions as stimuli, greatly restricting the generalizability of those data. It is not empirically established how different stimulus modalities and paradigms affect emotion-specific patterns of neural activation. However, it is intuitive that an emotion elicited by a lengthy induction procedure would necessarily be both qualitatively and quantitatively (in terms of arousal) different than one elicited by passively viewing a facial expression. Accordingly, we elected to explore this possibility within the meta-analysis (Chapter 2). We examined the core patterns of activation associated with data that used only facial expression, and compared that with our overall findings, as well as the remaining corpus of data. By isolating the effects that are the result of different paradigm modalities, we can make more accurate conclusions regarding the current research.

Similarly, it is important to examine emotional responses across multiple elicitation paradigms (e.g., viewing film clips and listening to autobiographical memory clips) within a single group of subjects. This type of approach can directly reveal regions that are active in response to a particular emotional state regardless of the elicitation method. Accordingly, the study reported in Chapter 3 used two different ecologically valid methods of emotion elicitation: film clips and autobiographical memory scripts to examine the core activations associated with each basic emotion state.

The use of a film clips as an elicitation method reduces inter-subject variability in the experience of each basic emotion state (by holding the stimuli constant), and the use

of autobiographical memories as an elicitation method provides a personally meaningful (and thus, more ecologically valid) emotional experience. In addition, presenting film clips and autobiographical memory cues allowed us to investigate differences in externally generated versus internally generated emotion states. We predicted that the distinct neural and ANS patterns associated with the discrete emotion states (happiness, disgust, etc.) would be largely independent of the particular way that they are elicited. That is not to say that differences will not arise as a result of paradigm modality (e.g., the neural correlates of fear elicited by viewing an aversive scene would not perfectly overlap with the neural correlates of fear elicited by an autobiographical recollection), but that there should be a set of regions that is commonly activated by a particular emotion state, regardless of the way it is elicited. Outside of the lab, emotional responses are locked to one type of stimulus (e.g., fearful responses are not restricted situations where one observes another person with a fearful facial expression void of any other sensory information), so it is important to study emotions across a wide range of contexts.

Film clips and autobiographical memories were selected as stimuli for multiple reasons. First, film clips have been used by several emotion researchers to successfully elicit emotion in the laboratory (e.g., Gross & Levenson, 1995; Kring & Gordon, 1998, and Rottenberg, Gross, Wilhem, Najmi & Gotlib, 2002). Second, film clips are more ecologically valid than most other stimulus possibilities. For example, pictures display static emotional scenes, void of motion and sound, whereas film clips present dynamic scenes that serve as a much more typical context in which people typically experience emotion. Additionally, using film clips rather than subject-generated stimuli (e.g., autobiographical recall, self-guided imagery) should increase consistency in the

emotional experience across participants. In contrast, autobiographical memories are capable of eliciting a more ecologically valid emotional response than film clips due to the personal nature of the stimulus. Such a response may be more complex and may index higher arousal than that of an experimenter-defined stimulus (Cabeza & St. Jaques, 2007). By using both types of stimuli, responses to highly arousing, personally meaningful, visually dynamic, and content consistent stimuli can all be assessed.

1.1.4 General Objectives

1.1.5 Study 1 Hypotheses

1.1.5.1 Consistency of Activation Patterns Associated with Basic Emotion States

Based on evidence that basic emotions are associated with characteristic biological signatures (e.g., Ekman et al., 1983, Damasio et al., 2000), we predicted that each basic emotion state (happiness, sadness, anger, fear, and disgust) would elicit a characteristic and reliable pattern of neural activation. These patterns were explored using ALE, where for a given emotion state, activation coordinates across studies were pooled together in the same space and their degree of overlap was evaluated.

1.1.5.2 Differentiability of Patterns Associated with Basic Emotion States

We predicted that all five basic emotion states (above) would be discriminable on the basis of the current neuroimaging evidence. This differentiation was expected to be identified using ALE, where cluster maps associated with each basic emotion were

created as in the consistency analyses. These maps were then directly contrasted to reveal clusters that were uniquely associated with one basic emotion state but not another.

1.1.6 Study 2 Hypotheses

1.1.6.1 Consistency of Neural Activations

We predicted that all basic emotion states (happiness, sadness, anger, fear, and disgust) would elicit reliable patterns of neural activation as indexed by pairwise contrasts of inclusive whole brain maps, conjunction analyses of film and memory activation maps for each emotion state, and ROI pairwise contrasts of each emotion state > neutral. Regions that reliably characterized and differentiated emotion states in the meta-analysis were selected as regions of interest (ROIs) (happiness: right STG, left ACC; sadness: left and right caudate; anger & disgust: left IFG; fear: left and right amygdala, left and right posterior insula; disgust: left and right anterior insula). These predictions are based on the results of neuroimaging experiments (e.g., Damasio et al, 2000) and meta-analyses (e.g., Vytal & Hamann, in press) that have indicated specific patterns of neural activation are associated with basic emotion states.

1.1.6.2 Distinctiveness of Neural Correlates of Basic Emotions

We predicted that basic emotion states would also elicit patterns of neural activation that are distinct from one another. We expected these patterns to be indexed by pairwise contrasts between basic emotion states using inclusive whole brain maps, conjunction analyses of film and memory activation maps for contrasts between each emotion state, and ROI pairwise contrasts between each emotion state. These predictions

are based on the results of neuroimaging experiments (e.g., Damasio et al, 2000) and meta-analyses (e.g., Vytal & Hamann, in press) that have indicated unique and differentiable patterns of neural activation are associated with basic emotion states.

1.1.6.3 Robustness of Neural Patterns Across Elicitation Methods

Prior research has not experimentally examined the effect(s) of elicitation method on neural or physiological activations as they relate to basic emotion states. Consequently, given that both paradigms used in this study have previously been shown to successfully elicit the target emotion states, and given that meta-analyses (e.g., Vytal & Hamann, in press) have shown that basic emotion states reliably exhibit discrete patterns of neural activity, core emotion-specific patterns were not expected to differ as a factor of how the emotion state was elicited. We expected modality-specific activations (e.g., visual cortex in response to film clips versus memory recollection), indexed by pairwise contrasts between modalities within each basic emotion state (e.g., happy films > happy memories), and by the areas activated by each basic emotion (e.g., happy films > neutral films) outside of the core conjunction (e.g., the conjunction between happy films and memories). However, the principal activations reflecting each basic emotion state were expected to remain virtually unaltered following a change in paradigm. Thus, we predicted that each basic emotion would be associated with consistent neural activations independent of the elicitation method (i.e., via film clips or autobiographical memories). For example, sadness should reliably activate a specific cluster of regions (e.g., caudate head, ACC) regardless of what type of event triggered the emotional response.

1.1.6.4 Individual Differences in Personality and Mood

Previous research has demonstrated that individuals with high levels of neuroticism and negative mood exhibit greater amygdala activation to aversive stimuli (Canli et al., 2001; Hariri et al., 2004). Based on these findings, we predicted that these individuals would exhibit greater amygdala activation, higher arousal ratings, and more negative valence ratings to fearful stimuli than those low on neuroticism and negative mood. Similarly, Canli et al. has also shown that individuals who were high on extraversion tended to exhibit greater amygdala activation when they were exposed to positive stimuli. Based on this finding, we predicted that individuals high on extraversion and positive mood would exhibit greater amygdala activation, higher arousal ratings, and more positive valence ratings to happiness stimuli than those low on extraversion and positive mood. Exploratory analyses investigated the role of personality and mood variables in differentiating among other emotional states.

1.1.6.5 Psychophysiological Patterns Associated with Basic Emotions

Based on previous research demonstrating that basic emotion states have distinct ANS correlates (Rainville et al., 2006), we predicted that basic emotion states would elicit differentiable patterns of ANS activity following a multivariate analysis. Previous reviews have noted that univariate analyses of the data may not be complex enough to detect subtleties in the relative contributions of the sympathetic and parasympathetic aspects of the ANS response (Cacioppo, Bernston, Larsen, Poehlmann, & Ito 2000), and successful differentiation has resulted from multivariate approaches (e.g., Rainville et al., 2006). Accordingly, it was hypothesized that emotion-specific patterns of ANS activity

may only be revealed by principal component analysis (PCA) followed by multivariate analysis of variance (MANOVA). However, both univariate and multivariate analyses will be applied to explore the physiological changes associated with basic emotion states.

Chapter 2

Study 1: Meta-analysis of Neuroimaging Support for Basic Emotions: *

*This chapter is derived in part from: Vytal, K. E. & Hamann, S. (in press). Neuroimaging support for discrete neural correlates of basic emotions: A voxel-based meta-analysis. *Journal of Cognitive Neuroscience*.

2.1 Precis

What is the basic structure of emotional experience and how is it represented in the human brain? One highly influential theory, discrete basic emotions (Ekman, 1972), proposes a limited set of basic emotions such as happiness and fear, which are characterized by unique physiological and neural profiles. Although many studies using diverse methods have linked particular brain structures with specific basic emotions, evidence from individual neuroimaging studies and from neuroimaging meta-analyses has been inconclusive regarding whether basic emotions are associated with both consistent and discriminable regional brain activations. We revisited this question, using Activation Likelihood Estimation (ALE), which allows spatially sensitive, voxel-wise statistical comparison of results from multiple studies, and examining substantially more studies than previous meta-analyses. The ALE meta-analysis yielded results consistent with basic emotion theory. Each of the emotions examined (fear, anger, disgust, sadness, and happiness) was characterized by consistent neural correlates across studies, as defined by reliable correlations with regional brain activations. In addition, the activation patterns associated with each emotion were discrete (discriminable from the other emotions in pairwise contrasts), and overlapped substantially with structure-function correspondences identified using other approaches, providing converging evidence that discrete basic emotions have consistent and discriminable neural correlates. Complementing prior studies that have demonstrated neural correlates for the affective dimensions of arousal and valence, the current meta-analysis results indicate that the key elements of basic emotion views are reflected in neural correlates identified by neuroimaging studies.

2.2 Introduction

Emotions are a key facet of human experience. A central question in the study of emotion is how best to characterize the basic structure of emotional experience. Discrete emotion theories (Darwin, 1872; Ekman, 1972) propose a limited set of basic emotions (e.g., happiness, sadness, anger, fear, and disgust) that have unique physiological and neural profiles. Other theoretical views, such as dimensional theories of emotion, conceptualize emotions using a framework in which affective states can be represented in terms of underlying factors such as emotional arousal (emotion strength), and emotional valence (degree of pleasantness or unpleasantness).

A key proposal of basic emotion theories is that basic emotions have consistent and specific psychophysiological and neural correlates. Ekman (1999) summarized this view: "It is necessary to posit emotion-specific central nervous system (CNS) activity in my account of basic emotions. The distinctive features of each emotion, including the changes not just in expression but in memories, imagery, expectations and other cognitive activities, could not occur without central nervous system organization and direction. There must be unique physiological [CNS] patterns for each emotion..." (Ekman, 1992, pp. 182). Although the predictions of basic emotion theories have drawn support from a wide variety of behavioral, neuropsychological, psychophysiological, and neuroimaging studies (e.g., Bechara, Damasio, Ponto, Parvizi, et al., 2000; Blair, Morris, Frith, Perrett, and Dolan, 1999; Damasio, Grabowski, Bechara et al. 2000; Ekman, 1992), recently the strength of the support for basic emotion theories has been challenged (e.g., Barrett and Russell, 1999; Barrett and Wager, 2006; Barrett, Lindquist, Bliss-Moreau, et al., 2007). For example, reviews of the psychophysiological literature have concluded that such

studies have not been able to identify consistent and specific psychophysiological correlates for basic emotions (Barrett and Wager 2006; Cacioppo et al., 2000; Zajonc and McIntosh, 1992).

Neuroimaging studies can assess activity related to experienced emotional states across the entire brain on a moment-to-moment basis, and thus one might expect that this approach would be more sensitive and better able to identify the consistent and specific biological correlates for basic emotions than other measures such as behavior or psychophysiology. However, the strength and consistency of the neuroimaging evidence supporting the predictions of basic emotion theories has also been questioned and some critiques have concluded that evidence for basic emotions from neuroimaging remains inconclusive (Barrett and Russell, 1999; Barrett and Wager, 2006). The existing literature directly relevant to evaluating whether basic emotions have differentiable neural correlates is relatively limited, in part because only a handful of neuroimaging studies have examined and contrasted several basic emotions concurrently in the same study. Meta-analytic methods applied to the neuroimaging literature can help overcome this limitation in the available literature, because such methods allow activation patterns associated with basic emotions across different studies to be compared. Such techniques can identify neural patterns that are consistent and specific to each emotion state. Meta-analyses can also assess whether these activation patterns are robust across experimental differences such as type of emotional stimuli and emotion-elicitation methods, and they can reduce problems associated with low experimental power in individual studies (Ioannidis & Lau, 1999).

Two meta-analytic reviews of the relevant basic emotion neuroimaging literature have been conducted to date (Murphy et al., 2003; Phan et al., 2002; see Bass, Aleman, & Kahn, 2004, Kober et al., 2008; Wager, Phan, Liberzon, & Taylor, 2003 for additional meta-analytic reviews of the neural correlates of emotion, but not basic emotion states). Both Phan et al. and Murphy et al. concluded that basic emotion theories are only partially supported by neuroimaging studies, and each review reached somewhat different conclusions regarding which specific neural correlates are associated with each basic emotion (Barrett & Wager, 2006). Because the status of the neuroimaging evidence supporting basic emotion theories is currently unresolved, we revisited these questions in the current meta-analytic study. We hypothesized that by using a more sensitive meta-analytic method (Activation Likelihood Estimation; ALE, Laird et al., 2005) than those used in previous reviews and by analyzing a substantially larger number of neuroimaging studies that have been published in the several years following the publication of these earlier reviews, we could potentially reveal differences between basic emotion states that were not detected in previous studies.

The current study differs from previous meta-analytic reviews in two primary respects: the meta-analytic methodology used and the number of studies included. We used the ALE method, which preserves three-dimensional spatial information in original activation maximum coordinate data, unlike label-based methods that convert activation coordinates into regional labels (e.g., prefrontal cortex), decreasing spatial information considerably. ALE allows for direct statistical comparison between the composite activation maps associated with discrete emotion states, and thus provides a means for assessing the discriminability of basic emotion states at the voxel level. Although the

analysis used by Murphy et al. (2003) did assess the differentiability of neural patterns associated with basic emotions states, their meta-analysis method divided the brain into only eight sectors of approximately equal volume. These sectors are larger than individual brain structures, and are orders of magnitude less spatially specific than the voxel level resolution afforded by ALE. Thus, this prior study could not assess the critical question relevant to the predictions of basic emotion theory, namely, whether basic emotions have consistent and specific correlates at the level of individual brain structures. Similarly, Phan et al. (2002) did not specifically assess whether each basic emotion could be discriminated from each of the other emotions based on regional activations. Their meta-analysis focused on determining which brain regions were more consistently associated with one particular emotion than other emotions, and it did not assess whether each basic emotion could be discriminated from every other emotion via regional activations. In addition to the methodological advantages associated with the current ALE meta-analysis, our review examined the considerably enlarged literature (50% more studies published subsequent to the most recent meta-analytic review; Murphy et al., 2003) that has resulted from the recent increase in the number of neuroimaging studies examining the neural correlates of emotion. It is important to note that although the overall majority of studies used facial expressions to explore the neural correlates of basic emotions, this larger literature introduces a wider-range of stimuli and methods with which basic emotions were studied. Together, these two considerations motivated a re-examination of whether the existing neuroimaging evidence supports the basic emotion view.

To address whether there are differentiable patterns of neural activity specific to each basic emotion we conducted two primary types of analysis, which can be characterized as assessing the consistency and discriminability of emotion-related activations, respectively. Consistency analyses determined the brain regions whose activity was most consistently and strongly associated with each of the individual basic emotions. Basic emotion theories predict that there should be characteristic regional brain activations that are consistently associated with the experience of each basic emotion. These neural correlates are predicted to also be discrete or discriminable, in the sense that each basic emotion is associated with some unique regional activations not shared by the other emotions. To test this prediction, we contrasted the activations associated with each basic emotion, assessing whether patterns of regional brain activation can discriminate among different basic emotions. The degree of support or lack of support for basic emotion theories was assessed primarily on the extent to which basic emotions were associated with consistent and discriminable regional activations.

In addition, we anticipated that the regions identified in the consistency and discriminability analyses would overlap to some degree, based on the view that some subset of the characteristic neural activations for each emotion also would comprise the activations that differentiated that emotion from others. Finally, we also predicted that the characteristic patterns of regional brain activity associated with basic emotions observed with neuroimaging should converge with the regions identified using other neuroscience methods such as neuropsychological studies. For example, because neuropsychological lesion studies in humans have demonstrated that the amygdala is critically implicated in the experience of fear and the acquisition of fear responses, one would predict that the

amygdala should be among the brain regions characteristic of the basic emotion of fear in our meta-analysis (Bechara, Damasio, Ponto et al., 2000).

2.3 Methods

2.3.1 Scope of the Review

To investigate patterns of neural activation associated with discrete basic emotions, we examined neuroimaging studies that included an explicit emotional elicitation task (e.g., mood induction), emotionally arousing stimuli (e.g., emotional pictures) or emotional facial expressions. Like Murphy et al. (2003), the current analysis considered studies that addressed any aspect of an emotional experience: expression, perception, interpretation, or subjective experience. Consequently, our meta-analysis examined neural activations across multiple studies that recruited a variety of different emotion-related processes. We elected to include all such studies, rather than focus on studies using a particular methodology such as emotion induction, because we were specifically interested in identifying the "core" neural patterns associated with basic emotions, reflected in the overlap of activations across different aspects of emotional experience.

Studies were selected based on a set of seven criteria that were adapted from inclusion criteria used in previous meta-analyses (e.g., Murphy et al., 2003; Phan et al., 2002). First, only studies conducted using $H_2{}^{15}O$ PET and fMRI were considered. Second, coordinates needed to be reported in standard stereotactic space (either MNI or Talairach). Third, studies must have reported whole-brain analyses (we excluded those studies reporting only region of interest [ROI] analyses) to ensure that all regions in the

brain were represented equivalently. Fourth, activation contrasts representing main effects of specific emotions relative to a baseline condition were required (e.g., viewing happy faces > viewing neutral faces) so that the activations associated with each emotion could be analyzed independently of any other emotion. This criterion also reduced the influence of stimulus type on the reported effects because effective control stimuli were well matched on all elements except for emotional arousal. Fifth, the main effects reported in a study were required to include at least one basic emotion state (happiness, sadness, anger, fear, or disgust). Sixth, studies had to report activations (deactivations were not included in the analysis because the nature of the analysis technique does not afford differentiation of activations from deactivations). Seventh, only data from healthy individuals were included because the objective was to capture typical emotional experience (studies of clinical patient groups were not considered).

Over 1,000 potential studies were identified by a search of electronic databases (Psych Info, Medline, Web of Science ISI), Google Scholar, previous meta-analyses (Murphy et al., 2003; Phan et al., 2002), and relevant peer-reviewed journals. Eighty-three neuroimaging studies (PET and fMRI) published from 1993 to 2008 were selected for the analysis (see Table 1 for a summary). The current analysis included 30 studies (approximately 100% more than Phan et al. 2002 and 50% more than Murphy et al. 2003) published after the studies included in the most recent meta-analysis (Murphy et al., 2003). Studies included in the ALE meta-analysis are preceded in the References section by an asterisk.

Table 1. Studies included in the meta-analysis

Study	Method	*N*	Age	Experimental Paradigm	Modality	Emotion
Aalto et al. (2002), *Neurorpt*.	PET	11f	18-44	Mood Induction	V (Films)	S
Aalto et al. (2005), *Brain Res. Protocols*	fMRI	11f	33.4	Viewing Emotional Films	V (Films)	S
Abel et al. (2003), *Neurorpt*.	fMRI	8m	N/A	Viewing Facial Expressions	V (Faces)	F
Abler et al. (2007), *J. Psych. Res*.	fMRI	12f	40.7	Viewing Emotional Pictures	V (Pictures)	D
Ashwin et al. (2007), *Neuropsychologia*	fMRI	13m	25.6	Viewing Facial Expressions	V (Faces)	F
Baker et al. (1997), *Psych. Med*.	fMRI	10m	18-35	Mood Induction	V (Scripts/Music)	H S
Beauregard et al. (1998), *Neurorpt*.	fMRI	3m, 4f	45	Viewing Emotional Films	V (Films)	S
Benuzzi et al. (2004), *Brain Res. Bul*.	fMRI	7m, 7f	21-27	Viewing Facial Expressions	V (Faces)	F
Benuzzi et al. (2008), *J. Neuro*.	fMRI	15f	23.5	Viewing Emotional Films	V (Films)	D
Blair et al. (1999), *Brain*	PET	13m	25	Viewing Facial Expressions	V (Faces)	A
Buchanan et al. (2000), *Cog. Brain Res*.	fMRI	10m	22-40	Emotional Prosody	A (Voices)	H S
Bystritsky et al. (2001), *Neurorpt*.	fMRI	3m, 3f	31.8	Mood Induction	A (Autobio Scripts)	F
Damasio et al. (2000), *Nat. Neuro*.	PET	53mix	N/A	Induced Mood	Autobio Recall	H S A F
Dolan et al. (1996), *Neuroimg*.	PET	8m	23	Viewing Facial Emotions	V (Faces)	H
Dougherty et al. (1999), Bio. Psych.	PET	8m	25	Mood Induction	A (Autobio Scripts)	A
Eugene et al. (2003), *Neuroimg*.	fMRI	10f	24	Viewing Emotional Films	V (Films)	S
Fischer et al. (2005), *Neuro. Lett*.	fMRI	11m, 11f	74.1	Viewing Facial Expressions	V (Faces)	A
Fitzgerald et al. (2004), *Neuro. Lett*.	fMRI	7m, 5f	31.2	Mood Induction	Autobio Recall	D
Fitzgerald et al. (2006), *Neuroimg*.	fMRI	10m, 10f	26	Viewing Facial Expressions	V (Faces)	H S A F D
George et al. (1995), *Bio. Psych*.	PET	11f	N/A	Induced Mood	Autobio Recall/ V (Faces)	S
George et al. (1996), *Am. J. Psych*.	PET	10m, 10f	35	Induced Mood	Autobio Recall/ V (Faces)	H S
Goldin et al. (2005), *Neuroimg*.	fMRI	13f	19.7	Viewing Emotional Films	V (Films)	H S
Grandjean et al. (2005), *Nat. Neuro*.	fMRI	8m, 7f	24.4	Emotional Prosody	A (Pseudo Sentences)	A
Grosbras et al. (2006), *Cer. Ctx*.	fMRI	10m, 10f	28.6	Viewing Emotional Films	V (Films)	A
Habel et al. (2005), *Neuroimg*.	fMRI	26m	33.4	Mood Induction	V (Faces)	H S
Hadjikhani et al. (2003), *Curr. Bio*.	fMRI	4m, 3f	N/A	Viewing Bodily Expressions	V (Bodily Expressions)	F
Hariri et al. (2003), *Bio. Psych*.	fMRI	5m, 6f	32	Viewing Emotional Pictures	V (Pictures)	F
Harris et al. (2007), *Psych. Sci*.	fMRI	10mix	N/A	Viewing Emotional Pictures	V (Pictures)	D
Hutcherson et al. (2005), *Neuroimg*.	fMRI	28f	18-21	Viewing Emotional Films	V (Films)	H S
Kesler/West et al. (2001), *Cog. Brain Res*.	fMRI	11m, 10f	21.6	Processing Facial Emotions	V (Faces)	H S A F
Killgore et al. (2004),	fMRI	12f	23.7	Viewing Facial Expressions	V (Faces)	H S

Neuroimg.						
Kilts et al. (2003), *Neuroimg*.	fMRI	9m, 4f	24.5	Viewing Facial Expressions	V (Faces)	H A
Kimbrell et al. (1999), *Bio. Psych*.	PET	10m, 8f	31.2, 34.7	Induced Mood	Autobio Recall	F
Lane et al. (1997), *J. Psych*.	PET	12f	23.3	Induced Mood	V (Film)/Recall	H S D
Lange et al. (2003), *Bio. Psych*.	fMRI	9m	29	Viewing Facial Expressions	V (Faces)	F
Lemche et al. (2007), *Neurorpt*.	fMRI	5f, 7m	27.3	Viewing Facial Expressions	V (Faces)	H S
Lennox et al. (2004), *Psych. Med*.	fMRI	6m, 6f	32.6	Viewing Facial Expressions	V (Faces)	H S
Liddell et al., (2005), *Neuroimg*.	fMRI	11m, 11f	32	Viewing Facial Expressions	V (Faces)	F
Liotti et al. (2000), *Bio. Psych*.	PET	8f	N/A	Mood Induction	V (Autobio Scripts)	S
Mayberg et al. (1999), *Am. J. Psych*.	PET	8f	36	Mood Induction	V (Autobio Scripts)	S
Michalopoulou et al. (2008), *Brit. J. Psych*.	fMRI	5m, 4f	32	Viewing Facial Expressions	V (Faces)	F
Mitterschiffthaler et al. (2007), *HBM*	fMRI	8m, 8f	30.8	Mood Induction	A (Music)	H S
Moll et al. (2005), *Cog. Beh. Neuro*.	fMRI	7m, 6f	22.5	Mood Induction	V (Statements)	D
Morris et al. (1998), *Brain*	PET	4m, 1f	42.8	Viewing Facial Expressions	V (Faces)	H F
Ottowitz et al. (2004), J. *Neuropsychiatry Clin. Neurosci*.	fMRI	8f	18-30	Mood Induction	V (Sentences)	S
Paradiso et al. (1997), *Am. J. Psych*.	PET	2m, 6f	62.6	Viewing Emotional Films	V (Film Clips)	H D
Paradiso et al. (2003), *J. Neuro.. Clin.. Neurosci*.	fMRI	9m, 8f	65	Mood Induction	V (Faces/Pictures)	S
Pardo et al. (1993), *Am. J. Psych*.	PET	3f	24	Mood Induction	Imagery	S
Pelletier et al. (2003), *Neurorpt*.	fMRI	5m, 4f	33	Mood Induction	V (Autobio Recall)	H S
Phillips et al. (1997), *Nat*.	fMRI	2m, 5f	27	Viewing Facial Expressions	V (Faces)	F D
Phillips et al. (1998), *Psych. Res.: Neuroimg*.	fMRI	7m, 1f	32	Viewing Facial Expressions	V (Faces)	H S
Phillips et al. (1998), *Proc. R. Soc. Lond. B*.	fMRI	6m	37	Vocal Expressions	V (Faces)/ A (Vocal)	F D
Phillips et al. (1999), *Psych. Res*.	fMRI	5mix	30	Viewing Facial Expressions	V (Faces)	A F D
Phillips et al. (2000), *Psych. Med*.	fMRI	7m, 7f	31	Viewing Emotional Pictures	V (Pictures)	D
Phillips et al. (2004), *Neuroimg*.	fMRI	5m, 5f	29.5	Viewing Facial Expressions	V (Faces)	F D
Pietrini et al. (2000), *Am. J. Psych*.	PET	8m, 7f	22	Mood Induction	Imagery	A
Pine et al. (2001), *Emotion*	fMRI	10m, 10f	13.9, 28.5	Visual Masking Paradigm	V (Faces)	H F
Salloum et al. (2007), *Alcohol. Clin. Exp. Res*.	fMRI	11m	36	Viewing Facial Expressions	V (Faces)	H S A F D
Sambataro et al. (2006), *Euro. J. Neuro*	fMRI	11m, 13f	26.8	Viewing Facial Expressions	V (Faces)	D
Sato et al. (2004), *Cog. Brain Res*.	fMRI	10m, 12f	26.5	Viewing Facial Expressions	V (Dynamic Faces)	H F
Schafer et al. (2005), *Int. J. Psychophys*.	fMRI	20m, 20f	23.93	Viewing Emotional Pictures	V (Pictures)	F
Schienle et al. (2002), *Neurorpt*.	fMRI	12f	26.3	Viewing Emotional Pictures	V (Pictures)	F D
Schienle et al. (2005), *Neuropsychobio*.	fMRI	63f	27.3	Viewing Emotional Pictures	V (Pictures)	D
Schienle et al. (2006), *Neuro. Lett*.	fMRI	12f	19-41	Viewing Emotional Pictures	V (Pictures)	F D
Shapira et al. (2003),	fMRI	3m,	38	Viewing Emotional Pictures	V (Pictures)	D

Bio. Psych.		5f				
Sprengelmeyer et al. (1998), *Proc. R. Soc. Lond. B*	fMRI	2m, 4f	23.5	Recognition of Facial Expressions	V (Faces)	A F D
Stark et al. (2003), *Int. J. Psychophys.*	fMRI	4m, 11f	29.1	Viewing Emotional Films	V (Pictures)	F D
Stark et al. (2005), *Int. J. Psychophys.*	fMRI	6m	N/A	Viewing Emotional Pictures	V (Films)	F D
Stark et al. (2007), *Neuroimg.*	fMRI	34m, 32f	24.7	Viewing Emotional Pictures	V (Pictures)	F D
Takahashi et al. (2008), *Cer. Ctx.*	fMRI	8m, 8f	21.5	Mood Induction	V (Sentences)	H
Thielscher et al. (2007), *J. Neuro.*	fMRI	10m, 15f	23	Viewing Facial Expressions	V (Faces)	F D
Vuilleumier et al. (2007), *Neuropsychologia*	fMRI	12mix	N/A	Viewing Facial Expressions	V (Faces)	F
Wang et al. (2005), *Emotion*	fMRI	5m, 7f	25.9	Visual Oddball Task	V (Pictures)	S
Whalen et al. (2001), *J. Neuro.*	fMRI	4m, 4f	25	Viewing Facial Expressions	V (Faces)	A F
Wicker et al. (2003), *Neuron*	fMRI	14m	N/A	Mood Induction	O	D
Williams et al. (2001), *Neuroimg.*	fMRI	11m	30	Viewing Facial Expressions	V (Faces)	A
Williams et al. (2004), *Cog. Brain Res.*	fMRI	15m, 7f	27.5	Viewing Facial Expressions	V (Faces)	F
Williams et al. (2005), *Neurorpt.*	fMRI	5m, 8f	24	Viewing Facial Expressions	V (Faces)	A F D
Winston et al. (2003), *Curr. Bio.*	fMRI	6m, 8f	30	Viewing Facial Expressions	V (Faces)	F
Wright et al. (2004), *Neurorpt.*	fMRI	4m, 4f	20-26	Viewing Emotional Pictures	V (Pictures)	F D

Note: Characteristics of all studies included in the meta-analysis. Abbreviations: For stimulus modality: V = visual; A = auditory; O = olfactory; For emotion category: H = happiness; S = sadness; A= anger; F = fear; D= disgust. Autobio = autobiographical.

2.3.2 Activation Likelihood Estimation

The current review used a recently developed neuroimaging meta-analysis method, ALE (Laird et al., 2005), which has considerable advantages over previously used label-based methods where anatomic locations of activations are analyzed according to their corresponding neural structure. ALE is a quantitative method of assessing relationships between function (i.e., cognitive or emotional processes) and regional brain activations. In an ALE analysis, relevant neuroimaging studies are collected and analyzed in relation to specific experimental conditions (e.g., viewing a frightening scene vs. a neutral scene) by extracting each reported three-dimensional focus of activation in the form of Talairach or MNI coordinates corresponding to activation maxima for contrasts between experimental conditions (see Figure 1). These sets of activation coordinates are then modeled as the centers of Gaussian probability distributions and are then combined (summated) to create statistical whole-brain ALE maps. ALE maps preserve considerably more spatial information from the original maxima, relative to label-based methods, and substantially increase the spatial sensitivity of the analysis. The ALE maps are composed of ALE statistics representing the likelihood that the voxel at that three-dimensional coordinate is active during the corresponding experimental condition across the entire set of studies analyzed (Laird et al., 2005). A further advantage of the ALE method is that these individual ALE statistic maps can then be directly compared statistically, by contrasting the voxel-wise differences between two ALE maps and comparing the resulting difference ALE map to a comparison null distribution generated by random permutation tests. To summarize the steps in the current ALE meta-analysis (for a complete description of the ALE method see Laird et al., 2005), three-dimensional

activation coordinates were extracted from the selected studies relevant studies for each basic emotion, converted to spatially smoothed activation foci volumes with a 10mm FWHM Gaussian kernel, and pooled across studies to create statistical whole-brain maps using GingerALE 1.1 (Laird et al., 2005).

Figure 1. Activation Likelihood Estimation analysis overview

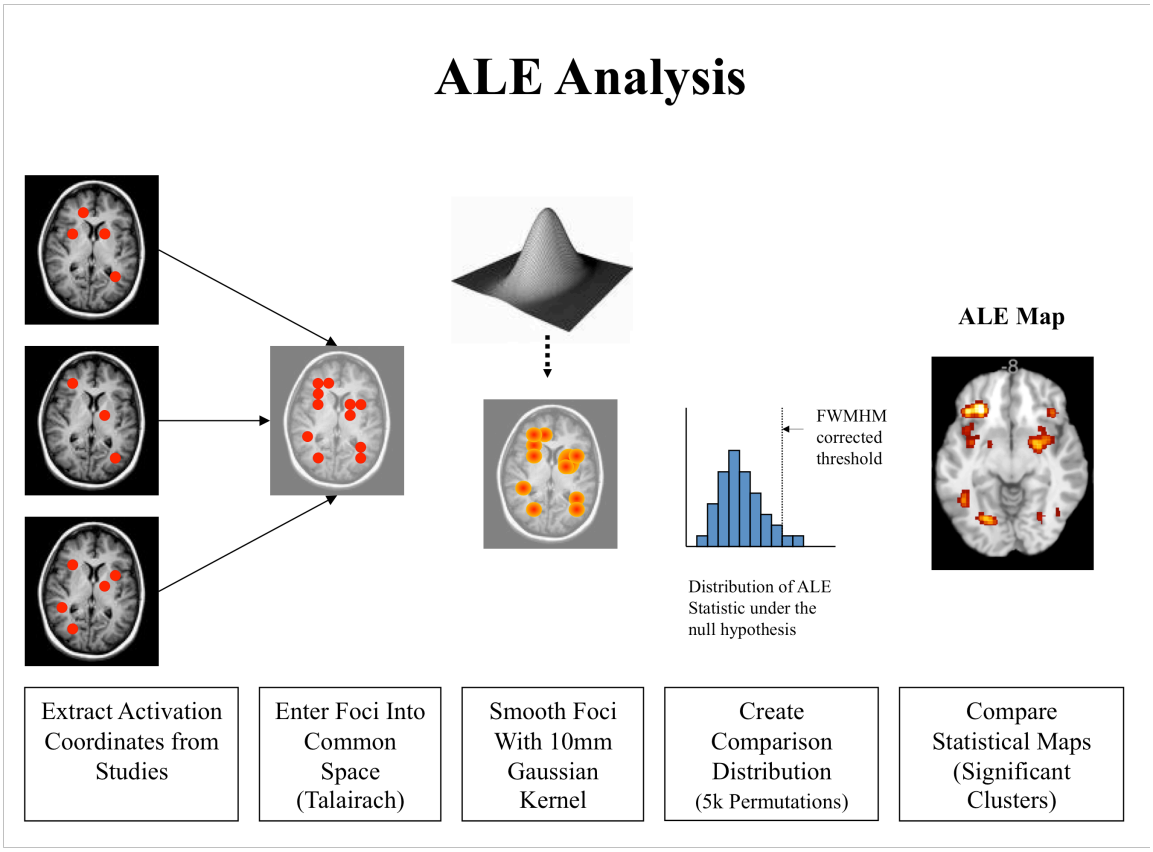


Figure Caption

An ALE analysis consists of the following steps: 1) extract the activation coordinates reported by studies 2) pool them together in a commons space 3) smooth them with a Gaussian kernel, and 4) test their degree of overlap against a random distribution.

For consistency analyses, ALE statistic maps were calculated for each of the five basic emotions analyzed, and each ALE map was then compared with a corresponding comparison null distribution of the ALE statistic based on 5,000 random spatial permutations across the brain of an equivalent number of activation foci. Similarly, for discriminability analyses, ALE statistic maps were compared by comparing the difference maps calculated from each pairwise contrast between individual emotion ALE maps (e.g., fear ALE map minus anger ALE map) across all basic emotions with a corresponding random null distribution. This null distribution was calculated by first generating 5,000 individual pairs of ALE maps, using the same permutation method as was used to compute individual ALE maps, second, calculating a difference map for each pair, and third, comparing the observed difference ALE map between the emotion pair with this null distribution. All thresholded ALE maps were corrected for multiple comparisons using the False Discovery Rate (FDR) algorithm ($q = .05$) and were overlaid on a canonical single-subject anatomical T1 brain template from the SPM5 image library. Only significant clusters that exceeded $100mm^3$ were reported.

In summary, the ALE meta-analysis was composed of consistency analyses and discriminability analyses. Consistency analyses identified the regional brain activations regions most consistently associated with each basic emotion. Discriminability analyses identified brain regions that were significantly differentially active when contrasting pairs of discrete emotions, thus addressing whether basic emotion states are discriminable based on regional activations.

2.4 Results

2.4.1 Activation Consistency Analyses

2.4.1.1 Happiness

The ALE analysis of activation foci associated with happiness revealed 9 significant clusters, with the largest (4880mm^3) located primarily in the right superior temporal gyrus (STG) (BA 22) (see Figure 2 and Table 2). Figure 2 displays ALE activation maps overlaid on eight axial slices from a canonical T1 anatomical image, centered on z=0, with the highest slice selected at a level that captured the most superior activation(s) across all statistical maps in the meta-analysis. The same display criteria were applied to all figures

Figure 2. Activation likelihood maps representing regional activity consistently associated with each basic emotion state

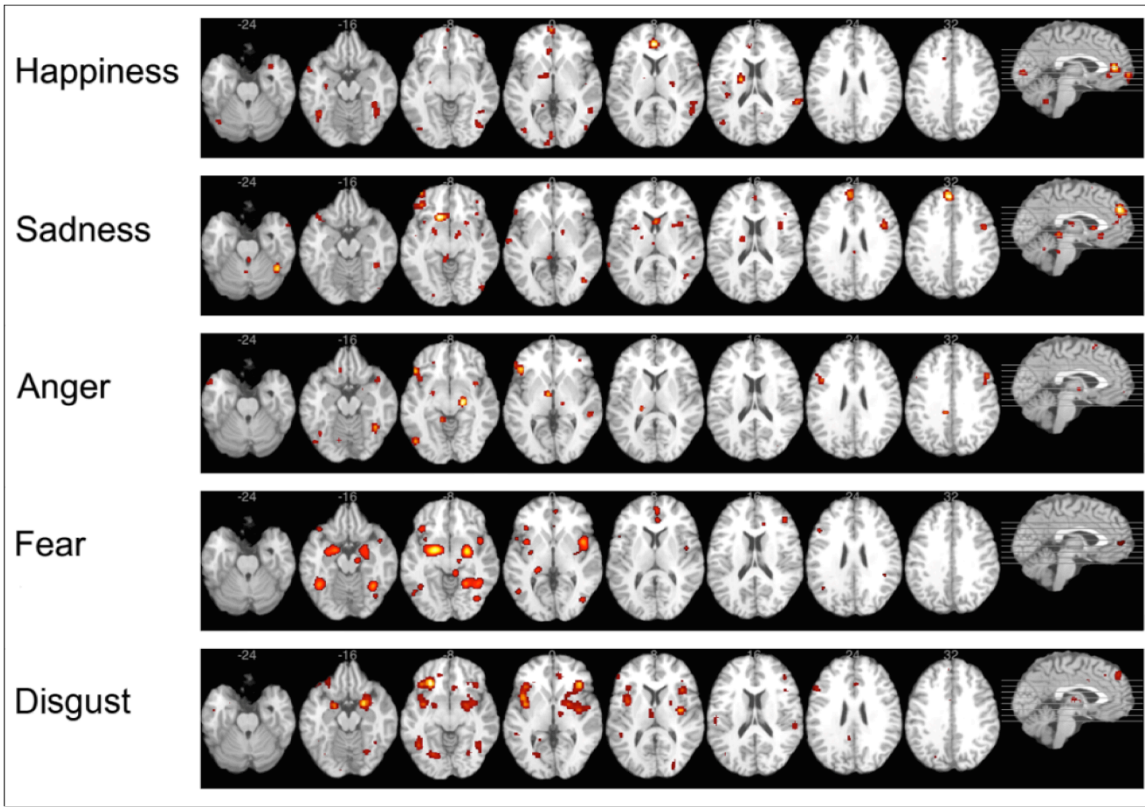


Figure Caption

Statistical map of significant ALE clusters associated with happiness, sadness, anger, fear, and disgust. The horizontal lines overlaid on the sagittal image (at far right) show the locations of the corresponding axial slices. All figures display slices in neurological convention, where the left side in the image corresponds to the left side of the image. ALE values are indicated by red-yellow color gradient clusters overlaid on a canonical structural image from SPM5. Rather than representing magnitude of activation, the color gradient represents the degree of overlap (i.e., activation likelihood or consistency) among the activation coordinates across studies that contributed to the analysis. The most prominent clusters associated with happiness are located in right STG (BA 22) and left

ACC (BA 24). The most prominent clusters associated with sadness are located in left caudate head and left medFG (BA 9) and right inferior frontal gyrus (BA 9). The most prominent clusters associated with anger are located in left IFG (BA 47) and right parahippocampal gyrus (BA 35). The most prominent clusters associated with fear are located in bilateral amygdala, right cerebellum, and right insula. The most prominent clusters associated with disgust are located in bilateral insula (BA 47).

Table 2. ALE activation clusters consistently associated with each basic emotion state

Happiness

Activation Focus			Region (> 100mm^3)	Size
x	y	z		
48	-53	-1	R STG (BA 22)*	4880
-2	42	4	L ACC (BA 24)*	3232
-40	-62	-18	L Cerebellum*	1176
-18	-9	17	L Thalamus	960
-4	-92	2	L Lingual Gyrus	888
-12	-6	2	L Thalamus	824
-39	-79	-3	L Inf Occ Gyrus*	528
-37	-31	18	L Insula*	288
25	-16	8	R Basal Ganglia (Put)*	200

Anger

Activation Focus			Region (>100mm^3)	Size
x	y	z		
-44	23	-3	L IFG (BA 47)*	2408
19	-19	-8	R PHG	1544
-44	-71	-11	L Fusiform Gyrus*	1480
39	8	-15	R IFG (BA 13)	1008
37	-55	-16	R Cerebellum*	1000
48	13	30	R MFG (BA 9)*	928
-45	12	26	L IFG (BA 9)*	904
-6	-9	1	L Thalamus*	568
-51	8	-22	L STG	464
-23	-7	-8	L Amygdala	128
5	45	-4	R ACC (BA 32)*	128
-11	24	-16	L medFG (BA 25)	120
12	-23	64	R medFG (BA 6)*	112

Fear

Activation Focus			Region (>100mm^3)	Size
x	y	z		
-23	-6	-9	L Amygdala*	5616
23	-11	-11	R Amygdala*	4248
33	-54	-10	R Cerebellum*	4176
43	3	-2	R Insula (BA 13)	2896
-40	-56	-14	L Fusiform Gyrus*	2848
-38	23	-7	L IFG (BA 47)*	1320
4	44	5	R ACC (BA 32)	1168
39	-73	-7	R Inf Occ Gyrus*	1072
38	10	20	R Insula (BA 13)*	368
43	-40	21	R Insula (BA 13)*	320
13	30	14	R ACC (BA 32)*	176

Sadness

Activation Focus			Region (>100mm^3)	Size
x	y	z		
-4	47	27	L medFG (BA 9)*	3120
39	6	21	R IFG (BA 9)	2576
-10	18	-8	L Caudate Head*	1960
-38	40	-8	L MFG (BA 10)*	1632
40	-51	-22	R Cerebellum*	1344
43	-66	4	R ITG	880
-5	-39	-5	L Cerebellum*	840
2	12	6	R Caudate Head	816
-17	-12	14	L Thalamus*	808
13	-5	-6	R PHG*	784
-37	14	-14	L IFG (BA 13)	632
3	8	62	R SFG*	512
-47	-7	41	L Precentral Gyrus	496
44	-78	-10	R Middle Occ Gyrus	456
-20	-1	-7	L Basal Ganglia (GP)	408
-59	-15	-1	L STG	400
40	22	-4	L IFG (BA 47)	352
-26	3	9	L Basal Ganglia (Put)	336
44	21	12	R IFG (BA 45)	272
24	9	-7	R Basal Ganglia (Put)	208
-50	25	1	L IFG (BA 45)	208
33	-22	19	R Insula (BA 13)	128

Disgust

Activation Focus			Region (>100mm^3)	Size
x	y	z		
30	4	-4	R IFG (BA 47/Insula)*	14208
-26	28	-10	L IFG (BA 47/Insula)*	10720
-22	-70	-6	L Lingual Gyrus*	1800
-20	-3	-14	L Amygdala	1352
-41	-55	-9	L Fusiform Gyrus*	1272
40	-58	-9	R Fusiform Gyrus	1104
-2	44	40	L medFG	960
27	-67	-12	R Cerebellum*	680
-50	19	26	R IFG (BA 9)	672
-4	-14	7	L Thalamus	512
-47	-44	4	L MTG	472
27	-83	10	R Middle Occ Gyrus	408
10	38	-1	R ACC	384
7	21	-9	R ACC (BA 32)	288
-14	38	-7	L medFG (BA 10)	264
-50	36	9	L IFG (BA 46)	200

Note: Each cluster greater than 400mm^3 is reported, along with the weighted central activation likelihood focus, the region corresponding to the cluster with the highest ALE score within the cluster, and the total cluster size in mm^3. Additional clusters of interest that surpassed a threshold of 100mm^3 are also reported. L and R indicate activations located in the left and right hemispheres, respectively. Inferior is abbreviated as Inf, occipital is abbreviated as Occ, globus pallidus is abbreviated as GP, putamen is abbreviated as Put, parahippocampal gyrus is abbreviated as PHG. Brodmann areas are provided to differentiate activations in larger regions that occur in multiple contrasts. * Indicates regions that overlapped with the re-analysis that involved only studies that used facial expressions.

2.4.1.2 Sadness

The ALE analysis of activation foci associated with sadness revealed 35 significant clusters, with the largest (3120mm^3) located primarily in the left medial frontal gyrus (medFG) (see Figure 2 and Table 2).

2.4.1.3 Anger

The ALE analysis of activation foci associated with anger revealed 13 significant clusters, with the largest (2408mm^3) located primarily in the left inferior frontal gyrus (IFG) (BA 47) (see Figure 2 and Table 2).

2.4.1.4 Fear

The ALE analysis of activation foci associated with fear revealed 11 significant clusters, with the largest (5616mm^3) located primarily in the left amygdala (see Figure 2 and Table 2).

2.4.1.5 Disgust

The ALE analysis of activation foci associated with disgust revealed 16 significant clusters, with the largest (14208mm^3) located primarily in the right insula and right IFG (BA 47) (see Figure 2 and Table 2).

2.4.2 Activation Discriminability Analyses

2.4.2.1 Happiness-Sadness

The ALE analysis of activation foci associated with happiness greater than sadness revealed 4 significant clusters, with the largest (424mm^3) located primarily in the right superior temporal gyrus (STG) (see Figure 2 and Table 3). The ALE analysis of activation foci associated with sadness greater than happiness revealed 12 significant clusters, with the largest (2536mm^3) located primarily in the right middle temporal gyrus (MTG) (BA 24) (see Figure 3 and Table 3). For all contrast analysis figures, clusters displayed in the red gradient correspond to the emotion state that is being subtracted from in the contrast; clusters displayed in the blue gradient correspond to the emotion state that is being subtracted.

Table 3. ALE activation clusters differentiating each basic emotion state

Happiness-Sadness				
Activation Focus			Region (>100mm^3)	Size
x	y	z		
			Happiness > Sadness	
60	-41	16	R STG*	424
0	39	7	L ACC (BA 32)*	344
-37	-31	18	L Insula (BA 13)	120
-1	57	-3	L medFG (BA 10)*	112
			Sadness > Happiness	
43	-65	7	R MTG	2536
-4	47	31	L medFG (BA 9)*	1976
-11	17	-9	L Caudate Head*	1760
-2	-21	11	L Thalamus*	888
-64	-47	7	L MTG	800
-21	-1	-8	L Basal Ganglia	624
41	21	-4	R IFG (BA 47)	528
44	21	13	R IFG (BA 45)	464
-38	15	-14	L IFG (BA 47)	464
40	6	22	R Basal Ganglia (Put)	408
-27	3	9	L Basal Ganglia (Put)	272
23	8	-7	R Basal Ganglia (Put)	272

Happiness-Disgust				
Activation Focus			Region (>100mm^3)	Size
x	y	z		
			Happiness > Disgust	
0	38	8	L ACC (BA 24)	672
-19	-10	17	L Thalamus	624
-1	58	-1	L medFG (BA 10)*	456
-13	-6	2	L Basal Ganglia (GP)	136
			Disgust > Happiness	
31	5	-4	R Basal Ganglia (Put)*	12008
-35	15	-3	L IFG (BA 47/Insula)*	9040
-22	-71	-6	L Lingual Gyrus*	1680
-20	-3	-15	L Amygdala	1184

Happiness-Anger				
Activation Focus			Region (>100mm^3)	Size
x	y	z		
			Happiness > Anger	
0	40	8	L ACC (BA 32)*	1032
58	-41	14	R STG (BA 22)*	824
-4	-92	2	L Lingual Gyrus	576
-18	-10	17	L Thalamus	496
-3	60	0	L medFG (BA 10)*	200
-35	-32	18	L Insula (BA 13)	128
			Anger > Happiness	
-43	21	-5	L IFG (BA 47)*	1536
20	-20	-9	R PHG	808
48	13	30	R IFG (BA 9)	752
36	6	-11	R IFG (BA 13)*	344
-44	11	26	L IFG (BA 9)*	336
-11	24	-16	L medFG (BA 25)	112

Happiness-Fear				
Activation Focus			Region (>100mm^3)	Size
x	y	z		
			Happiness > Fear	
55	-46	10	R STG (BA 22)*	1592
-3	38	10	L ACC (BA 32)*	776
-18	-9	17	L Thalamus	672
-2	59	-2	L medFG (BA 10)*	592
-5	32	-3	R ACC (BA 32)	192
-37	-31	18	L Insula (BA 13)	144
			Fear > Happiness	
-21	-6	-11	L Amygdala*	3192
25	-8	-11	R Amygdala*	2600
28	-53	-9	R Fusiform Gyrus*	2072
43	3	-2	R STG*	2056
-38	22	-8	L IFG (BA 47)	896
-46	-63	-4	L Middle Occ	568

								Gyrus*	
-1	44	40	L medFG (BA 8)	904	-35	5	1	L Insula	424
-41	-59	-7	L Fusiform Gyrus*	520	38	10	20	R Insula (BA 13)*	288
27	-83	10	R Cuneus	512	43	-41	20	R Insula (BA 13)*	192
7	21	-9	R ACC (BA 32)	296	13	30	14	R ACC (BA 32)*	168
10	37	0	R ACC	224	5	48	5	R medFG (BA 10)	120
-49	36	10	L IFG (BA 46)	168					
5	26	25	R ACC (BA 24)	120					

Sadness-Anger

Activation Focus			Region (>100mm^3)	Size
x	y	z		
			Sadness > Anger	
-34	47	28	L MFG (BA 9)	2088
37	7	17	R Insula (BA 13)	1528
-12	17	-9	Left Insula*	1328
2	11	6	R Caudate Head*	912
42	-67	4	R ITG	784
-38	35	-9	L MFG (BA 11)	768
-36	49	-4	L MFG (BA 10)	736
41	-52	-24	R Cerebellum*	608
-4	-37	-3	L Cerebellum*	400
-17	-11	13	L Thalamus*	400
44	22	13	R IFG (BA 45)	328
39	22	-4	R IFG (BA 47)	328
13	-4	-6	R Basal Ganglia (GP)	256
-1	-20	11	L Thalamus*	216
-32	12	-14	L IFG (BA 13)	192
23	8	-6	R Basal Ganglia (Put)	176
-7	60	3	L medFG (BA 10)	152
33	-22	19	R Insula (BA 13)	120
			Anger > Sadness	
20	-19	-9	R PHG	2536
-44	22	-4	L IFG (BA 47)*	1976
-47	-74	-11	L Fusiform Gyrus*	1760

Sadness-Fear

Activation Focus			Region (>100mm^3)	Size
x	y	z		
			Sadness > Fear	
-4	47	28	L medFG (BA 9)*	2840
-12	18	-9	L Caudate Head*	1248
44	6	28	R IFG (BA 9)	816
-39	35	-9	L Cerebellum*	752
41	-52	-23	R MFG (BA 10)	704
2	8	62	R Precentral Gyrus	592
-37	49	-6	R Cerebellum*	560
-4	-38	-5	R Thalamus	552
-17	-11	12	R MFG (BA 11)	552
45	-63	8	R Cerebellum*	464
-47	-7	41	L Caudate Head*	456
-60	-15	-1	L MFG (BA 47)*	312
39	39	-11	R medFG (BA 10)	280
-1	-20	11	L Basal Ganglia (Put)	112
			Fear > Sadness	
-20	-7	-10	L PHG/Amygdala*	2632
24	-10	-10	R Midbrain	2504
32	-53	-9	R Fusiform Gyrus*	2328
43	1	0	R Insula (BA 13)*	1376
4	47	4	R ACC (BA 32)*	336
-38	-52	-18	L IFG (BA 47)	304

Anger-Fear

Activation Focus			Region (>100mm^3)	Size
x	y	z		
			Anger > Fear	
-47	25	-3	L IFG (BA 47)*	784
49	14	30	R MFG (BA 9)	520

Sadness-Disgust

Activation Focus			Region (>100mm^3)	Size
x	y	z		
			Sadness > Disgust	
41	6	24	R IFG (BA 9)	1584
-4	48	27	L medFG (BA 9)*	1520
40	-51	-23	R Cerebellum*	1024

-8	-34	32	L Cingulate Gyrus*	176	-5	-39	-5	L Cerebellum*	808
20	-21	-8	R PHG	152	-13	16	-10	L Insula*	800
					1	11	6	R Caudate Head*	664
			Fear > Anger		-17	-11	14	L Thalamus	536
					2	8	62	R MFG (BA 47)*	456
-21	-7	-11	L Basal Ganglia (Put)*	3688	-47	-7	41	L Precentral Gyrus	440
34	-4	-5	R Insula (BA 13)*	3512	-40	36	-8	L MFG (BA 47)	376
29	-53	-8	R Cerebellum*	2080	-38	50	-7	R MFG (BA 11)	176
-38	-53	-16	L Fusiform Gyrus*	920	-29	49	4	L MFG (BA 10)	128
3	48	5	R ACC (BA 32)*	440					
43	-40	21	R Insula (BA 13)*	304				Disgust > Sadness	
38	10	20	R Insula (BA 13)*	296					
-36	4	2	L Insula	248	-34	15	-4	L IFG (BA 47)	6392
42	34	15	R MFG (BA 46)	224	31	-4	-6	R STG (BA 22)*	6288
-21	-34	-1	L PHG*	208	36	23	1	R Insula (BA 13)*	1144
5	34	6	R ACC (BA 24)	144	-23	-70	-4	L Lingual Gyrus*	600
					-50	19	26	L IFG (BA 9)	560
					-42	-56	-8	L Fusiform Gyrus*	448
					-20	-3	-17	L PHG/Amygdala	432
					40	-58	-9	R Fusiform Gyrus	424
					-13	38	-8	L medFG (BA 10)	136
					-3	44	43	L medFG (BA 8)	112

Anger-Disgust					Fear-Disgust				
Activation Focus			Region (>100mm^3)	Size	Activation Focus			Region (>100mm^3)	Size
x	y	z			x	y	z		
			Anger > Disgust					Fear > Disgust	
-46	26	-3	L IFG (BA 47)*	544	-21	-9	-10	L Amygdala*	2264
-46	-74	-11	L Fusiform Gyrus*	480	25	-52	-8	R PHG (BA 19)*	992
19	-21	-8	R PHG (BA 35)	456	43	6	-2	R Insula (BA 13)*	600
49	16	31	R MFG (BA 9)	112	-39	-55	-16	L Cerebellum	432
					4	48	5	R ACC (BA 32)*	352
			Disgust > Anger		25	-11	-10	R Amygdala*	328
					-21	-34	0	L PHG (BA 27)*	256
32	5	-2	R Basal Ganglia (Put)*	10696	42	-40	20	R Insula (BA 13)*	208
-34	14	-3	L Insula (BA 13)	7624	13	29	14	R ACC (BA 32)*	112
-23	-71	-6	L Lingual Gyrus*	1456					
-20	-3	-16	L PHG	1008				Disgust > Fear	
-1	43	40	L medFG (BA 8)	936					
-41	-53	-8	L Fusiform Gyrus*	648	34	28	-1	R Basal Ganglia*	2328
7	21	-9	R ACC (BA 32)	280	-26	28	-10	L IFG (BA 47)	2192
10	37	0	R ACC	240	-39	4	1	L Insula (BA 13)	2088
42	-61	-6	R Fusiform Gyrus	232	27	4	-15	R IFG (BA 47)*	1792
-19	-51	-3	L PHG (BA 19)	200	28	-5	4	R Basal Ganglia*	1544
-46	-10	-21	L Temporal Lobe (BA 20)	176	-2	44	40	L medFG (BA 8)	888
-49	36	9	L IFG (BA 46)	152	-20	-71	-6	L Lingual Gyrus*	736

4	26	24	R ACC (BA 24)	144	27	-82	10	R Cuneus (BA 30)	448
42	35	16	R MFG (BA 46)*	128	-47	-44	4	L MTG (BA 22)	432
-12	38	-7	L medFG (BA 10)	128	-13	38	-7	L medFG (BA 10)	256
					11	37	-1	R ACC	136
					4	26	25	R ACC (BA 24)	120

Note: Labels (e.g. “Happiness > Sadness”) indicate regions of consistently greater activity (i.e., activation likelihood) for the first emotion relative to the second. Each cluster greater than 400mm^3 in size is reported, along with the weighted central activation likelihood focus, the region corresponding to the cluster with the highest ALE score within the cluster, and the total cluster size in mm^3. Additional clusters of interest that surpassed a threshold of 100mm^3 were also reported. L and R indicate ALE clusters located in the left and right hemispheres, respectively. Inf = Inferior, Occ = Occipital, GP = Globus pallidus = GP, Put = Putamen, PHG = parahippocampal gyrus. Brodmann area labels are provided to differentiate ALE clusters in larger regions that occur in multiple contrasts. * Indicates regions that overlapped with the re-analysis that involved only studies that used facial expressions.

Figure 3. Activation likelihood maps for pairwise emotion contrasts, representing regional activations discriminating between basic emotion states

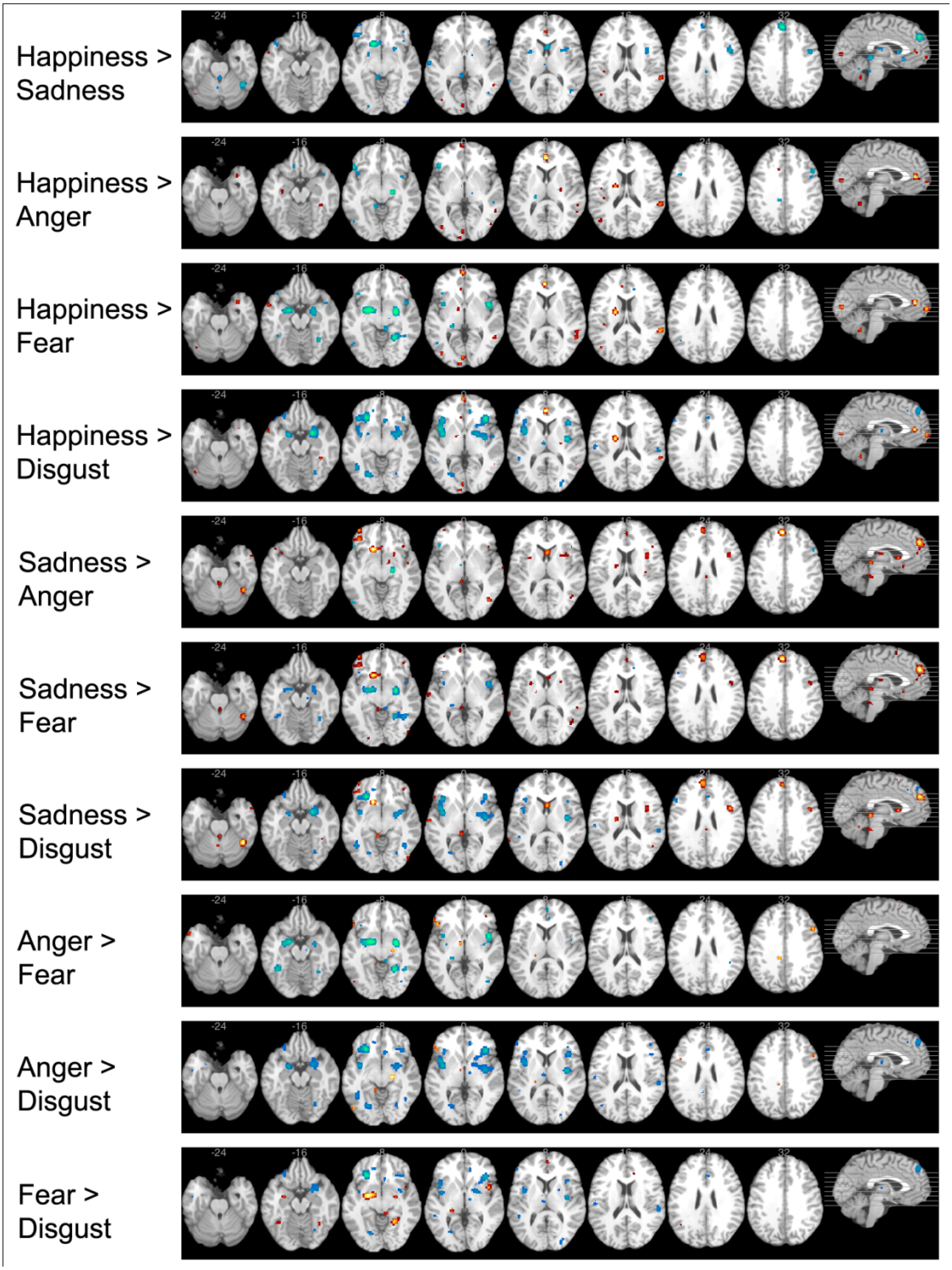


Figure Caption

Statistical maps of significant ALE clusters associated with all pairwise contrasts among emotion states. Clusters displayed in the red-yellow color gradient correspond to the emotion state that is being subtracted from in the contrast (i.e., the minuend; e.g., happiness); clusters displayed in the blue-green color gradient correspond to the emotion state that is being subtracted (i.e., the subtrahend; e.g., sadness). In the Happiness-Sadness contrast, the most prominent clusters associated with happiness are located in right STG (BA 22) and left ACC (BA 32). In the Happiness-Sadness contrast, the most prominent clusters associated with sadness are located in right MTG (BA 37) and left medFG (BA 9). In the Happiness-Anger contrast, the most prominent clusters associated with happiness are located in left ACC (BA 32) and right STG (BA 22). In the Happiness-Anger contrast, the most prominent clusters associated with anger are located in left IFG (BA 47) and right parahippocampal gyrus (BA 35). In the Happiness-Fear contrast, the most prominent clusters associated with happiness are located in right STG (BA 22) and left ACC (BA 32). In the Happiness-Fear contrast, the most prominent clusters associated with fear are located in bilateral amygdala. In the Happiness-Disgust contrast, the most prominent clusters associated with happiness are located in left ACC (BA 24) and left medFG (BA 10). In the Happiness-Disgust contrast, the most prominent clusters associated with disgust are located in bilateral amygdala. In the Sadness-Anger contrast, the most prominent clusters associated with sadness are located in left MFG (BA 9) and right insula (BA 13). In the Sadness-Anger contrast, the most prominent clusters associated with anger are located in the right parahippocampal gyrus (BA 35) and left IFG (BA 47). In the Sadness-Fear contrast, the most prominent clusters

associated with sadness are located in left medFG (BA 9) and left caudate head. In the Sadness-Fear contrast, the most prominent clusters associated with fear are located in bilateral amygdala. In the Sadness-Disgust contrast, the most prominent clusters associated with sadness are located in right IFG (BA 9) and left MFG (BA 9). In the Sadness-Disgust contrast, the most prominent clusters associated with disgust are located in bilateral insula and right STG (BA 22). In the anger-fear contrast, the most prominent clusters associated with anger are located in left IFG (BA 47) and right MFG (BA 9). In the Anger-Fear contrast, the most prominent clusters associated with fear are located in left putamen and right insula (BA 13). In the Anger-Disgust contrast, the most prominent clusters associated with anger are located in left IFG (BA 47) and left fusiform gyrus (BA 19). In the Anger-Disgust contrast, the most prominent clusters associated with disgust are located in right putamen and left insula (BA 13). In the Fear-Disgust contrast, the most prominent clusters associated with fear are located in left amygdala and right parahippocampal gyrus (BA 19). In the Fear-Disgust contrast, the most prominent clusters associated with disgust are located in left putamen and right IFG (BA 47).

2.4.2.2 Happiness-Anger

The ALE analysis of activation foci associated with happiness greater than anger revealed 6 significant clusters, with the largest (1032mm^3) located primarily in the left rostral anterior cingulate cortex (ACC) (BA 32) (see Figure 3 and Table 3). The ALE analysis of activation foci associated with anger greater than happiness revealed 6 significant clusters, with the largest (1536mm^3) located primarily in the IFG (BA 47) (see Figure 3 and Table 3).

2.4.2.3 Happiness-Fear

The ALE analysis of activation foci associated with happiness greater than fear revealed 6 significant clusters, with the largest (1592m^3) located primarily in the right STG (BA 22) (see Figure 3 and Table 3). The ALE analysis of activation foci associated with fear greater than happiness revealed 11 significant clusters, with the largest (3192m^3) located primarily in the left amygdala.

2.4.2.4 Happiness-Disgust

The ALE analysis of activation foci associated with happiness greater than disgust revealed 4 significant clusters, with the largest (672mm^3) located primarily in the left rostral ACC (BA 24) (see Figure 3 and Table 3). The ALE analysis of activation foci associated with disgust versus happiness revealed 11 significant clusters, with the largest (12008mm^3) located primarily in the right putamen (see Figure 3 and Table 3).

2.4.2.5 Sadness-Anger

The ALE analysis of activation foci associated with sadness greater than anger revealed 18 significant clusters, with the largest (2280mm^3) located primarily in the left MFG (BA 9) (see Figure 3 and Table 3). The ALE analysis of activation foci associated with anger greater than sadness revealed 3 significant clusters, with the largest (608mm^3) located primarily in the right parahippocampal gyrus (BA 35) (see Figure 3 and Table 3).

2.4.2.6 Sadness-Fear

The ALE analysis of activation foci associated with sadness greater than fear revealed 14 significant clusters, with the largest (20840mm^3) located primarily in the left medFG (see Figure 3 and Table 3). The ALE analysis of activation foci associated with fear revealed 6 significant clusters, with the largest (2632mm^3) located primarily in the left amygdala (see Figure 3 and Table 3).

2.4.2.7 Sadness-Disgust

The ALE analysis of activation foci associated with sadness greater than disgust revealed 12 significant clusters, with the largest (1584mm^3) located primarily in the right IFG (BA 9) (see Figure 3 and Table 3). The ALE analysis of activation foci associated with disgust greater than sadness revealed 10 significant clusters, with the largest (6392mm^3) located primarily in the left insula (see Figure 3 and Table 3).

2.4.2.8 Anger-Fear

The ALE analysis of activation foci associated with anger greater than fear revealed 4 significant clusters, with the largest (4784mm^3) located primarily in the left

IFG (BA 47) (see Figure 3 and Table 3). The ALE analysis of activation foci associated with fear greater than anger revealed 11 significant clusters, with the largest (3688mm^3) located primarily in the left putamen (see Figure 3 and Table 3).

2.4.2.9 Anger-Disgust

The ALE analysis of activation foci associated with anger greater than disgust revealed 4 significant clusters, with the largest (544mm^3) located primarily in the left IFG (BA 47) (see Figure 3 and Table 3). The ALE analysis of activation foci associated with disgust greater than anger revealed 15 significant clusters, with the largest (10696mm^3) located primarily in the right putamen (see Figure 3 and Table 3).

2.4.2.10 Fear-Disgust

The ALE analysis of activation foci associated with fear greater than disgust revealed 9 significant clusters, with the largest (2264mm^3) located primarily in the left amygdala (see Figure 3 and Table 3). The ALE analysis of activation foci associated with disgust greater than fear revealed 12 significant clusters, with the largest (2328mm^3) located primarily in the right putamen (see Figure 3 and Table 3).

2.4.3 Comparison with previous meta-analyses

The current meta-analysis identified consistent and discriminable patterns of neural activation associated with each basic emotion state. To further investigate the differences between the current findings and the findings of previous meta-analyses, we examined whether these differences were the result of the inclusion of additional data or

the use of a more sensitive meta-analytic method (ALE). Specifically, we compared our findings to those that would have been obtained were we to limit our data only to the studies included the previous meta-analyses. That is, we kept analysis method constant and varied the specific studies included to match the studies examined by Murphy et al. (2003). Phan et al. (2002) did not directly address the differentiability of emotion states in their analyses, and thus it was not necessary to reanalyze their data separately from that of Murphy et al. (2003).

Murphy et al. (2003) did not find that the neural correlates of happiness and sadness could be differentiated based on the distribution of activations across the eight spatial divisions of the brain they analyzed. In contrast, we found that the ALE method was able to discriminate between these two emotions, in addition to all pairwise emotion comparisons, (see Table 4) using the same dataset used by Murphy et al. Furthermore, the areas that differentiated basic emotion states when ALE was applied to the prior dataset substantially overlapped corresponding regions in the current meta-analysis. For example, seven of the ten pairwise contrasts between emotion states using Murphy et al.'s dataset revealed clusters that matched at least one of the three largest clusters for the corresponding pairwise contrasts in the current meta-analysis.

Table 4. ALE activation clusters differentiating each basic emotion state for re-analysis with reduced data set

Contrast	Regions
Happiness > Sadness	L ACC [BA 32] (1264mm^3), R MTG, L MTG, L Insula, R STG
Sadness > Happiness	R ACC [BA 24] (2096mm^3), L Caudate Head, R Insula, L medFG, L Cerebellum, L SFG, L MFG, R Insula, R MFG, L Thalamus, R medFG
Happiness > Anger	L ACC [BA 32] (1216mm^3), L Cerebellum, R MTG, L MTG, R Put, L Insula, L Thalamus
Anger > Happiness	R IFG (1552mm^3), R Thalamus, L STG, L Cingulate Gyrus, R PHG, L IFG, L Thalamus, L Cerebellum, R Cingulate Gyrus, R MFG, L MFG
Happiness > Fear	L ACC [BA 24] (1240mm^3), R MTG, L medFG, R STG, R Posterior Cingulate, L Insula, R ACC [BA 32]
Fear > Happiness	L Amygdala (3504mm^3), R Insula, R Put, R Thalamus, R Cingulate Gyrus, L SFG, L IFG, R PHG, L Thalamus
Happiness > Disgust	L ACC [BA 24] (2528mm^3), L medFG, L Cerebellum, R MTG, L MTG, R STG, R Supramarginal Gyrus, L GP, L ACC [BA 32], L Thalamus, L Insula, R Put
Disgust > Happiness	L Insula (3024mm^3), R STG, R Put, R Postcentral Gyrus, R Cuneus, L Thalamus, R IFG (Insula)
Sadness > Anger	L MFG (1068mm^3), R MFG, R Caudate Head, R Insula, L medFG, L Thalamus, R IFG, L MTG
Anger > Sadness	L IFG, (2256mm^3), R Cingulate, L Fusiform Gyrus, R PHG
Sadness > Fear	L Caudate Head (912mm^3), R MFG, R IFG, R Thalamus, R Cerebellum, L Put
Fear > Sadness	L Amygdala (2734m^3), R Insula, R Fusiform Gyrus, L IFG
Sadness > Disgust	L medFG (856mm^3), R Caudate Head, L Cerebellum, L Thalamus, R MFG, L MFG, L med FG
Disgust > Sadness	R STG (5478mm^3), L Insula, L Amygdala, R Insula, L Fusiform, R Insula, R Put
Anger > Fear	L IFG (982mm^3), L MFG, R MFG, L Cingulate Gyrus
Fear > Anger	R Insula (4913mm^3), L Put, L Amygdala, R ACC [BA 32], L Insula, L Fusiform Gyrus, L PGH, L Thalamus
Anger > Disgust	L IFG (1092mm^3), L STG, L Fusiform Gyrus, R PHG, L Cerebellum, R ACC [BA 32], L Cingulate Gyrus, L Thalamus, L MFG, R MFG, R Cingulate Gyrus, L Put, L medFG
Disgust > Anger	R STG (1608mm^3), R GP, R Postcentral Gyrus, L Thalamus, R IFG (Insula), L MTG
Fear > Disgust	L Amygdala (4544mm^3), R Cingulate Gyrus, L SFG, R Insula, R Precentral Gyrus, L Thalamus, R Thalamus, R Fusiform Gyrus, L IFG, R STG, R PHG, R Put, R Thalamus, R ACC [BA 32]
Disgust > Fear	R Put (2200mm^3), L GP, R Postcentral Gyrus, L Insula

Note: Each cluster greater than 400mm^3 is reported. The region corresponding to the largest cluster is reported first, with the total cluster size listed in parentheses. Additional clusters of interest that surpassed a threshold of 100mm^3 are also reported. L and R indicate ALE clusters located in the left and right hemispheres, respectively. Inferior is abbreviated as Inf, globus pallidus is abbreviated as GP, putamen is abbreviated as Put, parahippocampal gyrus is abbreviated as PHG. Brodmann areas are provided to differentiate activations in larger regions that occur in multiple contrasts.

In summary, we were able to differentiate between each of the basic emotions with the smaller dataset, even in cases where this was not possible in the original study, which used a different meta-analysis method. In addition, there was notable overlap between the results of the ALE analysis using the Murphy et al. dataset and the results of the current ALE meta-analysis. These results suggest that the greater sensitivity of the ALE method contributed an increased ability to discriminate between emotion states in the current meta-analysis. Furthermore, comparison of the results obtained with both datasets confirmed that the substantially larger number of studies we examined relative to previous studies also contributed significantly to the analysis, by allowing additional ALE clusters to be identified that discriminated between basic emotions.

2.4.4 Role of stimulus differences

The studies contributing to the activation foci in the ALE analysis employed a wide range of experimental materials and methods to examine emotion, such as facial expressions of emotion, emotional pictures, films, and scripts. Because studies differed in the frequency with which they used specific types of stimuli and elicitation methods, we examined whether such methodological differences could have contributed to the neural differences observed here. Notably, facial expressions of emotion were the most frequently used stimulus type for studies examining all basic emotions except for disgust, where facial expressions were the second most frequent stimulus type. Specifically, facial expressions were used as stimuli in 14 of 30 happiness studies, 11 of 33 sadness studies, 10 of 16 anger studies, 24 of 37 fear studies, and 9 of 29 disgust studies (11 of 29 disgust studies used picture stimuli). Because of insufficient numbers of associated studies, it was

not possible to examine the differential effects of every type of stimulus. Accordingly, we focused on the potential role of the most commonly used stimulus type, facial expressions.

To investigate the potential effects of stimulus material on the activation patterns associated with a given emotion, we conducted the ALE analysis a second time, including only those studies that used facial expressions as stimuli. In this way, we ruled out the possibility that systematic differences in stimulus type could contribute to activation differences differentiating basic emotions. Based on the hypothesis that stimulus differences did not contribute significantly to our original ALE results, we expected to obtain roughly similar results when we controlled for stimulus differences in this manner, though we also expected that the results would differ somewhat due to smaller number of studies. The results of this re-analysis confirmed that the ALE results obtained with studies employing facial emotion stimuli were similar to the results of the original analyses for each basic emotion. Overall, there was substantial overlap in the number of regional clusters identified in both analyses (Table 2). Furthermore, the regions that were central to the differentiation of each basic emotion state in the original analyses were also typically significant in the analysis limited to studies using facial emotion stimuli (Table 3). These results suggest that differences in stimulus type did not drive the primary finding of significant differentiation of emotion states, because when the potential effects of stimulus differences were eliminated, the characteristic patterns of neural activation associated with each basic emotion were still observed, and each basic emotion could still be differentiated on the basis of regional activations.

2.5 Discussion

The primary goal of this study was to assess the extent to which the current neuroimaging literature supports the proposal of basic emotion theories that different basic emotion states are associated with consistent, characteristic and discriminable patterns of brain activity. The results of the ALE meta-analysis supported the predictions of basic emotion theories. Each of the basic emotion states examined (anger, fear, sadness, anger, disgust) was consistently associated across studies with characteristic patterns of regional brain activity. For example, across a variety of different experimental paradigms and stimuli, we found that fear was associated with increased activation in the amygdala and insula, relative to emotionally neutral stimuli. Importantly, each basic emotion was reliably distinguished or differentiated from the other emotions on the basis of its characteristic pattern of brain activation. Specifically, every pairwise statistical contrast between the activation foci associated with emotion states (e.g., fear vs. anger) in the ALE analysis yielded a set of regional brain activations that reliably differentiated between each pair of emotions. Further, as predicted, the signature patterns of neural activation that characterized each emotion also most consistently differentiated that emotion from other emotions. This is in contrast with other possible scenarios, for example, where the regions that differentiate between emotions could have little overlap with the core, characteristic brain regions consistently activated by each emotion. Finally, the associations between emotion states and regions of brain activation identified in our ALE meta-analysis of the neuroimaging literature converge with the findings from other approaches including neuropsychological studies (e.g., Adolphs, Tranel, Damasio, and Damasio, 1994) and studies of nonhuman animals (e.g., Davis, 1992; 1994).

The current meta-analysis found that all five basic emotion states were associated with consistent and discriminable patterns of neural activation (Figure 3). Happiness consistently activated rostral ACC and right STG, and activity in both regions differentiated happiness from sadness, anger, fear and disgust (ACC only). Sadness consistently activated MFG and head of the caudate/subgenual ACC, and activity in both regions reliably differentiated sadness from happiness, anger, fear, and disgust. Anger consistently activated IFG and PHG, and both regions differentiated anger from all other emotion states. Fear consistently activated amygdala and insula, and these regions differentiated fear from happiness, sadness, anger (insula only), and disgust (posterior insula). Disgust consistently activated IFG/anterior insula, and these regions reliably differentiated disgust from all other emotion states. Together, these findings support the predictions of basic emotion theories by demonstrating that basic emotion states are associated with consistent patterns of brain activation and that these patterns differ significantly between emotions.

In contrast to the current meta-analysis, two previous meta-analyses (e.g., Phan et al., 2002; and Murphy et al., 2003) found more limited support for basic emotion theories. Phan et al., using a meta-analytic method based on counts of activated regions, found limited evidence for consistent associations between brain regions and basic emotions. For example, fear was more consistently associated with amygdala activation than any other emotion state, and sadness exhibited a greater association with subcallosal cingulate cortex activation in comparison to other emotions. Anger, happiness, and disgust did not consistently activate any brain region more than other emotions states. However, Phan et al. did not directly contrast activation patterns associated with each

basic emotion, so the extent to which these activations composed patterns that discriminated between basic emotions could not be addressed. Murphy et al. (2003) did address this question, and found reliably different spatial patterns of activation neural correlates for fear (amygdala), disgust (insula) and anger (globus pallidus and lateral OFC). However, happiness and sadness were not reliably differentiated, and the spatial divisions used in that study were too large to address the issue of discriminability at the level of specific brain regions.

Our meta-analysis differed from these previous meta-analyses in two important ways. We included a substantial amount of new data from thirty studies that were not included in the largest meta-analysis to date, and we used the more spatially sensitive ALE method. To determine the extent to which our method (ALE) vs. the inclusion of more data contributed to the increased ability to differentiate between neural patterns associated with basic emotions, we used the ALE method to analyze the smaller dataset analyzed by Murphy et al. and compared the results to those of the current meta-analysis. The results demonstrated that the ALE method was able to differentiate between all of the emotion states, including the pair of emotions that the previous meta-analysis was not able to differentiate, and suggested that both the increased sensitivity of the ALE method as well as the inclusion of additional studies contributed to the increased ability to discriminate among emotions.

Converging evidence from several domains suggest that discrete basic emotions are psychologically, physiologically and neurologically discriminable (e.g., Ekman et al., 1983, Murphy et al., 2003, Rainville et al., 2006). For example, therapeutic intervention studies of depression have demonstrated that reduction in depressive symptoms is

associated with increased activity in BA 24 (cingulate cortex), when deep brain stimulation or cognitive behavioral therapy (CBT) is used (Goldapple et al., 2004; Mayberg et al., 2005) and decreased activity in BA 9 (medial frontal cortex), when CBT is used (Goldapple et al., 2004). Mood fluctuations associated with happiness versus sadness may be supported by subregions of BA 24 (e.g., subgenual ACC) (Mayberg et al., 2005) that have subcortical projection to the brainstem and thalamus (areas that are involved in circadian rhythm maintenance) (Barbas et al., 2003; Ongur, An, & Price, 1998). These findings correspond with our results that implicate ACC (BA 24) and medFG (BA 9) are uniquely associated with happiness and sadness, respectively. Similarly, our results suggest an important role for IFG in anger, and this finding is complemented by the results of neuropsychological studies which indicate that damage to the IFG can increase violent and aggressive behaviors, consistent with a proposed regulatory role for the IFG in the expression of anger (Damasio et al., 1994; Grafman et al., 1996). The IFG may be engaged during exposure to angering stimuli as an automatic control to curb the potential for an overreaction such as unbridled rage. In addition, we found that disgust was associated with activity in the insula, and stimulation of this region has been shown to induce nausea (Penfeld & Faulk, 1955) and unpleasant sensations in the throat mouth and nose (Krolak-Salmon et al., 2003); both of which are involved in the experience of disgust. The visceral feeling that people experience in response to a disgusting stimulus may therefore reflect automatic simulation of these sensations, supported by the insula. Finally, the current meta-analytic review confirmed an important functional role for the amygdala in fear. The relationship between the amygdala and fear is perhaps the most robust structure-function association found across

studies, with converging evidence from meta-analyses of neuroimaging studies (e.g., Murphy et al.; Phan et al), animal models of fear (Davis, 1994), single-unit recording studies (Maren, 2001), and human lesion studies (Adolphs, Tranel, Damasio, & Damasio, 1994). The amygdala has been shown to direct attention to threat cues by modulating activity in primary visual cortex, as evidenced by effective connectivity (Pessoa et al., 2002) and lesion research (Vuilleumier et al., 2004). In addition, it has been suggested that amygdala activity may also indirectly influence thought and behavior through the modulation of prefrontal activity (Miller & Cohen, 2001), although this claim requires further exploration. A fearful response to a threatening stimulus may recruit the amygdala in order to focus attention to relevant cues and initiate an appropriate response to the threat.

Although our goal was to investigate the neural activations associated with basic emotions across a variety of contexts and elicitation methods, it is important to note that specific stimulus types were represented more than others in the studies comprising our meta-analysis. For example, facial emotion stimuli were the most frequently used type of stimulus in studies of happiness, sadness, anger, and fear. To examine the potential influence of stimulus differences on the results of our meta-analysis, we conducted an additional ALE analysis limited to studies that used facial expressions as stimuli. The results demonstrated that all five basic emotions were associated with unique and reliable patterns of neural activation, even when the analysis was limited to one stimulus type. Furthermore, the regions identified by this analysis overlapped with the regions identified by original consistency and discriminability analyses. These findings suggest that the primary finding, that the ALE analysis could differentiate among basic emotions on the

basis of neuroimaging evidence, was not driven by stimulus material. Although we acknowledge that the overlap between the original ALE analyses and the faces-only ALE analyses illustrates the large contribution of the facial expression data to the original ALE findings, 1) there was not absolute overlap between the original ALE analyses and the analysis examining the role of stimulus differences, and 2) an examination of the remaining data when facial expressions were excluded from the analysis demonstrated similar differentiation of basic emotions to that of the original ALE analyses and the ALE analysis with faces only, indicating that the original ALE findings were not simply a product of the facial expression studies.

Regarding limitations of this study, the spatial sensitivity of the current meta-analysis was limited by the resolution of the neuroimaging data in the studies analyzed (approximately 64 cubic mm voxels for fMRI), and subsequent data processing steps and summarization for publication further reduced the effective spatial resolution in individual studies. Another potential source of bias was the fact that a small minority of studies (12% of foci from all studies) gave preference in their analyses to a priori regions of interest by using more lenient thresholds for these regions, which would tend to increase the representation of these regions in the ALE analysis. Notably, the majority (72%) of these studies examined the neural correlates of fear and disgust, and thus any potential bias would be primarily limited to these two basic emotions. We examined the effect of excluding these foci obtained with more lenient thresholds from the ALE analyses, and found that their exclusion resulted in minimal and non-significant changes in the outcome of the meta-analysis.

The ALE method also makes some simplifying assumptions that may affect the

relative influence of individual activations and individual studies. All activation maxima above the significance threshold adopted in a particular study are given equivalent weight in the analysis, so that variations in activation intensity are not accounted for. Similarly, studies with greater numbers of activation maxima will contribute more towards the ALE map than studies with fewer maxima, though inspection of our individual studies did not reveal any systematic relationship between number of maxima per study and the results of the consistency and discriminability analyses. In addition to these considerations, the requirements of the analysis (e.g., analyses of whole-brain data) necessarily limited the number of studies that were included in the review. Another potential limitation includes publication biases such as the file-drawer problem (tendency for null findings not to be submitted), which is unavoidable.

The ALE approach taken here assessed correspondences between emotional processing and individual brain regions, rather than networks of regions. However, interactions between brain regions have been demonstrated to contribute importantly to emotion processing, and thus future meta-analyses should examine interactions and functional networks. Furthermore, we cannot conclude that these results reflect brain regions associated with the induction of basic emotion states because, like all previous meta-analytic studies, we included studies that addressed a wide range of emotion-related processes so that we could investigate the core neural signatures associated with basic emotions across a variety of contexts. Due to the fact that the majority of neuroimaging studies have used facial expressions to explore emotional processing, it will be important for future neuroimaging research to focus on investigating basic emotions using a wide range of methods and stimuli in order for experience of basic emotions to be more wholly

described. As the neuroimaging literature grows to incorporate a more diverse collection of methods exploring the neural correlates of basic emotions, it will be possible to better examine the effects of induction method and stimulus material on the patterns that characterize and differentiate emotion states. Although we focused on differentiating basic emotions on the basis of brain activation patterns, a recent meta-analysis used a complementary approach and a different voxel-based meta-analytic method (multilevel kernel density analysis [MKDA]) to explore the functional grouping of emotion-related activations in the brain (Kober et al., 2008). This study used a data-driven approach that ignored emotion labels such as happiness and sadness, and instead investigated the multivariate patterns of co-activation that emerged when activations from neuroimaging studies of emotion are examined (they identified six functionally distributed networks). Because Kober et al. (2008) explicitly avoided analyzing activations on the basis of basic emotion categories, it is difficult to compare their results with those of the current study.

The current meta-analysis also did not examine contextual, linguistic, and other influences on emotion states and their neurobiological correlates. We acknowledge that the experience and interpretation of emotional states can be strongly influenced by situational factors, both internal and external, and thus brain activity would be expected to reflect these factors. However, we sought to investigate the reliability of neural patterns associated with basic emotion categories, and thus did not explore the factors contributing to their variability here.

Emotions have been characterized by both dimensional and categorical theoretical frameworks. Dimensional views of emotion have proposed that emotions can be characterized in terms of component dimensions such as arousal (emotional strength) and

valence (pleasantness vs. unpleasantness). The dimensional approach to emotion has proven highly successful in accounting for a wide range of emotional phenomena and is theoretically more parsimonious than categorical approaches such as basic emotion theories (Lang, Bradley, & Cuthbert, 1990; Watson & Tellegen, 1985). Although dimensional and basic emotion theories have sometimes been characterized as being incompatible in some respects (e.g., Barrett, 2006), they are not necessarily mutually exclusive characterizations of emotional experience. A hybrid view combining dimensional descriptions of emotion states in terms of arousal and valence with additional characterization provided by basic emotion categories would be consistent with the current findings. For example, whereas a dimensional description in terms of arousal and valence can concisely characterize key aspects of emotional reactions to a photograph eliciting disgust, the basic emotion categorization of disgust captures facets of the experience of disgust not conveyed by the dimensional description, such as a somatic state of nauseation, elicitation of a facial expression of disgust, and CNS activation of the consistent and discriminable regional brain activations identified in the current study. Regarding the neural substrates corresponding to affective dimensions, several neuroimaging studies have identified discriminable neural correlates of emotional arousal (e.g., amygdala) and valence (e.g., subregions of prefrontal cortex) (Anderson, Christoff, Panitz, et al., 2003; Dolcos, LaBar, & Cabeza, 2004; Lewis, Critchley, Rotshtein, and Dolan, 2007). Taken together, the results of these studies and the current meta-analysis results indicate that both dimensional views and basic emotion views are supported by neuroimaging studies in the sense that the constructs associated with each view have identifiable neural correlates as assessed with neuroimaging. Further research

into the interplay between neural mechanisms underlying basic emotions and corresponding mechanisms associated with arousal and valence dimensions will help elucidate how each contributes to emotional experience and behavior.

2.6 Conclusions

When considered on a summary level across studies, the current neuroimaging literature supports the proposal that basic emotions have characteristic and unique neural correlates. Despite inconsistencies between previous meta-analyses and equivocal support for this claim in the past (e.g., Murphy et al., 2003, Phan et al., 2002), we have demonstrated full differentiation of five basic emotion states using a technique with increased spatial resolution and including a large body of data published after the most recent review. However, this claim has yet to be evaluated in the context of an experiment, where the neural responses can be evaluated across emotion states in a single group of individuals. In addition, although there has been some degree of variability in the types of stimuli used to study basic emotions, basic emotion research has been dominated by the use of facial expressions to elicit emotions (in part, because such research grew out of cross-cultural labeling of basic emotion expressions [Ekman, & Friesen, & Ellsworth, 1972; Izard, 1971]). The use of static expressions severely limits what conclusions one can make regarding such data; emotions are powerful, visceral, and elicited by a wide range of contexts (both internal and external) and should be studied using more ecologically valid methods. The following chapter addresses these critiques and attempts to extend the support for basic emotion theory to more naturalistic stimuli, further reinforcing the importance of acknowledging basic emotions at both the

psychological and neural level.

Chapter 3

Study 2: Neural Correlates of Basic Emotion States Elicited by Films and Memories

3.1 Precis

Ekman (1999) proposed that basic emotion states (i.e., happiness, sadness, anger, fear, and disgust) elicit characteristic and distinctive patterns of physiological and CNS activity. A recent quantitative meta-analytic review (Vytal & Hamann, in press) examined multiple neuroimaging studies and found that basic emotion states are associated with characteristic and dissociable activation patterns. However, the question of whether such dissociable activation patterns exist has not been investigated previously by directly contrasting each basic emotion within a single functional magnetic resonance imaging (fMRI) study. We used fMRI to scan 15 subjects (8 female) participants while they experienced basic emotion states elicited during alternating runs of films and autobiographical memories. Following each trial, subjects rated their elicited emotional state on valence, arousal, and emotion category. Ratings confirmed that the emotional stimuli were effective in eliciting the intended emotional responses. Results demonstrated that basic emotion states elicited distinctive and characteristic patterns of activation (e.g., sadness: caudate head, ACC disgust: insula) with the caveat that fear is variably associated with core activity depending on how it is assessed. Additionally, variability in these core patterns was associated with elicitation method (film vs. memory) and with personality and mood variables. These findings converge with previous evidence from other domains and provide further support for the proposal that basic emotions are associated with characteristic patterns of neural activation. In addition, they highlight the necessity to describe emotions on multiple levels (e.g., brain and physiology) and across different contexts to fully characterize emotional experience.

3.2 Introduction

Basic emotion theory proposes that certain emotions (e.g., happiness, sadness, anger, fear and disgust) are associated with characteristic profiles of nervous system activity (Ekman, 1999). Evidence in support of this claim has been provided by physiological research (e.g., Ekman et al., 1983; Rainville et al., 2006), neuroimaging research (e.g., Damasio et al., 2000) and meta-analytic reviews of these data (e.g., Murphy et al., 2003, Vytal & Hamann, in press). These findings suggest that there is truth to the claim that basic emotions are embodied (i.e., that they exhibit and are defined by their bodily states); however, inconsistencies both within and across studies have failed to lend clarity to how we experience emotions. Despite recent success using summary datasets to determine neural patterns associated with basic emotion states, experimental approaches to the study of basic emotions have struggled to identify and differentiate these patterns, primarily because of failure to successfully sustain and exclusively elicit these states. The widespread use of emotional facial expressions (approximately 50% of neuroimaging studies of emotion) has eclipsed the use of more sensory-rich emotional stimuli, which themselves present their own problems of emotional and temporal complexity. As a result, outside of meta-analytic evidence, the most robust support for basic emotions is provided by cross-cultural and developmental studies that demonstrate consistency in recognition of basic emotion expressions (e.g., Etcoff & Magee, 1992; Izard, 1994; Ludemann & Nelson, 1988). Undoubtedly, these findings are not persuasive evidence in support of basic emotion states as robust psychological and physiological phenomena. The objective of the current study was to resolve critiques of the support for basic emotion theory, to strengthen the existing behavioral data by approaching basic

emotions from a biological perspective, and to explore the neural signatures of emotion basic states elicited by personally-relevant autobiographical memories and emotionally powerful film clips.

Research supporting basic emotions has recently been scrutinized (Barrett & Wager, 2006; Cacioppo et al., 2000) on the basis of inconsistent findings across studies and between meta-analyses (e.g., Murphy et al., 2003, Phan et al., 2002). Previous meta-analyses of neuroimaging evidence, which have endeavored to offer clarity to the question of how best to describe affective experience, have at best, presented evidence in partial favor of the basic emotion view (see Table 5 for a comparison of results between meta-analyses). Phan et al found that certain emotion states (i.e., anger) were not associated with any reliable activity in the brain, and other states (i.e., happiness and sadness) were associated with overlapping patterns of activation and a lack of unique activations, rendering them inseparable. When findings are compared across studies, patterns of neural activity that seemed stable (e.g., lateral OFC activity associated with anger; Murphy et al.) are either different (e.g., IFG activity associated with anger; Vytal et al.) or non-existent in other reviews (e.g., Phan et al.). Further, when reviews were able to consistently find a primary region of activation associated with a basic emotion state, there was little correspondence among the regions identified for each basic emotion state; fear was the only emotion that was associated with activity in the same region (amygdala) across meta-analyses.

Table 5. Emotion-specific brain activations identified by previous and current meta-analyses

	Phan et al. (2002)		Murphy et al. (2003)		Vytal et al. (in press)	
	N	Brain Areas	*N*	Brain Areas	*N*	Brain Areas
Happiness	11	Basal Ganglia	11	Supracallosal ACC	30	ACC
Sadness	14	SCC	14	Supracallosal ACC	33	Caudate head
Anger	5	None	8	Lateral OFC	16	IFG
Fear	13	Amygdala	26	Amygdala	37	Amygdala
Disgust	5	Basal Ganglia	7	Insula & GP	27	Insula

Note. Table adapted and extended from Barrett et al. (2006). Supracallosal anterior cingulate cortex (ACC) is more specifically defined as rostral supracallosal ACC/dorsomedial PFC, and insula activation in Murphy et al. extends into the operculum. ACC activation in the current study was more specifically defined as rostral ACC activation (BA 24).

Despite inconsistencies, it is important to note that Vytal et al. was successful in characterizing and differentiating all five basic emotion states. Happiness consistently activated rostral ACC and right STG; sadness consistently activated MFG and head of the caudate/subgenual ACC; anger consistently activated IFG and PHG; fear consistently activated amygdala and posterior insula; disgust consistently activated IFG/anterior insula. Further, the regions that were associated with each basic emotion also differentiated it from all of the other basic emotions. Meta-analyses have not demonstrated consistency, but results from the latest review demonstrated that this type of quantitative summary has shown that the current corpus of data supports basic emotion theory.

On an individual level, neuroimaging studies have not typically attempted to characterize basic emotion states; rather, the focus has tended toward one or two emotions in the context of a different question (e.g., the differences in neural activation between disgust and fear as they apply to clinical interventions for depression and anxiety disorders; Liotti et al., 2000). Although interesting in their own right, these studies cannot fully describe emotional experience because they fail to characterize a variety of emotion states. Further, when only investigating the neural correlates of one or two states concurrently, less meaningful differences can be drawn about the differentiability of such patterns because the comparisons are being made between only two or three emotions. For example, a study may find that sadness activates ACC and medFG, whereas fear activates the amygdala and insula. These findings can demonstrate that sadness and fear have seemingly unique neural correlates, yet they would have overlooked the potential that sadness and happiness might both activate ACC and fear and disgust may both

activate the insula. It is therefore critical to consider multiple basic emotion states in a single paradigm so that the similarities and differences among the neural correlates of basic emotions can be fully captured.

Damasio et al. (2000) took this approach and investigated the neural signatures of happiness, sadness, anger, and fear using [^{15}O] positron emission tomography (PET), with the goal of identifying brain activity that organizes and controls internal biological states. They predicted that areas like the somatosensory cortices and midbrain would be commonly active during the self-generation of these emotional states, supporting the idea that they are grounded in the viscera. Not only did the findings support their hypothesis (re-experiencing personal life episodes engaged regions like the pons, midbrain, hypothalamus, insula and secondary somatosensory cortex) but they also demonstrated that these basic emotion states were associated with reliable neural correlates in a post-hoc whole brain analysis. Although they did not use pairwise contrasts to differentiate basic emotion states, they were able to distinguish regions that characterized one emotion state from neutral but not another. For example, they found that sadness was associated with left caudate activity, anger was associated with left motor cortex activity, and fear was associated with left thalamus activity. These findings are the foundation of what this study has attempted to demonstrate.

First, we investigated the consistent neural signatures associated with basic emotion states by duplicating one part of Damasio et al.'s analysis: we compared each emotion states to neutral using a variety of methods. Second, we directly compared each emotion state in pairwise contrasts to identify which regions were involved in reliably differentiating each basic emotion state. Third, we focused our analysis to regions of

interest, based on the regions that were shown to characterize and differentiate basic emotion states in the Vytal et al. meta-analysis. This approach allowed us to examine the signatures of basic emotion states from multiple directions to satisfy several predictions regarding basic emotion states in the brain.

In addition to investigating the neuroimaging evidence in support of basic emotion theory, we were also motivated to explore the physiological patterns associated with basic emotion states because of a similar trend in recent findings. Although a meta-analysis of psychophysiological studies of basic emotions (Cacioppo et al., 2000) concluded that the body of evidence in this domain is equivocal, three studies (Christie & Friedman, 2004; Rainville et al., 2006; Wilson & Hamann, 2010) have demonstrated that with the use of more sophisticated analyses, basic emotion states appear to have differentiable profiles of autonomic nervous system (ANS) activity. Christie et al. (2004) recorded skin conductance, blood pressure and ECG while subjects viewed films that evoked amusement, anger, contentment. Using pattern classification analyses, they demonstrated emotion-specific autonomic patterns for all emotions except disgust. Rainville et al. also used a multivariate analysis to show that happiness, sadness, anger, and fear could be differentiated on the basis of variables derived from cardiovascular and respiratory measures. Their subjects recalled one or two emotional events from the past, and a between-subjects multivariate analysis of factors revealed discrete patterns of physiological activity associated with all four basic emotion states. Wilson et al. applied the analytic techniques of Rainville et al. in order to replicate and extend their findings to all five basic emotion states. Subjects watched emotional film clips similar to those used in the current study and recalled emotional autobiographical memories while ECG,

respiration and impedance cardiogram data were recorded. Only the cardiorespiratory variables were successful in differentiating basic emotion states; a PCA followed by MANOVA found that differences in slow and fast heart-rate variation (HRV), coupled with or without changes in respiration rate differentiated happiness, sadness, anger, fear, and disgust.

Although Christie et al.'s multivariate approach has been successfully replicated in Rainville et al. and Wilson et al., their findings were not. Across studies, PCA components reflecting respiratory frequency and slow HRV were observed, but the directions in which the variables were coupled, as well as the emotion states they were concluded to represent, differ from study to study. Further, unlike the previous studies, Wilson et al. was unable to detect differences in heart rate (e.g., R-R interval) that corresponded with particular emotion states. Finding consistency in these patterns is necessary to demonstrate that they are core responses, yoked to these states. As a consequence, the current study sought to clarify these findings by exploring the cardiorespiratory patterns associated with the experience of watching emotional films. The use of films (versus autobiographical memories) introduced greater consistency across the stimuli used to elicit basic emotions, increasing the potential that reliable patterns could be detected. By approaching the characterization of basic emotions at two levels of biological study (the autonomic nervous system and the brain), we were able to detect corresponding differences that no previous study has ever attempted to investigate.

In addition, we included variables in our study that allowed us to address questions of individual and modality-specific differences in emotional responses. It is essential to describe the variability of emotional responses to capture the true nature of

emotions. This includes exploring how individual differences in internal states and perspectives are associated with changes in emotional responses in the brain. For example, Canli et al. (2001) and Hariri et al. (2004) have both demonstrated that personality variables modulate emotion-related responses in the amygdala. Individuals who were high on neuroticism tended to exhibit greater amygdala activation when they were exposed to negative stimuli, and individuals high on extraversion tended to exhibit greater amygdala activation when they were exposed to positive stimuli. Anecdotally, it is clear that we respond in different ways to similar or even identical situations. This point is extremely transparent when we turn to cases of emotional pathology. By honing in on what drives the variability in emotional responding to both internal and externally generated catalysts we will be better equipped to address the clinical cases that deviate even further from the mean. Ultimately, this investigation served to clarify the central tendencies and variability in how we process basic emotion states as well as to demonstrate whether or not basic emotions are useful categories with which to describe affective responses.

3.2.1.1 Hypotheses

3.2.1.1.1 Neuroimaging of Basic Emotions

Based on the results of neuroimaging experiments (e.g., Damasio et al, 2000) and meta-analyses (e.g., Vytal & Hamann, in press) that have indicated specific patterns of neural activation are associated with basic emotion states, we predicted that all basic emotion states (happiness, sadness, anger, fear, and disgust) would elicit reliable patterns of neural activation. We also predicted that basic emotion states would elicit patterns of

neural activation that are distinct from one another. Further, we predicted that regions comprising the signature core pattern of a particular emotion would also tend to discriminate it from other emotions. Regions that reliably characterized and differentiated emotion states in the meta-analysis were selected as regions of interest (ROIs) (happiness: right STG, left ACC; sadness: left and right caudate; anger & disgust: left IFG; fear: left and right amygdala, left and right posterior insula; disgust: left and right anterior insula).

3.2.1.2 Robustness of Neural Patterns Across Elicitation Methods

We predicted that modality-specific activations (e.g., visual cortex in response to film clips versus memory recollection) would surface when emotion states were considered based on how they were elicited. However, we expected the principal activations reflecting each basic emotion state to remain unaltered following a change in paradigm.

3.2.1.3 Psychophysiology

In addition to predicting core neural patterns associated with basic emotion states, we predicted that basic emotion states would be associated with differentiable patterns of ANS activity. Based on previous research (e.g., Rainville et al., 2006), we expected that a multivariate approach (i.e., principal component analysis (PCA) followed by multivariate analysis of variance (MANOVA)) would identify these patterns.

3.2.1.4 Individual Differences

Previous research has demonstrated personality factors are correlated with neural activity to emotional stimuli. Based on Canli et al., (2001) and Hariri et al. (2004), we predicted that individuals high on neuroticism and negative mood would exhibit greater amygdala activation, higher arousal ratings, and more negative valence ratings to fearful and disgusting stimuli than those low on neuroticism and negative mood. Similarly, we predicted that individuals high on extraversion and positive mood would exhibit greater amygdala activation, higher arousal ratings, and more positive valence ratings to happiness stimuli than those low on extraversion and positive mood.

3.3 Methods

3.3.1 Subjects

Sixteen healthy right-handed adults (8 female) free from any history of neurological or psychiatric impairment, and with English as a first language, were recruited on the Emory University campus. All subjects were paid for their participation. Written informed consent was acquired from subjects under a protocol that was approved by the Emory University Institutional Review Board. Fifteen subjects (8 female), with a mean age of 24.4 years successfully completed the fMRI session. One subject was excluded due to excessive motion. Psychological data were successfully recorded from 9 subjects (6 female), with a mean age of 22 years. Seven subjects were excluded due to problems with either ECG or respiration acquisition. A separate group of pilot subjects (n=10, 5 female) of similar age were recruited through the Psychology Research Participants pool at Emory University for a pilot study that determined the most emotionally evocative film clips unique to each basic emotion state.

3.3.2 Stimuli

The stimuli consisted of short film clips and autobiographical memories. Thirty-five film clips were selected based on results from a pilot study that identified 20 emotionally neutral and 3 emotionally arousing clips for each basic emotion state (15 total) (see Appendix A for a detailed description of the pilot study). Films clips were extracted from high-resolution videos on YouTube (http://www.youtube.com) and from DVDs. Neutral clips were matched on social content and were taken from the same movie or series as emotional clips when possible to better equate other dimensions (e.g., environment, characters). Examples of emotional film content included a young child getting shot in the arms of her father, family members embracing after being apart for a long time, and a character vomiting entrails. All films were presented in approximate wide-screen format to maximize size (see Appendix B for a detailed description of stimulus selection and presentation for both film clips and autobiographical memories).

Thirty-five autobiographical memories (20 neutral, 15 emotional) were selected by each participant. Subjects were asked to select memories from their recent and far past (i.e., >3 years ago) that specifically evoked each basic emotion state, as well as ones that were emotionally neutral. Emotional memories were reviewed to verify that they met the following conditions: 1) sufficiently detailed, 2) recollectively vivid (as rated by the participant), 3) situated in a specific place and time (i.e., not repetitive), 4) emotionally arousing, 5) specific to one basic emotion state (e.g., a memory that elicits sadness should not elicit any of the other basic emotions). Examples of emotional memories included watching a father being sent to jail, talking to a sibling who is attempting suicide, and

having sexual intercourse for the first time. Emotionally neutral memories were required to meet similar criteria except that they were expected to be emotionally unarousing. Examples of neutral memories included attending a sibling's school performance, baking cookies as a Resident Advisor for a dormitory hall, and grocery shopping for dinner ingredients with a roommate. Subjects selected brief 1-3 word cues to refer to each memory. Cues were later presented as reminders in the scanner during the recall period.

3.3.3 Trial structure

Film clip trials began with a brief (500ms) fixation cross followed by a 20s film and two 3-second ratings (see Figure 4). During the film clip, subjects were instructed to press a button when they first began to feel an emotional response. After the film clip, subjects rated the valence of the clip from 1 (representing "highly negative") to 4 (representing "highly positive") and the arousal level of the clip from 1 (representing "no or low arousal" to 4 (representing "high arousal"). Trials were separated by a 3-second intertrial interval.

Figure 4. Film clip trial

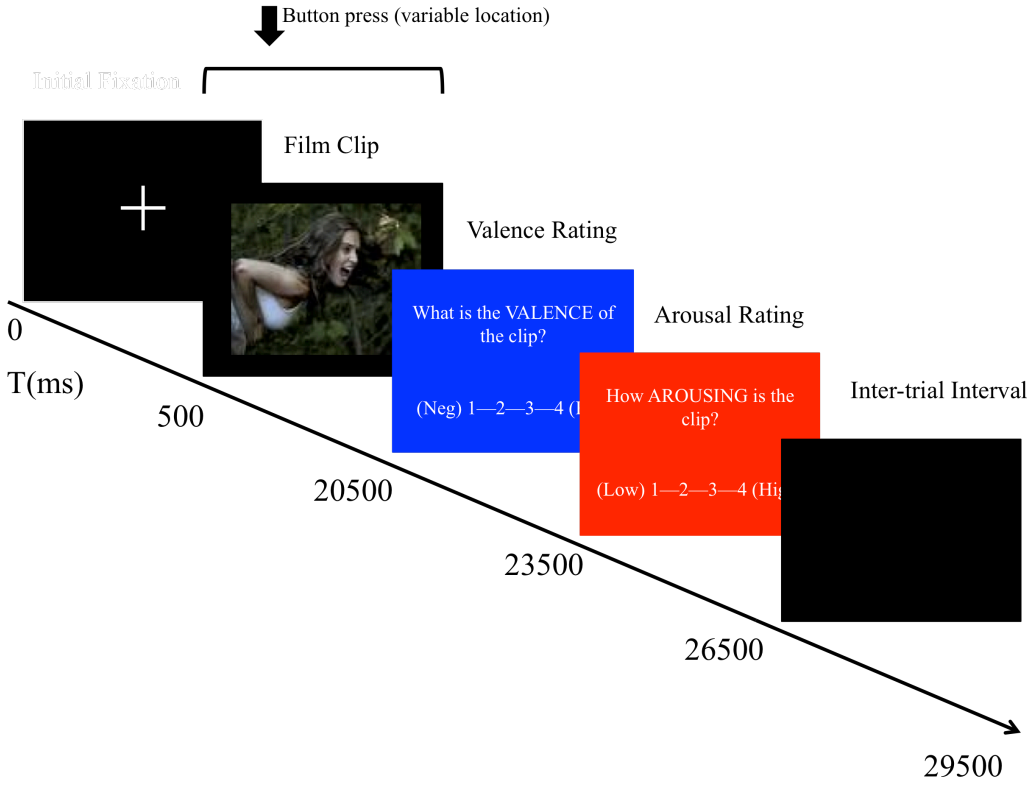


Figure Caption

Illustration of one film clip trial. Each trial began with a fixation cross, followed by a video. Subjects made a button press when they began to feel an emotional response. After the clip, subjects made valence and arousal ratings. Trials were separated by 3-second intertrial intervals.

Similar to film clip trials, autobiographical memory trials began with a 500ms fixation period, followed by a 30-second recall period (see Figure 5 for an illustration of a full trial). During the first 3 seconds of the recall period, subject saw a cue presented on the screen. After the recall period, subjects rated the valence and arousal of the event on scales identical to those used during film clip trials. In addition, subjects rated how well the target emotion (i.e., the emotion the memory was selected to elicit) was elicited by the event from 1 (representing, for example, "no ANGER") to 4 (representing, for example, "A lot of ANGER"). Trails were separated by 3-second intertrial intervals.

Figure 5. Autobiographical memory trial

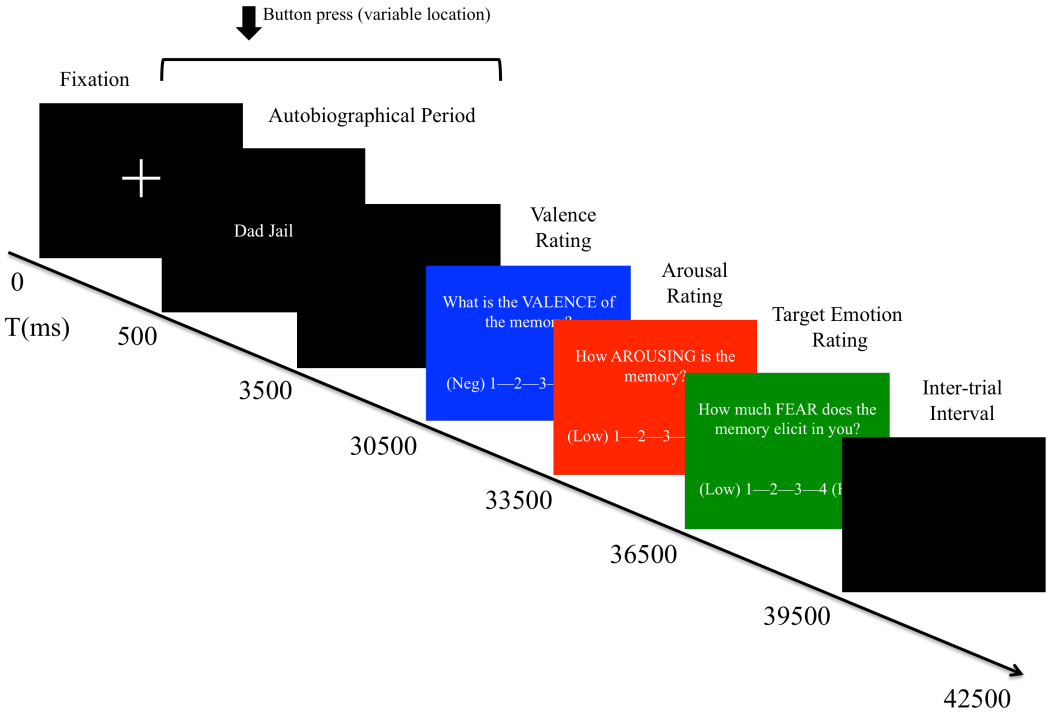


Figure Caption

Illustration of one film clip trial. Each trial began with a fixation cross, followed by a memory cue. Subjects made a button press when they began to feel an emotional response. After the recall period, subjects made valence, arousal and target emotion ratings. Trials were separated by 3-second intertrial intervals.

3.3.4 Procedure

Subjects participated in three sessions: an introductory session, an fMRI session, and a rating session where psychophysiological data were recorded (see Appendix B for a detailed description of the procedure and Figure 6 for an overview). During the first session, subjects reviewed the memories they had prepared, they practiced the tasks they would complete in the scanner (both the film clips and the autobiographical memory trials), and they completed 2 personality questionnaires (the NEO-FFI and MPQ-Harmavoidance scale, see Appendix D for detailed descriptions of these measures). The NEO-FFI is a self-report inventory that measures neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness personality factors (Costa & McRae, 1992). The neuroticism and extraversion factors were used to predict individual differences in brain activity associated with emotional experience. The MPQ is a self-report questionnaire that measures 11 major scales, one of which we extracted for use in this study. All items (true-false) that measured harmavoidance were identified and combined to compose an MPQ harmavoidance scale. Individual differences in harmavoidance were also used to explore differences in brain activity associated with emotional experience.

Figure 6. Procedure overview

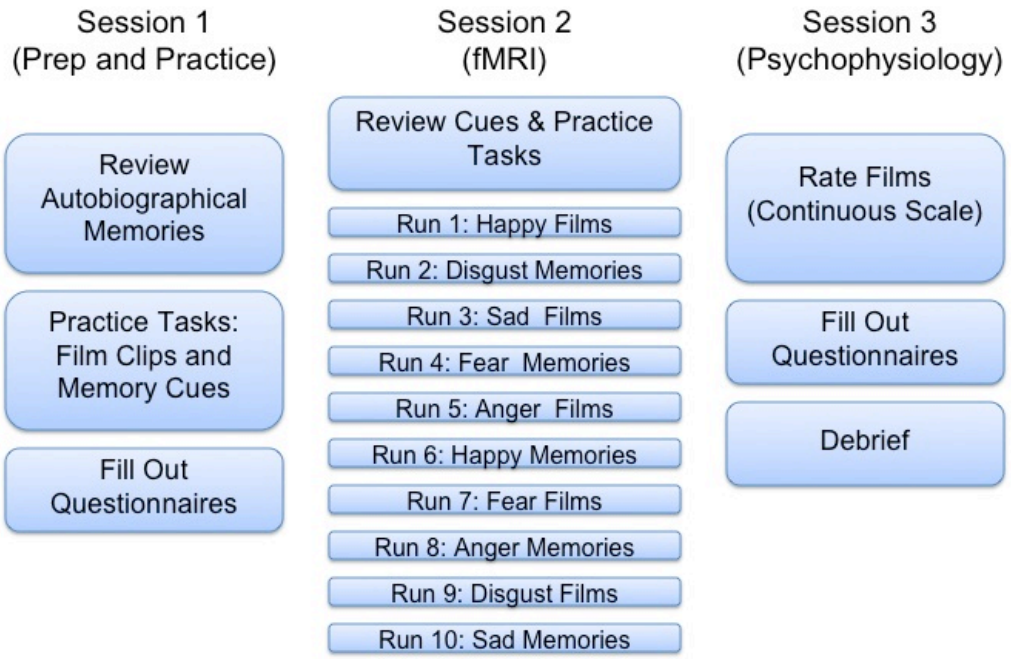


Figure Caption

Subjects participated in three sessions. In the first session, they provided us with autobiographical memories and practiced the tasks that they would perform in the scanner. In the second session, participants were scanned while they recalled their autobiographical memories and watched film clips. In the third session, we acquired autonomic nervous system activity while subjects rated their emotional response to the same set of films on a moment-to-moment basis.

During the second session, subjects completed two brief measures of mood (the positive and negative affective schedule [PANAS] and state-trait anxiety inventory [STAI], see Appendix D for detailed descriptions of these measures) and then were prepared for the scanner. After practicing the experimental tasks in the scanner during an anatomic scan, subjects were scanned while they watched film clips and recalled memories over 10 functional runs. Each run presented only one modality (i.e., film clips or autobiographical memory cues), and one emotion state (e.g., Happiness). Only one emotion state was presented in each run to minimize the effects of slow drift (magnetic field changes over time) and maximize the emotional experience associated with each stimulus. Run order and stimulus order were counterbalanced to reduce order effects. After the functional scans, subjects were escorted back to the Psychology building where they completed the third and final session.

In the third session, we recorded ECG and respiration using a Biopac MP100 system while subjects rated a subset of the film clips (25 total: 15 emotional, 10 neutral) they had seen in the scanner. During each film, subjects made a continuous rating of their internal emotional state on a 30-point scale. Subjects were instructed to indicate their current emotional response from low to high on a moment-to-moment basis. After each film, subjects rated the valence and arousal of the clips on scales identical to those used in the scanning session. Finally, subjects rated each film based on how well it elicited each of the basic emotion states. When the session was over, subjects were debriefed and compensated for their time.

3.3.5 Neuroimaging Acquisition

Anatomical and functional whole-brain imaging data were obtained using a Siemens 3T Trio MRI scanner. Forty-three 3mm-thick axial slices were acquired approximately parallel to the anterior-posterior commissures in order to capture cortical and subcortical regions involved in emotional processing. Functional scans were acquired using T2*-weighted gradient-echo sequences (TR = 2160ms, TE = 30ms, 64 x 64 matrix, 3 x 3 x 3mm voxel size). Structural scans were acquired using a gradient 256 x 256 matrix, 1 x 1 x 1 mm voxel size. Head movement was limited by foam padding and medical tape places across the forehead. Parameters were based on those used in previous neuroimaging studies conducted at the biomedical imaging technology center scanning suite at Emory University. These parameters have been shown to optimize the tradeoff between spatial and temporal resolution in the data, while preserving the blood-oxygen-level-dependent (BOLD) signal and spatial range of the data acquired.

3.3.6 Neuroimaging Analysis

Standard preprocessing of functional data was performed. First, ArtRepair 4 software (Mazaika, Hoeft, Glover, & Reiss, 2009) was used to repair compromised slices via interpolation (compromised slices were defined as those greater than 5 SD from the mean for that slice across a given run). Next, functional images were motion-corrected using Statistical Parametric Mapping software (SPM8, Wellcome Department of Cognitive Neurology, London, UK). ArtRepair 4 was used to deweight and interpolate between bad volumes (i.e., those affected by motion or other artifacts). Normalization was performed in a three-step process: first, each subject's T1 was coregistered to their mean EPI image, ensuring that the images are in the same space; second, the coregistered

T1 was segmented to create a normalization parameter file, and third, the normalization parameter file was used to normalize the volumes for each run. Images were smoothed with a Gaussian filter of 8mm full width at half maximum.

Group data was analyzed in a two-stage random effect analysis implemented in SPM8. Emotion states (happiness, sadness, anger, fear, disgust, and neutral) were modeled as separate blocks for film clips (20s) versus autobiographical memories (30s). Rating periods and intertrial intervals were unmodeled and served as the implicit baseline. In the first step of the analysis, contrasts were defined to assess differences between the conditions of interest at the individual level. These summary statistic images were then entered into a second stage analysis to assess activations across conditions at the group level. This two-stage analysis accounted for within and between subject variance by treating each subject as a random variable.

A conjunction analysis was performed in order to examine the core patterns of activation associated with each basic emotion state. To remove differences in the activation patterns that were specific to the elicitation method, statistical maps were calculated by subtracting the neutral condition within each run, separately for films and memories. Then, the film contrast and memory contrast for a particular emotion state were converted into binary masks based on the critical T threshold (2.624) corresponding to a p-value of .01. These masks were then multiplied using the Imcalc function in SPM8 to calculate the conjunction between films and memories for each emotion (resulting in a threshold of $p < .001$). This calculation resulted in maps that display basic emotion activations that were common to both modalities (i.e., the core activations) for each basic emotion state.

To assess the differentiability of basic emotion states, pairwise contrasts of emotion states were examined in a similar conjunction analysis. The film contrast and memory contrasts for a particular pairwise comparison between emotion states (e.g., Anger Films > Disgust Films; Anger Memories > Disgust Memories) were converted into binary masks based on the critical T threshold (2.624) corresponding to a p-value of .01. These masks were then multiplied using the Imcalc function in SPM8 to calculate the conjunction between films and memories for each pairwise comparison (resulting in a threshold of $p < .001$). This calculation resulted in maps that displayed activations that differentiated emotions across both modalities (i.e., the differentiating activations) for each pairwise contrasts between basic emotions.

In addition, the differentiability of basic emotion states was investigated using data from the random-effects analysis. After subtracting activations associated with the neutral (control) condition, contrasts of interest included all pairwise comparisons between emotion states (Happiness > Sadness, Happiness > Anger, Happiness > Fear, Happiness > Disgust, Sadness > Anger, Sadness > Fear, Sadness > Disgust, Anger > Fear, Anger > Disgust, Fear > Disgust, and all the reverse comparisons). These comparisons were computed for both elicitation methods separately (i.e., for film clips and autobiographical memory scripts) in order to assess differences in emotion-specific activation patterns that might be better captured within elicitation modality (i.e., Sad Films > Happy Films), as well as for all stimuli considered together for each emotion state (i.e., all sad films and sad memories > all happy films and memories).

Modality-specific activations were assessed by comparing activation maps associated with films to those associated with memories for each basic emotion state

(e.g., anger films > anger memories) and for all emotion states considered together (e.g., emotional films > emotional memories). All activation maps were overlaid on a representative high-resolution structural T1-weighted image from a single subject from the SPM8 canonical image set, coregistered to Montreal Neurological Institute (MNI) space, a commonly used approximation of canonical Talairach space. Contrast thresholds were set at $p < .001$, uncorrected, with an extent threshold of 5 voxels. Small-volume corrections ($p < .05$) were used to focus whole brain analyses on a priori regions of interest (regions consisted of the same set of regions used in the ROI analysis below). These analyses were used to identify activations that may have been undetectable in the ROI analyses because the signal is calculated across the entire volume. Activation coordinate locations were verified based on anatomical markers and by the use of the Talairach Daemon (an automated labeling atlas) (Lancaster et al., 2000). Labels were determined based on the nearest gray matter.

ROIs were based on a priori regions based on converging evidence from the literature and Vytal and Hamann (in press). Regions that reliably characterized and differentiated emotion states in the meta-analysis were selected as ROIs (right STG, left ACC, left medFG, left caudate head, left IFG, right PHG, bilateral amygdala, bilateral insula). All ROIs were created by selecting appropriate automated anatomical labeling (AAL) atlas masks for each region (Tzourio-Mazoyer et al., 200) in WFUPickatlas (http://www.fmri.wfubmc.edu/cms/software#PickAtlas). Left and right amygdala masks were dilated by 1mm to capture adjacent activity that may have shifted as a result of motion or smoothing over the small structure. Left and right anterior insula were bounded at the caudal MNI boundary of y=8; left and right posterior insula were defined as insula

cortex posterior to that boundary. These divisions were based on cytoarchitectural features of the agranular insula (Ongur et al., 2003). Marsbar toolbox (Brett, Anton, Valabregue, & Poline, 2002) was used to estimate and specify the peristimulus time function for the temporal window containing the peak of the hemodynamic response for each event through the application of a finite impulse response functions model of the hemodynamic response (Burock & Dale, 2000, Ollinger, Shulman, & Corbetta, 2001). Percent signal change in each ROI was reported for the five emotion conditions (happiness, sadness, anger, fear and disgust) and the control condition (neutral). The neutral condition from each run was subtracted as a baseline, and the resulting values were entered into a one-way ANOVA. Planned t-tests ($p < .05$, one-tailed) were used to compare activation across the five conditions.

3.3.7 Psychophysiology

3.3.7.1 Acquisition

Physiological activity was recorded at a sampling rate of 1000Hz and processed using the Biopac MP100 system. Recording parameters and analyses were modeled after a previous study that successfully differentiated basic emotions on the basis of ANS activity (Rainville et al., 2006). All electrode leads were to maintain consistency in susceptibility to interference across leads. Respiration was recorded using a tension transducer attached to a strain-gage belt placed over the rib cage at the level of the fifth thoracic vertebrae. The respiration belt was adjusted for each subject during the training phase so that a normal breath created a visible change in amplitude recording. Changes in thoracic circumference were measured with a Biopac TSD201 respiratory effort

transducer. Respiration variables were derived from the respiration data. ECG was recorded using the standard Einthoven triangle configuration (three lead montage), with 2 leads placed under the left and right breastbone. Changes in electrical activity produced by the heart were measured using a Biopac ECG100C amplifier. Inter-beat interval (R-R intervals) variables were all derived from the ECG data.

3.3.7.2 Analysis

Using AcqKnowledge software (BIOPAC Systems Inc., Goleta, California), the onset of the film clip in each trial was identified based on the audio channel recording. Epochs extending 20 seconds past that marker were defined as experimental events. Events were subsequently categorized according to their corresponding emotional state and variables of interest were calculated for each of these categories. For each 20-second trial, we extracted time domain measures of cardiovascular and respiratory activity. Prior to epoch extraction, R-R intervals were determined using a modified Pan-Tompkins QRS detector (Pan & Tompkins; 1985). Respiration data was downsampled to 62.5Hz and band-passed between 0.05-1Hz using a digital finite impulse response filter with Bartlett windowing. Respiratory sinus arrhythmia was calculated using the peak-to-valley method (Grossman, Van Beek, & Wientjes, 1990).

Based on Rainville et al. (2006), the following variables were derived from the respiration and ECG measures: (1) mean respiratory period, (2) median respiratory period, (3) standard deviation of the respiratory period, (4) mean of the relative respiratory amplitude, (5) median of the relative respiratory amplitude, (6) standard deviation of the relative respiratory amplitude, changes per respiratory cycle, (7) mean of

the averaged R-R within each respiratory cycle, (8) mean of the averaged R-R within each respiratory cycle, (9) standard deviation of the averaged R-R within each respiratory cycle (slow RR changes between respiratory cycles), (10) mean of the standard deviation of RR calculated within each respiratory cycle (fast R-R changes within respiratory cycles; respiratory sinus arrhythmia), (11) median of the standard deviation of RR calculated within each respiratory cycle (fast R-R changes within respiratory cycles; respiratory sinus arrhythmia), (12) standard deviation of the standard deviation of R-R calculated within each respiratory cycle (fast RR changes within respiratory cycles; respiratory sinus arrhythmia), (13) mean of the maximum excursion of the RR interval (RR max RR min) within each respiratory cycle (fast RR changes within respiratory cycles; respiratory sinus arrhythmia), (14) median of the maximum excursion of the RR interval (RR max RR min) within each respiratory cycle (fast RR changes within respiratory cycles; respiratory sinus arrhythmia), (15) standard deviation of the maximum excursion of the RR interval (RR max RR min) within each respiratory cycle (fast RR changes within respiratory cycles; respiratory sinus arrhythmia), (16) mean R-R interval, (17) median R-R interval, (18) standard deviation of the R-R interval (overall variation in RR).

All variables were examined in a univariate analysis first to determine whether or not basic emotion states differed from neutral. A second univariate analysis (pairwise comparisons) was performed on log-transformed data (log(emotional/neutral) to determine whether or not basic emotions could be differentiated on any of the measures. Multivariate patterns of activity were not explored because there were very few variables that differentiated emotional from neutral stimuli.

3.4 Results

3.4.1 Behavioral

3.4.1.1 Ratings in the scanner

Behavioral ratings verified that the film clips and autobiographical memories elicited the expected emotional responses. Ratings in the scanner demonstrated that happy films and memories were evaluated high on positive valence and emotional arousal, whereas sad film and memories, anger films and memories, fear films and memories, and disgust films and memories were evaluated high on negative valence and emotional arousal (see Figures 7 and 8). Neutral films and memories were rated as valence neutral (i.e., emotionally neutral) and low on emotional arousal (see Table 5 for means and SDs). Target emotion ratings in the scanner demonstrated that each basic emotion state was elicited well by the each memory, and neutral memories did not elicit the target emotion (see Figure 9). Neutral stimuli were rated significantly lower on emotional arousal than emotional stimuli, higher on valence (i.e., more positive, which corresponds to neutral) than negative stimuli, lower on valence (i.e., more negative, which corresponds to neutral) than positive stimuli, and lower on target emotion ratings than emotional stimuli (i.e., they did not elicit target emotions) (see Table 6 for pairwise contrasts between emotion and neutral).

Table 6. fMRI session ratings of arousal, valence, and target emotion

Target Emotion	*Arousal*		*Valence*		*Target Emotion Rating*	
Films						
Happiness	3.35	(0.33)	3.58	(0.29)		
Sadness	3.65	(0.28)	1.08	(0.15)		
Anger	3.31	(0.37)	1.23	(0.26)		
Fear	3.38	(0.48)	1.15	(0.21)		
Disgust	3.65	(0.26)	1.08	(0.15)		
Neutral	1.36	(0.27)	2.38	(0.18)		
Memories						
Happiness	3.35	(0.35)	3.50	(0.70)	3.81	(0.37)
Sadness	3.54	(0.34)	1.19	(0.38)	3.17	(0.48)
Anger	3.33	(0.63)	1.29	(0.36)	3.62	(0.71)
Fear	3.13	(0.47)	1.29	(0.50)	3.29	(0.63)
Disgust	3.50	(0.30)	1.17	(0.24)	3.67	(0.34)
Neutral	1.38	(0.31)	2.46	(0.12)	1.09	(0.34)

Figure Caption

fMRI session ratings of arousal, valence, and success with eliciting the target emotion (memories only) according to emotion condition. *M* (*SD*).

Table 7. Pairwise contrasts between emotion conditions and neutral across fMRI session ratings

	Arousal	*Valence*	*Target Emotion*
Films			
Happiness - Neutral	*23.5*	*13.1*	
Sadness - Neutral	*31.2*	*-28.0*	
Anger - Neutral	*20.0*	*-19.1*	
Fear - Neutral	*13.9*	*-17.2*	
Disgust - Neutral	*23.9*	*-20.8*	
Memories			
Happiness - Neutral	*14.9*	*6.1*	*30.5*
Sadness - Neutral	*13.3*	*-13.0*	*14.4*
Anger - Neutral	*18.1*	*-20.0*	*26.0*
Fear - Neutral	*11.5*	*-8.6*	*9.9*
Disgust - Neutral	*15.0*	*-20.7*	*21.7*

Figure Caption

Pairwise contrasts (*t)* between ratings of each emotion condition and neutral. Arousal, valence, and target emotion ratings are reported (fMRI session). $df(14)$. $p < 0.001$ for all contrasts.

Figure 7. Valence ratings inside the scanner

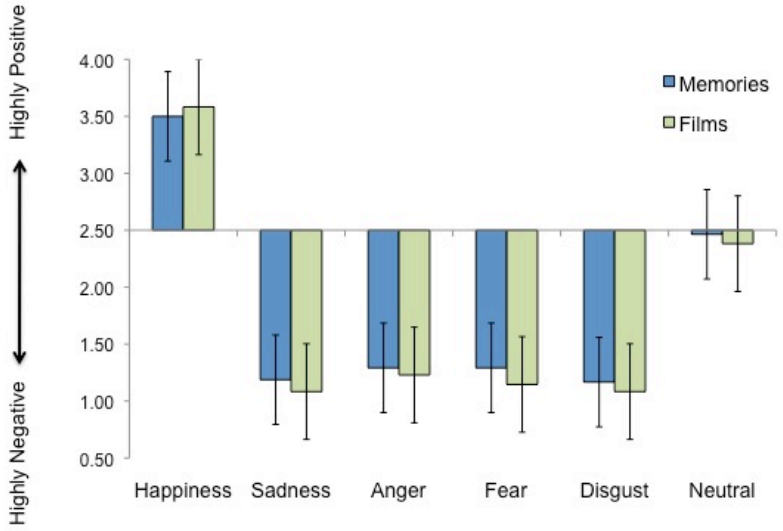


Figure Caption

Ratings inside the scanner confirmed that subjects evaluated happy films and memories as emotionally positive, all other films and memories as emotionally negative, and all neutral films and memories as emotionally neutral.

Figure 8. Arousal ratings inside the scanner

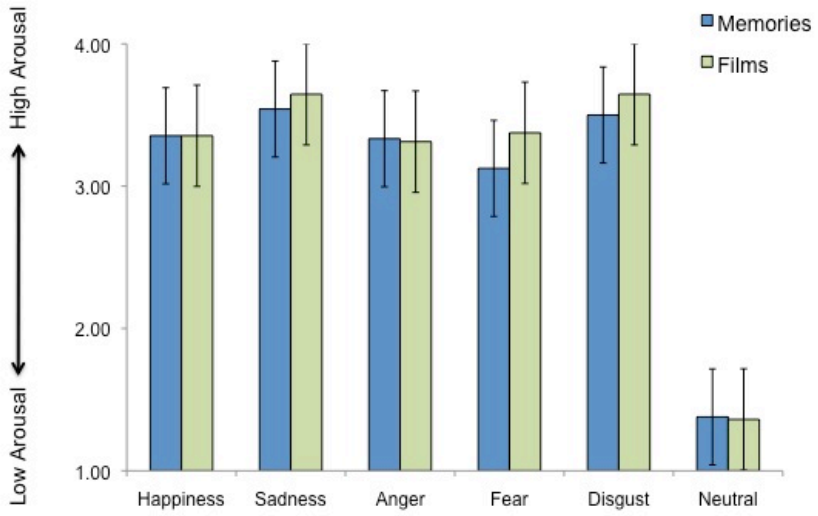


Figure Caption

Ratings inside the scanner confirmed that subjects evaluated all emotional films and memories as emotionally arousing, and all neutral films and memories as emotionally unarousing.

Figure 9. Target emotion ratings of autobiographical memories in the scanner

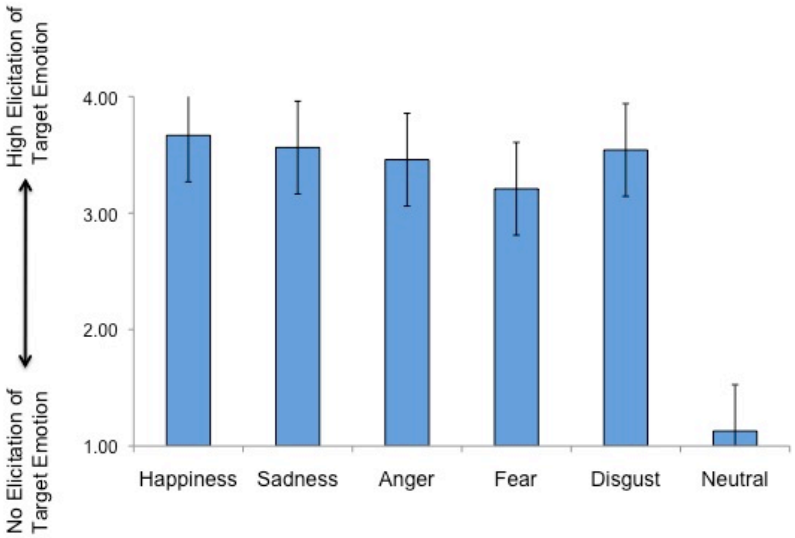


Figure Caption

Ratings inside the scanner confirmed that all memories elicited the expected emotion state. Neutral films elicited very little to none of the expected emotion state.

In the scanner, subjects made a button press when they first began to feel an emotion related to a film or memory. We collected these data to estimate the time point when subjects started to experience an emotion during each event. If these data demonstrated that subjects did not begin to feel an emotion until the latter half of the trial, we could then use the responses to remodel our events accordingly. However, the data suggest that subjects began to experience an emotional response approximately 6-7 seconds into both film clips and memory recollection on average (films *M*(7.15) *SEM*(.7), memories *M*(6.28) *SEM*(.92)). We modeled our events at the start of each film or memory event, and thus captured ample time (13 seconds, on average) beyond when subjects began to feel an emotional response.

3.4.1.2 Rating session ratings

Ratings outside the scanner confirmed ratings inside the scanner: happy films were rated high on positive valence arousal; all other emotional films (sad, anger, fear, disgust) were rated high on negative valence and arousal (see Figures 10 and 11, and Table 7 for means and SDs). Neutral films were again rated as emotionally neutral on valence and low on emotional arousal. Basic emotion ratings indicate that each film elicited the expected basic emotion state (e.g., happy films elicited happiness but not sadness, anger, fear, or disgust) (see Figure 12).

Table 8. Rating session ratings of arousal, valence, and basic emotion elicitation

Target Emotion	*Arousal*		*Valence*		*Basic Emotion Ratings*									
					Happiness		*Sadness*		*Anger*		*Fear*		*Disgust*	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Happiness	3.36	0.32	3.64	0.34	**3.47**	**0.29**	1.11	0.35	1.02	0.09	1.00	0.00	1.00	0.00
Sadness	3.51	0.21	1.09	0.23	1.00	0.00	**3.76**	**0.29**	1.42	0.39	1.29	0.31	1.11	0.16
Anger	3.09	0.41	1.20	0.25	1.09	0.23	1.64	0.57	**3.38**	**0.45**	1.40	0.34	1.49	0.47
Fear	3.13	0.57	1.16	0.25	1.29	0.53	1.31	0.44	1.16	0.31	**3.60**	**0.34**	1.49	0.35
Disgust	3.58	0.46	1.09	0.15	1.20	0.35	1.16	0.21	1.16	0.21	1.33	0.31	**3.87**	**0.21**
Neutral	1.28	0.27	2.37	0.27	1.27	0.21	1.13	0.23	1.06	0.14	1.10	0.12	1.03	0.06

Note: Rating session ratings of arousal, valence, and success with eliciting basic emotions for all films according to emotion condition. For valence: 1; highly negative, 2.5; neutral; 4; highly positive, for all other ratings 1; low, 4; high. Basic emotion ratings are in bold for the corresponding target emotion. *M* (*SD*).

Figure 10. Valence ratings outside the scanner

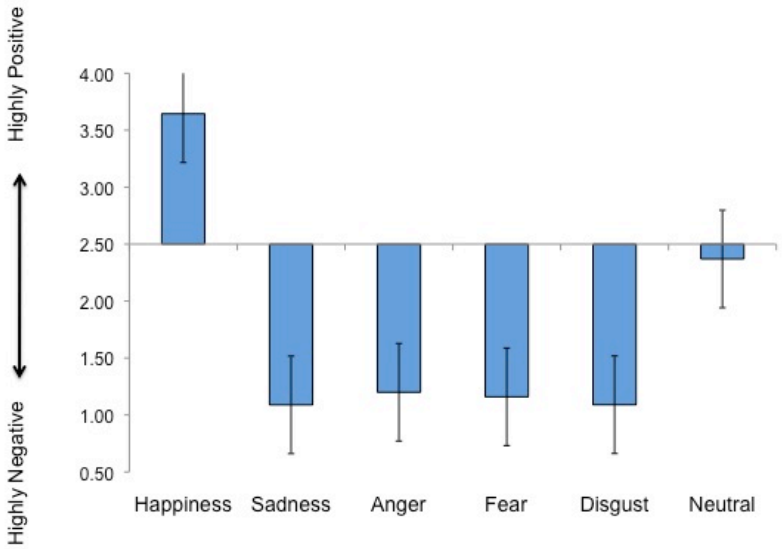


Figure Caption

Ratings outside the scanner (psychophysiology session) confirmed that subjects evaluated happy films as emotionally positive, all other films as emotionally negative, and all neutral films as emotionally neutral.

Figure 11. Arousal ratings outside the scanner

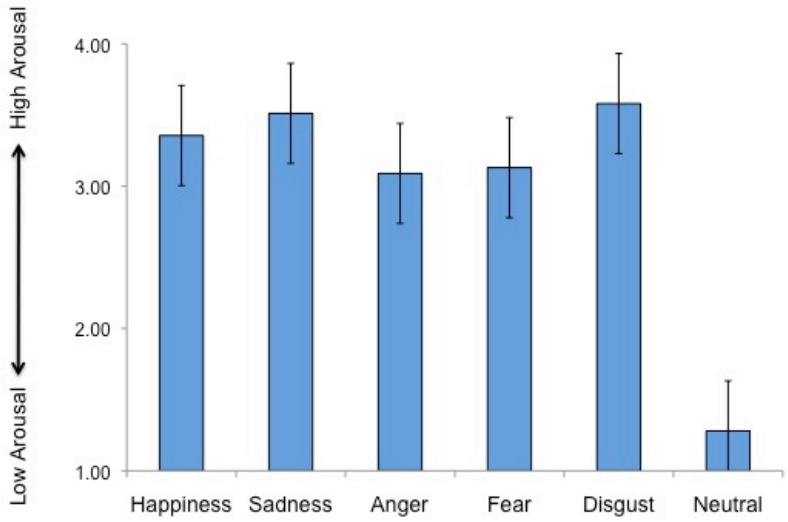


Figure Caption

Ratings outside the scanner confirmed that subjects evaluated all emotional films as emotionally arousing, and all neutral films as unarousing.

Figure 12. Basic emotion ratings outside the scanner

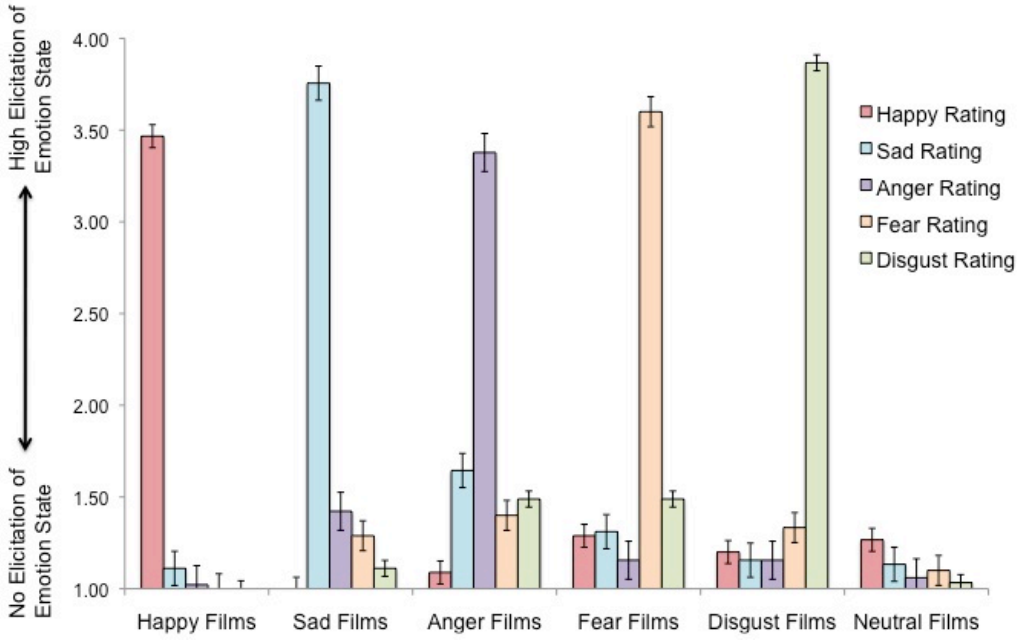


Figure Caption

Ratings outside the scanner confirmed that all basic emotional films uniquely elicited the expected emotion state. Neutral films elicited very little to none of the expected emotion state.

During each film clip, subjects also rated their emotional response on a continuous scale from 1 (representing "no emotional response") to 30 (representing "high emotional response"). These data provide additional information regarding the temporal unfolding of emotional experience. Further, they allow us to make inferences regarding the response profiles associated with different basic emotion states (e.g., fear might be more transient, whereas sadness might be more prolonged). Continuous rating data was analyzed for one subject in order to provide a small sample of typical emotional responses associated with different emotional states. Time points of ratings were rounded down to the nearest 500ms, creating 40 bins across each trial.

As expected, neutral films elicited very few and very minimal responses (see Figures 13-22). Any responses that did occur exhibited long durations of low emotional response and thus may reflect more of a slight change in mood state rather than a discrete emotional response. The profiles of neutral and emotional clips were strikingly different. Emotional clips tended to elicit an emotional response that intensified throughout the film and peaked somewhere near the end (see Figures 23-37). Fear and disgust films elicited the most rapid increases in emotional response; happiness, anger, and sadness tended to elicit responses that grew over longer durations. All of the emotional films elicited responses (>20 on the emotional response scale) that sustained until the end of the clip and likely beyond.

Figure 13. Emotional responses across a neutral clip (1)

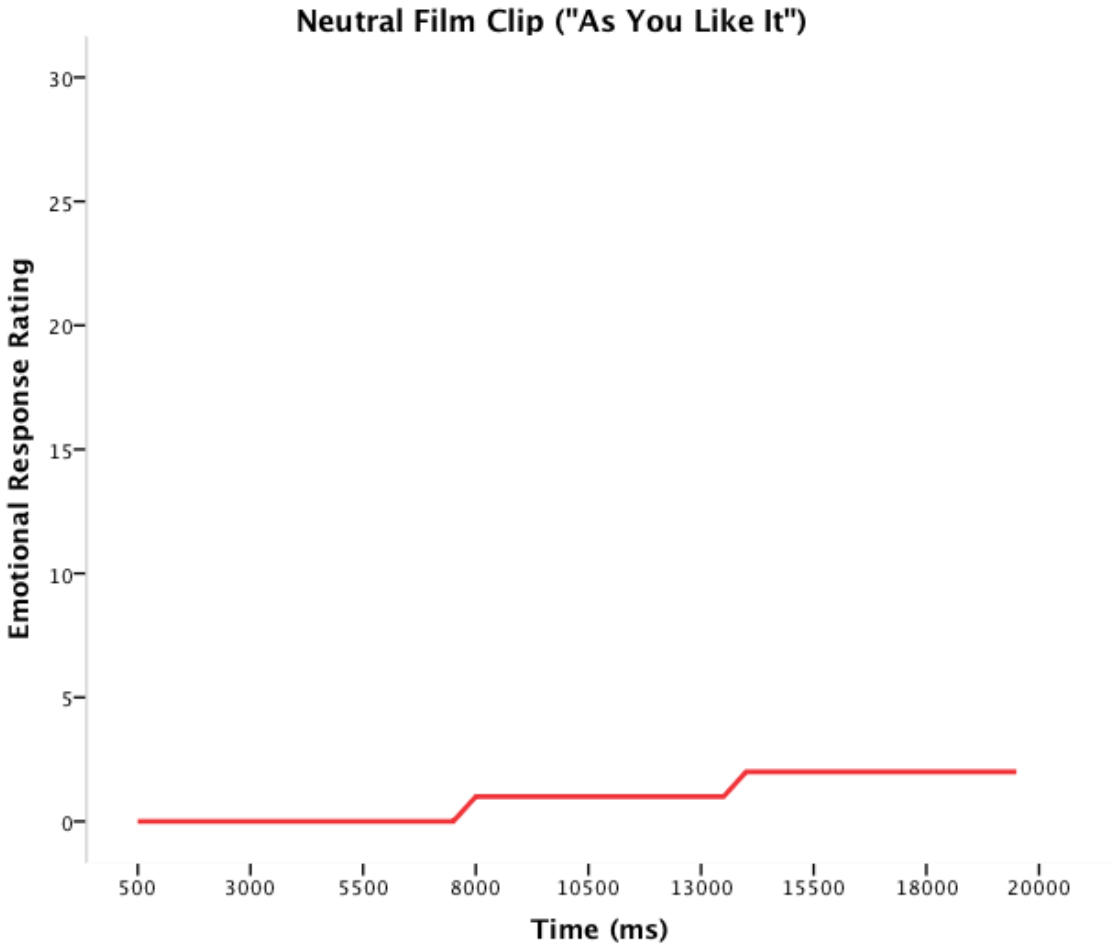


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 14. Emotional responses across a neutral clip (2)

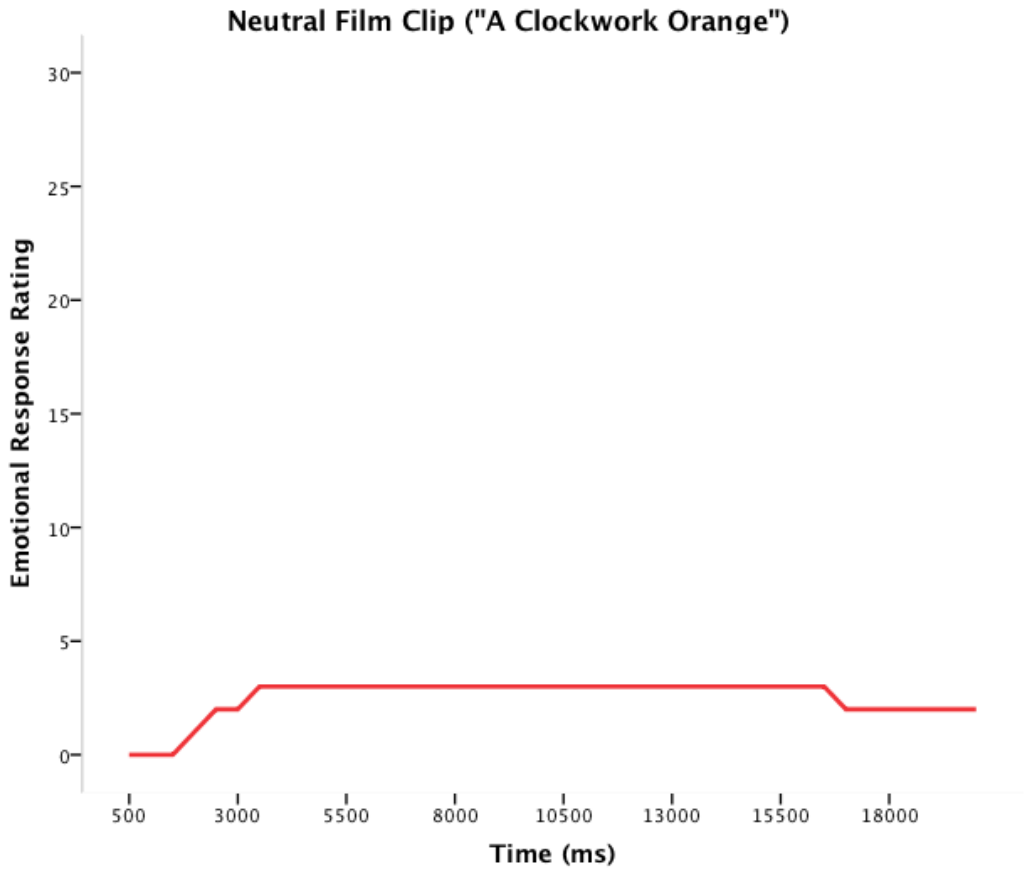


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 15. Emotional responses across a neutral clip (3)

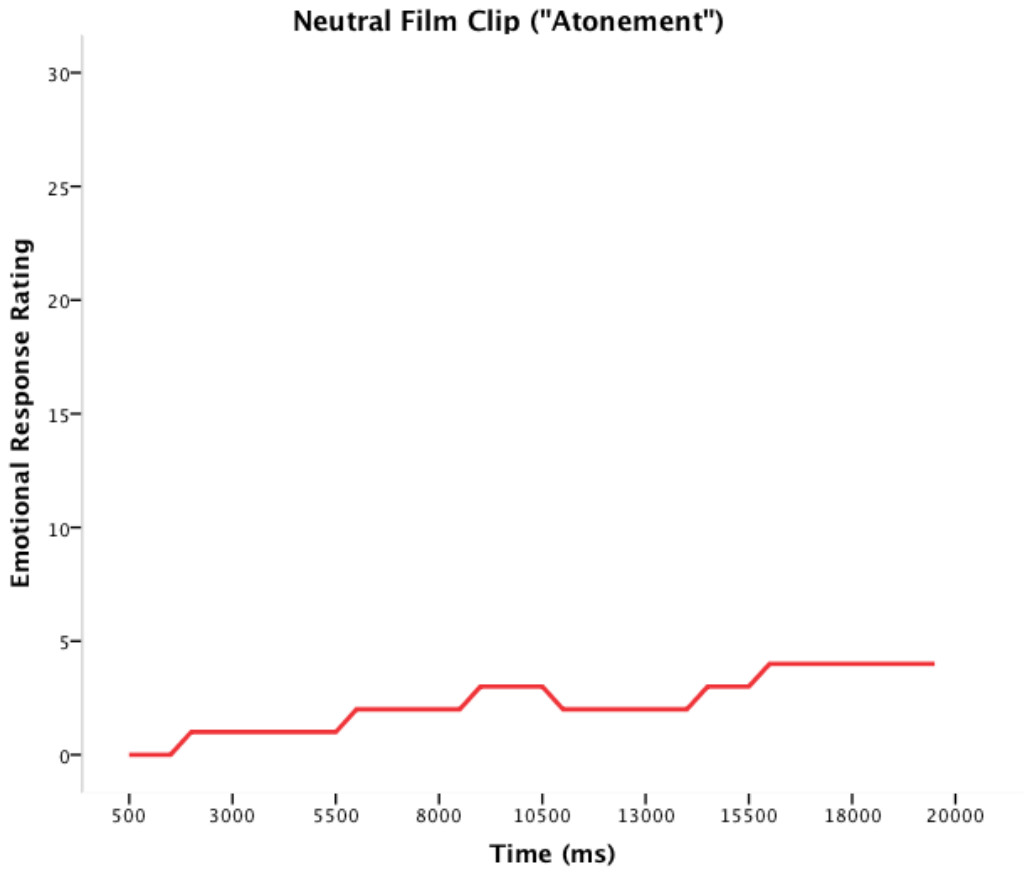


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 16. Emotional responses across a neutral clip (4)

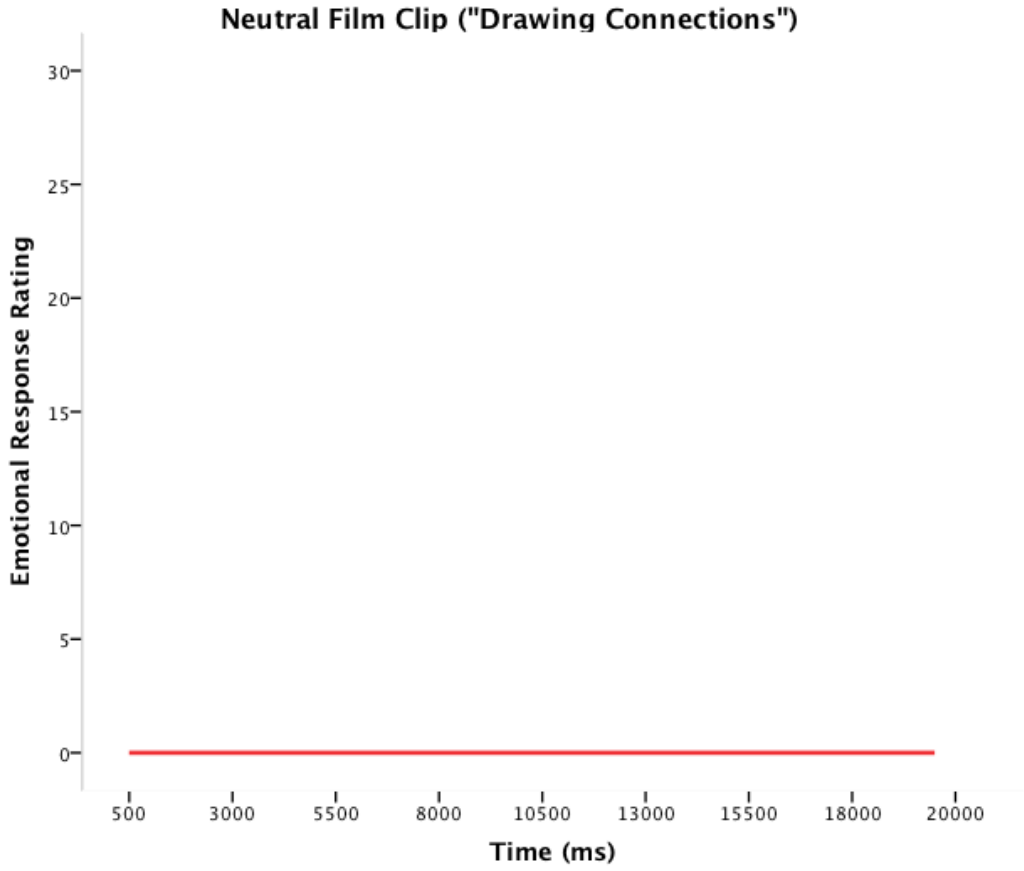


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 17. Emotional responses across a neutral clip (5)

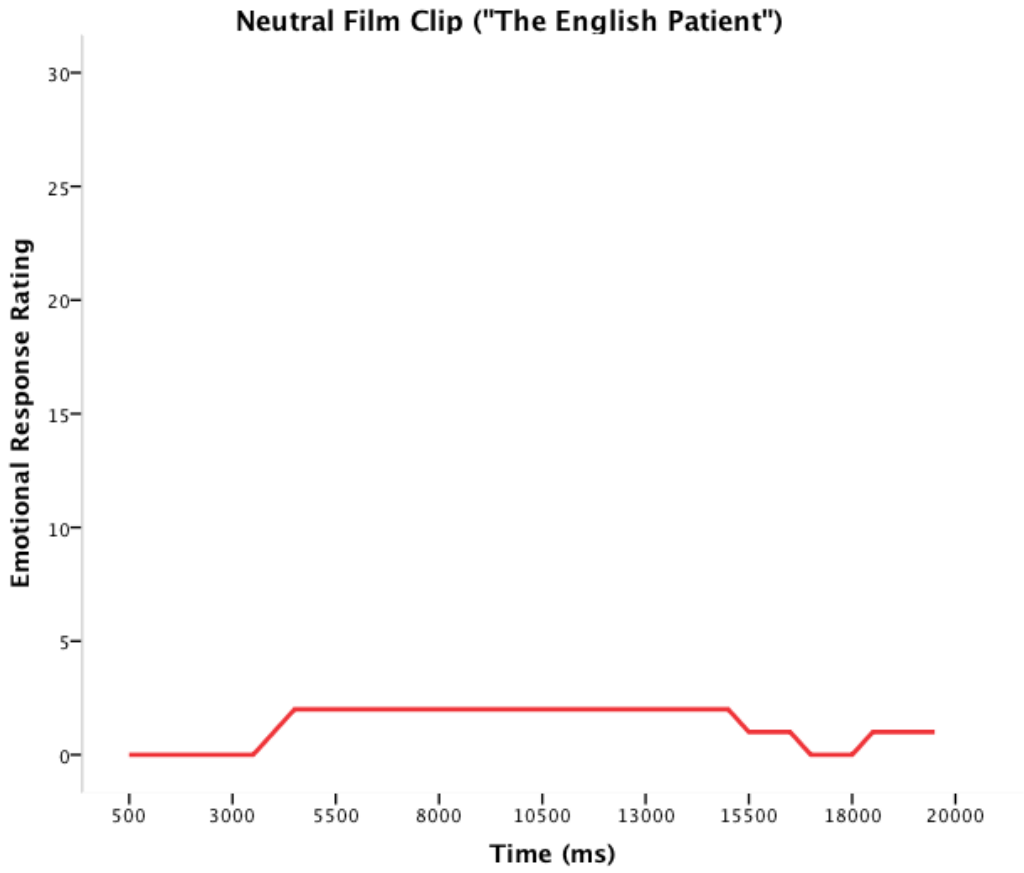


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 18. Emotional responses across a neutral clip (6)

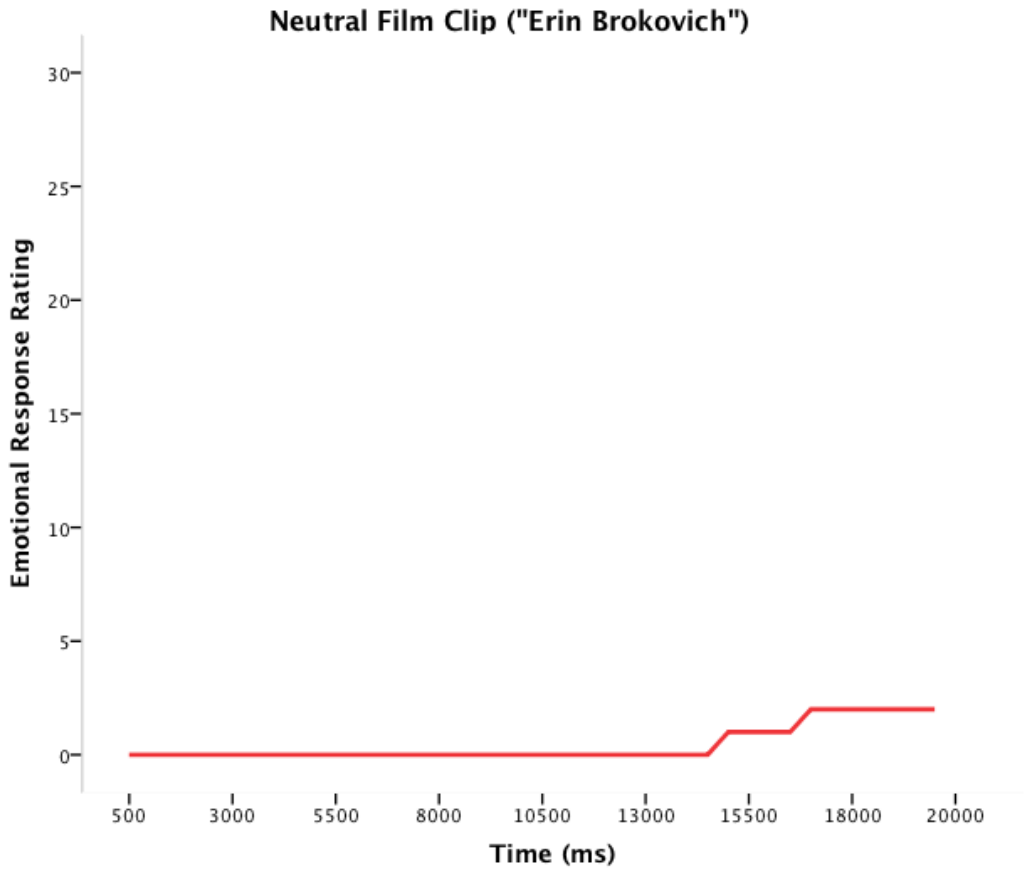


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 19. Emotional responses across a neutral clip (7)

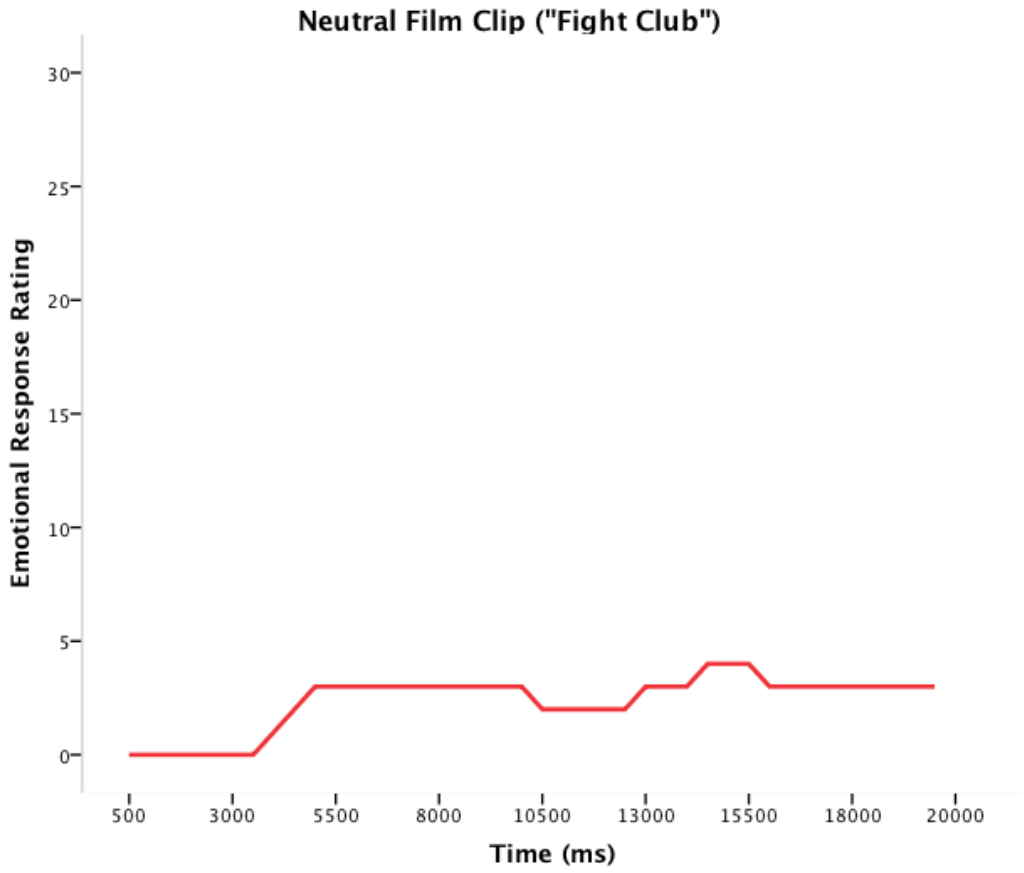


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 20. Emotional responses across a neutral clip (8)

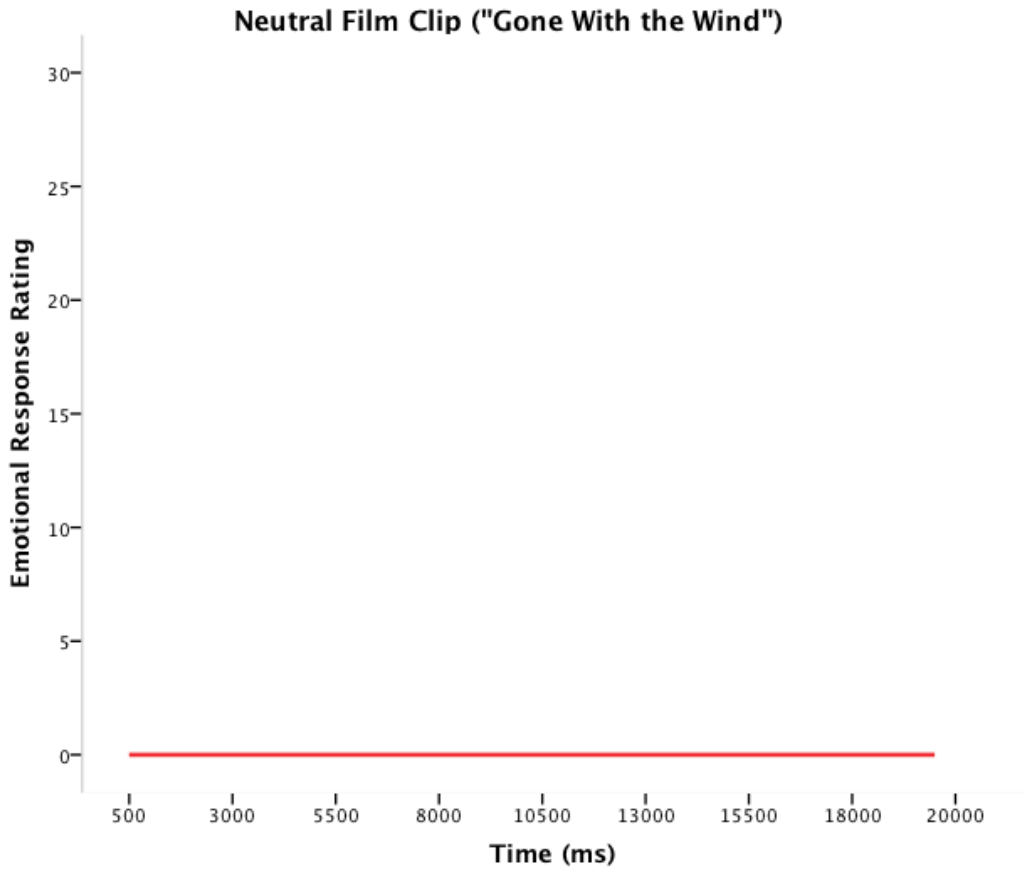


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 21. Emotional responses across a neutral clip (9)

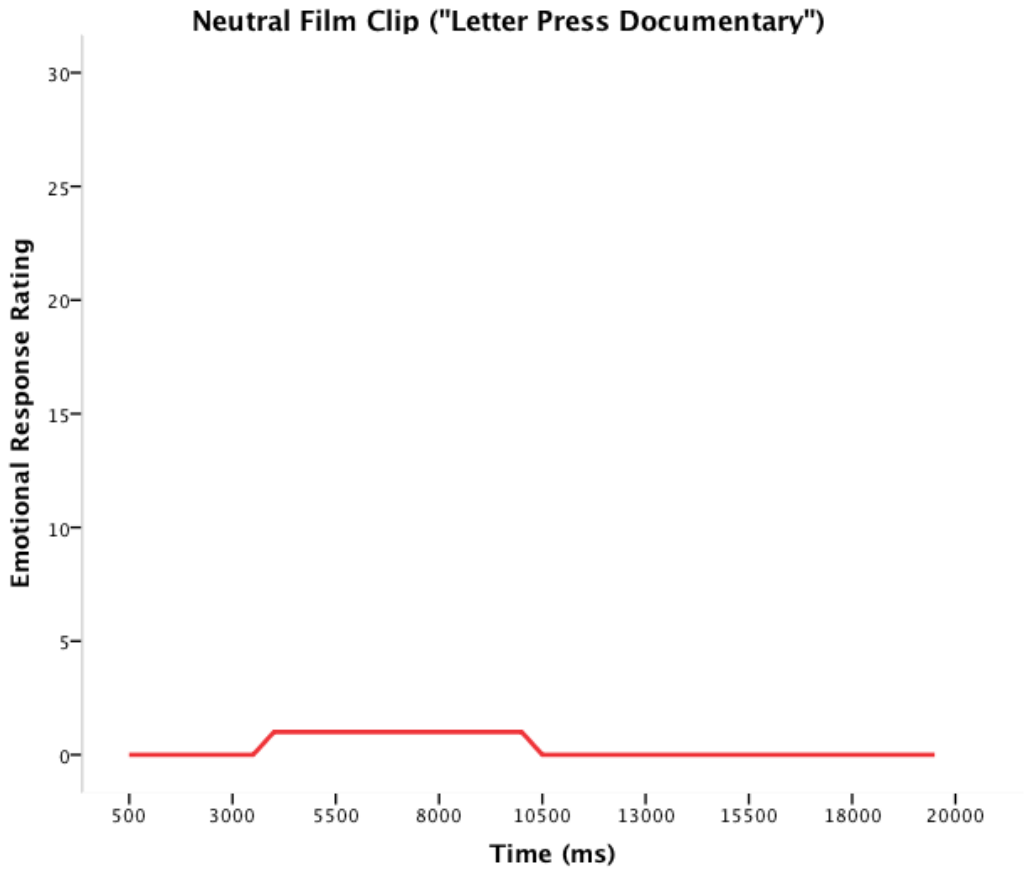


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 22. Emotional responses across a neutral clip (10)

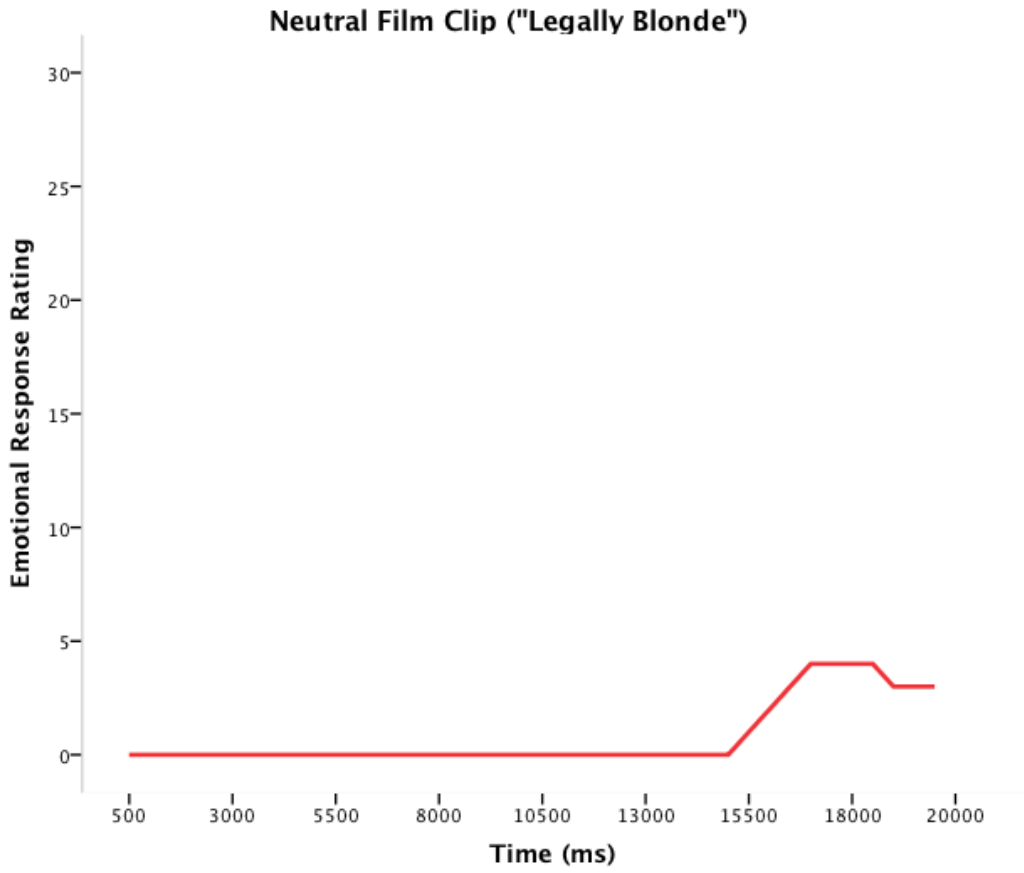


Figure Caption

Continuous emotional responses across a neutral film clip from one subject.

Figure 23. Emotional responses across a happy clip (1)

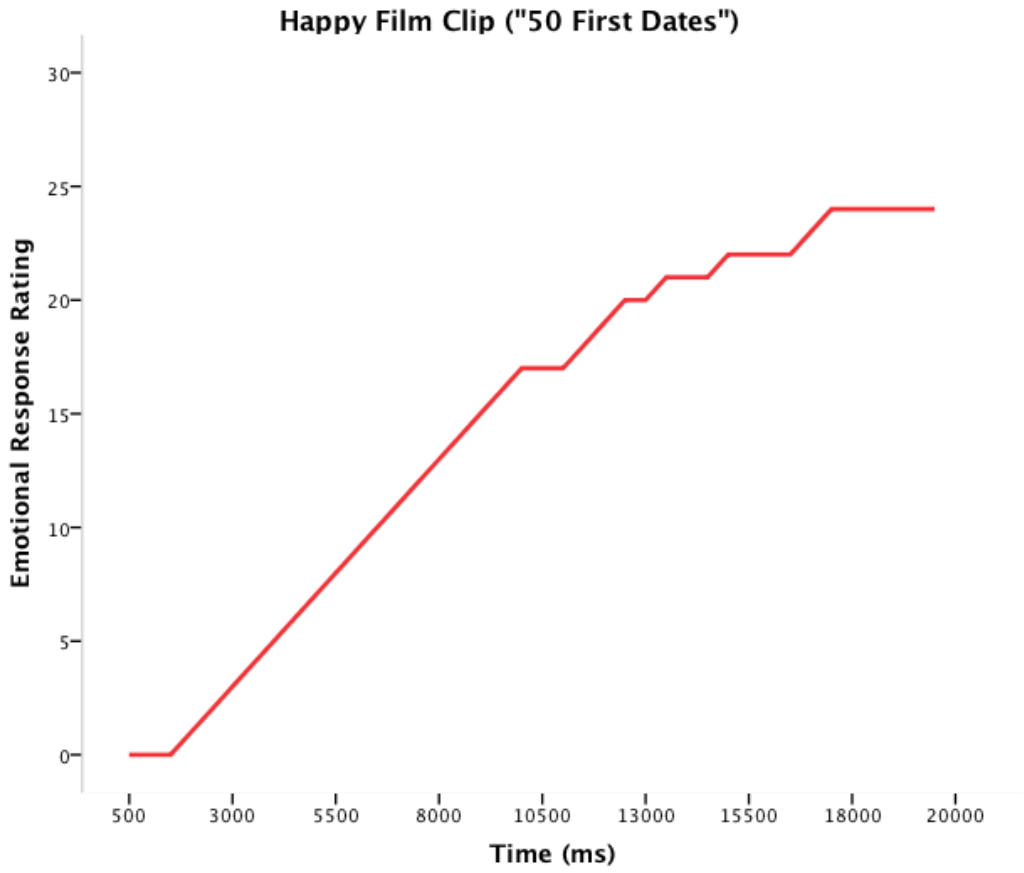


Figure Caption

Continuous emotional responses across a happy film clip from one subject.

Figure 24. Emotional responses across a happy clip (2)

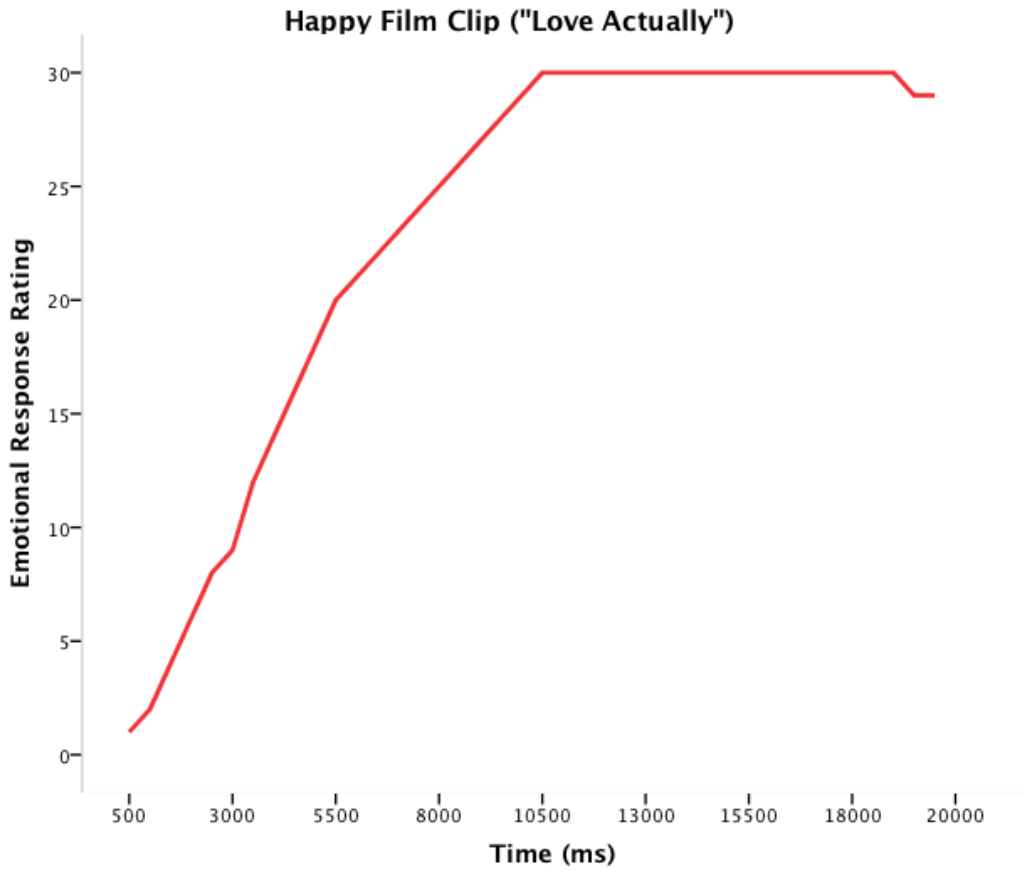


Figure Caption

Continuous emotional responses across a happy film clip from one subject.

Figure 25. Emotional responses across a happy clip (3)

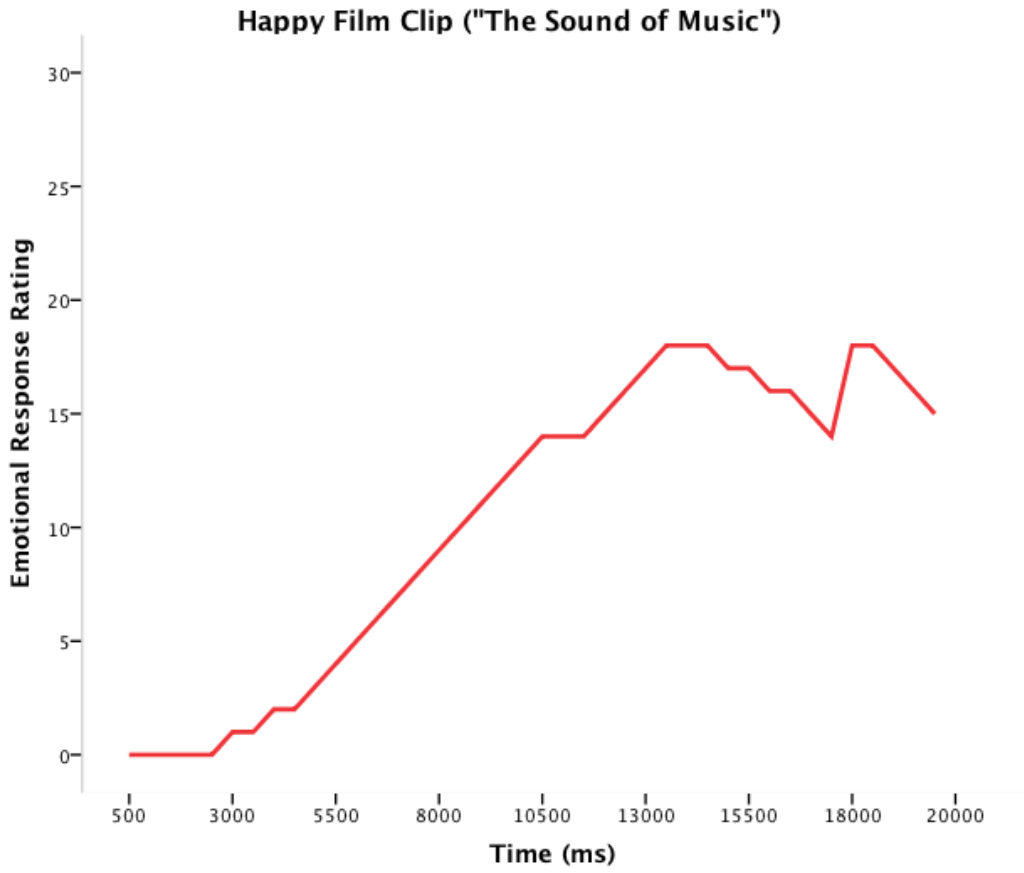


Figure Caption

Continuous emotional responses across a happy film clip from one subject.

Figure 26. Emotional responses across a sad clip (1)

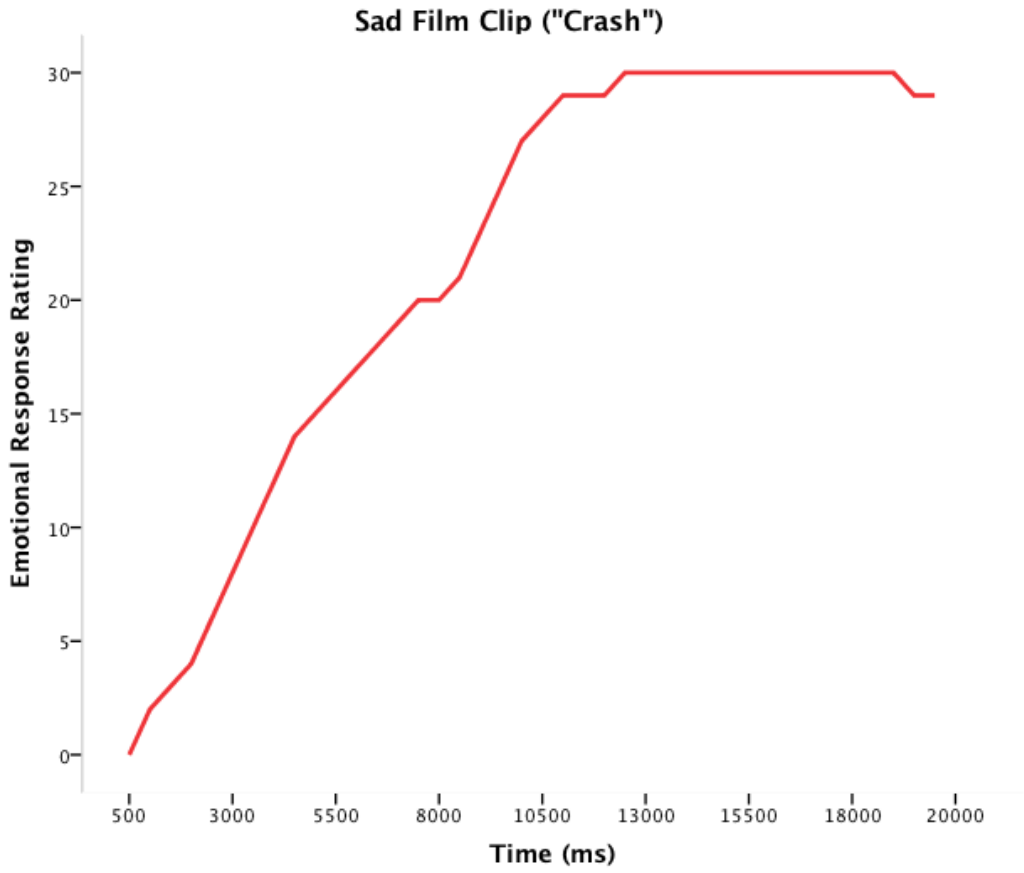


Figure Caption

Continuous emotional responses across a sad film clip from one subject.

Figure 27. Emotional responses across a sad clip (2)

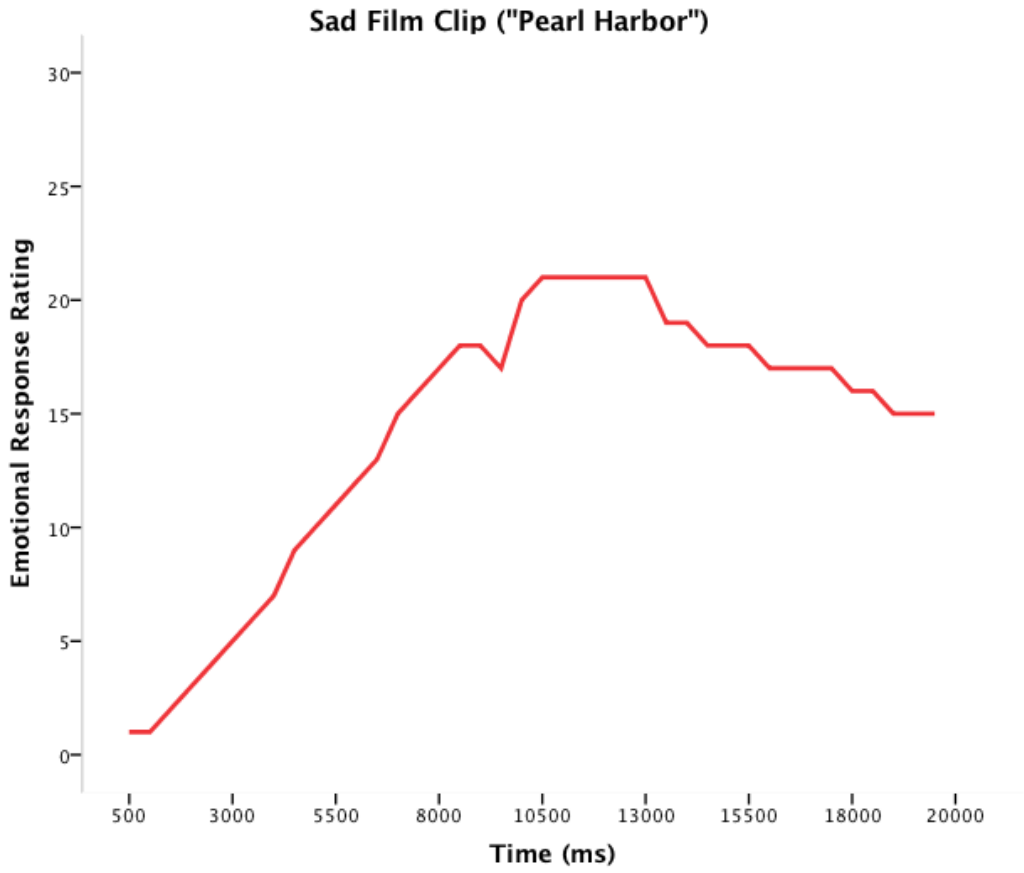


Figure Caption

Continuous emotional responses across a sad film clip from one subject.

Figure 28. Emotional responses across a sad clip (3)

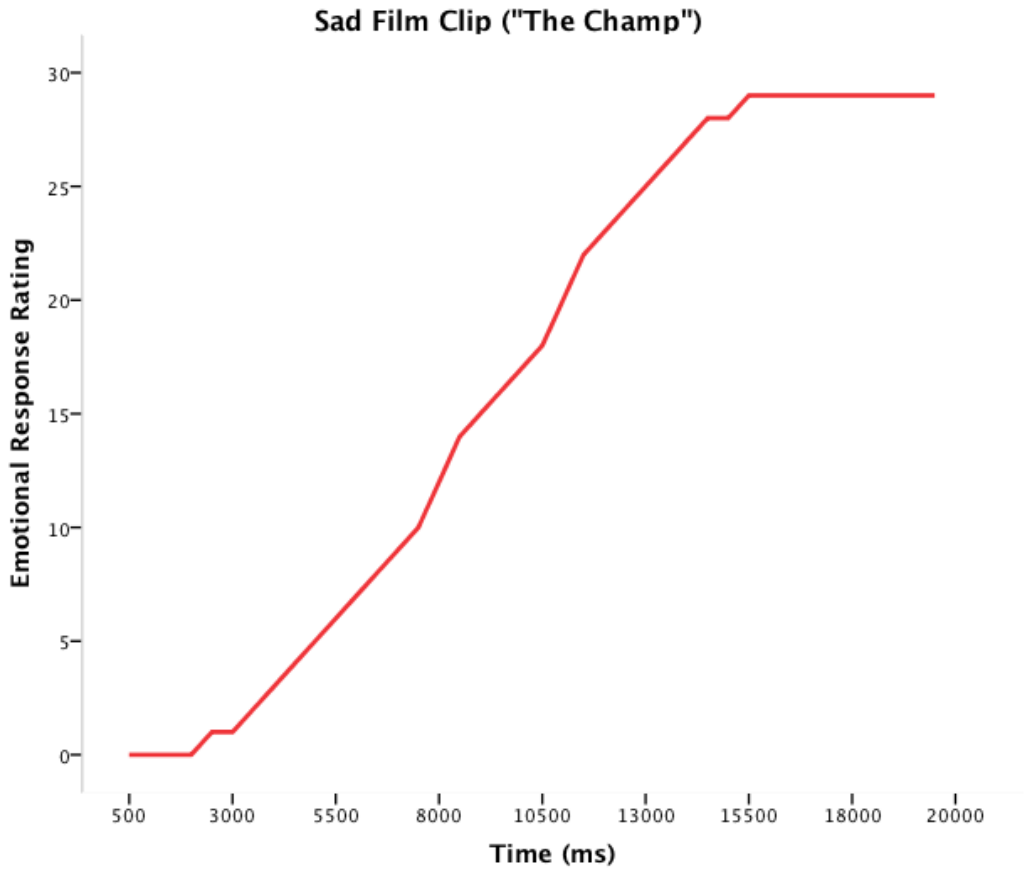


Figure Caption

Continuous emotional responses across a sad film clip from one subject.

Figure 29. Emotional responses across an anger clip (1)

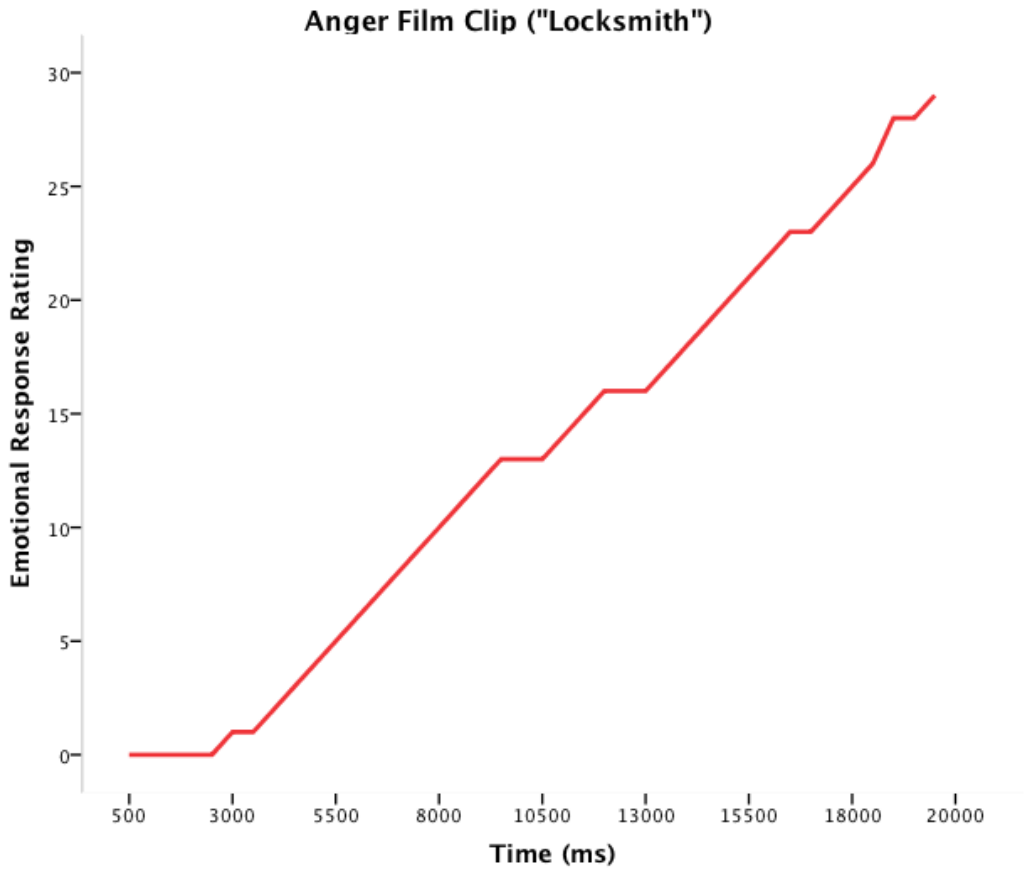


Figure Caption

Continuous emotional responses across an anger film clip from one subject.

Figure 30. Emotional responses across an anger clip (2)

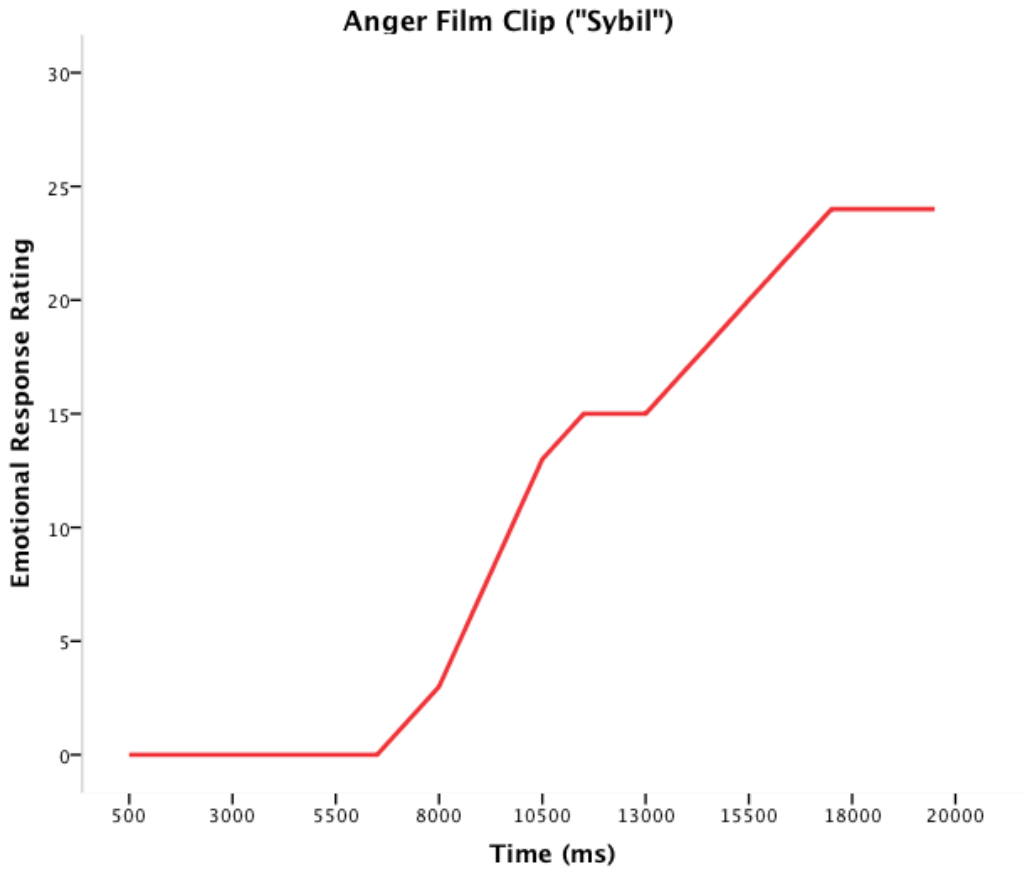


Figure Caption

Continuous emotional responses across an anger film clip from one subject.

Figure 31. Emotional responses across an anger clip (3)

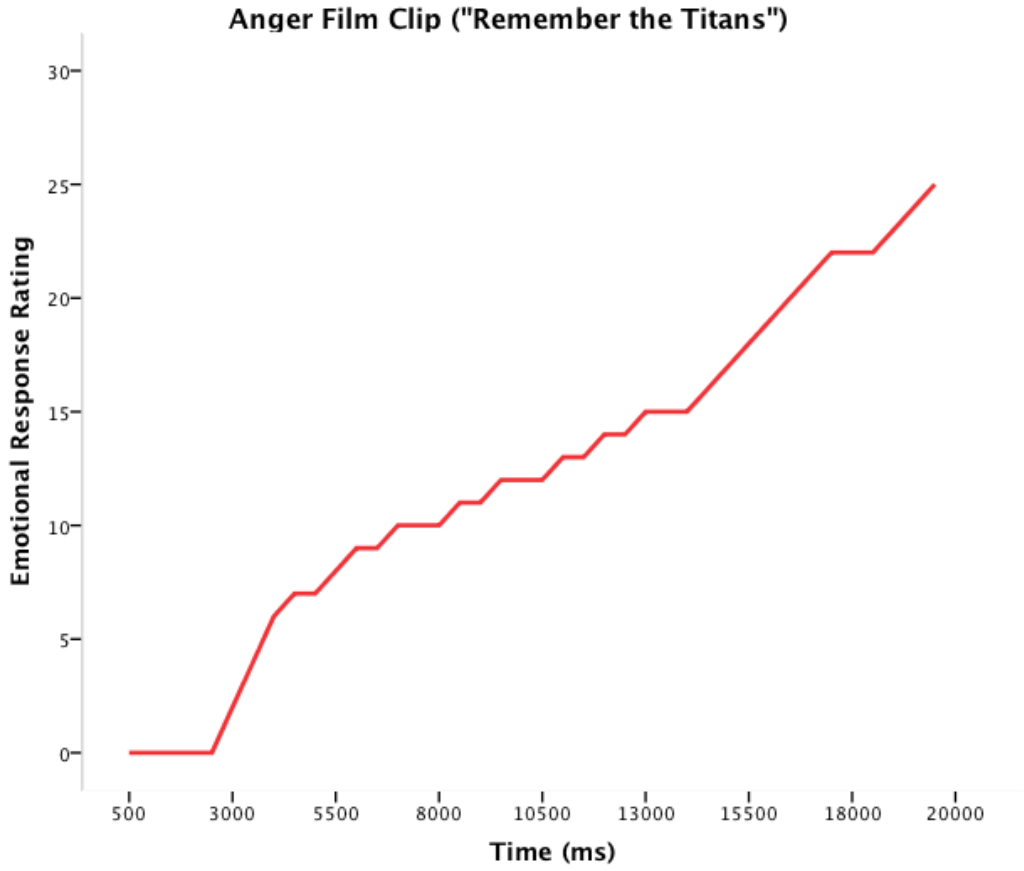


Figure Caption

Continuous emotional responses across an anger film clip from one subject.

Figure 32. Emotional responses across a fear clip (1)

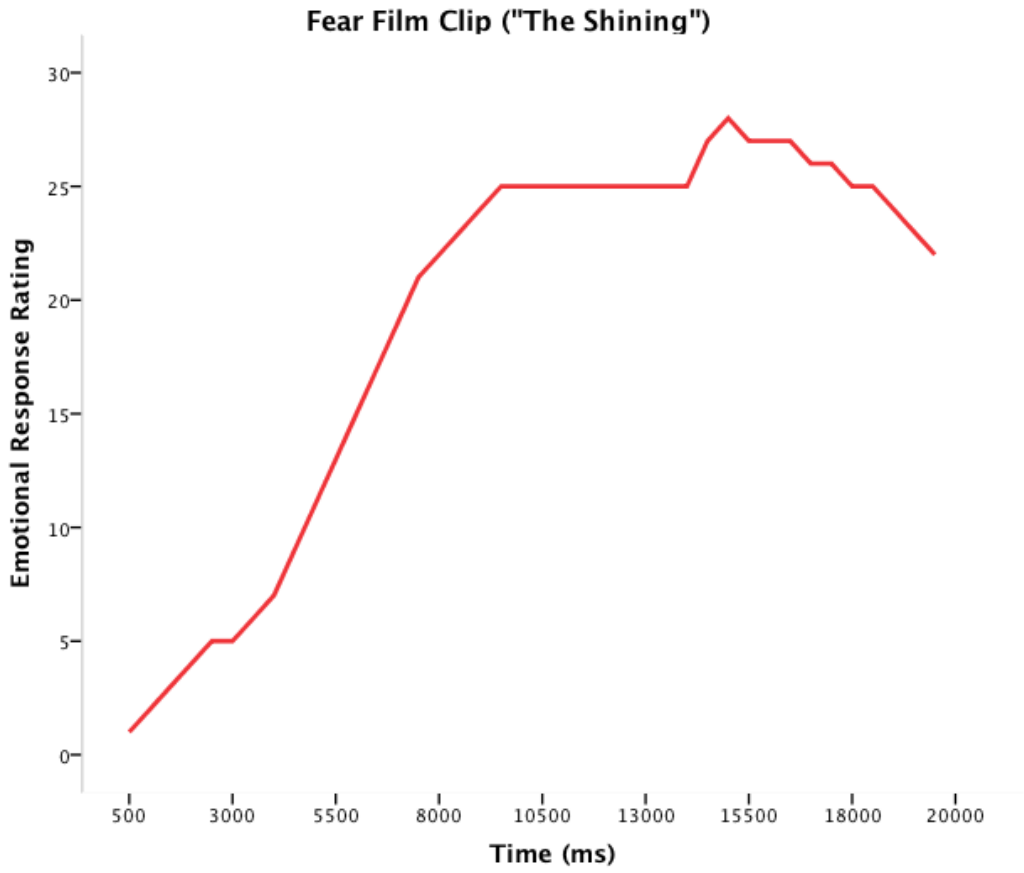


Figure Caption

Continuous emotional responses across a fear film clip from one subject.

Figure 33. Emotional responses across a fear clip (2)

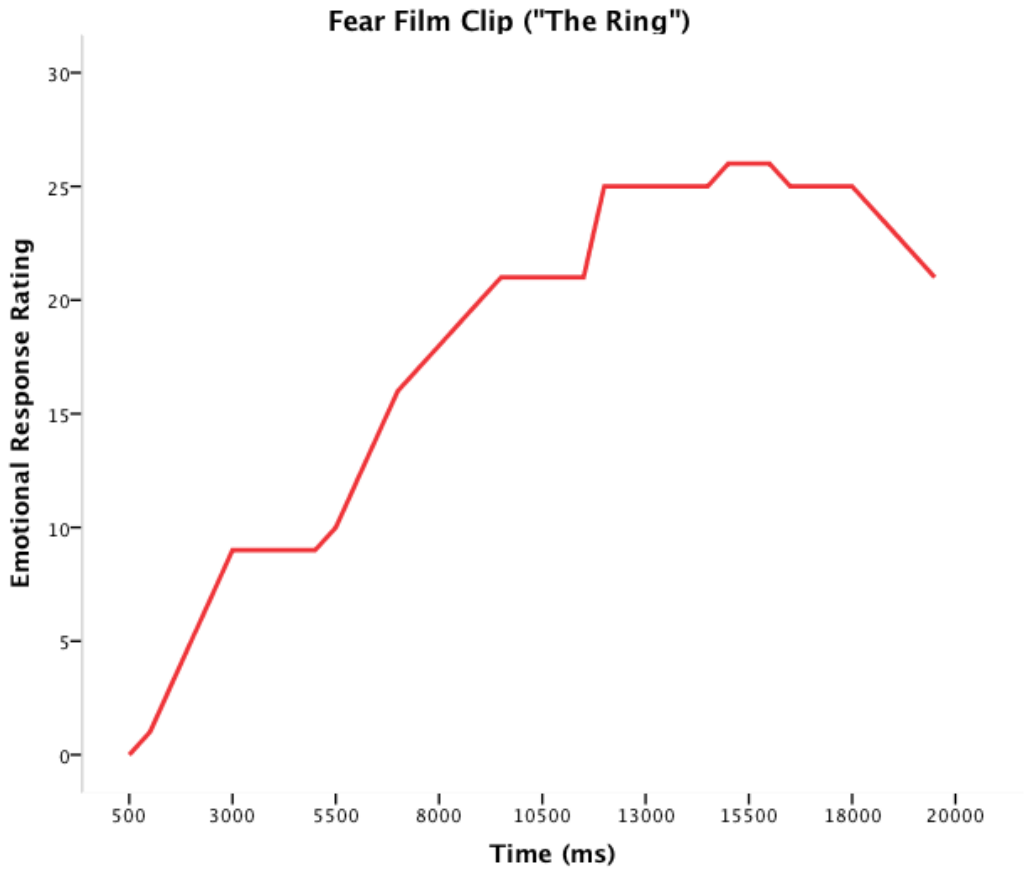


Figure Caption

Continuous emotional responses across a fear film clip from one subject.

Figure 34. Emotional responses across a fear clip (3)

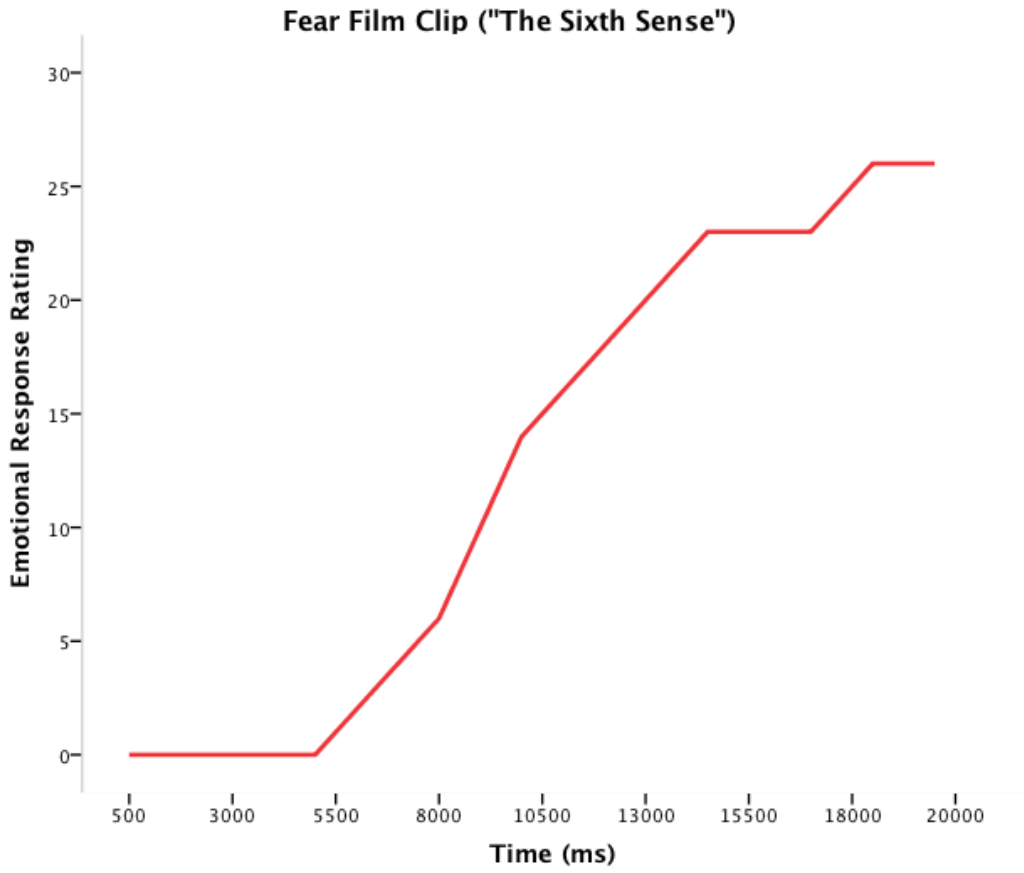


Figure Caption

Continuous emotional responses across a fear film clip from one subject.

Figure 35. Emotional responses across a disgust clip (1)

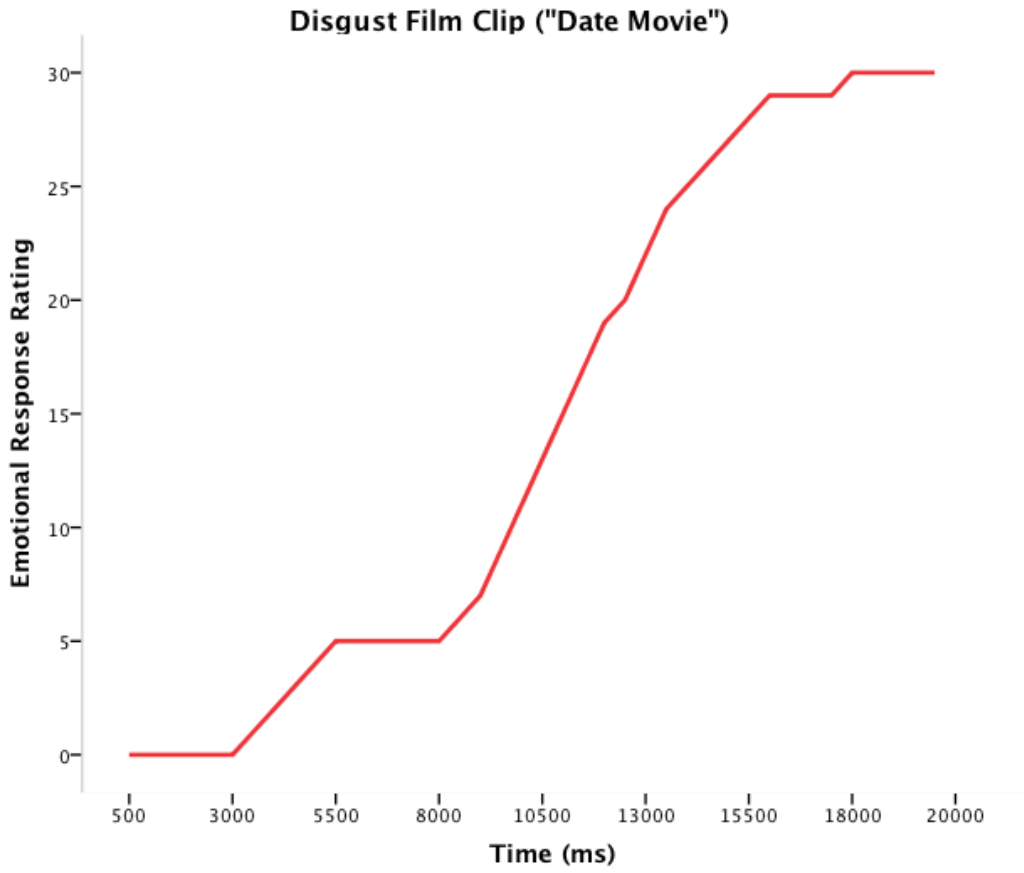


Figure Caption

Continuous emotional responses across a fear film clip from one subject.

Figure 36. Emotional responses across a disgust clip (2)

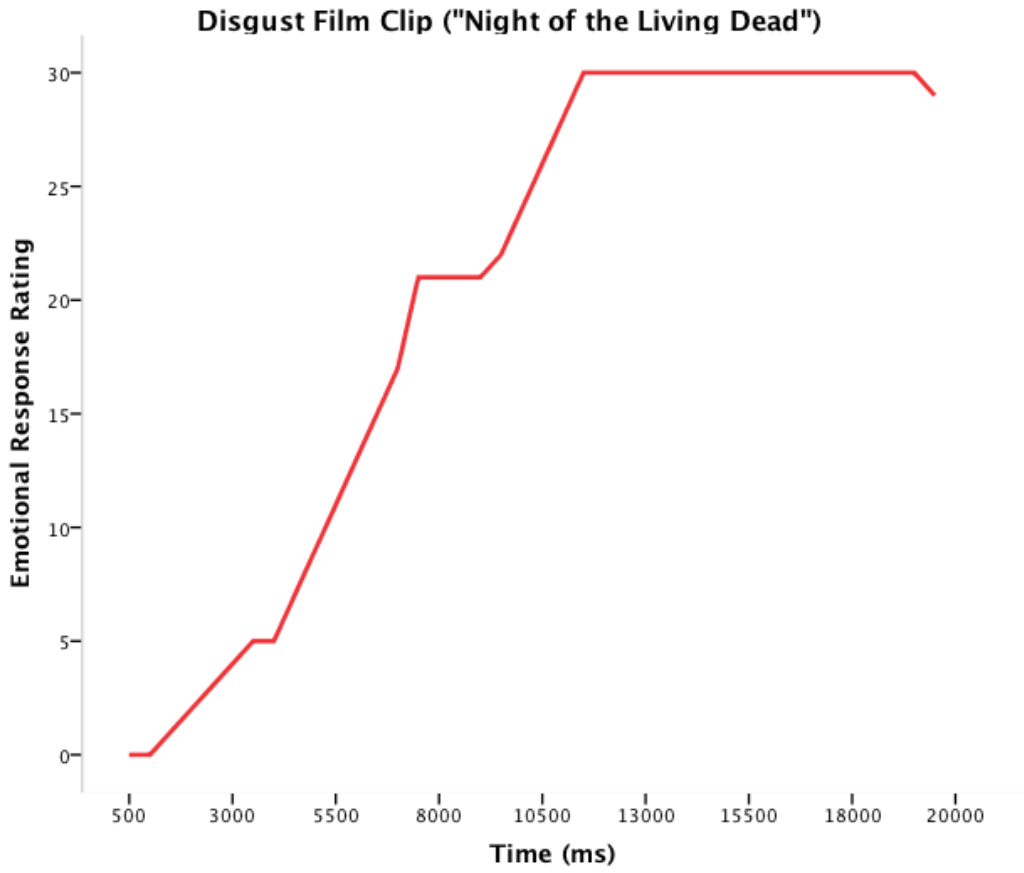


Figure Caption

Continuous emotional responses across a fear film clip from one subject.

Figure 37. Emotional responses across a disgust clip (3)

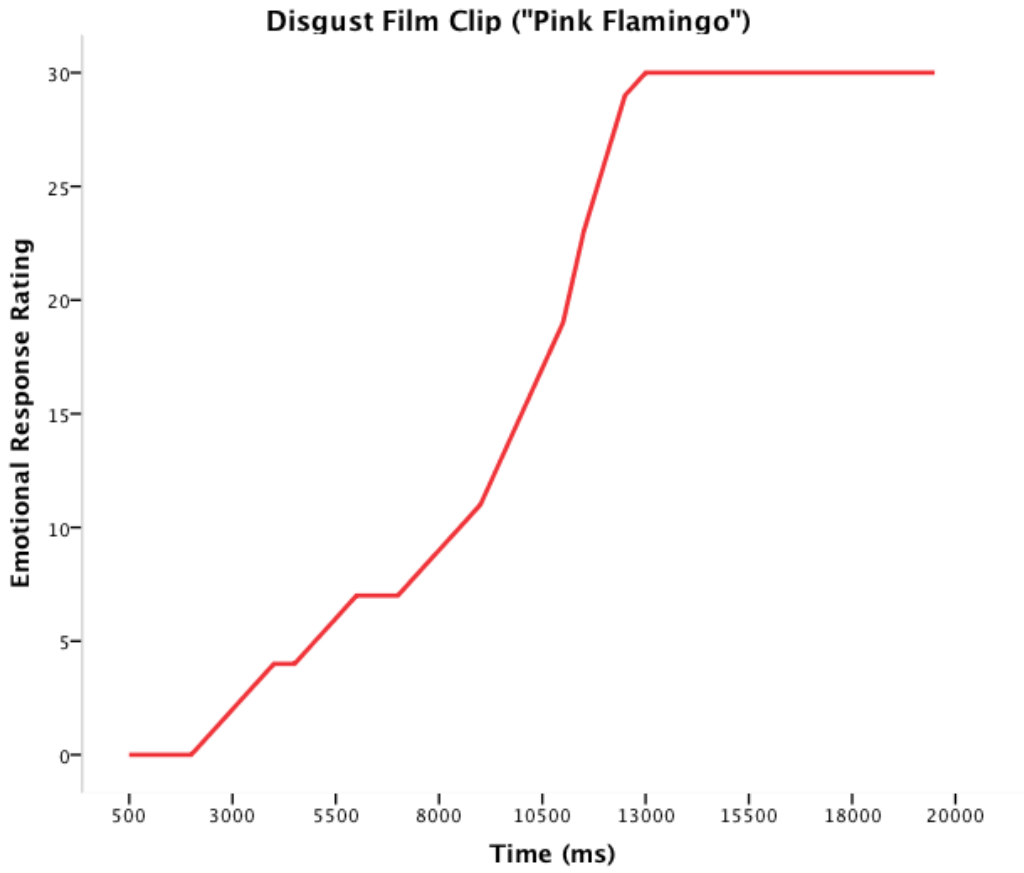


Figure Caption

Continuous emotional responses across a fear film clip from one subject.

3.4.2 Neuroimaging

3.4.2.1 Basic emotion consistency analyses

3.4.2.2 Consistency conjunction analyses (conjunction of activations elicited by films and memories for each basic emotion state)

Consistency conjunction analyses assessed the overlap between activation maps associated with an emotion state elicited by films and an emotion state elicited by memories. This was achieved by calculating within-modality pairwise contrasts of each emotion state with neutral (e.g., overlap between Anger Films > Neutral Films and Anger Memories > Neutral Memories) and multiplying binarized versions of those maps. This revealed overlapping clusters of activity that were present during emotional experience elicited by both films and memories. This analysis technique was used to demonstrate consistent activations associated with each basic emotion state.

3.4.2.2.1 Happy

The conjunction of happy films and happy memories revealed clusters located in the right posterior insula and right hippocampus extending into the parahippocampal cortex (see Figure 38). These clusters represent the core activations associated with happiness (see Table 9 for a list of core activations associated with each of the basic emotion states). Clusters for all conjunction analyses are displayed in red, as opposed to a gradient because the activation maps were converted into binary maps in order to calculate the conjunction.

Table 9. Clusters associated with the conjunction of films and memories for each basic emotion state

Region	*HEM*	*Coordinate (MNI)*		
		x	*y*	*z*
Core Happy Clusters				
Hippocampus/Parahippocampal G.	R	35	-36	5
Insula	R	30	-34	25
Core Sad Clusters				
Med. Frontal G.	L	0	60	23
Thalamus	R	2	-7	12
Thalamus	R	2	-26	1
Thalamus	L	-14	-11	-5
Putamen/Thalamus	R	23	-11	3
Caudate	R	15	23	6
Caudate	L	-8	19	6
Cingulate/Med. Frontal G.	L	-18	18	39
Pos. Cingulate	L	-4	-50	26
Core Anger Clusters				
Inf. Frontal G.	L	-34	23	16
Caudate Body	L	-13	14	15
Ant. Cingulate	R	7	20	15
Sup. Frontal G.	R	4	13	67
Cerebellum	R	10	-45	-35
Core Disgust Clusters				
Thalamus	R	10	-3	-5
Globus Pallidus	L	-16	-5	-5
Inf. Frontal G.	L	-38	38	-5
Mid. Frontal G.	L	-48	47	7

Inf. Frontal G.	R	37	15	-28

Note: Activation clusters at a p threshold of .001, uncorrected. Coordinates represent approximations of the center of each cluster. HEM = hemisphere; L = left; R = right; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

Figure 38. Core activations associated with happiness

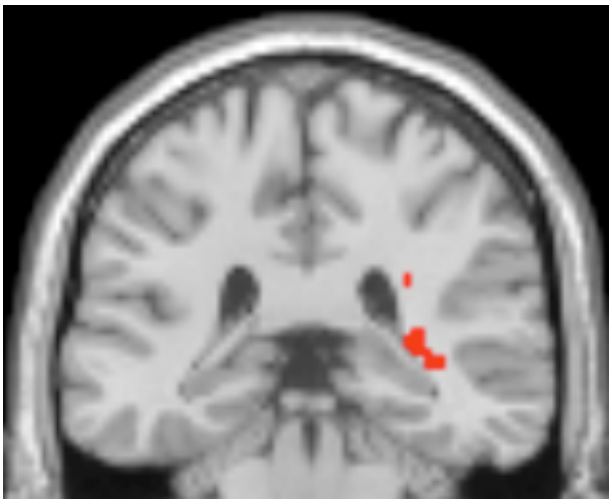


Figure Caption

Clusters in the right hippocampus, parahippocampal cortex, and insula characterized happiness. Contrast represents the overlap between happy films > neutral films and happy memories > neutral memories.

3.4.2.2.2 Sad

The conjunction of sad films and sad memories revealed clusters located in the right posterior insula and right hippocampus extending into the parahippocampal cortex (see Figure 39 and Table 9). These clusters represent the core activations associated with sadness.

Figure 39. Core activations associated with sadness

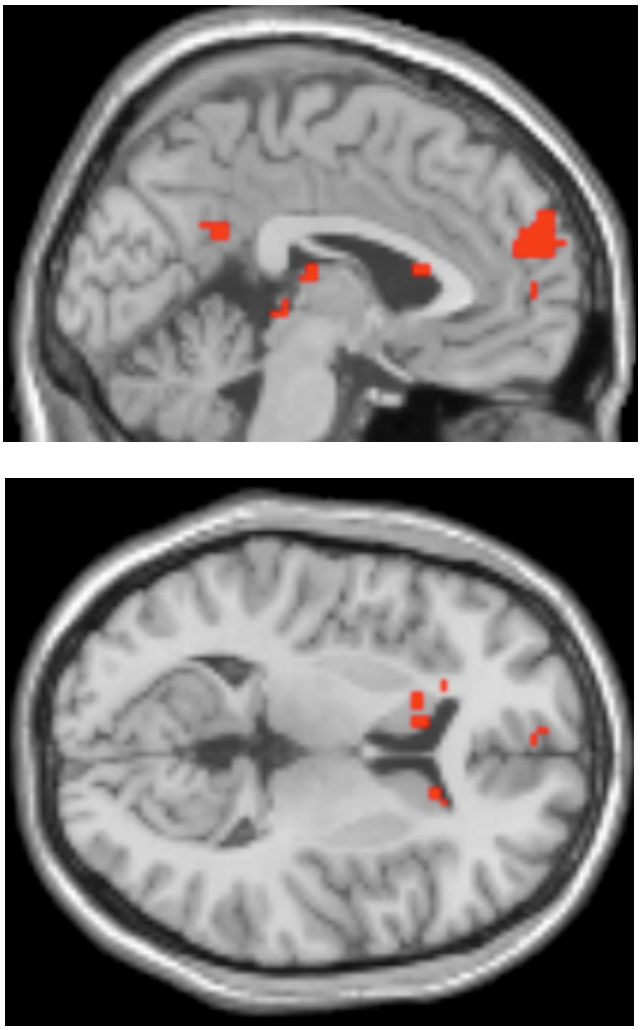


Figure Caption

Clusters in the left medFG, left posterior cingulate, bilateral thalamus (sagittal view), and bilateral caudate head (axial view) characterized sadness. Contrast represents the overlap between sad films > neutral films and sad memories > neutral memories.

3.4.2.2.3 Anger

The conjunction of anger films and anger memories revealed clusters located in the left IFG, left caudate body, right ACC, right superior frontal gyrus, and right cerebellum (see Figure 40 and Table 9). These clusters represent the core activations associated with anger.

Figure 40. Core activations associated with anger

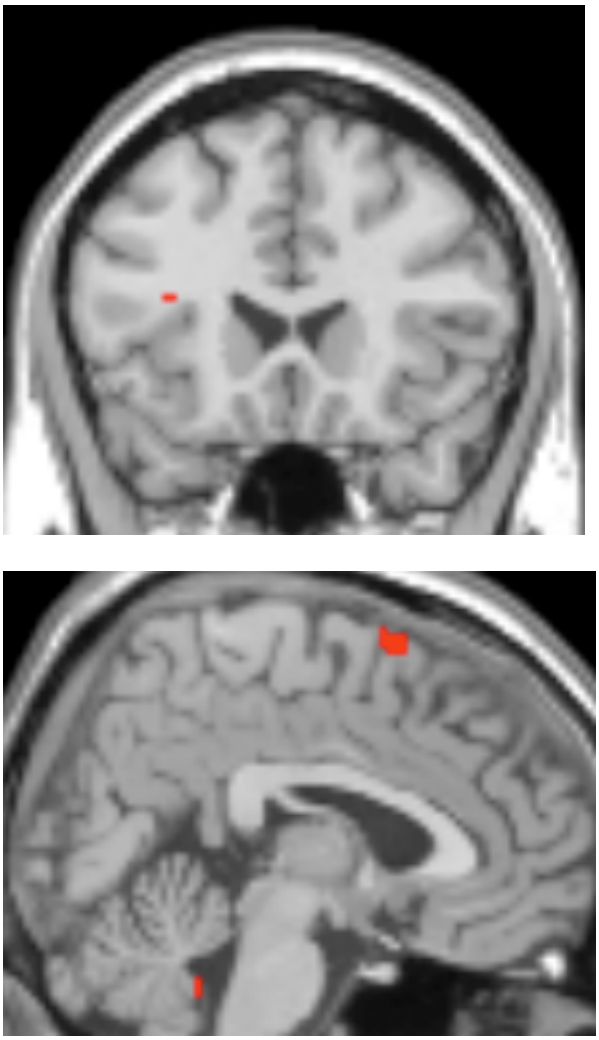


Figure Caption

Clusters in the left IFG (coronal view), right superior frontal gyrus, and right cerebellum characterized anger. Contrast represents the overlap between anger films > neutral films and anger memories > neutral memories.

3.4.2.2.4 Fear

The conjunction of fear films and fear memories did not reveal any significant clusters at a threshold of $p < 0.001$. The contrast of fear memories > neutral memories did not contribute any significant clusters at $p < 0.01$, and consequently, the conjunction of that contrast with fear films > neutral films could not be calculated. When the threshold was lowered to an exploratory level of $p < 0.05$ for the memory contrast, five significant activation clusters survived. A second conjunction analyses with the memory contrast at a more lenient threshold did not reveal any overlap. These results indicate that fear memories may have elicited a qualitatively different fear response than fear films. However, due to the fact that fear memories did not show any differences in activation from neutral memories at $p > 0.001$, the distinction between fear as elicited by films and fear elicited by memories might simply be a quantitative one. Ratings in the scanner would suggest otherwise, yet it is possible that subjects believed they were experiencing fear and that it was simply not comparable to the level of fear elicited by the film clips. The rating scale restricted subjects to only four responses (1; no fear, 2; a little fear, 3; moderate fear and 4; a lot of fear) and because subjects selected their own memories, they may have been biased toward the higher end of the narrow range. With a greater range in the response scale, we may have been able to detect a potential difference in emotional experience between fear films and fear memories.

3.4.2.2.5 Disgust

The conjunction of disgust films and disgust memories revealed clusters located in the left MFG, bilateral IFG, left thalamus, and right globus pallidus (see Figure 41 and Table 9). These clusters represent the core activations associated with disgust.

Figure 41. Core activations differentiating disgust

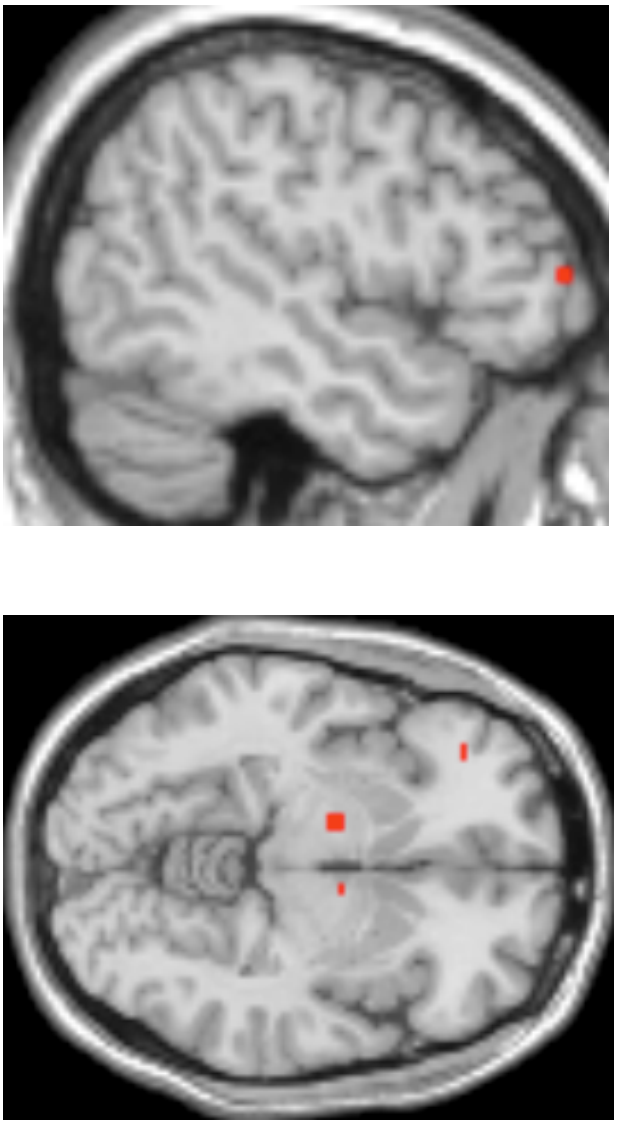


Figure Caption

Clusters in the left MFG (sagittal view), left IFG, left globus pallidus, and left thalamus (axial view) characterized disgust. Contrast represents the overlap between disgust films > neutral films and disgust memories > neutral memories.

3.4.2.3 Inclusive whole-brain core emotion analyses (each emotion state elicited by films, each emotion state elicited by memories, and each emotion state elicited by the combination of both films and memories)

In addition to conjunction analyses, whole brain data were investigated in order to characterize consistent activations associated with basic emotion states that included activations outside of the conjunction overlap (i.e., the contrasts included all activations associated with a given emotion state). Results are reviewed for all basic emotion states within modality (i.e., films and autobiographical memories separately) as well as with modality collapsed (i.e., films and memories combined).

3.4.2.3.1.1 Happy

3.4.2.3.1.1.1 Films

Activity in left anterior cingulate cortex ACC, left STG, bilateral posterior insula, left pons, bilateral midbrain, and left thalamus characterized happiness as elicited by films (see Table 10 for a summary of all peak coordinates and their related statistics)

Table 10. Inclusive whole brain basic emotion consistency contrasts

Region	*HEM*	*Coordinate (MNI)*			*k* (volume)	*Z*
		x	*y*	*z*		
		Happiness				
		Happy Films > Neutral Films				
Pos. Insula	R	36	-40	28	21	4.77
Lingual G.	R	21	-76	1	1654	4.43
Parahippocampal G.	R	39	-57	-5	LM	4.35
Cerebellum	R	18	-54	-14	LM	4.19
Lingual G.	L	-39	-79	1	249	4.42
Fusiform G.	L	-39	-49	-20	LM	3.50
Fusiform G.	L	-45	-73	-14	LM	3.34
Pons	L	-6	-37	-38	12	4.19
Pos. Cingulate	L	-12	-52	7	26	4.15
Midbrain	L	-9	-28	-14	95	4.05
Midbrain	R	9	-28	-17	LM	3.81
Sup. Temporal G.	L	-57	-25	10	36	4.01
Thalamus	L	-24	-25	-2	49	3.74
Globus Pallidus	L	-15	-4	-8	LM	3.45
Thalamus	L	-12	-13	-2	LM	3.41
Thalamus	L	-24	-25	-2	11	3.61
Sup. Temporal G.	L	-54	-7	4	22	3.52
Pos. Insula	L	-48	-7	-5	LM	3.43
Caudate Body	L	-18	20	1	27	3.52
ACC (BA 33)	L	-3	20	10	LM	3.49
Pos. Cingulate	R	12	-46	7	23	3.43
Pos. Cingulate	R	3	-43	7	LM	3.42
Caudate Body	R	21	17	7	7	3.39
Thalamus	L	-3	-7	-8	8	3.35
		Happy Memories > Neutral Memories				
Cingulate G.	R	24	11	19	11	3.72
		Happy (Films + Memories) > Neutral (Films + Memories)				
Pos. Insula (BA 13)	R	36	-40	28	9	3.94

Lingual G.	L	-15	-82	4	45	3.76
Lingual G.	R	3	-91	4	LM	3.28
Cuneus	L	-5	-94	4	LM	3.27
Cerebellum	R	33	-58	-23	115	3.76
Cerebellum	R	35	-58	-14	LM	3.58
Lingual G.	R	5	-73	-2	Lm	3.55
Mid. Temporal G.	R	42	-49	7	54	3.76
Caudate Tail	R	35	-37	7	LM	3.56
Pos. Insula (BA 13)	R	33	-40	15	LM	3.19
Midbrain/Hypothalamus	R	3	-10	-14	14	3.68
Caudate Body/ACC (BA24)	L	-6	8	19	7	3.57
Midbrain	R	12	-28	-14	10	3.55
Lingual G.	R	12	-79	7	16	3.44
Pos. Cingulate	R	6	-43	7	8	3.43
Caudate Body/ACC (BA24)	L	-3	17	13	5	3.38
Sup. Temporal G.*	R	45	-46	13	83	3.64
Sup. Temporal G.*	R	39	-34	4	LM	3.15
Sup. Temporal G.*	R	42	-37	13	LM	3.13
Sup. Temporal G.*	R	39	-34	10	LM	2.70
Sup. Temporal G.*	R	53	-37	10	LM	2.05
Sup. Temporal G.*	R	51	-1	-8	180	2.82
Sup. Temporal G.*	R	54	-7	1	LM	2.75
Sup. Temporal G.*	R	53	-22	7	LM	2.53
Sup. Temporal G.*	R	55	-19	10	LM	2.53

Sadness

Sad Films > Neutral Films

Globus Pallidus	L	-12	-7	-11	262	5.06
Globus Pallidus/Amygdala	R	21	-10	-11	LM	4.72
Thalamus	L	-5	-13	1	LM	4.31
Precuneus	L	-9	-52	31	70	4.15
Med. Frontal G.	L	-12	59	25	25	4.02
Sup. Frontal G.	L	-18	53	34	LM	3.22
Caudate Body	L	-15	5	16	85	3.88
Thalamus	L	-15	-15	15	LM	3.87
Caudate Body	L	-12	17	10	LM	3.50
Inf. Frontal G. (BA 47)	R	45	17	-26	26	3.82
Mid. Temporal G.	R	54	11	-29	LM	3.30
Sup. Temporal G.	L	-48	14	-32	6	3.79

Cerebellum	L	0	-64	4	32	3.67
Pos. Cingulate	L	-3	-54	16	LM	3.14
Ant. Cingulate C. (BA 32)	R	15	23	13	20	3.61
Putamen	R	27	11	-17	9	3.59
Ant. Insula (BA 13)	R	54	11	1	8	3.52
Mid. Temporal G.	L	-48	-73	28	46	3.40
Mid. Temporal G.	L	-51	-73	13	LM	3.37
Mid. Temporal G.	L	-42	-73	13	LM	3.33
Med. Frontal G.	L	-6	56	-2	5	3.37
Mid. Occipital G.	R	42	-64	1	12	3.33
Mid. Temporal G.	R	45	-54	13	LM	3.22

Sad Memories > Neutral Memories

Thalamus	L	0	-4	19	82	4.13
Caudate Body	L	-9	11	19	LM	3.92
Caudate Body	L	-12	20	15	LM	3.80
Caudate Body	L	-9	23	-2	9	3.55
Caudate Head	L	-3	17	1	LM	3.41
Caudate Body	R	18	32	4	17	3.51
Caudate Head	R	9	26	4	LM	3.50
Caudate Body	L	-21	29	13	7	3.32

Sad (Films + Memories) > Neutral (Films + Memories)

Precuneus	R	18	-55	46	8	3.50
Lingual G.	R	3	-67	7	42	3.48
Pos. Cingulate	R	15	-67	7	LM	3.25
Inf. Parietal Lobe	L	-63	-28	34	13	3.28

Anger

Anger Films > Neutral Films

Sup. Temporal G.	R	54	-31	7	1619	6.10
Sup. Temporal G.	R	51	-49	19	LM	5.43
Inf. Frontal G. (BA 47)	R	51	17	-26	LM	5.29
Inf. Frontal G.	L	-57	-13	1	3613	5.84
Mid. Temporal G.	L	-51	-49	10	LM	5.33
Sup. Temporal G.	L	-54	-28	7	LM	5.24
Inf. Frontal G. (BA 13)	L	-48	29	4	310	5.21

Inf. Frontal G. (BA 45)	L	-54	35	1	LM	5.04
Inf. Frontal G.	L	-35	17	22	LM	3.79
Med. Frontal G. (BA 9)	R	12	59	31	723	4.67
Sup. Frontal G.	L	-5	23	54	LM	4.50
Sup. Frontal G.	L	-3	35	58	LM	4.38
Mid. Frontal G.	R	39	20	31	237	4.51
Mid. Frontal G.	R	51	8	43	LM	4.22
Mid. Frontal G.	R	30	23	28	LM	4.14
Cerebellum	R	27	-70	-23	268	4.51
Cerebellum	R	24	-70	-32	LM	4.48
Fusiform G.	R	42	-45	-23	LM	4.47
Cerebellum	R	0	-55	-32	95	4.30
Pons	L	-9	-49	-35	LM	4.07
Cerebellum	L	-24	-70	-32	30	4.12
Fusiform G.	L	-39	-43	-20	39	4.04
Med. Frontal G.	L	-3	59	-14	33	3.79
Mid. Frontal G.	L	-42	2	55	50	3.76
Mid. Frontal G.	L	-35	-1	49	LM	3.57
Mid. Frontal G.	L	-42	14	52	LM	3.19
Inf. Frontal G. (BA 45)	R	54	35	-2	36	3.72
Inf. Frontal G. (BA 45)	R	39	32	1	LM	3.53
Inf. Frontal G. (BA 47)	R	51	38	-11	LM	3.43
Cerebellum	L	-6	-76	-29	12	3.63
Cerebellum	L	-36	-76	-20	18	3.32

Anger Memories > Neutral Memories

Caudate Body	L	-6	14	13	8	3.69
Parahippocampal G.	R	30	-40	4	18	3.61
Caudate Tail	R	24	-37	13	LM	3.51
Caudate Body	L	-21	20	4	18	3.48
Claustrum	L	-27	17	16	LM	3.32
Ant. Insula (BA 13)	L	-36	20	13	LM	3.20

Anger (Films + Memories) > Neutral (Films + Memories)

Sup. Temporal G.	L	-57	-13	1	5821	5.29
Sup. Temporal G.	R	54	-34	7	LM	5.18
Midbrain	L	-12	-10	-8	LM	5.17

Inf. Frontal G. (BA 45)	L	-54	26	7	393	4.72
Mid. Frontal G.	L	-42	17	52	LM	4.14
Mid. Frontal G.	L	-36	23	19	LM	3.78
Inf. Frontal G.	R	54	26	22	253	4.46
Mid. Frontal G.	R	42	23	40	LM	4.04
Mid. Frontal G.	R	48	17	37	LM	3.93
Sup. Frontal G.	R	9	50	40	902	4.32
Med. Frontal G.	R	5	47	31	LM	4.30
Sup. Frontal G.	R	15	41	49	LM	4.22
Parahippocampal G.	L	-21	-25	-23	21	3.66
Parahippocampal G.	L	-18	-31	-14	LM	3.18
Cerebellum	L	-15	-76	-29	26	3.58
Cerebellum	L	-21	-70	-32	LM	3.5
Cerebellum	L	-30	-57	-29	LM	3.17
Med. Frontal G. (BA 10)	L	-3	59	-17	33	3.56
Med Frontal G. (BA 10)	L	-9	53	-14	LM	3.49
Cerebellum	L	-9	-52	-26	6	3.26
Inf. Frontal G.*	L	-54	26	7	549	4.72
Inf. Frontal G.*	L	-57	23	10	LM	4.71
Inf. Frontal G.*	L	-36	23	19	LM	3.78
Inf. Frontal G.*	L	-48	14	28	LM	3.24
Inf. Frontal G.*	L	-39	35	-2	LM	2.51

Fear

Fear Films > Neutral Films

Mid. Occipital G.	R	39	-70	16	148	5.13
Precuneus	R	30	-73	19	LM	4.51
Pos. Cingulate	R	33	-75	7	LM	4.27
Mid. Occipital G.	L	-39	-79	19	363	4.81
Cuneus	L	-24	-79	25	LM	4.24
Precuneus	L	-18	-73	43	LM	3.87
Precuneus	R	24	-49	46	30	4.10
Precentral G.	R	36	11	31	32	3.76
Precuneus	R	9	-52	52	21	3.73
Sup. Frontal G.	L	-21	53	13	6	3.42
Parahippocampal G.	L	-30	-49	-8	23	3.39
Fusiform G.	L	-30	-58	-11	LM	3.33
Parahippocampal G.	L	-33	-40	-11	LM	3.15
Parahippocampal G.	R	33	-43	-8	15	3.31

Fear Memories > Neutral Memories

Parahippocampal G.	R	33	-40	4	10	1.91

Fear (Films + Memories) > Neutral (Films + Memories)

Mid. Temporal G.	R	36	-64	28	422	4.78
Precuneus	R	27	-51	40	LM	4.72
Precuneus	R	30	-52	43	LM	4.53
Mid. Temporal G.	L	-39	-82	16	203	4.42
Mid. Temporal G.	L	-30	-75	28	LM	4.15
Cerebellum	L	-33	-64	-8	66	4.02
Precentral Gyrus (BA 6)	R	39	5	31	38	3.99
Fusiform G.	R	48	-49	-8	19	3.75
Mid. Frontal G.	L	-21	2	55	9	3.62
Precuneus	L	-24	-58	43	8	3.50
Fusiform G.	L	-48	-67	-5	9	3.37
Precuneus	L	-15	-70	46	10	3.37

Disgust

Disgust Films > Neutral Films

Ant. Insula	R	57	14	-2	712	5.07
Ant. Insula	R	54	14	16	LM	4.39
Ant. Insula	R	39	2	-5	LM	4.28
Inf. Parietal Lobule	L	-36	-46	58	298	4.89
Inf. Parietal Lobule	L	-57	-31	46	LM	4.88
Ant. Insula	L	-27	26	-8	306	4.63
Ant. Insula	L	-33	20	-17	LM	3.95
Ant. Insula	L	-33	8	-14	LM	3.95
Fusiform G.	R	48	-52	-5	220	4.58
Fusiform G.	R	45	-51	-8	LM	4.29
Fusiform G.	R	35	-54	-11	LM	4.29
Fusiform G.	L	-45	-67	-8	284	4.47
Ant. Insula	L	-33	8	-14	LM	4.12
Mid. Temporal G.	R	48	-52	-5	LM	3.79
Precuneus	R	27	-64	40	275	4.47
Precuneus	R	30	-45	45	LM	4.31
Postcentral G.	R	60	-13	19	297	4.30

Postcentral G./Insula	R	60	-19	25	LM	4.27
Supramarginal G.	R	60	-34	31	LM	3.53
Postcentral G./Insula	L	-57	-22	19	55	4.18
Cuneus	R	27	-82	10	19	3.75
Mid. Occipital G.	L	-33	-88	1	54	3.74
Mid. Frontal G.	R	33	-1	55	29	3.74
Caudate Body	L	-12	8	10	16	3,74
Caudate Body	R	18	8	10	64	3.67
Thalamus	R	15	-1	10	LM	3.34
Mid. Frontal G.	R	12	-10	4	LM	3.28
Cingulate G.	L	-30	2	58	11	3.39

Disgust Memories > Neutral Memories

Pos. Insula	L	-21	-46	13	9	3.48

Disgust (Films + Memories) > Neutral (Films + Memories)

Ant. Insula	L	-33	8	-14	507	4.74
Ant. Insula	L	-39	2	-11	LM	4.58
Ant. Insula	L	-39	25	1	LM	4.53
Ant. Insula	R	54	11	-8	515	4.33
Ant. Insula	R	57	14	13	LM	4.12
Inf. Frontal G./Insula	R	48	32	-2	LM	4.05
Inf. Parietal Lobule	L	-60	-31	43	27	4.25
Mid. Temporal G.	R	48	-49	-2	504	4.24
Parahippocampal G.	R	45	-51	-8	LM	4.15
Mid. Temporal G.	R	45	-52	10	LM	3.97
Inf. Frontal G.	R	36	11	22	32	4.15
Fusiform G.	L	-42	-52	-20	128	3.92
Fusiform G.	L	-45	-57	-5	LM	3.85
Cerebellum	L	-30	-57	-17	LM	3.56
Inf. Frontal G.	L	-51	44	4	6	3.83
Mid. Frontal G.	R	45	2	52	26	3.83
Cuneus	R	27	-79	13	15	3.80
Postcentral G./Insula	L	-57	-22	19	26	3.70
Caudate Body	L	-12	8	10	17	3.68
Thalamus	R	9	-10	1	73	3.62

Thalamus	R	15	-13	7	LM	3.60
Caudate Body	R	18	8	13	LM	3.35
Mid. Occipital G.	L	-33	-85	1	21	3.58
Inf. Parietal Lobule	L	-33	-43	49	42	3.57
Precuneus	L	-33	-49	55	LM	3.57
Precuneus	L	-27	-58	52	LM	3.21
Precuneus	R	27	-52	49	17	3.44
Sup. Frontal G.	R	9	11	67	11	3.33
Inf. Frontal G.	L	-57	14	7	5	3.31
Ant. Insula*	L	-30	26	-8	244	4.42
Ant. Insula*	L	-39	20	1	LM	4.18
Ant. Insula*	L	-30	17	-20	LM	4.15
Ant. Insula*	L	-33	11	-14	LM	3.98
Ant. Insula*	L	-39	20	-8	LM	3.97
Ant. Insula*	L	-35	25	4	LM	3.87
Ant. Insula*	R	48	11	-8	205	3.92
Ant. Insula*	R	27	14	-14	LM	3.54
Ant. Insula*	R	42	28	-5	LM	3.02
Ant. Insula*	R	35	29	-2	LM	2.98
Ant. Insula*	R	25	29	4	LM	2.42
Ant. Insula*	R	35	20	13	LM	1.95
Ant. Insula*	R	35	11	13	LM	1.88

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. The contrast threshold for fear memories was set at an exploratory $p < .05$ (k=5) when no clusters were revealed at more stringent thresholds. Clusters detected by a small-volume correction ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.3.1.1.2 Memories

Activity in right cingulate gyrus characterized happiness as elicited by autobiographical memories (see Table 10 for related statistics).

3.4.2.3.1.1.3 Overall (Films and Memories)

Activity in left ACC/caudate, bilateral insula (see Figure 42), midbrain, and posterior insula characterized happiness as elicited by the combination of films and autobiographical memories (i.e., overall) (see Table 10 for a summary of all peak coordinates and their related statistics). A small volume correction in the right superior temporal gyrus (STG) revealed additional activity associated with overall happiness.

Figure 42. Happiness Overall

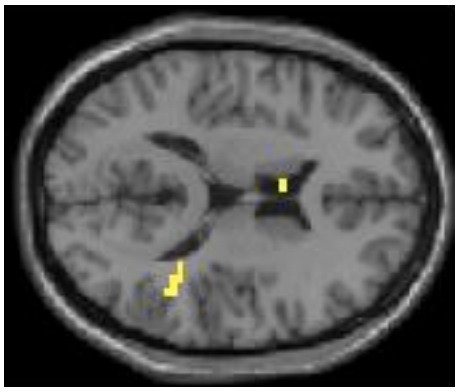


Figure Caption

Activation in the right posterior insula associated with happiness elicited by the combination of both films and memories. $p < 0.001$, uncorrected.

3.4.2.3.1.2 Sad

3.4.2.3.1.2.1 Films

Activity in left caudate body, left medial frontal gyrus (medFG), right anterior insula, and bilateral globus pallidus characterized sadness as elicited by autobiographical memories (see Table 10 for a summary of all peak coordinates and their related statistics).

3.4.2.3.1.2.2 Memories

Activity in left thalamus, and bilateral caudate body and head (see Figure 43) characterized sadness as elicited by autobiographical memories (see Table 10 for a summary of all peak coordinates and their related statistics).

Figure 43. Sad Films > Neutral Films

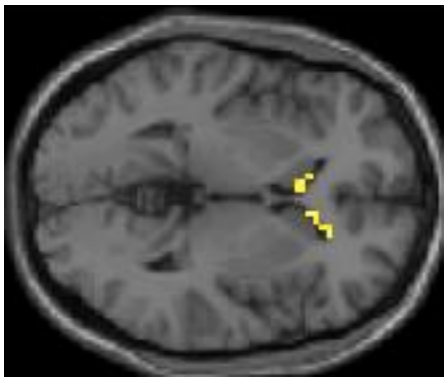


Figure Caption

Activation in the left caudate associated with the recollection of sad memories. $p < 0.001$, uncorrected.

3.4.2.3.1.2.3 Overall (Films and Memories)

Activity in right precuneus and right posterior cingulate characterized sadness as elicited by the combination of films and autobiographical memories (i.e., overall) (see Table 10 for a summary of all peak coordinates and their related statistics).

3.4.2.3.1.3 Anger

3.4.2.3.1.3.1 Films

Bilateral activity in STG, IFG (see Figure 44), MFG and medFG characterized anger as elicited by films (see Table 10 for a summary of all peak coordinates and their related statistics).

Figure 44. Anger Films > Neutral Films

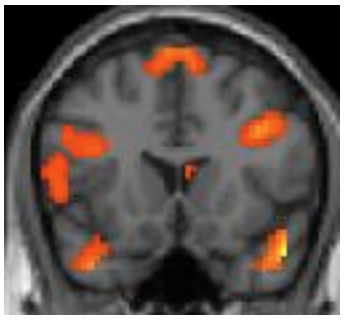


Figure Caption

Activation in the right inferior frontal gyrus, bilateral MFG, and SFG associated with anger films. $p < 0.001$, uncorrected.

3.4.2.3.1.3.2 Memories

Activity in right PHG, left caudate body, right caudate tail, and left anterior insula characterized anger as elicited by autobiographical memories (see Table 10 for a summary of all peak coordinates and their related statistics).

3.4.2.3.1.3.3 Overall (Films and Memories)

Similar to the contrast involving films only, bilateral activity in STG, IFG, MFG and medFG characterized anger as elicited by the combination of films and autobiographical memories (i.e., overall) (see Table 10 for a summary of all peak coordinates and their related statistics). A small volume correction in the left IFG revealed additional activity associated with overall anger.

3.4.2.3.1.4 Fear

3.4.2.3.1.4.1 Films

Activity in bilateral precuneus, left SFG, and bilateral PHG (see Figure 45) characterized fear as elicited by films (see Table 10 for a summary of all peak coordinates and their related statistics).

Figure 45. Fear Films > Neutral Films

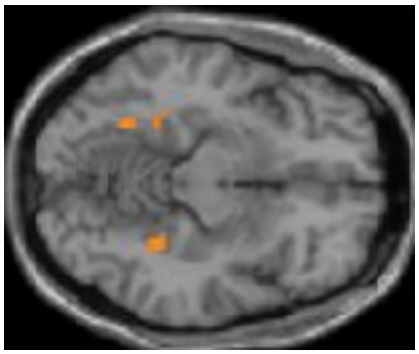


Figure Caption

Activation in bilateral parahippocampal gyrus associated with fear films. $p < 0.001$, uncorrected.

3.4.2.3.1.4.2 Memories

Activity in right PHG characterized fear as elicited by autobiographical memories (see Table 10 for a related statistics).

3.4.2.3.1.4.3 Overall (Films and Memories)

Activity in right precuneus and right posterior cingulate characterized fear as elicited by the combination of films and autobiographical memories (i.e., overall) (see Table 10 for a summary of all peak coordinates and their related statistics).

3.4.2.3.1.5 Disgust

3.4.2.3.1.5.1 Films

Activity in bilateral anterior insula, bilateral caudate body, right fusiform gyrus and right precuneus characterized disgust as elicited by films (see Table 10 for a summary of all peak coordinates and their related statistics).

3.4.2.3.1.5.2 Memories

Activity in left posterior insula characterized disgust as elicited by autobiographical memories (see Table 10 for related statistics).

3.4.2.3.1.5.3 Overall (Films and Memories)

Similar to the contrast involving films only, activity in bilateral anterior insula (see Figure 46), bilateral caudate body, bilateral precuneus, and left fusiform gyrus characterized disgust as elicited by the combination of films and autobiographical

memories (i.e., overall) (see Table 10 for a summary of all peak coordinates and their related statistics). A small volume correction performed in the left and right anterior insula revealed additional activity associated with overall disgust.

Figure 46. Disgust Overall

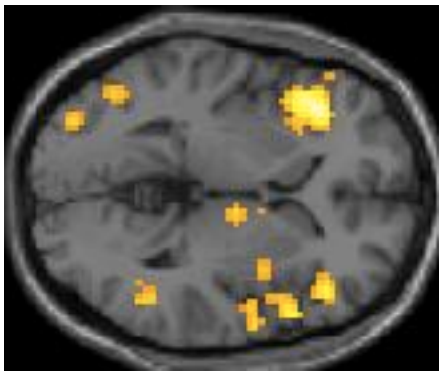


Figure Caption

Activation in the bilateral anterior insula associated with disgust elicited by the combination of both films and memories. $p < 0.001$, uncorrected.

3.4.2.4 Differentiability conjunction analyses (conjunction of regions that differentiated one emotion state from another in both film and memory contrasts)

Differentiability conjunction analyses assessed the overlap between pairwise contrasts of each emotion state within modality (e.g., overlap between Anger Films > Disgust Films and Anger Memories > Disgust Memories). This analysis technique was used to demonstrate differentiation of basic emotion states.

3.4.2.4.1 Happiness

3.4.2.4.1.1 Happy > Sad

The conjunction of regions more active during happiness versus sadness across films and memories did not reveal any significant clusters. See the reverse contrast below for regions differentiating the two emotions.

3.4.2.4.1.2 Happy > Anger

The conjunction of regions more active during happiness versus anger across films and memories revealed clusters located in the left OFC, right insula, right precuneus, and right cingulate (see Figure 47). These clusters represent the core activations that differentiated happiness from anger (see Table 11 for a list of core activations differentiating each of the basic emotion states). Clusters for all conjunction analyses are displayed in red, as opposed to a gradient because the activation maps were converted into binary maps in order to calculate the conjunction.

Table 11. Clusters associated with the conjunction of films and memories for each pairwise contrast differentiating basic emotion states

Region	*HEM*	*Coordinate (MNI)*		
		x	*y*	*z*
Happy > Anger				
Orbitofrontal C.	L	-37	44	-16
Pos. Insula	R	37	-39	27
Precuneus/Cingulate G.	R	22	-39	44
Cingulate G.	R	23	-15	44
Happy > Disgust				
Ant. Cingulate C.	R	11	37	-8
Caudate	L	-18	26	8
Cingulate C.	R	20	-7	37
Hippocampus	L	-33	-37	0
Hippocampus	R	32	-38	4
Pos. Insula	L	-27	-35	28
Pos. Insula	R	41	-39	28
Pos. Cingulate C.	R	11	-53	20
Lingual G.	R	11	-53	6
Sad > Happy				
Med. Frontal G.	L	-11	57	28
Sad > Anger				
Ant. Cingulate C.	L	-18	41	1
Ant. Cingulate C.	R	18	41	-3
Sad > Fear				
Med. Frontal G.	L	-6	54	-8

Ant. Cingulate	L	-6	32	-4
Inf. Frontal G.	R	42	18	-25
Mid. Temporal G.	R	51	1	-25
Globus Pallidus	R	24	-5	-7
Pos. Insula	R	34	-5	19
Globus Pallidus	R	13	-10	-13
Pos. Insula	R	50	-18	20
Postcentral G.	R	45	-19	63
Postcentral G.	L	-57	-19	32
Precuneus	L	-9	-60	32
Mid. Temporal G.	R	45	-59	8
Cerebellum	R	13	-64	4
Occipital/Mid. Temporal G.	L	-46	-71	4
Cerebellum	L	-33	-82	-28

Sad > Disgust

Ant. Cingulate	R	3	52	-11
Ant. Cingulate/Med. Frontal G.	R	21	41	7
Caudate Head	L	-10	22	2
Cingulate G.	L	-18	18	36
Caudate	L	-21	-18	25
Caudate/Insula	L	-24	-29	25
Pos. Cingulate	R	6	-49	28
Pos. Cingulate	R	2	-49	8
Cingulate G./Precuneus	R	2	-46	35
Cingulate G./Precuneus	R	18	-57	32

Anger > Happy

Cerebellum	R	23	-65	-32

Anger > Fear

Sup. Temporal G.	R	51	14	-28
Sup. Frontal G.	L	-3	5	68
Mid. Frontal G.	L	-43	0	55
Precentral G.	L	-48	-12	25
Mid. Temporal G.	L	-51	-18	-11
Cerebellum	L	-9	-45	-34

Cerebellum	R	9	-45	-36
Cerebellum	R	23	-67	-23
Cerebellum	R	23	-70	-32

Anger > Disgust

Sup. Frontal G.	R	23	30	54

Disgust > Happy

Postcentral G.	R	65	-21	31
Postcentral G.	L	-63	-26	32
Supramarginal G.	L	-53	-33	45
Sup. Parietal Lobule	L	-30	-51	52

Disgust > Sad

Inf. Frontal G.	L	-51	43	4
Inf. Frontal G.	L	-49	46	8

Disgust > Anger

Mid. Frontal G.	L	-46	43	12
Mid. Frontal G.	L	-24	6	60
Insula	L	-40	0	9
Postcentral G.	L	-62	-21	33
Postcentral G.	R	64	-20	36
Postcentral G.	L	-21	-20	57
Precuneus	L	-34	-48	56
Fusiform G.	L	-46	-50	-16
Precuneus	L	-26	-62	55
Precuneus	R	21	-68	44

Disgust > Fear

Mid. Frontal G.	L	-49	46	8
Claustrum	R	26	24	8
Inf. Frontal G.	R	35	17	-28
Inf. Frontal G./Insula	R	58	13	0
Sup. Temporal G.	R	61	-3	4

Insula	R	39	-3	9
Insula	L	-36	13	3
Inf. Frontal G./Insula	L	-54	13	-2
Amygdala/Inf. Frontal G.	L	-32	2	-16
Thalamus	R	10	2	-4
Cingulate G.	L	-2	-4	32
Postcentral G.	L	-62	-22	32
Insula	R	42	-31	14
Fusiform G.	L	-44	-52	-13

Note: Activation clusters at a p threshold of .001, uncorrected. Coordinates represent approximations of the center of each cluster. HEM = hemisphere; L = left; R = right; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

Figure 47. Core activations differentiating happiness from anger

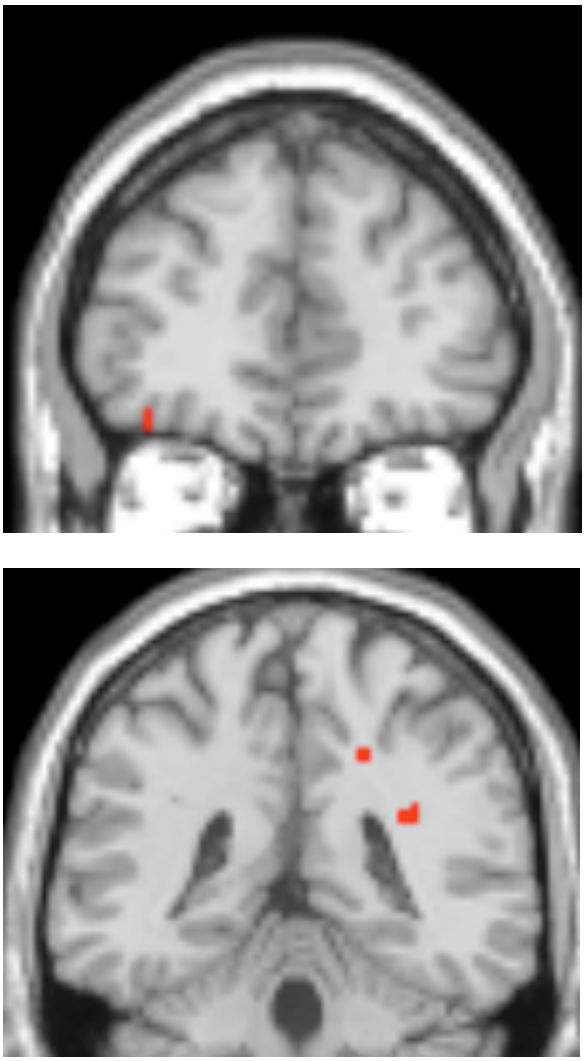


Figure Caption

Clusters in the left lateral OFC (top coronal), right precuneus/cingulate, and right insula (bottom coronal) differentiated happiness from anger. Contrast represents the overlap between happy films > anger films and happy memories > anger memories.

3.4.2.4.1.3 Happy > Fear

The conjunction of regions more active during happiness versus fear across films and memories did not reveal any significant clusters.

3.4.2.4.1.4 Happy > Disgust

The conjunction of regions more active during happiness versus disgust across films and memories revealed clusters located in the right ACC, right cingulate, right posterior cingulate, right lingual gyrus, left caudate, bilateral hippocampus, and bilateral posterior insula (see Figure 48 and Table 11). These clusters represent the core activations that differentiated happiness from disgust.

Figure 48. Core activations differentiating happiness from disgust

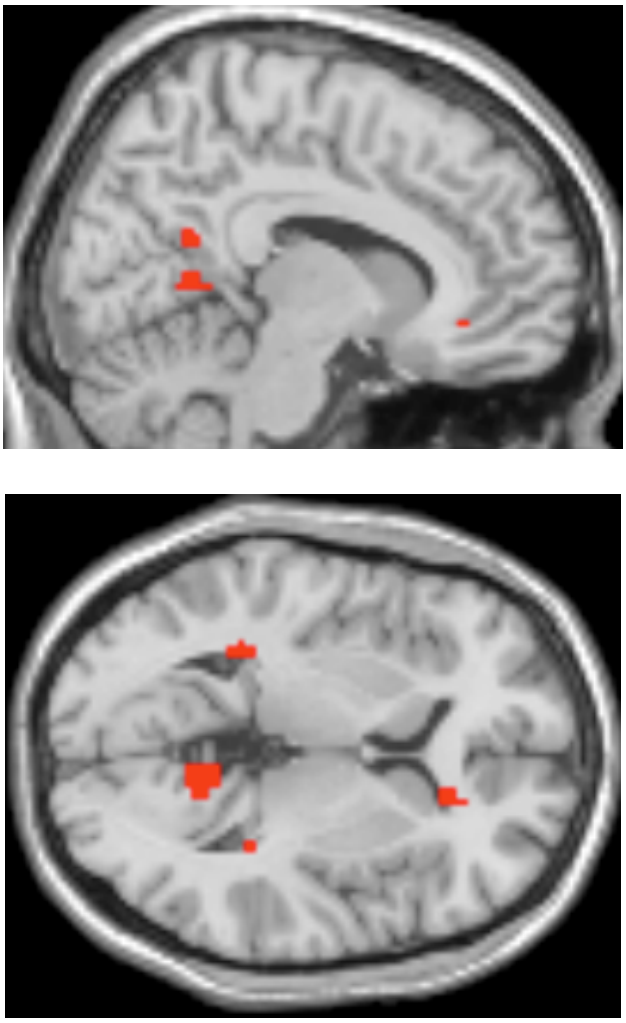


Figure Caption

Clusters in the right anterior and posterior ACC (top sagittal), and bilateral hippocampus (bottom axial) differentiated happiness from anger. Contrast represents the overlap between happy films > disgust films and happy memories > disgust memories.

3.4.2.4.2 Sadness

3.4.2.4.2.1 Sad > Happy

The conjunction of regions more active during sadness versus happiness across films and memories revealed a cluster located in the left MFG (see Figure 49 and Table 11). This cluster represents the core activation that differentiated sadness from happiness.

Figure 49. Core activation differentiating sadness from happiness

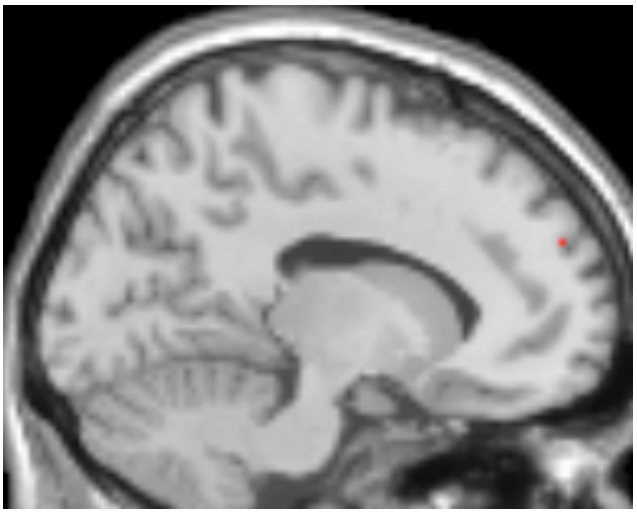


Figure Caption

Cluster in the left MFG. Contrast represents the overlap between sad films > happy films and sad memories > happy memories.

3.4.2.4.2.2 Sad > Anger

The conjunction of regions more active during sadness versus anger across films and memories revealed clusters located in the left and right ACC (see Figure 50 and Table 11). These clusters represent the core activations that differentiated sadness from anger.

Figure 50. Core activations differentiating sadness from anger

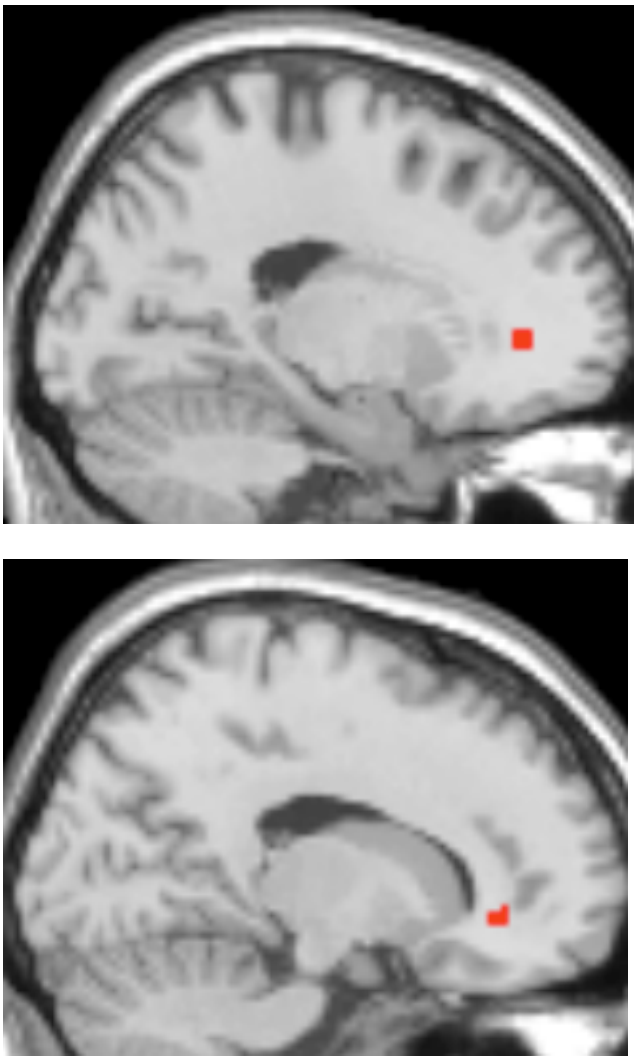


Figure Caption

Clusters in the left (top sagittal) and right ACC (bottom sagittal). Contrast represents the overlap between sad films > anger films and sad memories > anger memories.

3.4.2.4.2.3 Sad > Fear

The conjunction of regions more active during sadness versus fear across films and memories revealed clusters located in the left medFG, left ACC, right IFG, right globus pallidus, right insula, and left precuneus among others (see Figure 51 and Table 11). These clusters represent the core activations that differentiated sadness from fear.

Figure 51. Core activations differentiating sadness from fear

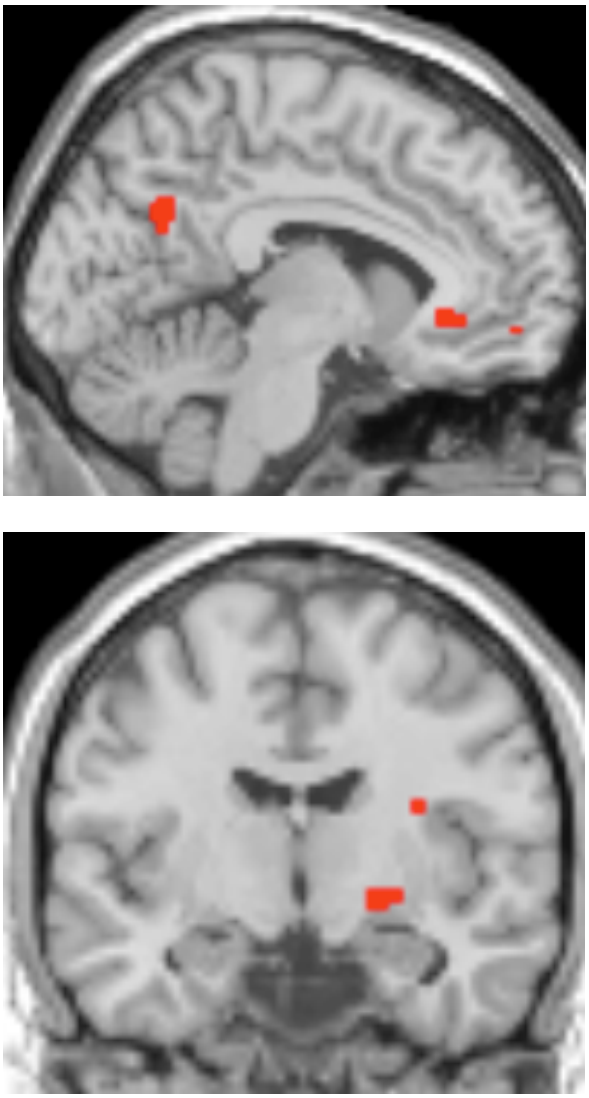


Figure Caption

Clusters in the left ACC, left medFG, left precuneus (top sagittal), right globus pallidus, and right insula (bottom coronal). Contrast represents the overlap between sad films > fear films and sad memories > fear memories.

3.4.2.4.2.4 Sad > Disgust

The conjunction of regions more active during sadness versus disgust across films and memories revealed clusters located in the right ACC, right medFG, left caudate head, right posterior cingulate, and right precuneus among others (see Figure 52 and Table 11). These clusters represent the core activations that differentiated sadness from disgust.

Figure 52. Core activations differentiating sadness from disgust

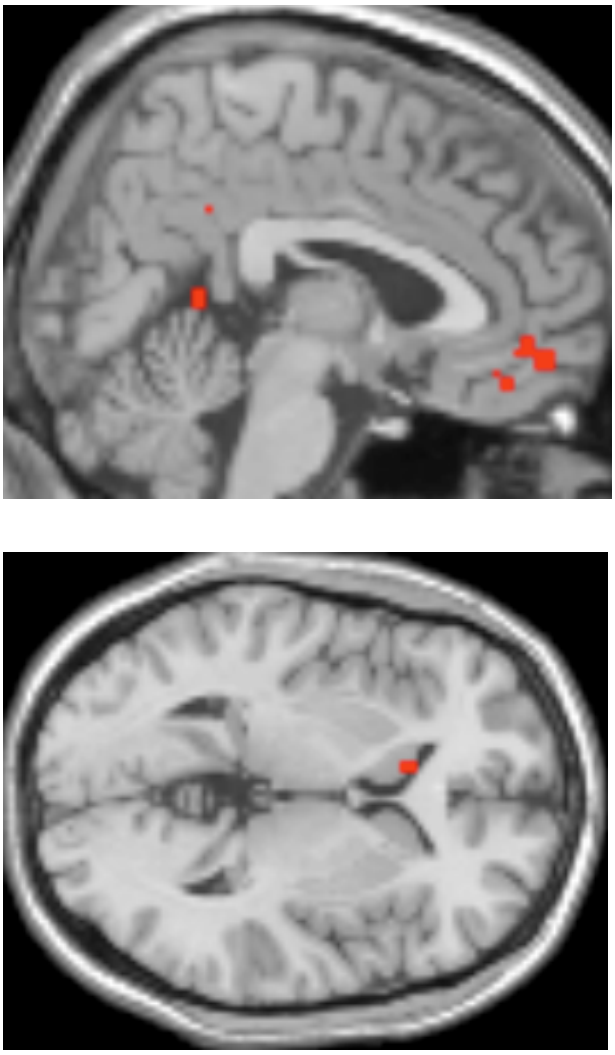


Figure Caption

Clusters in the right ACC, right medFG, right posterior cingulate (top sagittal), and left caudate head (bottom axial). Contrast represents the overlap between sad films > disgust films and sad memories > disgust memories.

3.4.2.4.3 Anger

3.4.2.4.3.1 Anger > Happy

The conjunction of regions more active during anger versus happiness across films and memories revealed a cluster located in the right cerebellum (see Figure 53 and Table 11). This cluster represents the core activation that differentiated anger from happiness.

Figure 53. Core activation differentiating anger from happiness

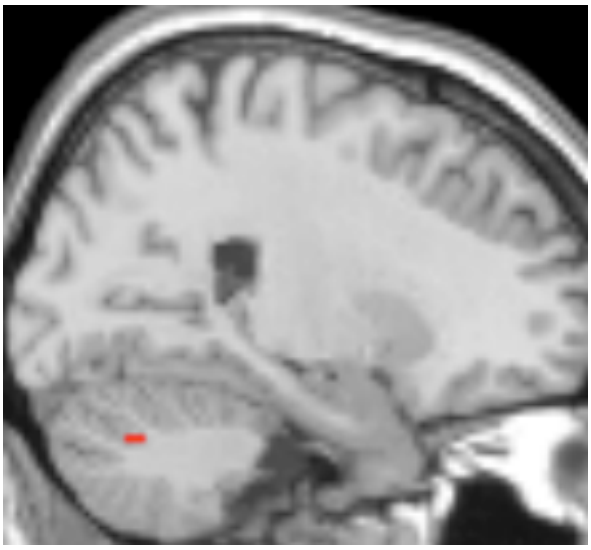


Figure Caption

Cluster in the right cerebellum. Contrast represents the overlap between anger films > happy films and anger memories > happy memories.

3.4.2.4.3.2 Anger > Sad

The conjunction of regions more active during anger versus sadness across films and memories did not reveal any significant clusters. See the reverse contrast above for regions differentiating the two emotions.

3.4.2.4.3.3 Anger > Fear

The conjunction of regions more active during anger versus fear across films and memories revealed clusters located in right STG, left SFG, left MFG, left MTG, left precentral gyrus, and bilateral cerebellum right ACC (see Figure 54 and Table 11). These clusters represent the core activations that differentiated anger from fear.

Figure 54. Core activations differentiating anger from fear

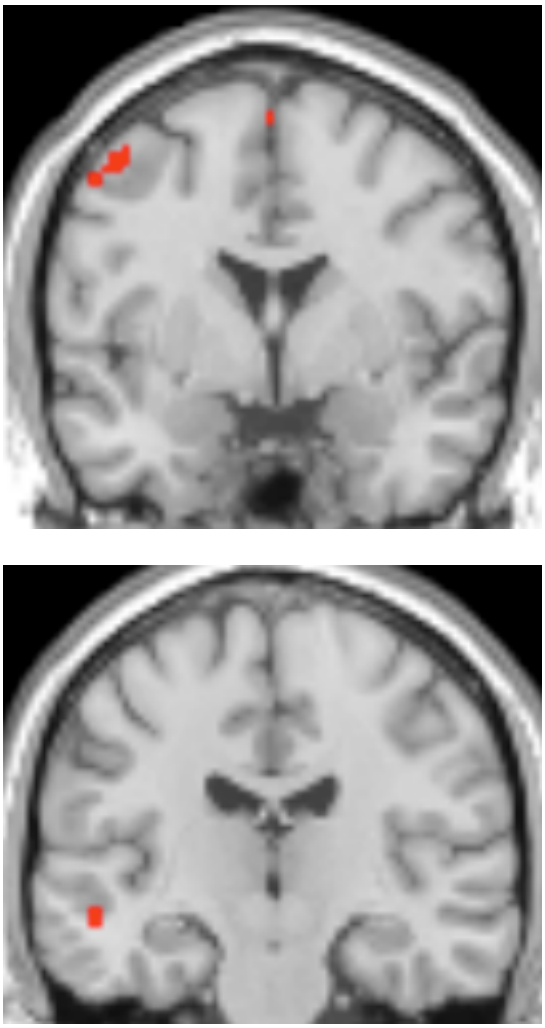


Figure Caption

Clusters in the left MFG, left SFG (top coronal), and left STG (bottom coronal). Contrast represents the overlap between anger films > fear films and anger memories > fear memories.

3.4.2.4.3.4 Anger > Disgust

The conjunction of regions more active during anger versus disgust across films and memories revealed a cluster located in the right SFG/MFG (see Figure 55 and Table 11). This cluster represents the core activation that differentiated anger from disgust.

Figure 55. Core activations differentiating anger from disgust

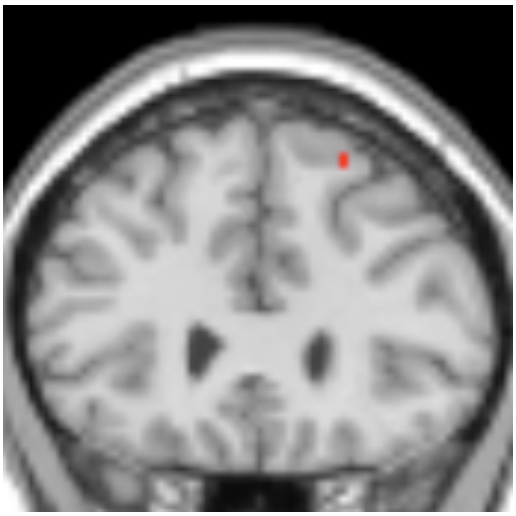


Figure Caption

Cluster in the right SFG. Contrast represents the overlap between anger films > disgust films and anger memories > disgust memories.

3.4.2.4.4 Fear

The conjunction of regions more active during fear versus any basic emotion state across films and memories did not reveal any significant clusters.

3.4.2.4.5 Disgust

3.4.2.4.5.1 Disgust > Happy

The conjunction of regions more active during disgust versus happiness across films and memories revealed clusters located in bilateral postcentral gyrus, left superior parietal lobule, and left supramarginal gyrus (see Figure 56 and Table 11). These clusters represent the core activations that differentiated anger from fear.

Figure 56. Core activations differentiating disgust from happiness

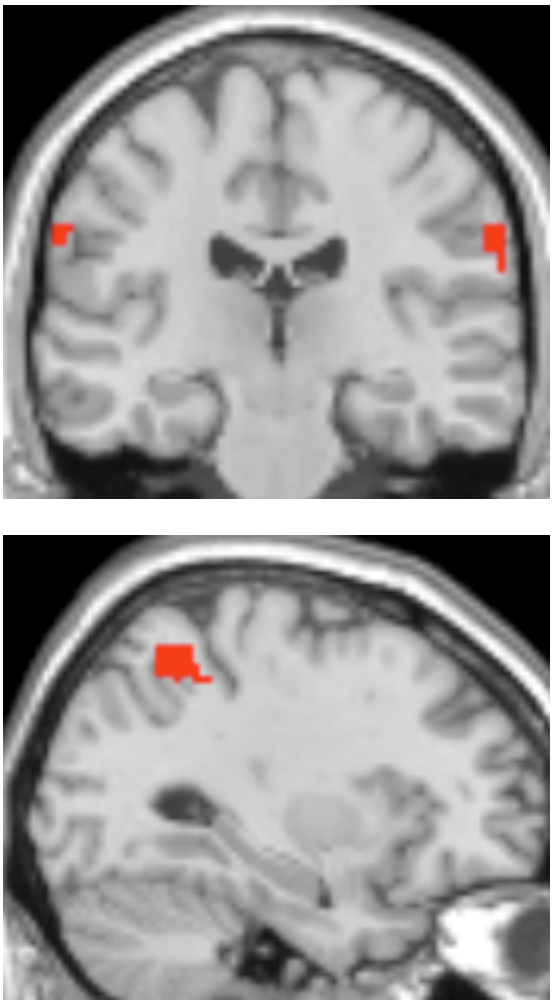


Figure Caption

Clusters in bilateral postcentral gyrus (top coronal) and left superior parietal lobule (bottom sagittal). Contrast represents the overlap between disgust films > happy films and disgust memories > happy memories.

3.4.2.4.5.2 Disgust > Sad

The conjunction of regions more active during disgust versus sadness across films and memories revealed clusters located in left IFG (see Figure 57 and Table 11). These clusters represent the core activations that differentiated disgust from sadness.

Figure 57. Core activations differentiating disgust from sadness

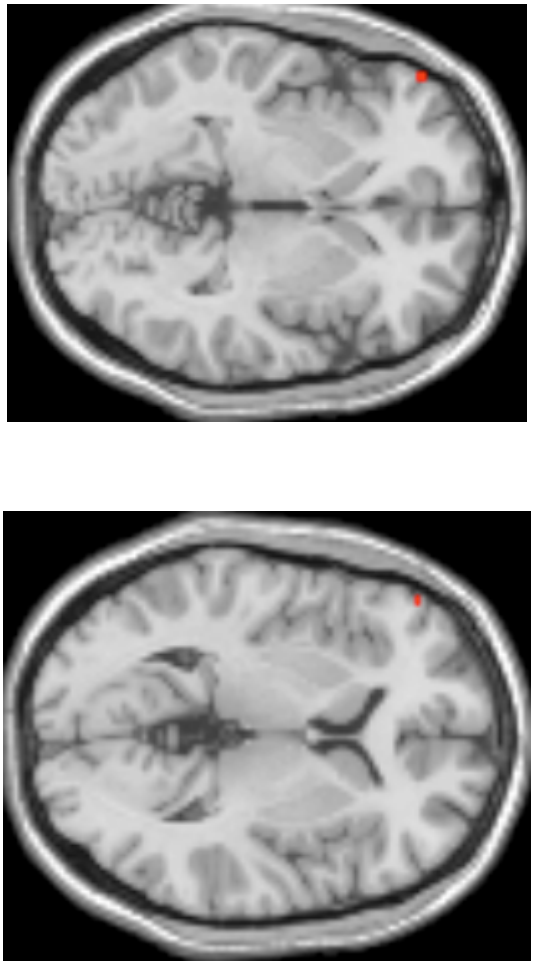


Figure Caption

Clusters in the left IFG (top sagittal: superior cluster, bottom sagittal: inferior cluster). Contrast represents the overlap between disgust films > sad films and disgust memories > sad memories.

3.4.2.4.5.3 Disgust > Anger

The conjunction of regions more active during disgust versus anger across films and memories revealed clusters located in left MFG, left insula, and bilateral precuneus among others (see Figure 58 and Table 11). These clusters represent the core activations that differentiated disgust from anger.

Figure 58. Core activations differentiating disgust from anger

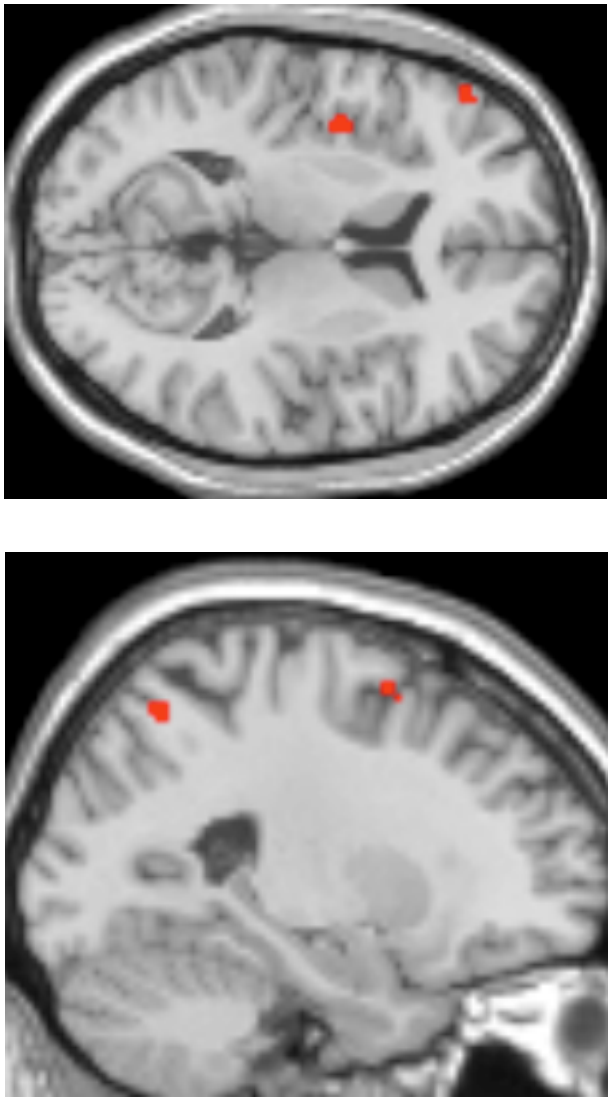


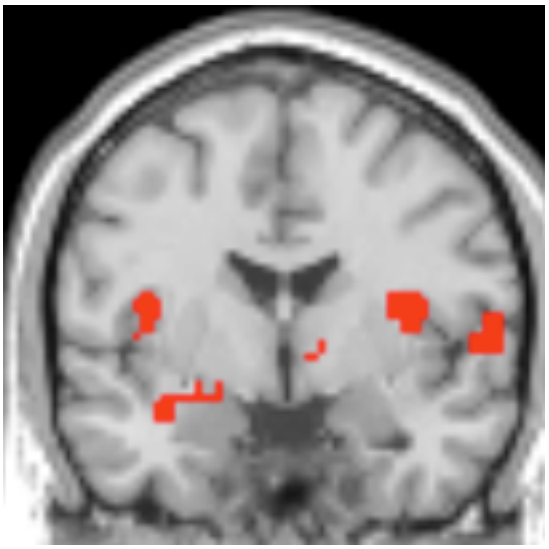
Figure Caption

Clusters in the left insula, left MFG (top axial), and left MFG and left precuneus (bottom sagittal). Contrast represents the overlap between disgust films > anger films and disgust memories > anger memories.

3.4.2.4.5.4 Disgust > Fear

The conjunction of regions more active during disgust versus fear across films and memories revealed clusters located in bilateral insula, bilateral IFG, left amygdala, and left MFG among others (see Figure 59 and Table 11). These clusters represent the core activations that differentiated disgust from fear.

Figure 59. Core activations differentiating disgust from fear



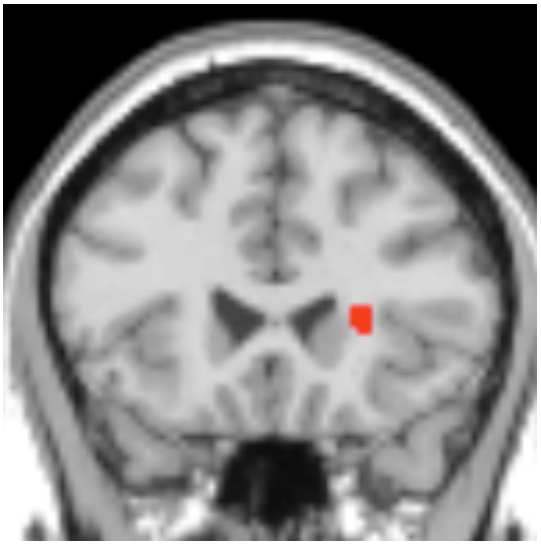


Figure Caption

Clusters in the left and right insula, left amygdala, right thalamus (top coronal) and right MFG (bottom coronal). Contrast represents the overlap between disgust films > fear films and disgust memories > fear memories.

3.4.2.4.6 Inclusive whole-brain emotion pairwise contrasts (regions that differentiate one emotion state from other emotion states)

In addition to conjunction analyses (where only the overlap between emotions elicited by films and emotions elicited by memories was assessed), inclusive whole-brain contrasts (where all activations associated with an emotion state were considered) were used to assess differentiability of basic emotion states. All possible pairwise contrasts were calculated between emotions, first within modality (films and memories separately), and then overall (films and memories together).

3.4.2.4.6.1 Happy > Sad

3.4.2.4.6.1.1 Films

Activity in bilateral STG and left cuneus differentiated happiness elicited by films from sadness elicited by films (see Table 11 for a summary of all peak coordinates and their related statistics).

Table 12. Inclusive whole-brain contrasts: Happy > Sad

		Coordinate (MNI)				
Region	*HEM*	*x*	*y*	*z*	*k* (volume)	*Z*
HAPPINESS - SADNESS						
Happy Films > Sad Films						
Cuneus	L	-12	-82	7	17	3.55
Sup. Temporal G.	R	54	2	-5	18	3.49
Sup. Temporal G.	L	-54	-10	7	29	3.43
Happy (Films + Memories) > Sad (Films + Memories)						
Sup. Temporal G.*	R	57	-4	-2	34	2.31

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.1.2 Memories

Happy memories were not differentiated from sad memories at a threshold of $p <$ .001. For additional regions differentiating the two emotions, see the following contrast.

3.4.2.4.6.1.3 Overall (Films and Memories)

A small volume correction in the right STG revealed additional activity associated with differentiating overall happiness from overall sadness (see Table 12 for relevant statistics).

3.4.2.4.6.2 Happy > Anger

3.4.2.4.6.2.1 Films

Activity in left ACC, bilateral cingulate, and right insula differentiated happiness elicited by films from anger elicited by films (see Table 13 for a summary of all peak coordinates and their related statistics).

Table 13. Inclusive whole-brain contrasts: Happy > Anger

		Coordinate (MNI)				
Region	*HEM*	*x*	*y*	*z*	*k* (volume)	*Z*
		HAPPINESS - ANGER				
		Happy Films > Anger Films				
Cingulate G.	R	21	-34	40	15	4,29
Cingulate G.	L	-6	-22	22	13	4,07
Pos. Insula	R	33	-40	28	26	3,88
Cingulate G.	R	9	-25	22	5	3,46
Ant. Cingulate (BA 24)	L	-9	29	10	10	3.45
Ant. Cingulate (BA 33)	L	-3	20	10	LM	3.31
Lingual G.	R	21	-79	1	11	3.38
		Happy Memories > Anger Memories				
Pos. Insula	R	36	-40	25	5	3.95
Cingulate G.	R	21	-22	46	5	3.65
		Happy (Films + Memories) > Anger (Films + Memories)				
Pos. Insula (BA 13)	R	36	-40	28	37	4.30
Cingulate G.	R	21	-34	40	14	3.99
Ant. Cingulate*	L	-15	47	-2	7	1.81
Ant. Cingulate*	L	-12	41	-2	LM	1.75

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.2.2 Memories

Activity in right cingulate and right posterior insula differentiated happiness elicited by memories from anger elicited by memories (see Table 13 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.2.3 Overall (Films and Memories)

Activity in right cingulate and right posterior insula differentiated overall happiness from overall anger. A small volume correction in the left ACC revealed additional activity associated with differentiating overall happiness from overall anger (see Table 13 for relevant statistics).

3.4.2.4.6.3 Happy > Fear

3.4.2.4.6.3.1 Films

Activity in left STG, right cuneus, right caudate tail, and left ITG differentiated happiness elicited by films from fear elicited by films (see Table 14 for a summary of all peak coordinates and their related statistics).

Table 14. Inclusive whole-brain contrasts: Happy > Fear

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
HAPPINESS - FEAR						
Happy Films > Fear Films						
Lingual G.	L	-12	-82	10	204	4.13
Cuneus	R	15	-78	13	LM	3.84
Lingual G.	L	0	-94	7	LM	3.82
Cerebellum/Fusiform	R	36	-58	-20	24	3.81
Sup. Temporal G.	L	-57	-4	4	22	3.56
Mid. Occipital G.	L	-45	-82	1	28	3.49
Inf. Temporal G.	L	-51	-73	4	LM	3.42
Caudate Tail	R	36	-34	4	5	3.41
Happy (Films + Memories) > Fear (Films + Memories)						
Cuneus	L	-12	-82	7	71	4.10
Lingual G.	L	0	-94	7	LM	3.90
Pos. Insula	R	36	-40	28	16	3.72
Mid. Occipital G.	L	-51	-73	4	6	3.43
Cuneus	R	12	-79	13	5	3.31
Sup. Temporal G.*	R	39	-34	10	324	2.60
Sup. Temporal G.*	R	38	-34	4	LM	2.58
Sup. Temporal G.*	R	50	2	-5	LM	2.50
Sup. Temporal G.*	R	50	-10	7	LM	2.48
Sup. Temporal G.*	R	51	-4	-8	LM	2.32
Sup. Temporal G.*	R	50	-19	7	LM	2.31
Sup. Temporal G.*	R	51	-34	10	LM	2.10
Sup. Temporal G.*	R	48	2	-11	LM	2.04
Sup. Temporal G.*	R	45	2	-17	LM	1.98
Sup. Temporal G.*	R	45	-45	13	LM	1.79
Ant. Cingulate*	L	-9	14	25	11	1.74
Ant. Cingulate*	L	-9	32	16	2	1.72

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume

corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.3.2 Memories

Happy memories were not differentiated from fear memories at a threshold of $p < .001$. For additional regions differentiating the two emotions, see the following contrast.

3.4.2.4.6.3.3 Overall (Films and Memories)

Activity in right posterior insula and bilateral cuneus differentiated overall happiness from overall fear. A small volume correction in the left ACC and right STG revealed additional activity associated with differentiating overall happiness from overall fear (see Table 14 for relevant statistics).

3.4.2.4.6.4 Happy > Disgust

3.4.2.4.6.4.1 Films

Activity in left caudate body, right posterior cingulate, and left cuneus differentiated happiness elicited by films from disgust elicited by films (see Table 15 for a summary of all peak coordinates and their related statistics).

Table 15. Inclusive whole-brain contrasts: Happy > Disgust

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
		HAPPINESS - DISGUST				
		Happy Films > Disgust Films				
Caudate Body	L	-9	23	1	7	3.71
Pos. Cingulate	R	12	-52	13	14	3.55
Cuneus	L	-12	-85	10	6	3.32
		Happy Memories > Disgust Memories				
Cingulate G.	R	21	-31	43	22	4.41
		Happy (Films + Memories) > Disgust (Films + Memories)				
Cuneus	L	-12	-82	7	60	4.51
Caudate Tail	L	-15	-25	25	17	3.90
Pos. Cingulate	R	12	-55	7	13	3.42
Ant. Cingulate*	L	-15	41	-5	60	2.16
Ant. Cingulate*	L	0	47	-5	LM	2.13
Ant. Cingulate*	L	-3	38	-8	LM	2.12

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.4.2 Memories

Activity in right cingulate differentiated happiness elicited by memories from disgust elicited by memories (see Table 15 for related statistics).

3.4.2.4.6.4.3 Overall (Films and Memories)

Activity in left cuneus, left caudate tail, and right posterior cingulate differentiated overall happiness from overall disgust. A small volume correction in the left ACC revealed additional activity associated with differentiating overall happiness from overall disgust (see Table 15 for relevant statistics).

3.4.2.4.6.5 Sad > Happy

3.4.2.4.6.5.1 Films

Sadness elicited by films was not differentiated from happiness elicited by films at a threshold of $p < .001$. For additional regions differentiating the two emotions, see the overall contrast.

3.4.2.4.6.5.2 Memories

Sadness elicited by memories was not differentiated from happiness elicited by memories at a threshold of $p < .001$. For additional regions differentiating the two emotions, see the overall contrast.

3.4.2.4.6.5.3 Overall (Films and Memories)

Activity in left thalamus differentiated overall sadness from overall happiness (see Table 15 for a summary of all peak coordinates and their related statistics). A small volume correction in the left ACC revealed additional activity associated with differentiating overall sadness from overall happiness (see Table 16 for relevant statistics).

Table 16. Inclusive whole-brain contrasts: Sad > Happy

		Coordinate (MNI)				
Region	*HEM*	*x*	*y*	*z*	*k* (volume)	*Z*
SADNESS - HAPPINESS Sad (Films + Memories) > Happy (Films + Memories)						
Thalamus	L	0	-25	-2	5	3.24
Ant. Cingulate*	L	-9	29	-5	83	2.76
Ant. Cingulate*	L	-9	47	15	LM	2,28
Ant. Cingulate*	L	-9	41	1	LM	2.01

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.6 Sad > Anger

3.4.2.4.6.6.1 Films

Activity in left cingulate differentiated sadness elicited by films from anger elicited by films (see Table 17 for a summary of related statistics).

Table 17. Inclusive whole-brain contrasts: Sad > Anger

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
		SADNESS - ANGER				
		Sad Films > Anger Films				
Cingulate G.	L	-6	-22	22	5	3.75
		Sad Memories > Anger Memories				
Ant. Cingulate	R	18	38	-2	65	3.96
Ant. Cingulate (BA 32)	R	21	47	4	LM	3.67
Med. Frontal G. (BA 9)	R	12	62	4	LM	3.46
Fusiform G.	L	-24	-46	-20	9	3.94
Pos. Cingulate	R	33	-67	16	32	3.92
Sup. Parietal Lobule	R	48	-61	55	LM	3.64
Precuneus	R	3	-61	55	25	3.8
Precentral G.	L	-57	-1	7	39	3.8
Sup. Temporal G.	L	-54	-16	10	LM	3.35
Thalamus	R	3	-4	13	28	3.78
Caudate Body/Head	R	6	2	7	LM	3.71
Cerebellum	R	6	-85	-20	12	3.78
Caudate Head	R	9	8	-11	13	3.76
Caudate Head	R	15	14	-11	LM	3.59
Cingulate G.	R	0	-4	46	39	3.74
Pos. Insula	L	-36	-22	10	24	3.67
Pos. Insula	L	-36	-13	16	LM	3.48
Sup./Mid. Temporal G.	R	60	-1	-11	26	3.65
Cuneus	R	21	-76	31	7	3.62
Pos. Cingulate	R	3	-49	10	25	3.61
Lingual G.	R	9	-55	-2	LM	3.30
Sup. Frontal G.	R	18	35	52	22	3.59
Sup. Frontal G.	R	21	25	52	LM	3.39
Postcentral G.	L	-48	-19	43	15	3.58
Cerebellum	R	9	-40	-20	9	3.57
Cerebellum	L	-6	-43	-17	LM	3.33
Thalamus	R	0	-25	10	9	3.56

Putamen	L	-33	2	-11	12	3.53
Hippocampus	L	-36	-19	-20	5	3.52
Postcentral G.	L	-39	-22	34	9	3.48
Precuneus	R	21	-61	34	16	3.46
Precuneus	L	-18	-43	55	10	3.42
Parahippocampal G.	R	15	-1	-14	6	3.41
Sad (Films + Memories) > Anger (Films + Memories)						
Ant. Cingulate (BA 32)	L	-21	38	1	25	4.59
Precuneus	R	33	-40	46	85	4.45
Cingulate G.	R	21	-31	43	LM	3.83
Ant. Cingulate (BA 32)	R	18	38	-2	13	3.58
Med. Frontal G.	R	18	-13	61	8	3.55
Precuneus	L	-33	-40	52	25	3.44
Postcentral G.	L	-36	-22	34	6	3.42
Med. Frontal G./ACC	L	-9	56	-2	5	3.37
Caudate*	L	-9	17	-2	57	2.45
Caudate*	L	-3	14	-2	LM	2.28
Caudate*	L	-3	8	-5	LM	2.23
Caudate*	L	-15	17	-11	LM	2.22
Caudate*	R	3	8	-5	11	2.04
Caudate*	R	18	23	10	9	2.18
Caudate*	R	15	20	13	LM	1.95

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.6.2 Memories

Activity in right ACC (BA 32), right medFG, right SFG and right caudate body/head cingulate differentiated sadness elicited by memories from anger elicited by memories (see Table 17 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.6.3 Overall (Films and Memories)

Activity in bilateral ACC, bilateral medFG, right cingulate and bilateral precuneus differentiated overall sadness from overall anger (see Table 17 for a summary of all peak coordinates and their related statistics). A small volume correction in the left and right caudate revealed additional activity associated with differentiating overall sadness from overall anger (see Table 17 for relevant statistics).

3.4.2.4.6.7 Sad > Fear

3.4.2.4.6.7.1 Films

Activity in right STG and right middle occipital gyrus body differentiated sadness elicited by films from fear elicited by films (see Table 18 for a summary of all peak coordinates and their related statistics).

Table 18. Inclusive whole-brain contrasts: Sad > Fear

Region	*HEM*	*Coordinate (MNI)*			*k* (volume)	*Z*
		x	*y*	*z*		
SADNESS - FEAR						
Sad Films > Fear Films						
Sup. Temporal G.	R	48	14	-26	14	3.52
Mid. Occipital G.	R	45	-64	1	13	3.50
Sad Memories > Fear Memories						
Pos. Cingulate	R	24	-70	7	75	5.82
Precentral G.	L	-30	14	22	21	5.22
Precentral G.	L	-33	5	22	LM	4.15
Caudate Head	L	-9	23	-2	49	5.18
Caudate Head	R	3	14	-5	LM	4.53
Caudate Head	R	9	20	-2	LM	4.51
Pons	R	12	-37	-23	9	5.13
Putamen	L	-30	5	-14	8	4.84
Thalamus	R	21	-4	4	38	4.75
Thalamus	R	27	-13	7	LM	4.2
Thalamus	L	-15	-16	-5	12	4.61
Sup. Temporal G.	L	-54	8	-8	11	4.59
Pons	L	-6	-37	-35	5	4.54
Precentral G.	L	-60	-4	10	21	4.46
Sup. Temporal G.	L	-51	-31	10	47	4.41
Sup. Temporal G.	L	-63	-40	19	LM	4.02
Precentral G.	L	-51	-7	52	6	4.41
Caudate Head	L	-18	14	-8	5	4.34
Putamen	R	33	-1	13	7	4.32
Cerebellum	L	-24	-61	-26	5	4.11
Cerebellum	R	27	-61	-20	8	3.26
Precuneus	R	33	-40	49	8	3.26
Caudate Body/Head	R	3	5	7	6	3.25
Sad (Films + Memories) > Fear (Films + Memories)						

Caudate Head	L	-9	29	-2	109	4.25
Ant. Cingulate (BA 32)	R	0	41	-8	LM	3.67
Ant. Cingulate (BA 32)	R	0	50	-8	LM	3.64
Caudate Body	R	12	23	13	53	4.04
Caudate Head	R	18	32	1	LM	3.44
Mid. Temporal G.	R	48	-61	4	36	3.99
Precuneus	L	-12	-61	34	41	3.98
Precuneus	L	-3	-64	22	LM	3.48
Inf. Temporal G.	L	-51	-73	1	26	3.83
Med. Frontal G.	R	18	59	1	20	3.70
Cerebellum	R	9	-61	1	21	3.69
Postcentral G.	R	42	-22	64	18	3.61
Cerebellum	R	42	-49	-20	6	3.55
Sup. Temporal G.	R	42	14	-26	24	3.53
Inf. Frontal G.	R	33	11	-26	LM	3.29
Putamen	R	21	-7	-5	10	3.43
Postcentral G.	R	33	-19	46	8	3.38
Sup. Temporal g.	R	48	-1	-26	7	3.38
Med. Frontal G./ACC	R	9	47	19	5	3.34
Parahippocampal G.	L	-12	-10	-14	8	3.32
Med. Frontal G.	L	-12	41	22	5	3.24
Caudate*	L	-3	14	-1	225	3.47
Caudate*	L	-15	17	16	LM	3.2
Caudate*	L	-18	17	4	LM	2.28
Caudate*	L	-15	-13	22	LM	2.23
Caudate*	L	-18	-22	19	LM	2.2
Caudate*	L	-18	2	19	LM	2.18
Caudate*	R	15	20	13	225	3.69
Caudate*	R	5	20	-2	LM	3.28
Caudate*	R	15	11	19	LM	2.98
Caudate*	R	12	23	1	LM	2.93
Caudate*	R	15	28	-2	LM	2.9
Caudate*	R	21	14	13	LM	2.52
Caudate*	R	15	-13	22	5	1.77
Caudate*	R	12	-7	16	1	1.69

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to

each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.7.2 Memories

Activity in bilateral caudate head, left STG, right posterior cingulate and bilateral thalamus differentiated sadness elicited by memories from fear elicited by memories (see Table 18 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.7.3 Overall (Films and Memories)

Activity in bilateral caudate head, right ACC, and right medFG differentiated overall sadness from overall fear (see Table 18 for a summary of all peak coordinates and their related statistics). A small volume correction in the left and right caudate revealed additional activity associated with differentiating overall sadness from overall fear (see Table 18 for relevant statistics).

3.4.2.4.6.8 Sad > Disgust

3.4.2.4.6.8.1 Films

Activity in left caudate tail, right posterior cingulate, right precuneus, and right cingulate differentiated sadness elicited by films from disgust elicited by films (see Table 19 for a summary of all peak coordinates and their related statistics).

Table 19. Inclusive whole-brain contrasts: Sad > Disgust

Region	*HEM*	*Coordinate (MNI)*			*k* (volume)	*Z*
		x	*y*	*z*		
SADNESS - DISGUST						
Sad Films > Disgust Films						
Precuneus	R	12	-58	28	170	4.07
Precuneus	L	-12	-55	31	LM	3.97
Cingulate G.	R	12	-13	25	5	3.76
Pos. Cingulate	R	24	-43	16	13	3.56
Caudate Tail	L	-21	-25	22	7	3.53
Mid. Temporal G.	R	45	-64	28	10	3.44
Pos. Cingulate	R	12	-52	7	8	3.35
Sad Memories > Disgust Memories						
Caudate Head	L	-9	23	-5	13	3.94
Insula/Caudate Tail	L	-27	-28	22	7	3.92
Caudate Body	L	-18	-16	22	12	3.79
Caudate Head	R	9	23	1	34	3.75
Ant. Cingulate C.	R	15	32	-2	LM	3.59
Parahippocampal G.	R	36	-61	10	10	3.50
Thalamus	L	-3	-1	16	11	3.44
Cingulate/Med. Frontal G.	L	-12	32	22	7	3.38
Ant. Cingulate (BA 32)	L	-12	41	16	LM	3.14
Med. Frontal G.	R	18	41	25	5	3.31
Sad (Films + Memories) > Disgust (Films + Memories)						
Cingulate G.	R	0	-46	34	168	4.53
Cingulate G.	R	6	-52	31	LM	4.04
Pos. Cingulate	L	-9	-52	28	LM	3.62
Caudate Tail/Body	L	-18	-22	22	33	4.04
Mid. Temporal G.	R	45	-58	28	12	3.80
Caudate Body/Head	L	-12	20	4	7	3.48
Pos. Cingulate	R	9	-55	7	6	3.27
Cingulate*	L	-18	-22	22	160	4.04

Cingulate*	L	-12	2-	4	LM	3.48
Cingulate*	L	-12	-1	19	LM	2.35
Cingulate*	L	-5	14	-8	LM	2.34
Cingulate*	L	-12	14	16	LM	2.14
Cingulate*	R	15	26	1	64	2.65
Cingulate*	R	12	20	4	LM	2.48
Cingulate*	R	12	14	16	LM	2.28
Cingulate*	R	15	-13	22	3	2.07
Cingulate*	R	18	2	22	1	1.78

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.8.2 Memories

Activity in bilateral caudate head, right ACC, left cingulate/medFG, and left thalamus differentiated sadness elicited by memories from disgust elicited by memories (see Table 19 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.8.3 Overall (Films and Memories)

Activity in left caudate head, bilateral posterior cingulate, and right cingulate differentiated overall sadness from overall disgust (see Table 19 for a summary of all peak coordinates and their related statistics). A small volume correction in the left and right caudate revealed additional activity associated with differentiating overall sadness from overall disgust (see Table 19 for relevant statistics).

3.4.2.4.6.9 Anger > Happy

3.4.2.4.6.9.1 Films

Activity in bilateral IFG, bilateral MFG, and bilateral STG differentiated anger elicited by films from happiness elicited by films (see Table 20 for a summary of all peak coordinates and their related statistics).

Table 20. Inclusive whole-brain contrasts: Anger > Happiness

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
ANGER - HAPPINESS						
Anger Films > Happy Films						
Sup. Temporal G.	L	-54	-13	-5	833	5.06
Sup. Temporal G.	L	-54	-1	-14	LM	4.83
Mid. Temporal G.	L	-63	-37	4	LM	4.55
Sup. Temporal G.	R	51	-31	1	179	4.82
Sup. Frontal G.	R	9	47	46	189	4.27
Med. Frontal G.	R	6	59	34	LM	3.81
Sup. Frontal G.	R	21	50	28	LM	3.32
Inf. Frontal G.	R	54	26	16	78	4.18
Inf. Frontal G.	R	48	20	-26	19	3.96
Sup. Temporal G.	R	54	14	-23	LM	3.40
Sup. Temporal G.	R	48	-49	22	101	3.96
Sup. Temporal G.	R	60	-46	22	LM	3.79
Sup. Temporal G.	R	57	-13	-11	65	3.91
Sup. Temporal G.	R	57	2	-14	LM	3.44
Inf. Frontal G.	L	-51	35	-5	9	3.79
Ant. Cingulate	R	6	47	-17	18	3.74
Ant. Cingulate	R	6	38	-17	LM	3.33
Pons	R	6	-49	-35	6	3.66
Mid. Frontal G.	R	42	17	34	13	3.65
Pos. Cingulate	L	-3	-58	31	43	3.51
Inf. Frontal G.	L	-57	26	7	11	3.31
Inf. Frontal G.	L	-54	20	19	LM	3.18
Med. Frontal G.	R	3	53	16	5	3.25
Anger (Films + Memories) > Happy (Films + Memories)						
Sup. Temporal G.	R	51	-31	1	116	4.40
Mid. Temporal. G.	L	-54	-55	13	218	3.89
Mid. Temporal. G.	L	-63	-37	4	LM	3.57
Sup. Temporal G.	L	-54	-16	-5	LM	3.56
Cerebellum	L	-9	-67	-32	35	3.74
Cerebellum	L	-18	-64	-32	LM	3.71
Cerebellum	L	-21	-76	-29	LM	3.61
Mid. Frontal G.	R	45	14	40	28	3.73
Sup Temporal G.	L	-57	5	-14	5	3.55
Cerebellum	R	21	-67	-32	6	3.54
Inf. Frontal G.	R	57	26	16	16	3.41

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume

corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.9.2 Memories

Anger elicited by memories was not differentiated from happiness elicited by memories at a threshold of $p < .001$. For additional regions differentiating the two emotions see the overall contrast.

3.4.2.4.6.9.3 Overall (Films and Memories)

Activity in right IFG, bilateral STG, right MFG, and bilateral cerebellum differentiated overall anger from overall happiness (see Table 20 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.10 Anger > Sad

3.4.2.4.6.10.1 Films

Activity in left IFG, left posterior insula, bilateral SFG, bilateral STG, and bilateral STG differentiated anger elicited by films from sadness elicited by films (see Table 21 for a summary of all peak coordinates and their related statistics).

Table 21. Inclusive whole-brain contrasts: Anger > Sadness

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
ANGER - SAD						
Anger Films > Sad Films						
Mid. Temporal G.	L	-51	-40	-2	1068	4.88
Sup. Temporal G.	L	-57	-13	-2	LM	4.65
Pos. Insula	L	-45	-28	-2	LM	4.54
Sup. Temporal G.	R	54	-31	7	482	4.79
Sup. Temporal G.	R	63	-10	-5	LM	4.34
Sup. Temporal G.	R	60	2	-11	LM	4.30
Inf. Frontal G.	L	-54	26	7	43	3.76
Precentral G.	L	-48	-1	49	17	3.67
Precentral G.	L	-39	2	58	LM	3.29
Sup. Frontal G.	L	-6	8	70	10	3.66
Sup. Frontal G.	R	9	50	46	21	3.65
Sup. Frontal G.	L	-3	53	43	LM	3.43
Sup. Frontal G.	R	21	53	31	5	3.64
Med. Frontal G.	R	9	59	34	3	3.59
Precuneus	R	3	-61	37	8	3.44
Sup. Frontal G.	L	-6	23	61	5	3.38
Sup. Temporal G.	R	51	-52	22	12	3.31
Cerebellum	R	27	-64	-23	7	3.29
Precentral G.	R	54	2	46	1	3.27
Sup. Frontal G.	R	21	70	-29	2	3.21
Cerebellum	L	-36	-64	-29	1	3.18
Sup. Frontal G.	R	21	44	46	1	3.15
Cerebellum	L	-24	-70	-32	1	3.12
Anger (Films + Memories) > Sad (Films + Memories)						
Sup. Temporal G.	L	-57	-13	-5	577	5.03
Mid. Temporal G.	L	-66	-28	1	LM	4.64
Sup. Temporal G.	L	-51	-25	1	LM	4.3
Sup. Temporal G.	R	57	-31	10	119	4.24
Sup. Temporal G.	R	66	-7	-2	58	4.18
Inf. Frontal G.	L	-51	26	4	6	3.42
Precentral G.	L	-51	-1	49	6	3.39

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to

each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.10.2 Memories

Anger elicited by memories was not differentiated from sadness elicited by memories at a threshold of $p < .001$. For additional regions differentiating the two emotions see the overall contrast.

3.4.2.4.6.10.3 Overall (Films and Memories)

Activity in bilateral superior temporal, left IFG, and left MTG differentiated overall anger from overall sadness (see Table 21 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.11 Anger > Fear

3.4.2.4.6.11.1 Films

Activity in left IFG, bilateral STG, left precuneus, and left medFG differentiated anger elicited by films from fear elicited by films (see Table 22 for a summary of all peak coordinates and their related statistics).

Table 22. Inclusive whole-brain contrasts: Anger > Fear

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
ANGER – FEAR						
Anger Films > Fear Films						
Sup. Temporal G.	R	48	-25	1	853	5.69
Sup. Temporal G.	R	54	-31	7	LM	5.51
Sup. Temporal G.	R	63	-10	-8	LM	5.48
Sup. Temporal G.	L	-51	-22	-2	1277	5.45
Sup. Temporal G.	L	-66	-22	1	LM	5.44
Sup. Temporal G.	L	-57	-13	1	LM	5.28
Precuneus	L	0	-67	28	115	4.33
Precuneus	L	-3	-55	34	LM	3.64
Inf. Frontal G.	L	-45	29	4	74	3.85
Inf. Frontal G.	L	-54	26	7	LM	3.83
Inf. Frontal G.	L	-51	35	-11	LM	3.61
Sup. Frontal G.	R	15	59	28	72	3.64
Med. Frontal G.	R	0	56	37	LM	3.45
Sup. Frontal G.	R	12	47	46	16	3.43
Sup. Frontal G.	L	-9	32	55	7	3.32
Anger Memories > Fear Memories						
Precentral G.	L	-42	-7	28	14	4.12
Caudate body	L	-9	14	13	9	3.54
Med. Frontal G.	L	-3	5	64	13	3.46
Claustrum	L	-27	17	16	7	3.25
Sup. Temporal G.	L	-36	14	10	LM	3.11
Anger (Films + Memories) > Fear (Films + Memories)						
Sup. Temporal G.	R	57	-28	4	266	4.26
Sup. Temporal G.	R	60	-19	1	LM	4.12
Pos. Insula	R	48	-28	1	LM	4.00
Sup. Temporal G.	L	-51	-22	1	320	4.13
Sup. Temporal G.	L	-66	-40	7	LM	3.51
Sup. Temporal G.	L	-51	-40	7	LM	3.39
Pos. Insula	L	-51	-16	19	20	3.60
Sup. Temporal G.	R	54	11	-26	20	3.49

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to

each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.11.2 Memories

Activity in left STG, left medFG, and left caudate body differentiated anger elicited by memories from fear elicited by memories (see Table 22 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.11.3 Overall (Films and Memories)

Activity in bilateral STG and bilateral posterior insula differentiated overall anger from overall fear (see Table 22 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.12 Anger > Disgust

3.4.2.4.6.12.1 Films

Activity in bilateral STG, right ACC, right IFG, and right PHG differentiated anger elicited by films from disgust elicited by films (see Table 23 for a summary of all peak coordinates and their related statistics).

Table 23. Inclusive whole-brain contrasts: Anger > Disgust

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
ANGER - DISGUST Anger Films > Disgust Films						
Sup. Temporal G.	L	-66	-25	4	497	4.96
Sup. Temporal G.	L	-60	-10	-5	LM	4.66
Sup. Temporal G.	L	-54	11	-23	LM	4.24
Sup. Temporal G.	R	48	-31	4	47	3.84
Sup. Temporal G.	R	60	-13	-8	18	3.57
Ant. Cingulate	R	6	38	-17	13	3.57
Precuneus	R	3	-64	28	115	3.56
Precuneus	R	15	-58	25	LM	3.55
Precuneus	L	-6	-55	37	LM	3.52
Inf. Frontal G.	R	51	17	-26	6	3.50
Sup. Frontal G.	R	15	41	49	26	3.50
Parahippocampal G.	R	12	-52	1	15	3.38
Anger (Films + Memories) > Disgust (Films + Memories)						
Pons	L	-18	-34	-26	10	3.97
Med. Frontal G.	R	9	59	34	23	3.66
Sup. Frontal G.	R	6	50	46	LM	3.55
Sup. Temporal G.	R	45	-31	4	22	3.62
Sup. Temporal G.	L	-60	-13	-5	69	3.57
Sup. Temporal G.	L	-66	-22	1	LM	3.56
Sup. Temporal G.	L	-66	-24	4	LM	3.22
Cerebellum	L	0	-49	-32	26	3.38
Pons/Cerebellum	L	0	-40	-32	LM	3.28

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.12.2 Memories

Anger elicited by memories was not differentiated from disgust elicited by memories at a threshold of $p < .001$. For additional regions differentiating the two emotions see the overall contrast.

3.4.2.4.6.12.3 Overall (Films and Memories)

Activity bilateral STG, right medFG, left pons, and left cerebellum differentiated overall anger from overall disgust (see Table 23 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.13Fear > Happy

3.4.2.4.6.13.1 Films

Activity in bilateral MFG, right MTG, left posterior cingulated, and left precuneus differentiated fear elicited by films from happiness elicited by films (see Table 24 for a summary of all peak coordinates and their related statistics).

Table 24. Inclusive whole-brain contrasts: Fear > Happiness

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
FEAR - HAPPINESS						
Fear Films > Happiness Films						
Mid. Occipital G.	L	-36	-79	22	43	3.76
Pos. Cingulate	L	-30	-70	22	LM	3.23
Precuneus	L	-24	-70	28	LM	3.19
Mid. Frontal G.	L	-24	5	52	8	3.31
Precuneus	L	-18	-73	43	7	3.29
Precuneus	L	-18	-67	52	5	3.25
Mid. Temporal G.	R	39	-70	22	5	3.18
Mid. Frontal G.	R	27	-1	49	5	3.13
Fear (Films + Memories) > Happy (Films + Memories)						
Pos. Cingulate	L	-27	-67	25	5	3.11

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.13.2 Memories

Fear elicited by memories was not differentiated from happiness elicited by memories at a threshold of $p < .001$. For additional regions differentiating the two emotions see the overall contrast.

3.4.2.4.6.13.3 Overall (Films and Memories)

Activity in left posterior cingulate differentiated overall fear from overall happiness (see Table 24 for related statistics).

3.4.2.4.6.14Fear > Sad

3.4.2.4.6.14.1 Films

Activity in bilateral PHG and left precuneus differentiated fear elicited by films from sadness elicited by films (see Table 25 for a summary of all peak coordinates and their related statistics).

Table 25. Inclusive whole-brain contrasts: Fear > Sadness

Region	*HEM*	*Coordinate (MNI)* *x*	*Y*	*z*	*k* (volume)	*Z*
FEAR – SADNESS						
Fear Films > Sad Films						
Mid. Occipital G.	R	33	-73	19	27	4.07
Mid. Occipital G.	L	-36	-82	19	73	3.76
Precuneus	L	-27	-73	28	LM	3.19
Parahippocampal G.	L	-33	-40	-11	48	3.55
Parahippocampal G.	L	-30	-49	-8	LM	3.51
Parahippocampal G.	R	30	-46	-11	29	3.44
Fear (Films + Memories) > Sad (Films + Memories)						
Parahippocampal G.	L	-30	-43	-8	26	3.08
Mid. Occipital G.	L	-33	-88	13	8	2.97
Parahippocampal G.	R	30	-43	-8	7	2.80

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.14.2 Memories

Fear elicited by memories was not differentiated from sadness elicited by memories at a threshold of $p < .001$. For additional regions differentiating the two emotions see the overall contrast.

3.4.2.4.6.14.3 Overall (Films and Memories)

Activity in bilateral PHG differentiated overall fear from overall sadness (see Table 25 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.15Fear > Anger

3.4.2.4.6.15.1 Films

Activity in bilateral precuneus and left PHG differentiated fear elicited by films from anger elicited by films (see Table 26 for related statistics).

Table 26. Inclusive whole-brain contrasts: Fear > Anger

Region	*HEM*	*Coordinate (MNI)* *X*	*y*	*z*	*k* (volume)	*Z*
		FEAR - ANGER				
		Fear Films > Anger Films				
Precuneus	L	-21	-70	46	100	4.22
Cerebellum	L	-36	-85	-19	92	3.88
Mid. Occipital G.	L	-33	-76	22	LM	3.67
Precuneus	R	18	-67	46	71	3.73
Precuneus	R	27	-64	40	LM	3.67
Precuneus	R	18	-58	55	LM	3.22
Parahippocampal G.	L	-33	-43	-8	10	3.40
		Fear (Films + Memories) > Anger (Films + Memories)				
Precuneus	R	27	-67	40	21	3.62
Precuneus	L	-18	-46	52	6	3.54

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.15.2 Memories

Fear elicited by memories was not differentiated from anger elicited by memories at a threshold of $p < .001$. For additional regions differentiating the two emotions see the overall contrast.

3.4.2.4.6.15.3 Overall (Films and Memories)

Activity in bilateral precuneus differentiated overall fear from overall sadness (see Table 26 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.16Fear > Disgust

3.4.2.4.6.16.1 Films

Activity in bilateral PHG, right posterior cingulate, bilateral cingulate, and right MFG differentiated fear elicited by films from disgust elicited by films (see Table 27 for related statistics).

Table 27. Inclusive whole-brain contrasts: Fear > Disgust

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
		FEAR - DISGUST				
		Fear Films > Disgust Films				
Parahippocampal G.	L	-33	-37	-11	10	3.82
Pos. Cingulate	R	21	-43	16	9	3.73
Parahippocampal G.	R	30	-46	-5	6	3.69
Cingulate G.	R	9	-46	43	17	3.60
Cingulate G.	L	-30	-85	22	10	3.52
Precuneus	L	-15	-43	40	10	3.50
Parahippocampal G.	R	18	-28	-17	5	3.44
Pos. Cingulate	R	15	-55	25	11	3.42
Parahippocampal G.	L	-30	-46	-5	6	3.35
Mid. Frontal G.	R	24	23	40	7	3.28
		Fear (Films + Memories) > Disgust (Films + Memories)				
Pons	R	18	-22	-26	5	3.40

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.16.2 Memories

Fear elicited by memories was not differentiated from disgust elicited by memories at a threshold of $p < .001$. For additional regions differentiating the two emotions see the overall contrast.

3.4.2.4.6.16.3 Overall (Films and Memories)

Activity in right pons differentiated overall fear from overall disgust (see Table 27 for a summary of coordinates and their related statistics).

3.4.2.4.6.17Disgust > Happy

3.4.2.4.6.17.1 Films

Activity in bilateral anterior insula, bilateral posterior insula, right IFG, and left fusiform gyrus differentiated disgust elicited by films from happiness elicited by films (see Table 28 for related statistics).

Table 28. Inclusive whole-brain contrasts: Disgust > Happiness

Region	*HEM*	*Coordinate (MNI)*			*k* (volume)	*Z*
		x	*y*	*z*		
DISGUST - HAPPINESS						
Disgust Films > Happiness Films						
Inf. Frontal G.	R	51	14	19	173	4.48
Pos. Insula	R	39	-10	-2	LM	3.81
Pos. Insula	R	39	5	19	LM	3.74
Inf. Frontal G.	R	60	-19	25	133	4.06
Postcentral g./Insula	R	60	-19	37	LM	3.93
Postcentral G.	R	57	-25	49	LM	3.59
Inf. Parietal Lobule	L	-60	-31	43	18	3.69
Postcentral G./Insula	L	-60	-19	22	22	3.64
Inf. Parietal Lobule	R	39	-37	43	25	3.52
Ant. Insula	L	-27	26	-8	7	3.49
Fusiform G.	L	-42	-64	-8	7	3.34
Inf. Frontal G./Insula	R	42	29	-2	6	3.31
Inf. Frontal G./Insula	R	33	29	-11	7	3.27
Disgust Memories > Happiness Memories						
Inf. Parietal Lobule	L	-45	-34	43	14	3.47
Inf. Frontal G.	L	-60	17	10	7	3.33
Disgust (Films + Memories) > Happy (Films + Memories)						
Inf. Parietal Lobule	R	42	-34	43	27	4.30
Ant. Insula	R	30	29	-5	32	4.28
Inf. Parietal Lobule	L	-54	-31	40	64	4.20
Inf. Parietal Lobule	L	-45	-37	46	LM	3.46
Inf. Frontal G.	R	54	14	19	24	4.16
Postcentral G.	R	60	-22	40	153	3.98
Ant. Insula	R	63	-34	25	LM	3.75
Inf. Parietal Lobule	R	57	-25	49	LM	3.59
Inf. Frontal G./Insula	L	-30	26	-8	42	3.98
Pos. Insula	L	-36	26	4	LM	3.44
Pos. Insula	R	39	5	19	136	3.97
Pos. Insula	R	39	5	-8	LM	3.87
Pos. Insula	R	39	-7	-5	LM	3.66
Precuneus	L	-27	-52	52	99	3.82
Inf. Parietal Lobule	L	-35	-46	58	LM	3.57
Fusiform G.	L	-45	-67	-8	11	3.46
Caudate Body	R	15	2	1	10	3.38
Thalamus	R	15	-13	7	6	3.28
Postcentral G./Insula	L	-60	-19	22	5	3.24

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.17.2 Memories

Activity in left IFG differentiated disgust elicited by memories from happiness elicited by memories (see Table 28 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.17.3 Overall (Films and Memories)

Activity in bilateral anterior insula, bilateral posterior insula, bilateral IFG, and right thalamus differentiated overall disgust from overall happiness (see Table 28 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.18Disgust > Sad

3.4.2.4.6.18.1 Films

Activity in bilateral PHG, and left precuneus differentiated disgust elicited by films from sadness elicited by films (see Table 29 for a summary of all peak coordinates and their related statistics).

Table 29. Inclusive whole-brain contrasts: Disgust > Sadness

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*Z*	*k* (volume)	*Z*
DISGUST – SADNESS Disgust Films > Sad Films						
Inf. Parietal Lobule	L	-57	-22	19	36	4.40
Postcentral G.	L	-36	-52	52	86	4.28
Mid. Occipital G.	L	-57	-31	46	56	4.24
Mid. Occipital G.	L	-33	-88	4	46	4.08
Pos. Insula	R	39	2	-8	145	3.95
Pos. Insula	R	39	-7	-2	LM	3.65
Precentral G.	R	57	14	-2	LM	3.48
Postcentral G./Pos. Insula	R	60	-19	25	49	3.93
Precuneus	R	30	-52	49	113	3.91
Precuneus	R	36	-40	43	LM	3.52
Inf. Parietal Lobule	R	42	-40	55	LM	3.37
Precuneus	R	30	-67	31	14	3.79
Mid. Temporal G.	L	-30	-1	58	27	3.64
Fusiform G.	L	-42	-49	-14	23	3.64
Fusiform G.	L	-48	-64	-5	22	3.47
Ant. Insula	R	42	29	-2	29	3.44
Pos. Insula	L	-39	5	-2	28	3.43
Pos. Insula	L	-36	5	-14	LM	3.37
Fusiform G.	L	-30	-61	-8	10	3.39
Disgust (Films + Memories) > Sad (Films + Memories)						
Inf. Frontal G.	L	-42	41	-5	9	4.21
Pos. Insula	L	-39	5	-2	25	3.91
Pos. Insula	L	-36	5	-11	LM	3.31
Inf. Frontal G.	L	-36	20	-17	8	3.51
Ant. Insula	L	-51	38	16	13	3.44
Inf. Frontal G.	L	-51	44	4	LM	3.41
Pos. Insula	L	-39	-10	-5	8	3.38

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. =

superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.18.2 Memories

Disgust elicited by memories was not differentiated from sadness elicited by memories at a threshold of $p < .001$. For additional regions differentiating the two emotions see the overall contrast.

3.4.2.4.6.18.3 Overall (Films and Memories)

Activity in left IFG and left anterior and posterior insula differentiated overall disgust from overall sadness (see Table 29 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.19Disgust > Anger

3.4.2.4.6.19.1 Films

Activity in bilateral posterior insula, right anterior insula, right IFG, and bilateral precuneus differentiated disgust elicited by films from anger elicited by films (see Table 30 for a summary of all peak coordinates and their related statistics).

Table 30. Inclusive whole-brain contrasts: Disgust > Anger

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
DISGUST - ANGER						
Disgust Films > Anger Films						
Precuneus	R	24	-64	49	560	5.29
Precuneus	R	24	-61	40	LM	5.27
Inf. Parietal Lobule	R	36	-34	40	LM	5.14
Ant. Insula	R	39	8	19	209	4.81
Inf. Frontal G.	R	51	14	19	LM	4.57
Pos. Insula	R	39	2	-5	LM	4.1
Precuneus	L	-24	-61	52	274	4.67
Precuneus	L	-27	-52	55	LM	4.65
Inf. Parietal Lobule	L	-60	-31	43	LM	3.73
Fusiform G.	L	-42	-64	-8	88	4.3
Fusiform G.	L	-30	-67	-11	LM	3.28
Fusiform G.	R	48	-52	-8	23	3.69
Mid. Occipital G.	L	-30	-91	10	39	3.66
Postcentral G./Insula	L	-57	-22	22	11	3.42
Pos. Insula	L	-39	2	-11	12	3.40
Disgust Memories > Anger Memories						
Mid. Frontal G.	L	-48	44	7	29	4.41
Fusiform G.	L	-51	-52	-14	32	3.62
Pos. Insula	L	-42	2	13	10	3.36
Disgust (Films + Memories) > Anger (Films + Memories)						
Precuneus	R	24	-64	46	112	5.16
Inf. Parietal Lobule	R	39	-37	43	219	4.68
Inf. Parietal Lobule	R	60	-31	31	LM	3.62
Postcentral G.	R	60	-19	31	LM	3.56
Inf. Parietal Lobule	L	-33	-52	55	254	4.63
Inf. Parietal Lobule	L	-45	-43	58	LM	3.98
Inf. Parietal Lobule	L	-60	-31	43	LM	3.79
Mid. Frontal G.	L	-33	41	-14	9	4.00
Pos. Insula	R	39	5	-8	74	3.63
Pos. Insula	R	39	-16	-2	LM	3.58
Pos. Insula	R	36	-4	10	LM	3.50
Ant. Insula	R	33	32	-11	5	3.59
Pos. Insula	L	-39	2	-8	14	3.44
Pos. Insula	L	-39	-1	13	5	3.42
Mid. Frontal G.	L	-27	5	52	6	3.27

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.19.2 Memories

Activity in left posterior insula, left MFG, and left fusiform gyrus differentiated disgust elicited by memories from anger elicited by memories (see Table 30 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.19.3 Overall (Films and Memories)

Activity in bilateral posterior insula, right anterior insula, and left MFG differentiated overall disgust from overall anger (see Table 30 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.20Disgust > Fear

3.4.2.4.6.20.1 Films

Activity in bilateral anterior insula, right posterior insula, right cingulate, and left thalamus differentiated disgust elicited by films from fear elicited by films (see Table 31 for a summary of all peak coordinates and their related statistics).

Table 31. Inclusive whole-brain contrasts: Disgust > Fear

Region	*HEM*	*Coordinate (MNI)* *x*	*y*	*z*	*k* (volume)	*Z*
DISGUST - FEAR						
Disgust Films > Fear Films						
Postcentral G./Insula	L	-57	-19	16	465	5.11
Inf. Parietal Lobule	L	-54	-31	40	LM	5.02
Inf. Parietal Lobule	L	-36	-46	55	LM	4.76
Inf. Frontal G./Insula	L	-33	20	-17	403	5.07
Ant. Insula	L	-30	11	-14	LM	4.39
Ant. Insula	L	-42	26	1	LM	4.12
Cerebellum	L	-42	-64	-11	191	4.75
Cerebellum	L	-39	-52	-20	LM	3.77
Pos. Insula	R	39	2	-5	508	4.73
Ant. Insula	R	51	14	-11	LM	4.18
Putamen/Insula	R	27	14	-14	LM	3.82
Postcentral G./Insula	R	60	-16	25	345	4.26
Postcentral G.	R	54	-19	34	LM	4.12
Postcentral G.	R	63	-16	40	LM	3.95
Inf. Parietal Lobule	R	45	-34	49	138	4.07
Inf. Parietal Lobule	R	42	-37	58	LM	3.77
Precentral G.	R	-57	5	37	9	3.94
Cerebellum	R	36	-64	-11	41	3.85
Inf. Temporal G.	R	45	-64	-5	LM	3.63
Cingulate G.	R	0	8	28	25	3.78
Cingulate G.	R	0	14	19	LM	3.49
Sup. Temporal G.	R	45	-49	10	21	3.53
Sup. Temporal G./Insula	R	42	-34	13	LM	3.41
Globus Pallidus	L	-15	-7	-11	10	3.52
Thalamus	L	-12	-7	-2	LM	3.16
Ant. Insula	R	39	11	19	16	3.46
Disgust Memories > Fear Memories						
Inf. Parietal Lobule	L	-66	-25	31	11	3.68
Ant. Insula	L	-30	8	16	8	3.32
Pos. Insula	L	-36	2	22	LM	3.18
Disgust (Films + Memories) > Fear (Films + Memories)						
Fusiform G.	L	-42	-55	-11	202	5.24
Fusiform G.	L	-48	-64	-8	LM	3.96
Mid. Temporal G.	L	-51	-67	7	LM	3.55
Pos. Insula	L	-36	5	-11	431	4.86
Pos. Insula	L	-42	-4	-8	LM	4.77
Ant. Insula	L	-51	8	-5	LM	4.63
Sup. Temporal G.	L	-54	-31	10	498	4.49

Pos. Insula	L	-51	-19	16	LM	4.43
Inf. Parietal Lobule	L	-30	-49	55	LM	4.38
Sup. Temporal G.	R	63	-4	4	1267	4.38
Sup. Temporal G.	R	48	14	-20	LM	4.29
Postcentral G./Insula	R	60	-13	13	LM	4.28
Precentral G.	L	-60	8	31	10	3.93
Putamen	R	27	23	7	14	3.69
Pos. Insula	L	-39	-4	13	17	3.66
Caudate Body	L	-21	14	19	6	3.65
Cingulate G.	R	15	-16	37	9	3.59
Cingulate G.	L	-3	-4	34	21	3.59
Mid. Temporal G.	R	48	-52	10	18	3.49
Fusiform G.	R	36	-64	-11	6	3.42

Note: Activation clusters of 5 contiguous voxels at a p threshold of .001. Clusters detected by small-volume corrections ($p < 0.05$) are denoted by a star. Small volume corrections were performed on a priori ROIs (identical to the ROI analysis) specific to each emotion state. Local maxima = (LM); HEM = hemisphere; L = left; R = right; k = cluster volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Pos. = posterior; C. = cortex; G. = gyrus.

3.4.2.4.6.20.2 Memories

Activity in left anterior and posterior insula differentiated disgust elicited by memories from fear elicited by memories (see Table 31 for a summary of all peak coordinates and their related statistics).

3.4.2.4.6.20.3 Overall (Films and Memories)

Activity in left anterior and posterior insula, bilateral MTG, bilateral STG, bilateral cingulate, and right putamen differentiated overall disgust from overall fear (see Table 31 for a summary of all peak coordinates and their related statistics).

3.4.2.5 ROI Analyses

Regions of interest (ROI) analyses were performed on anatomically-defined ROIs. Regions were selected based on those that characterized and differentiated basic emotion states in the meta-analysis, with converging evidence in other domains (e.g., nonhuman animal research). The following sections present the mean percent signal change across in each ROI for each emotion state with the neutral baseline subtracted. Table 32 presents means and SDs of percent signal change in each modality (films and memories) for each basic emotion state. Table 33 presents means and SDs of percent signal change in for each basic emotion state averaged across modality. Table 34 presents pairwise comparison statistics between all emotion conditions (as well as the neutral condition) for each ROI. Table 35 presents pairwise comparison statistics between all emotion conditions (as well as the neutral condition) for the average mean percent signal change collapsed across modality in each ROI.

Table 32. Descriptive statistics of ROI percent signal change in each emotion condition separately for memories and films

	Happy		Neutral (Happy)		Sadness		Neutral (Sadness)		Anger	
Region of Interest	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Films										
Left Amygdala	0.127	0.224	-0.106	0.330	0.175	0.367	-0.047	0.236	0.153	0.471
Right Amygdala	0.118	0.244	-0.024	0.273	0.244	0.301	0.058	0.183	0.173	0.254
Right STG	0.358	0.346	0.074	0.456	0.219	0.341	0.160	0.336	0.700	0.369
Left ACC	0.003	0.380	-0.071	0.180	0.003	0.271	-0.104	0.236	-0.049	0.348
Left Caudate	0.005	0.167	-0.075	0.176	0.068	0.195	-0.036	0.160	0.048	0.220
Right Caudate	-0.014	0.148	-0.079	0.187	0.098	0.236	-0.004	0.163	0.110	0.213
Left IFG	0.240	0.276	0.130	0.258	0.175	0.233	0.150	0.199	0.370	0.414
Left Anterior Insula	0.148	0.258	0.026	0.165	0.178	0.209	0.052	0.149	0.167	0.321
Right Anterior Insula	0.119	0.259	0.035	0.225	0.168	0.323	0.087	0.224	0.185	0.328
Left Posterior Insula	0.055	0.162	0.009	0.165	-0.038	0.168	-0.028	0.117	0.038	0.242
Right Posterior Insula	0.043	0.171	-0.042	0.241	-0.049	0.265	-0.068	0.153	0.085	0.257
Memories										
Left Amygdala	-0.211	0.328	-0.262	0.373	-0.299	0.301	-0.464	0.264	-0.265	0.412
Right Amygdala	-0.196	0.207	-0.187	0.270	-0.254	0.335	-0.374	0.326	-0.224	0.384
Right STG	0.358	0.346	0.074	0.456	0.219	0.341	0.160	0.336	0.700	0.369
Left ACC	0.003	0.380	-0.071	0.180	0.003	0.271	-0.104	0.236	-0.049	0.348
Left Caudate	-0.116	0.201	-0.124	0.221	-0.109	0.274	-0.259	0.207	-0.174	0.276
Right Caudate	-0.152	0.160	-0.143	0.188	-0.151	0.254	-0.280	0.235	-0.181	0.268
Left IFG	-0.295	0.301	-0.207	0.266	-0.274	0.303	-0.323	0.282	-0.260	0.455
Left Anterior Insula	-0.189	0.248	-0.125	0.223	-0.170	0.289	-0.268	0.272	-0.178	0.318
Right Anterior Insula	-0.222	0.296	-0.151	0.306	-0.262	0.404	-0.329	0.326	-0.242	0.404
Left Posterior Insula	-0.036	0.213	0.060	0.203	-0.115	0.222	-0.089	0.262	-0.078	0.381
Right Posterior Insula	-0.069	0.250	0.012	0.308	-0.101	0.296	-0.148	0.277	-0.056	0.384

	Neutral (Anger)		Fear		Neutral (Fear)		Disgust		Neutral (Disgust)	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Films										
Left Amygdala	-0.046	0.303	-0.099	0.338	-0.163	0.241	0.313	0.395	-0.098	0.309
Right Amygdala	0.031	0.198	-0.060	0.331	0.344	0.282	0.344	0.382	-0.090	0.282
Right STG	0.128	0.268	0.144	0.297	0.038	0.369	0.450	0.269	0.125	0.301
Left ACC	-0.045	0.206	-0.084	0.214	-0.076	0.175	-0.142	0.338	-0.148	0.211
Left Caudate	-0.045	0.168	-0.084	0.160	-0.124	0.144	-0.088	0.226	-0.141	0.146

Right Caudate	-0.024	0.189	-0.047	0.190	-0.110	0.179	0.026	0.209	-0.054	0.157
Left IFG	0.161	0.307	0.216	0.215	0.228	0.230	0.366	0.414	0.166	0.217
Left Anterior Insula	0.063	0.236	0.035	0.265	0.009	0.159	0.315	0.230	-0.009	0.188
Right Anterior Insula	0.071	0.223	0.002	0.299	0.007	0.227	0.333	0.288	-0.035	0.231
Left Posterior Insula	0.082	0.167	-0.041	0.224	0.019	0.159	0.158	0.364	-0.011	0.161
Right Posterior Insula	0.049	0.189	-0.062	0.246	-0.032	0.219	0.270	0.278	-0.059	0.174
Memories										
Left Amygdala	-0.159	0.385	-0.482	0.444	-0.277	0.328	-0.191	0.279	-0.181	0.348
Right Amygdala	-0.143	0.292	-0.313	0.405	-0.169	0.284	-0.104	0.248	-0.093	0.286
Right STG	0.128	0.268	0.144	0.297	0.038	0.369	0.450	0.269	0.125	0.301
Left ACC	-0.045	0.206	-0.084	0.214	-0.076	0.175	-0.142	0.338	-0.148	0.211
Left Caudate	-0.235	0.215	-0.269	0.200	-0.206	0.189	-0.063	0.198	-0.078	0.156
Right Caudate	-0.219	0.191	-0.234	0.171	-0.152	0.151	-0.097	0.217	-0.097	0.175
Left IFG	-0.261	0.317	-0.373	0.351	-0.221	0.241	-0.084	0.308	-0.217	0.261
Left Anterior Insula	-0.209	0.248	-0.228	0.327	-0.168	0.224	-0.030	0.290	-0.106	0.206
Right Anterior Insula	-0.223	0.306	-0.265	0.401	-0.129	0.292	-0.090	0.304	-0.095	0.308
Left Posterior Insula	0.020	0.358	-0.158	0.349	-0.016	0.269	0.048	0.275	0.039	0.253
Right Posterior Insula	0.026	0.360	-0.177	0.320	0.010	0.203	0.008	0.288	-0.001	0.288

Note: Table presents mean percent signal change and standard deviations in each emotion condition across different regions of interest.

Table 33. Descriptive statistics of ROI percent signal change in each emotion condition collapsed across modality

	Happy		Neutral (Happy)		Sadness		Neutral (Sadness)		Anger	
Region of Interest	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Left Amygdala	-.0422	0.118	-0.184	0.303	-0.062	0.215	-0.256	0.183	-0.056	0.384
Right Amygdala	-0.039	0.124	0.124	0.208	-0.005	0.217	-0.158	0.202	-0.026	0.245
Right STG	0.088	0.236	-0.028	0.308	-0.002	0.241	-0.059	0.250	0.288	0.288
Left ACC	-0.091	0.267	-0.110	0.179	-0.077	0.188	-0.209	0.197	-0.144	0.274
Left Caudate	-0.055	0.153	-0.100	0.149	-0.020	0.195	-0.148	0.156	-0.063	0.201
Right Caudate	-0.083	0.118	-0.111	0.144	-0.026	0.203	-0.142	0.160	-0.036	0.200
Left IFG	0.013	0.013	-0.036	0.205	-0.050	0.160	-0.060	0.210	0.084	0.412
Left Anterior Insula	-0.007	0.191	-0.050	0.115	0.021	0.216	-0.062	0.172	-0.004	0.219
Right Anterior Insula	-0.026	0.216	-0.051	0.157	-0.036	0.279	-0.069	0.187	-0.029	0.245
Left Posterior Insula	0.032	0.103	0.038	0.099	-0.073	0.125	-0.024	0.109	-0.020	0.212
Right Posterior Insula	0.011	0.128	-0.013	0.157	-0.076	0.144	-0.070	0.109	0.021	0.237

	Neutral (Anger)		Fear		Neutral (Fear)		Disgust		Neutral (Disgust)	
Region of Interest	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Left Amygdala	-0.103	0.306	-0.291	0.311	-0.220	0.241	0.061	0.197	-0.140	0.230
Right Amygdala	-0.056	0.200	-0.187	-0.187	0.217	0.319	0.120	0.151	-0.091	0.165
Right STG	0.021	0.316	-0.090	0.290	-0.037	0.274	0.176	0.183	0.015	0.218
Left ACC	-0.119	0.158	-0.176	0.191	-0.115	0.156	-0.111	0.270	-0.089	0.130
Left Caudate	-0.140	0.158	-0.177	0.151	-0.165	0.126	-0.075	0.152	-0.110	0.114
Right Caudate	-0.122	0.160	-0.141	0.151	-0.131	0.137	-0.036	0.150	-0.076	0.117
Left IFG	-0.030	0.282	-0.044	0.247	0.026	0.177	0.128	0.257	-0.022	0.205
Left Anterior Insula	-0.063	0.174	-0.050	0.199	-0.043	0.125	0.139	0.203	-0.054	0.106
Right Anterior Insula	-0.067	0.199	-0.085	0.235	-0.026	0.175	0.119	0.213	-0.058	0.123
Left Posterior Insula	0.062	0.184	-0.050	0.184	0.032	0.134	0.099	0.219	0.007	0.124
Right Posterior Insula	0.056	0.210	-0.076	0.182	-0.001	0.132	0.137	0.216	-0.040	0.116

Note: Table presents mean percent signal change and standard deviations in each emotion condition across different regions of interest.

Table 34. ROI pairwise comparisons between emotion conditions separated by memories and films

	Paired comparisons									
Region of Interest	H vs. N		H vs. S		H vs. A		H vs. F		H vs. D	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Films										
Left Amygdala	***2.85***	***0.014***	0.08	0.934	0.33	0.743	0.43	0.189	-1.04	0.319
Right Amygdala	*2.12*	*0.053*	-0.84	0.417	-1.03	0.323	0.71	0.488	***-2.56***	***0.023***
Right STG	***0.30***	***0.010***	*1.97*	*0.069*	***-2.37***	***0.033***	1.30	0.215	-0.35	0.734
Left ACC	0.71	0.487	-3.19	0.754	0.76	0.458	0.70	0.499	0.54	0.598
Left Caudate	***2.34***	***0.035***	-0.56	0.585	-0.41	0.689	0.77	0.453	0.45	0.661
Right Caudate	*1.91*	*0.077*	-0.72	0.483	***.2.574***	***0.022***	0.04	0.972	-0.28	0.783
Left IFG	1.26	0.230	0.57	0.522	-0.17	0.867	1.10	0.292	0.33	0.747
Left Anterior Insula	***2.24***	***0.042***	-0.12	0.910	0.28	0.787	1.39	0.185	***-2.71***	***0.017***
Right Anterior Insula	1.45	0.168	0.46	0.964	-0.40	0.695	1.30	0.216	-2.95	0.110
Left Posterior Insula	0.87	0.398	0.75	0.467	1.31	0.211	1.36	0.195	-1.12	0.281
Right Posterior Insula	1.59	0.134	0.82	0.425	0.86	0.402	1.81	0.920	-2.99	0.100
Memories										
Left Amygdala	1.11	0.287	-1.05	0.314	1.50	0.159	*2.06*	*0.060*	0.82	0.428
Right Amygdala	-0.20	0.843	-1.43	0.174	0.89	0.390	1.44	0.173	0.04	0.973
Right STG	2.97	0.100	*1.97*	*0.069*	-2.37	0.330	1.30	0.215	-0.35	0.734
Left ACC	0.71	0.487	-0.32	0.754	0.76	0.458	0.70	0.499	0.54	0.598
Left Caudate	0.21	0.840	-1.84	0.087	-0.83	0.422	1.02	0.323	-0.14	0.889
Right Caudate	-0.26	0.801	-1.67	0.118	-8.17	0.427	1.14	0.272	-0.16	0.876
Left IFG	-1.39	0.186	-1.28	0.221	-0.81	0.430	0.65	0.527	***-2.46***	***0.027***
Left Anterior Insula	-1.50	0.155	***-2.21***	***0.044***	-1.17	0.263	-0.08	0.938	*-2.01*	*0.065*
Right Anterior Insula	-1.30	0.214	-1.34	0.202	-0.54	0.597	0.78	0.447	-0.86	0.406
Left Posterior Insula	*-2.01*	*0.064*	-0.75	0.463	0.04	0.971	0.77	0.454	-1.54	0.147
Right Posterior Insula	-1.55	0.144	-1.32	0.207	0.02	0.988	1.41	0.181	-1.21	0.246

	S vs. N		S vs. A		S vs. F		S vs. D		A vs. N	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Films										
Left Amygdala	***2.68***	***0.019***	0.19	0.850	1.21	0.249	-1.55	0.145	***2.66***	***0.020***
Right Amygdala	2.72	0.170	0.14	0.893	1.42	0.176	-2.09	0.055	2.85	0.130
Right STG	0.83	0.423	***-4.76***	***< 0.001***	-0.45	0.659	-2.03	0.062	***10.08***	***< 0.001***
Left ACC	2.32	0.036	1.69	0.114	1.33	0.206	1.05	0.310	-0.07	0.948
Left Caudate	***3.89***	***0.002***	0.24	0.817	1.10	0.288	0.81	0.433	***3.16***	***0.007***
Right Caudate	***2.75***	***0.016***	-0.60	0.560	0.68	0.508	0.37	0.719	***4.41***	***0.001***
Left IFG	0.55	0.590	-1.17	0.262	0.52	0.613	-0.64	0.536	***4.13***	***0.001***
Left Anterior Insula	***2.74***	***0.016***	0.33	0.748	1.33	0.236	-3.02	0.009	1.52	0.151
Right Anterior Insula	1.43	0.173	-0.34	0.741	0.92	0.376	-3.39	0.004	1.38	0.190

Left Posterior Insula	-0.23	0.820	0.50	0.626	0.66	0.522	-2.33	0.035	-0.84	0.413
Right Posterior Insula	0.39	0.704	-0.21	0.838	0.57	0.577	-3.47	0.004	0.64	0.531
Memories										
Left Amygdala	2.00	0.067	3.05	0.009	***3.90***	***0.002***	1.88	0.830	-1.38	0.190
Right Amygdala	1.89	0.800	2.63	0.200	***3.02***	***0.009***	1.69	0.113	0.89	0.390
Right STG	0.83	0.423	***-4.76***	***< 0.001***	-0.45	0.659	-2.03	0.620	***10.08***	***< 0.001***
Left ACC	***2.32***	***0.036***	1.69	0.114	1.33	0.206	1.05	0.310	-0.07	0.948
Left Caudate	***2.31***	***0.037***	1.86	0.085	***3.36***	***0.005***	2.67	0.018	1.44	0.173
Right Caudate	1.88	0.081	1.72	0.108	***3.33***	***0.005***	2.45	0.028	0.83	0.420
Left IFG	0.52	0.610	0.43	0.674	1.82	0.090	-0.98	0.346	0.01	0.990
Left Anterior Insula	1.42	0.178	1.00	0.335	***2.48***	***0.027***	0.34	0.739	0.46	0.651
Right Anterior Insula	0.71	0.487	1.40	0.184	***2.24***	***0.042***	0.72	0.484	-0.23	0.822
Left Posterior Insula	-0.40	0.697	1.48	0.162	1.47	0.165	-0.48	0.639	-1.83	0.088
Right Posterior Insula	0.63	0.537	***2.60***	***0.021***	***2.44***	***0.029***	0.45	0.662	-1.27	0.224

	A vs. F		A vs. D		F vs. N		F vs. D		D vs. N	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Films										
Left Amygdala	1.12	0.285	-1.25	0.233	0.62	0.546	***-2.93***	***0.012***	***2.76***	***0.016***
Right Amygdala	1.31	0.212	-1.56	0.142	0.43	0.673	***-3.87***	***0.002***	***3.76***	***0.002***
Right STG	***4.91***	***< 0.001***	*2.09*	*0.056*	1.25	0.233	.1.832	0.088	***3.10***	***0.008***
Left ACC	0.06	0.956	-0.08	0.935	-0.13	0.898	-0.18	0.858	0.07	0.948
Left Caudate	0.93	0.369	0.75	0.465	0.08	0.437	-0.29	0.776	1.09	0.295
Right Caudate	1.35	0.197	1.03	0.319	1.37	0.193	-0.32	0.752	1.86	0.084
Left IFG	***2.35***	***0.034***	0.82	0.424	-0.19	0.850	-1.30	0.214	***2.35***	***0.034***
Left Anterior Insula	1.29	0.219	***3.19***	***0.007***	0.36	0.729	***-5.14***	***< 0.001***	4.57	***< 0.001***
Right Anterior Insula	1.70	0.111	-2.59	0.220	-0.64	0.950	***-4.50***	***0.001***	***4.11***	***0.001***
Left Posterior Insula	0.28	0.783	-2.06	0.580	-0.92	0.373	-2.97	0.100	1.86	0.084
Right Posterior Insula	1.15	0.269	-3.03	0.009	-0.49	0.635	***-4.03***	***0.001***	***3.78***	***0.002***
Memories										
Left Amygdala	1.07	0.306	-0.99	0.339	-2.19	0.470	-1.96	0.720	-0.15	0.887
Right Amygdala	-1.18	0.260	-1.70	0.112	*-2.04*	*0.060*	-1.70	0.112	-0.18	0.861
Right STG	***4.91***	***< 0.001***	*2.09*	*0.056*	1.25	0.233	-1.83	0.088	***3.10***	***0.008***
Left ACC	0.06	0.956	-0.08	0.935	-0.13	0.898	-0.18	0.858	0.07	0.948
Left Caudate	2.89	0.120	1.32	0.208	-1.15	0.268	-1.51	0.153	0.41	0.690
Right Caudate	***2.61***	***0.021***	1.02	0.327	-1.61	0.131	-1.47	0.163	-0.01	0.993
Left IFG	1.70	0.112	-1.57	0.140	-1.75	0.103	***-2.63***	***0.020***	***2.24***	***0.042***
Left Anterior Insula	1.57	0.140	-0.66	0.518	-1.11	0.287	-1.74	0.104	1.41	0.180
Right Anterior Insula	1.73	0.105	-0.26	0.795	*-2.14*	*0.051*	-1.53	0.148	0.07	0.945
Left Posterior Insula	0.84	0.415	-1.71	0.109	***-2.93***	***0.011***	***-2.14***	***0.050***	0.16	0.875
Right Posterior Insula	1.37	0.191	-1.16	0.268	***-3.29***	***0.005***	***-2.38***	***0.032***	0.13	0.898

Note: Table presents pairwise contrasts between all emotion conditions for each region of interest (mean percent signal change). Neutral contrasts were calculated separately for each run. Significant differences ($p < 0.05$) are in bold and italicized. Effects approaching significance ($p < 0.08$) are italicized only. *df*(14) for all contrasts except the left amygdala where *df*(13).

Table 35. ROI pairwise contrasts between emotion conditions, collapsed across modality

	Paired comparisons									
Region of Interest	H vs. N		H vs. S		H vs. A		H vs. F		H vs. D	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Left Amygdala	***2.70***	***0.018***	-0.54	0.600	1.12	0.281	***1.94***	***0.074***	-0.56	0.588
Right Amygdala	1.66	0.119	-1.20	0.251	0.68	0.510	1.40	0.185	***-2.33***	***0.035***
Right STG	1.86	0.084	0.24	0.504	-1.81	0.092	1.58	0.136	-0.70	0.498
Left ACC	0.29	0.779	-1.27	0.225	0.55	0.594	0.96	0.352	0.49	0.630
Left Caudate	1.47	0.164	-1.77	0.099	-0.82	0.424	1.03	0.319	0.21	0.834
Right Caudate	1.19	0.253	-1.68	0.116	*-1.91*	*0.077*	0.80	0.440	-0.32	0.756
Left IFG	0.58	0.571	0.40	0.697	-0.96	0.353	1.55	0.144	-0.96	0.352
Left Anterior Insula	1.17	0.261	-1.21	0.247	-0.31	0.758	1.45	0.170	***-3.18***	***0.007***
Right Anterior Insula	0.62	0.546	-0.15	0.879	-0.25	0.809	*2.02*	*0.063*	***-2.30***	***0.037***
Left Posterior Insula	-0.15	0.882	0.75	0.466	1.59	0.135	*2.04*	*0.060*	-1.40	0.183
Right Posterior Insula	0.68	0.509	0.59	0.567	1.59	0.133	***2.48***	***0.027***	***-2.70***	***0.017***

	S vs. N		S vs. A		S vs. F		S vs. D		A vs. N	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Left Amygdala	***3.44***	***0.004***	*2.08*	*0.058*	***2.95***	***0.011***	-0.08	0.934	0.85	0.413
Right Amygdala	***3.23***	***0.006***	*2.10*	*0.054*	***2.75***	***0.016***	-1.11	0.287	0.71	0.492
Right STG	0.88	0.393	***-3.41***	***0.004***	1.24	0.234	-1.21	0.245	***6.12***	***<0.001***
Left ACC	*2.01*	*0.064*	***2.48***	***0.027***	***2.70***	***0.017***	***2.43***	***0.029***	-0.48	0.641
Left Caudate	***3.23***	***0.006***	1.31	0.211	***3.37***	***0.005***	***2.18***	***0.047***	***2.74***	***0.016***
Right Caudate	***2.51***	***0.025***	0.71	0.489	***2.97***	***0.010***	1.66	0.120	***3.05***	***0.009***
Left IFG	0.28	0.783	-1.70	0.112	1.17	0.263	***-2.99***	***0.010***	***2.39***	***0.031***
Left Anterior Insula	***2.73***	***0.016***	0.53	0.605	***2.29***	***0.038***	***-2.55***	***0.023***	1.31	0.210
Right Anterior Insula	0.89	0.391	-0.09	0.930	***2.04***	***0.061***	***-2.68***	***0.018***	0.67	0.511
Left Posterior Insula	-1.43	0.175	0.65	0.528	0.60	0.559	***-2.65***	***0.019***	*-1.96*	*0.071*
Right Posterior Insula	-0.20	0.844	0.57	0.579	1.31	0.212	***-3.68***	***0.002***	-0.74	0.470

	A vs. F		A vs. D		F vs. N		F vs. D		D vs. N	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Left Amygdala	1.23	0.242	-1.56	0.142	-0.87	0.400	***-3.65***	***0.003***	***2.43***	***0.031***
Right Amygdala	1.11	0.288	***-3.15***	***0.007***	***-2.59***	***0.021***	***-4.80***	***0.000***	***4.03***	***0.001***
Right STG	***4.90***	***0.001***	1.69	0.113	-0.83	0.420	***-3.11***	***0.008***	***4.33***	***0.001***
Left ACC	0.70	0.493	-0.04	0.966	-1.36	0.196	-0.69	0.502	-0.45	0.663
Left Caudate	*2.06*	*0.059*	1.42	0.178	-0.26	0.796	-1.31	0.212	1.13	0.278
Right Caudate	***2.30***	***0.038***	1.74	0.103	-0.23	0.820	-1.37	0.192	1.50	0.156
Left IFG	***4.00***	***0.001***	-0.53	0.607	-1.34	0.201	***-2.81***	***0.014***	***3.06***	***0.009***
Left Anterior Insula	1.75	0.102	***-2.97***	***0.010***	-0.15	0.879	***-4.52***	***0.000***	***3.99***	***0.001***
Right Anterior Insula	***0.02***	***0.043***	***-2.15***	***0.049***	-1.07	0.301	***-3.77***	***0.002***	***3.17***	***0.007***
Left Posterior Insula	0.00	0.998	***-2.51***	***0.025***	-1.86	0.084	***-2.80***	***0.014***	1.43	0.175
Right Posterior Insula	1.14	0.274	***-3.48***	***0.004***	-1.59	0.134	***-4.25***	***0.001***	***3.42***	***0.004***

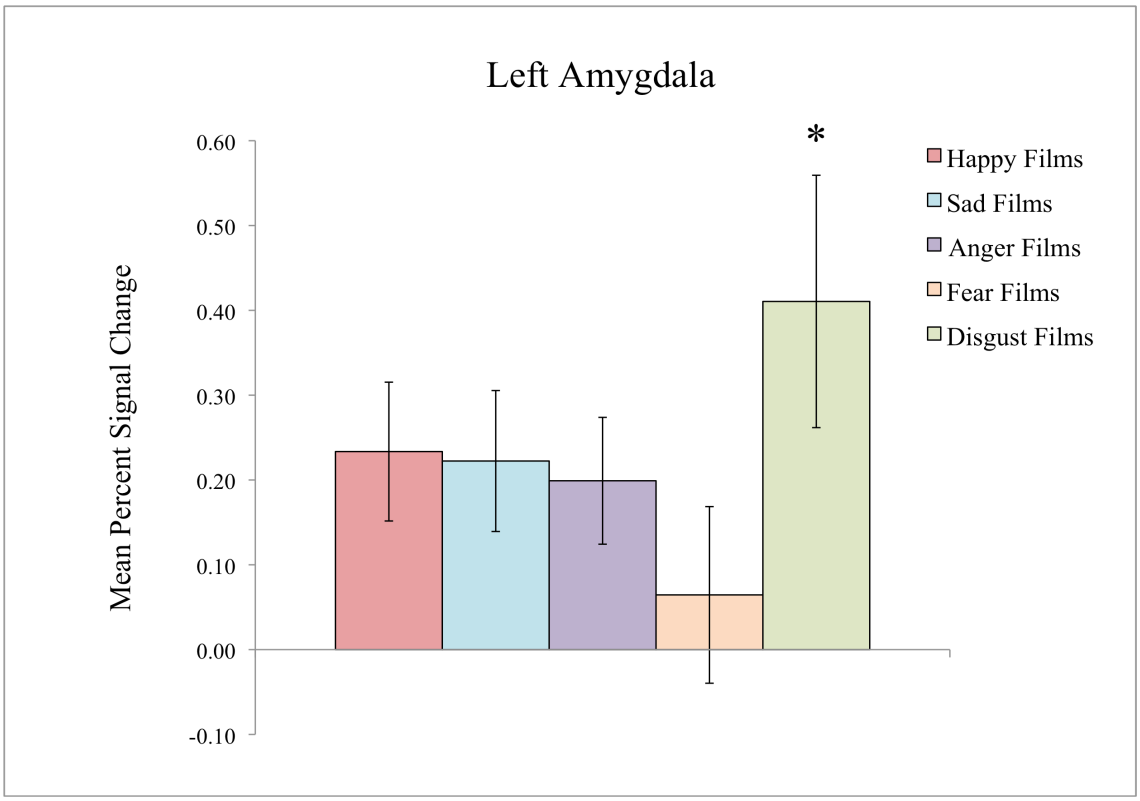
Note: Table presents pairwise contrasts between all emotion conditions, in addition to neutral, for each region of interest (average of films and memories: mean percent signal change). Neutral contrasts were calculated separately for each run. Significant differences ($p < 0.05$) are in bold and italicized. Differences approaching significance ($p < 0.08$) are italicized only. *df*(14) for all contrasts except the left amygdala where *df*(13).

3.4.2.5.1 Left Amygdala

3.4.2.5.1.1 Films

Mean percent signal change in the left amygdala was greater during disgust films than during fear films (see Table 32 and Figure 60). Although disgust has previously been shown to be associated with amygdala activity and not fear (Stark et al., 2003), we expected fear films to engage the amygdala to a greater extent than all other emotion states. These data suggest that perhaps the association between fear and the amygdala, and disgust and the amygdala may change depending on the context or method of emotion elicitation.

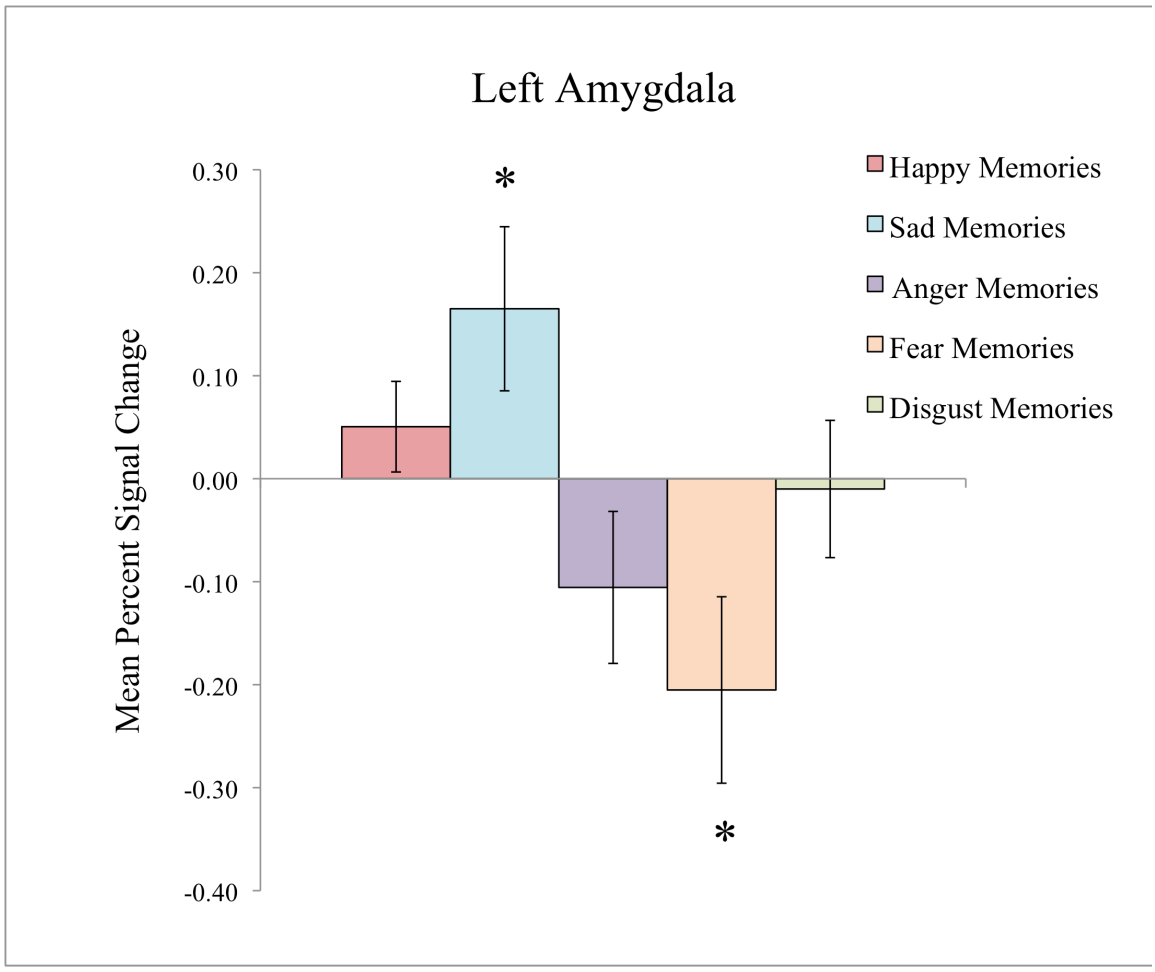
Figure 60. Mean percent signal change in the left amygdala during film viewing



3.4.2.5.1.2 Memories

Mean percent signal change in the left amygdala was greater during sad memory recollection than during fear and anger memory recollection, and greater during disgust memory recollection than fear memory recollection (see Table 34 and Figure 61). Again, these data do not support the hypothesis that fear-inducing stimuli would engage the amygdala to a greater extent than all other emotion states.

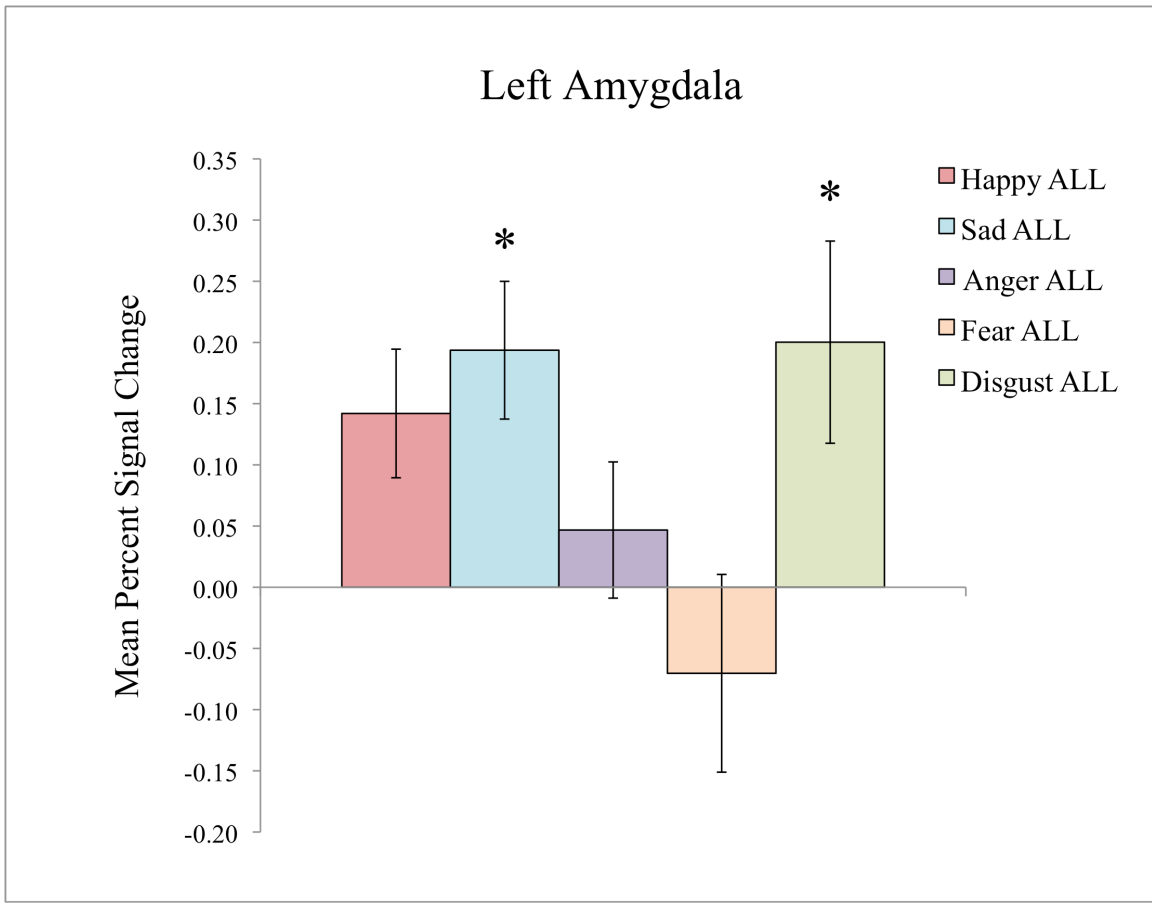
Figure 61. Mean percent signal change in the left amygdala during memory recollection



3.4.2.5.1.3 Overall (Films and Memories)

Mean percent signal change in the left amygdala was greater during the experience of sadness and disgust across elicitation methods than during the experience of fear (see Table 34 and Figure 62). Again, these data do not support the hypothesis that fear-inducing stimuli would engage the amygdala to a greater extent than all other emotion states.

Figure 62. Mean percent signal change in the left amygdala across modalities

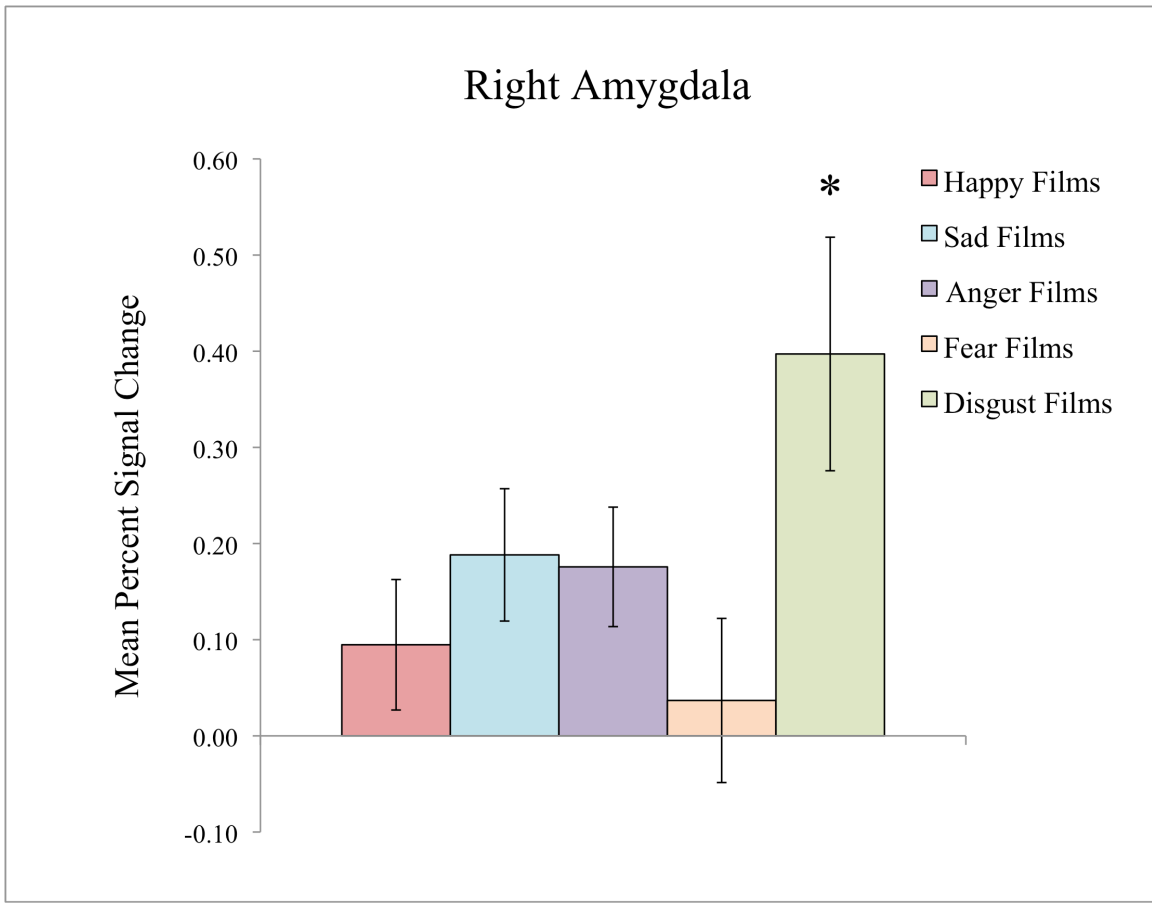


3.4.2.5.2 Right Amygdala

3.4.2.5.2.1 Films

Mean percent signal change in the right amygdala was greater during disgust films than during any other film condition (see Table 34 and Figure 63). Again, these data do not support the hypothesis that fear-inducing stimuli would engage the amygdala to a greater extent than all other emotion states.

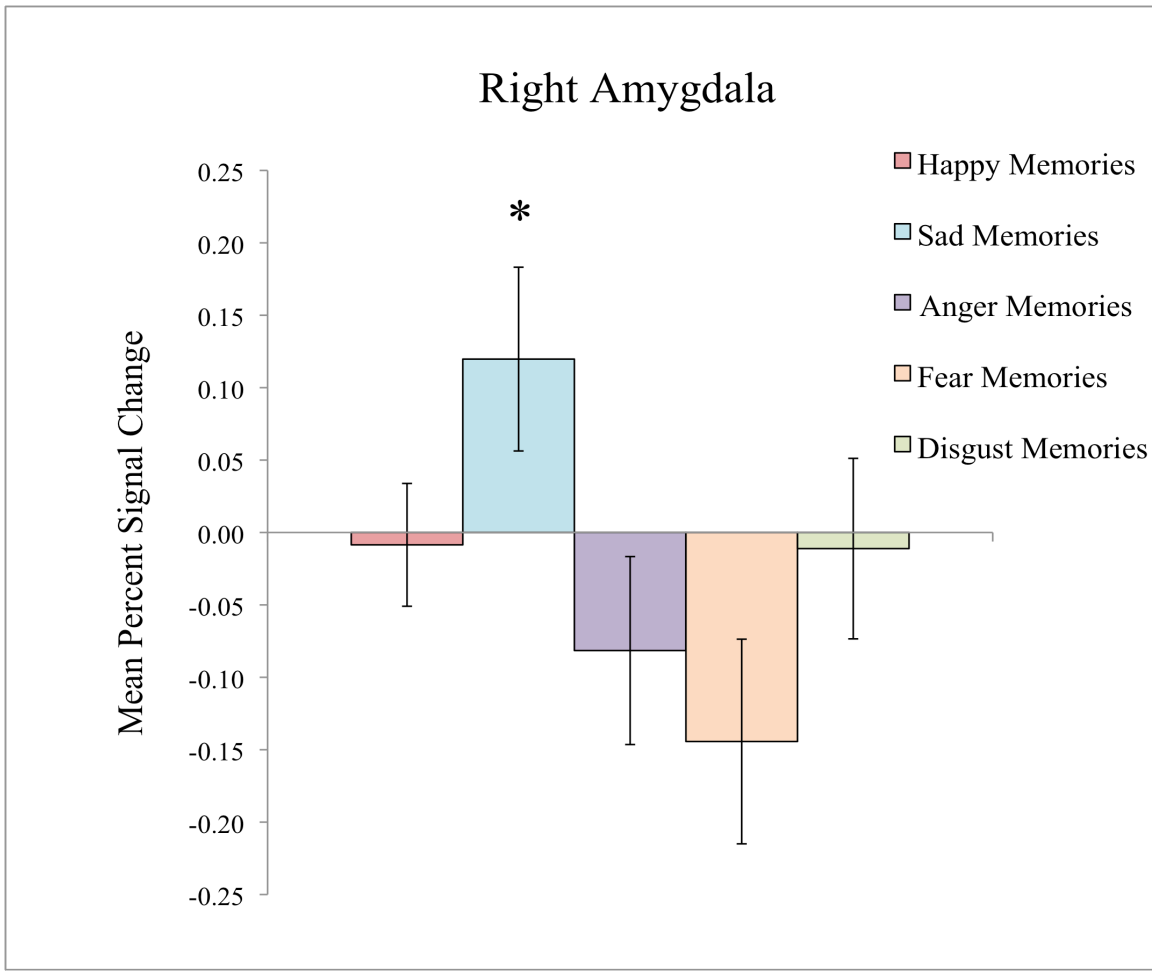
Figure 63. Mean percent signal change in the right amygdala during film viewing



3.4.2.5.2.2 Memories

Mean percent signal change in the right amygdala was greater during the recollection of sadness memories than during the recollection of anger memories and fear memories (see Table 34 and Figure 64). Again, these data do not support the hypothesis that fear-inducing stimuli would engage the amygdala to a greater extent than all other emotion states.

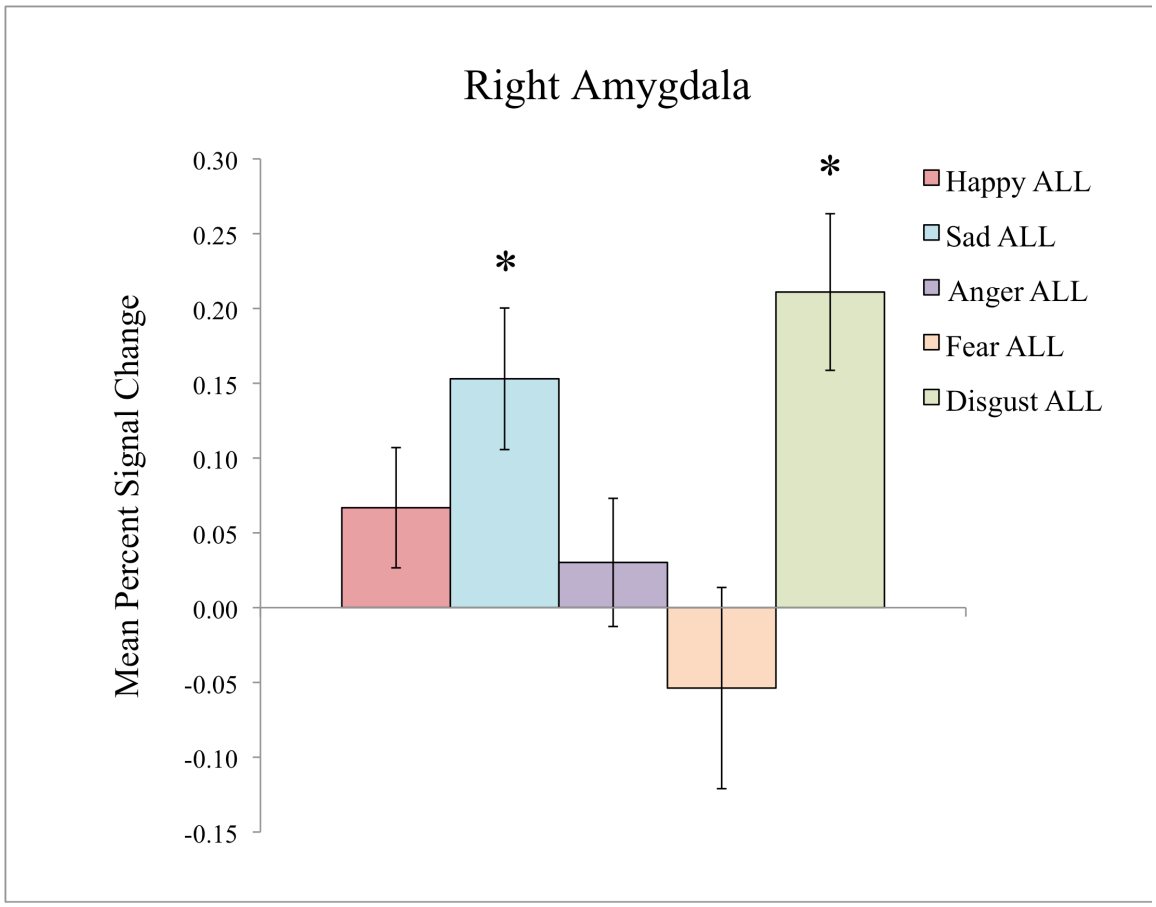
Figure 64. Mean percent signal change in the left amygdala during memory recollection



3.4.2.5.2.3 Overall (Films and Memories)

Mean percent signal change in the left amygdala was greater during the experience of sadness and disgust across elicitation methods than during the experience of all other emotion states (except for happiness: mean percent signal change did not differ between sadness and happiness, although it did differ in the direction indicated between disgust and happiness) (see Table 34 and Figure 65). Again, these data do not support the hypothesis that fear-inducing stimuli would engage the amygdala to a greater extent than all other emotion states.

Figure 65. Mean percent signal change in the left amygdala across modalities

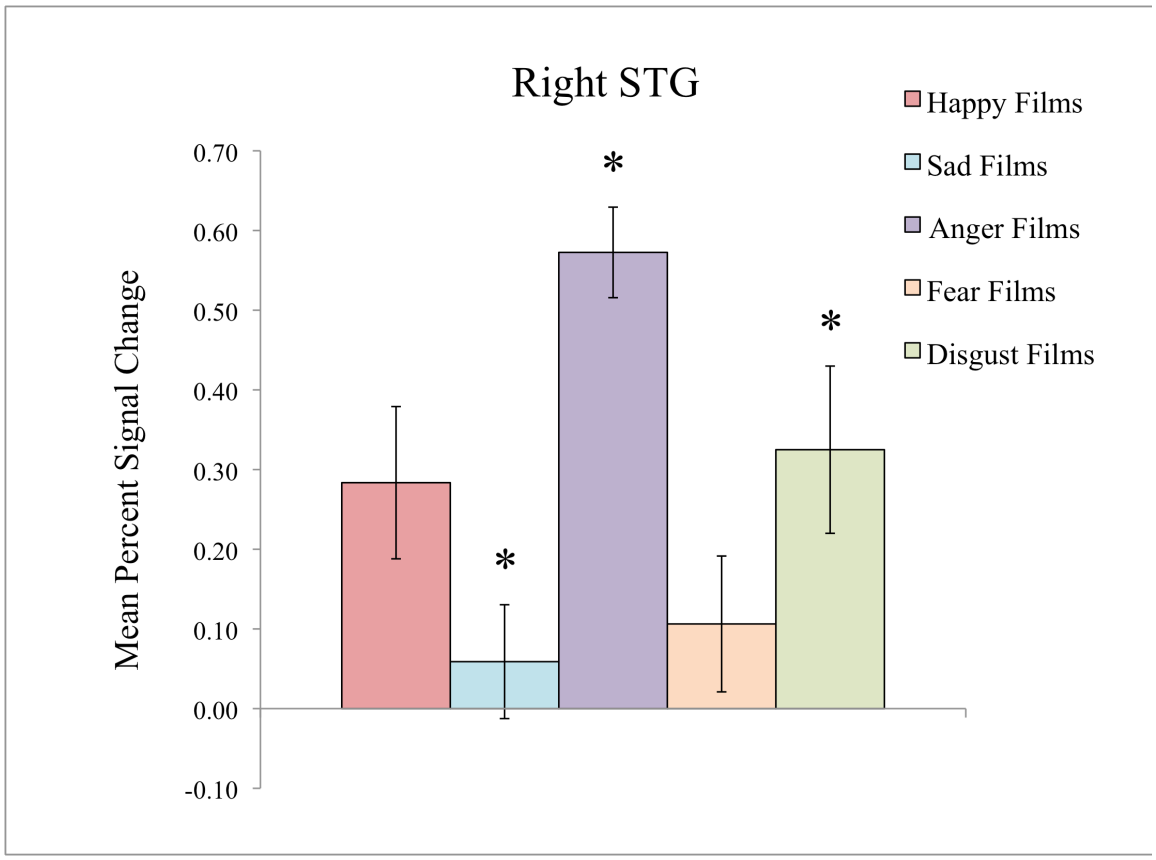


3.4.2.5.3 Right Superior Temporal Gyrus

3.4.2.5.3.1 Films

Mean percent signal change in the right STG was greater during anger films than during any other film condition (see Table 34 and Figure 66). In addition, mean percent signal change in the right STG was greater during disgust films than sad films. These data do not support the prediction that happiness would uniquely engage right STG.

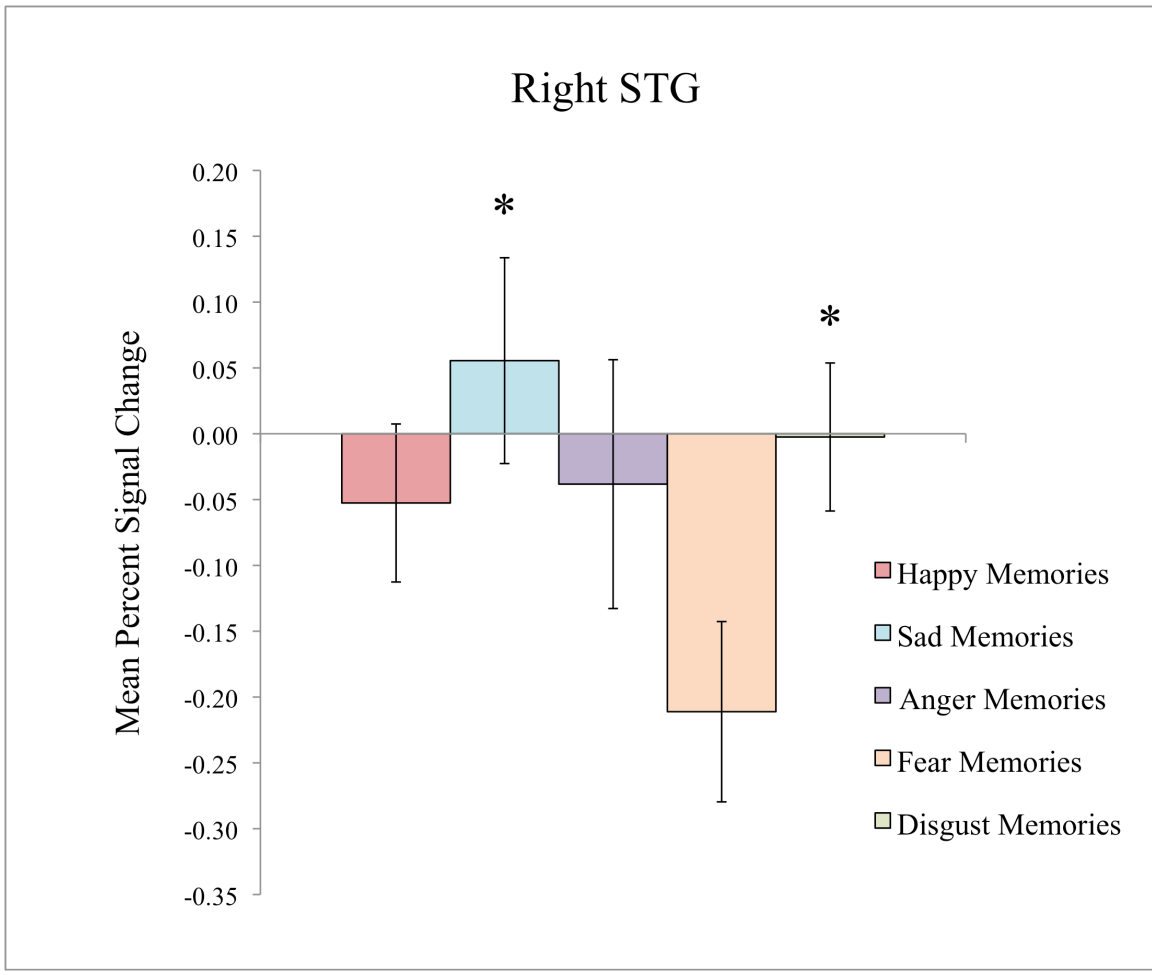
Figure 66. Mean percent signal change in the right superior temporal gyrus during film viewing



3.4.2.5.3.2 Memories

Mean percent signal change in the right STG was greater during sad and disgust memory recollection than during fear memory recollection (see Table 34 and Figure 67). These data do not support the prediction that happiness would uniquely engage right STG.

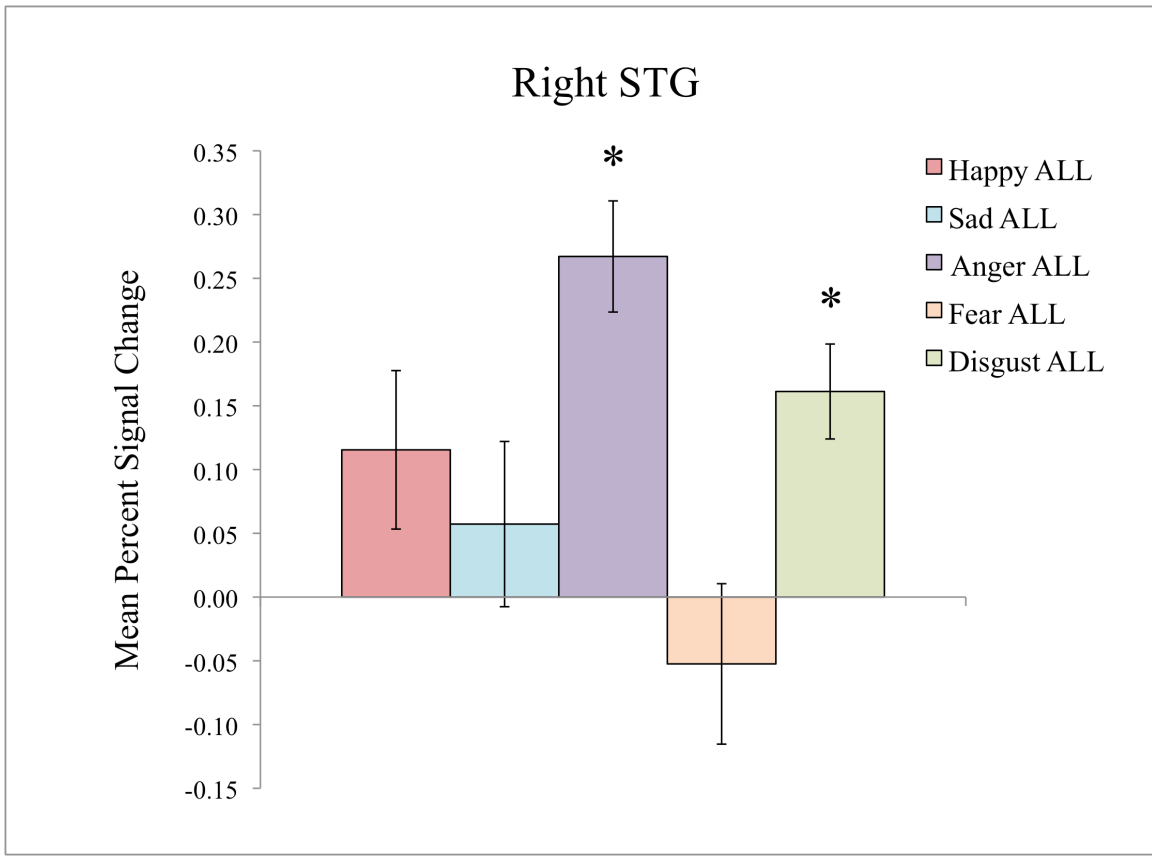
Figure 67. Mean percent signal change in the right superior temporal gyrus during memory recollection



3.4.2.5.3.3 Overall (Films and Memories)

Mean percent signal change in the right superior temporal gyrus was greater during the experience of anger and disgust across elicitation methods than during the experience of sadness and fear (see Table 34 and Figure 68). These data do not support the prediction that happiness would uniquely engage right STG.

Figure 68. Mean percent signal change in the right superior temporal gyrus across modalities

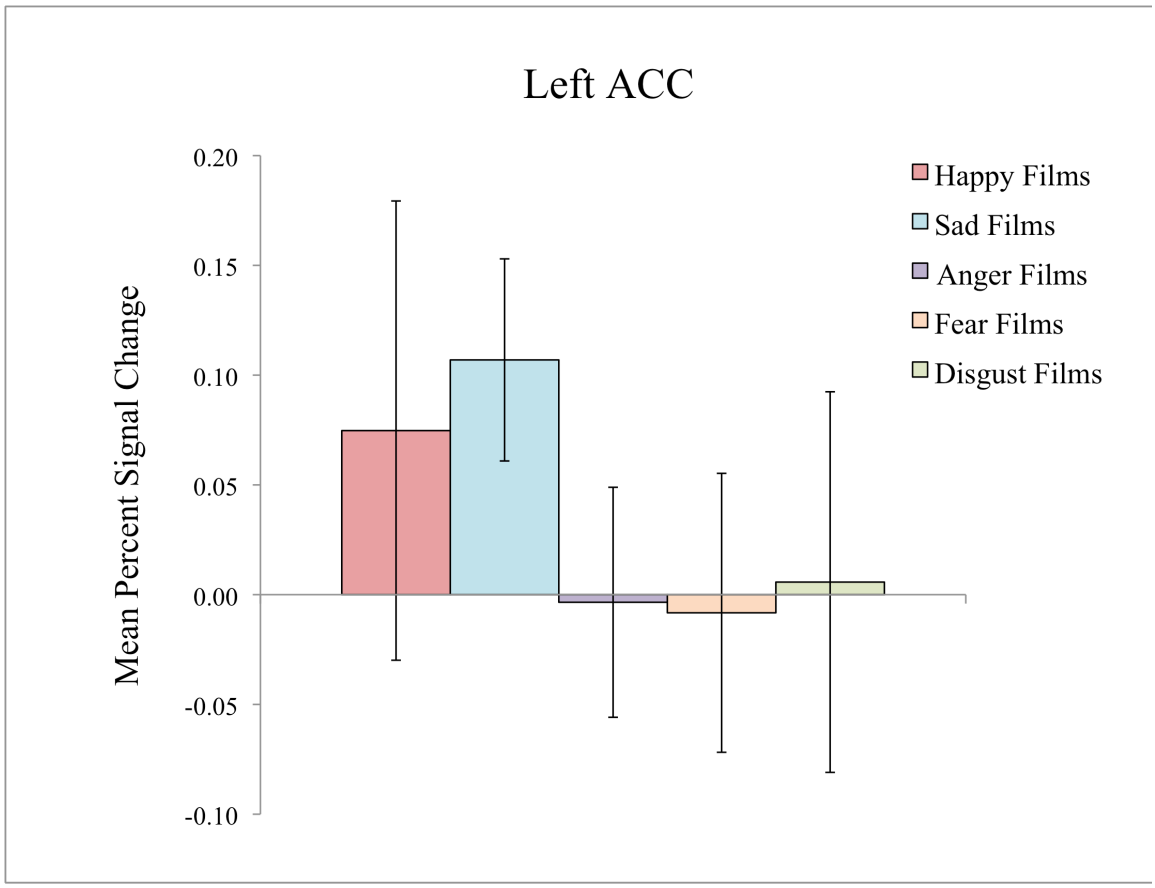


3.4.2.5.4 Left Anterior Cingulate Gyrus

3.4.2.5.4.1 Films

Mean percent signal change in the left ACC did not differ between film conditions (see Table 34 and Figure 69). These data do not support the hypothesis that happiness-inducing stimuli would engage the left ACC to a greater extent than all other emotion states.

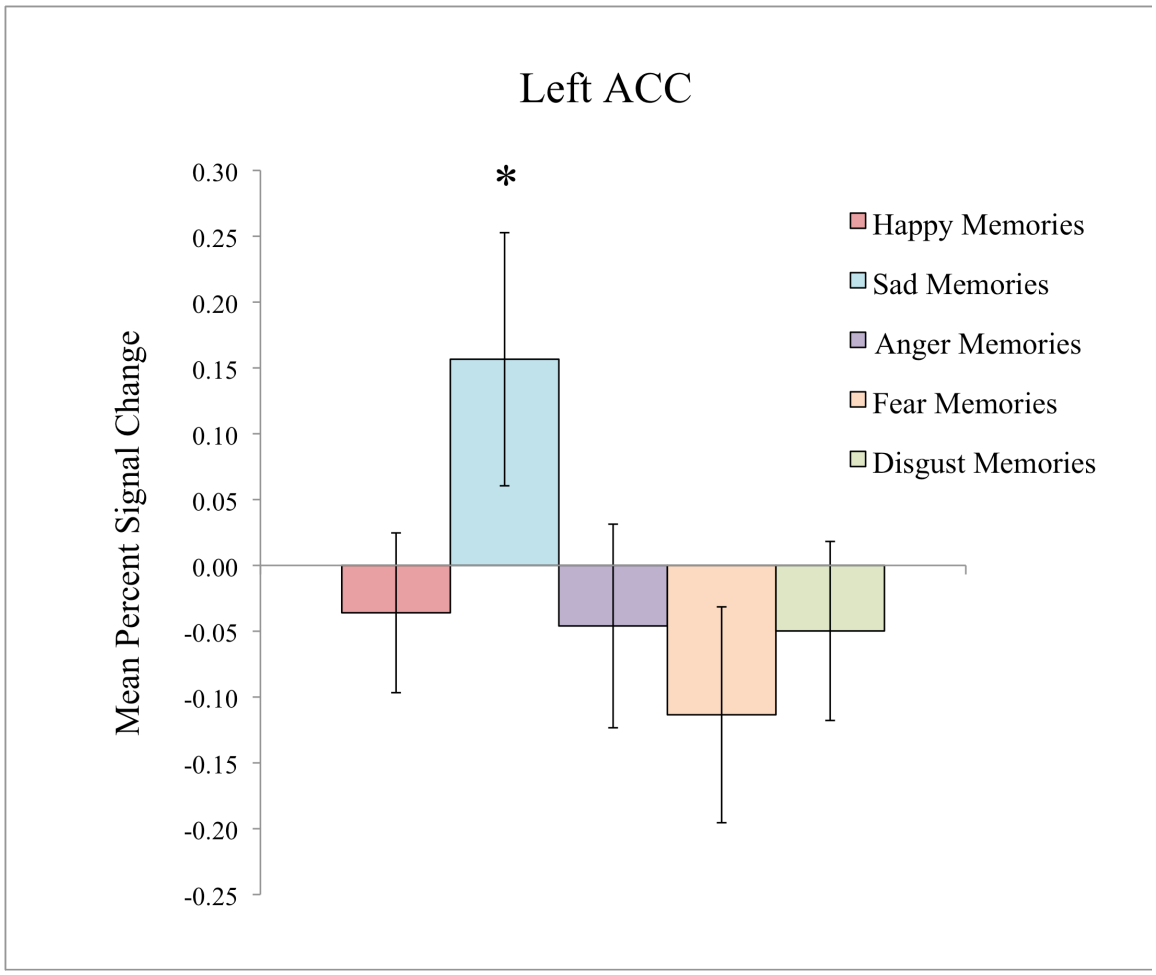
Figure 69. Mean percent signal change in the left anterior cingulate during film viewing



3.4.2.5.4.2 Memories

Mean percent signal change in the left ACC was greater during the recollection of sad memories than during any other type of memory recollection (see Table 34 and Figure 70). Again, these data do not support the hypothesis that happiness-inducing stimuli would engage the ACC to a greater extent than all other emotion states. However, these findings do fit with results from Vytal et al., which suggest that sadness also engages the ACC in a subregion (subgenual) that is distinct from that of happiness.

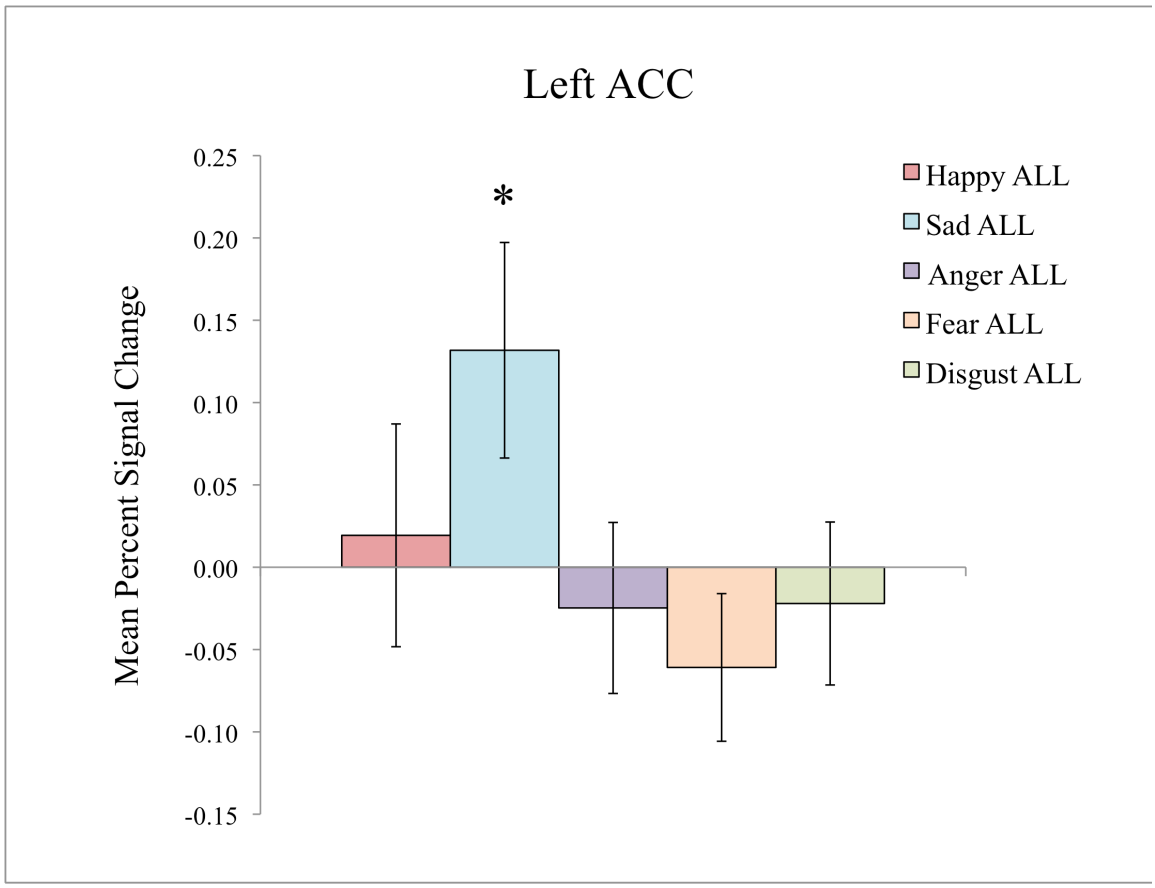
Figure 70. Mean percent signal change in the left anterior cingulate during memory recollection



3.4.2.5.4.3 Overall (Films and Memories)

Mean percent signal change in the left ACC was greater during the experience of sadness across elicitation modalities than during the experience of anger, fear or disgust (see Table 34 and Figure 71). Mean percent signal change in the left ACC did not differ between happiness and sadness. Again, these data do not support the hypothesis that happiness-inducing stimuli would uniquely engage the left ACC; yet they fit with results from the Vytal et al. meta-analysis that suggest that subgenual ACC plays a role in the experience of sadness.

Figure 71. Mean percent signal change in the left anterior cingulate across modalities

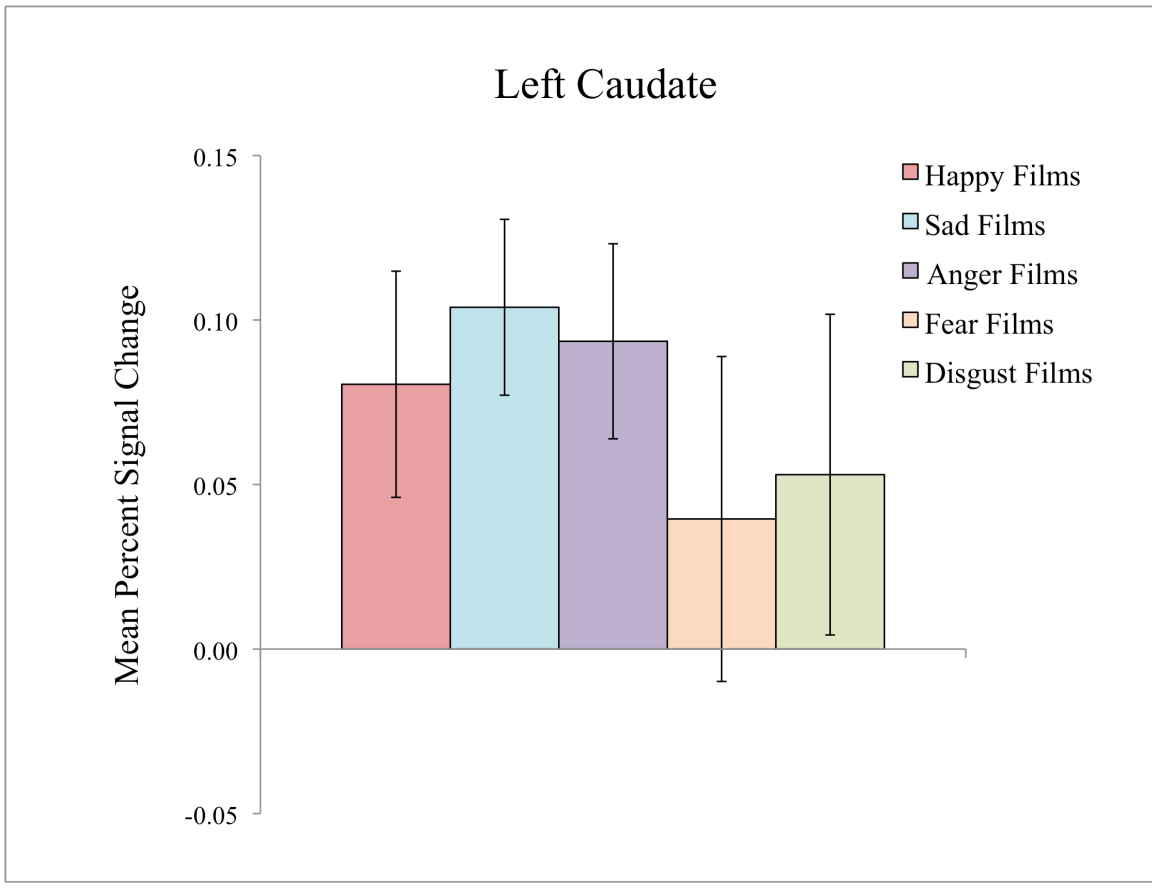


3.4.2.5.5 Left Caudate

3.4.2.5.5.1 Films

Mean percent signal change in the left caudate did not differ between film conditions (see Table 34 and Figure 72). These data do not support the hypothesis that sadness-inducing stimuli would engage the caudate to a greater extent than all other emotion states.

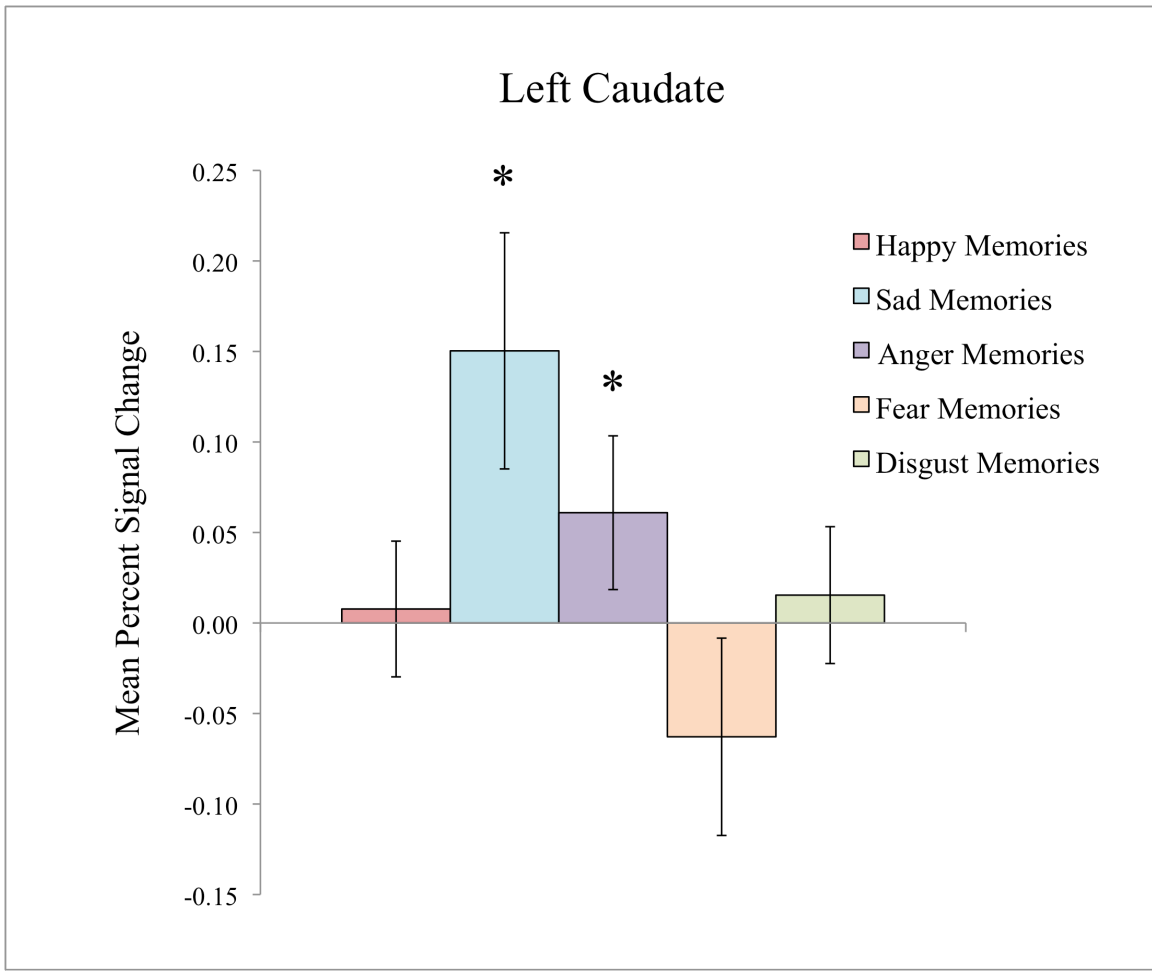
Figure 72. Mean percent signal change in the left caudate during film viewing



3.4.2.5.5.2 Memories

Mean percent signal change in the left caudate was greater during recollection of sad memories than during the recollection of happy, fear, or disgust memories (see Table 34 and Figure 73). These findings fit with our hypothesis that sadness-inducing stimuli would engage the caudate. In addition, recollection of anger memories was associated with a greater increase in mean percent signal change in the left caudate when compared with fear.

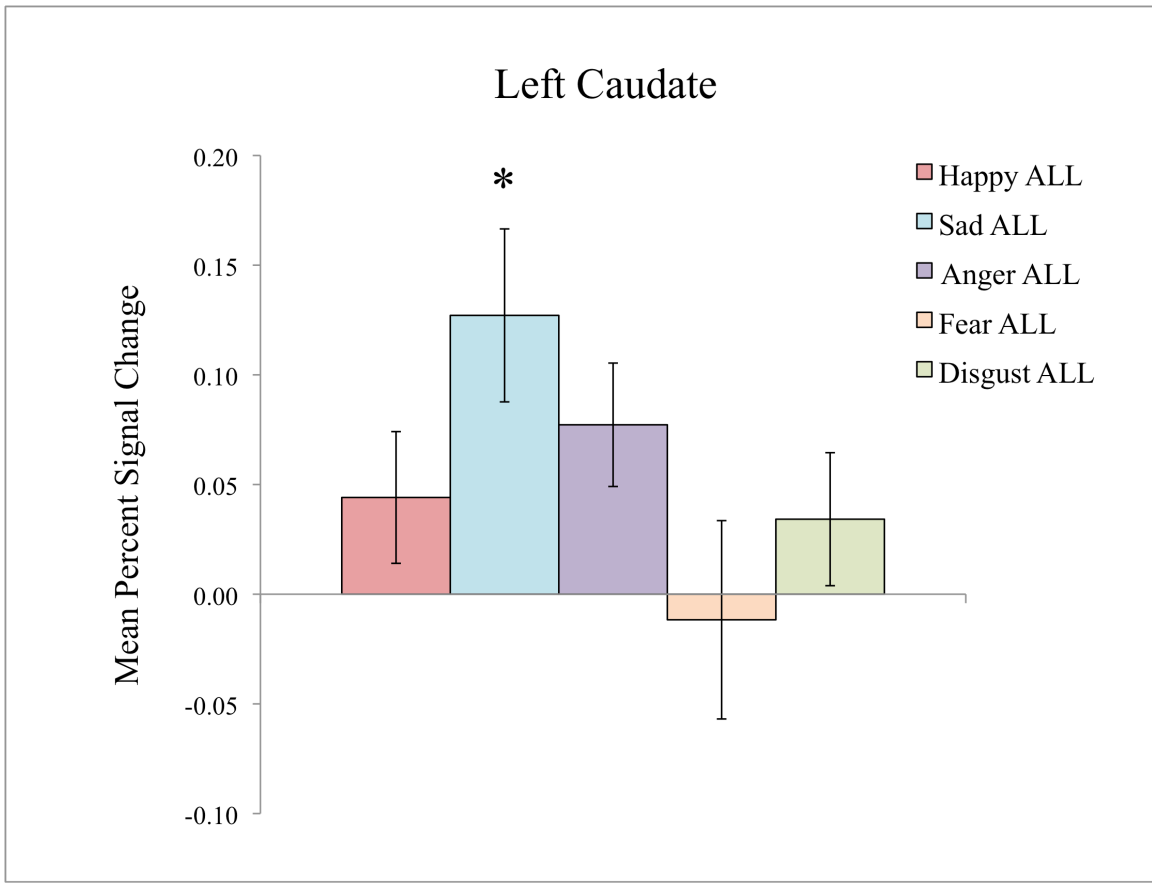
Figure 73. Mean percent signal change in the left caudate during memory recollection



3.4.2.5.5.3 Overall (Films and Memories)

Mean percent signal change in the left caudate was greater during the experience of sadness than during the experience of happiness (trend), fear, and disgust (mean percent signal change did not significantly differ between sadness and anger) (see Table 34 and Figure 74). Again, these data support the hypothesis that sadness-inducing stimuli would engage the caudate to a greater extent than other emotion states.

Figure 74. Mean percent signal change in the left caudate across modalities

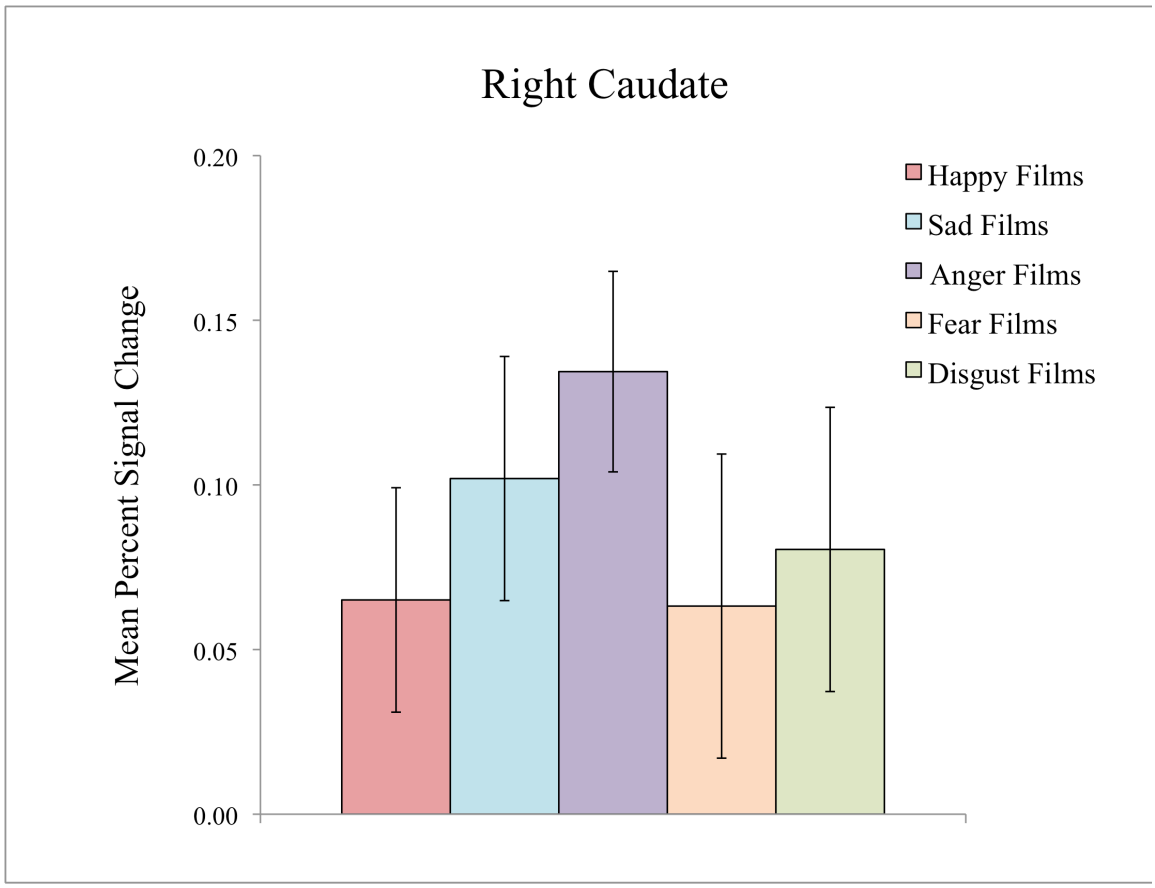


3.4.2.5.6 Right Caudate

3.4.2.5.6.1 Films

Mean percent signal change in the right caudate did not differ between any of the film conditions (see Table 34 and Figure 75). These data do not support the hypothesis that sadness-inducing stimuli would engage the caudate to a greater extent than all other emotion states.

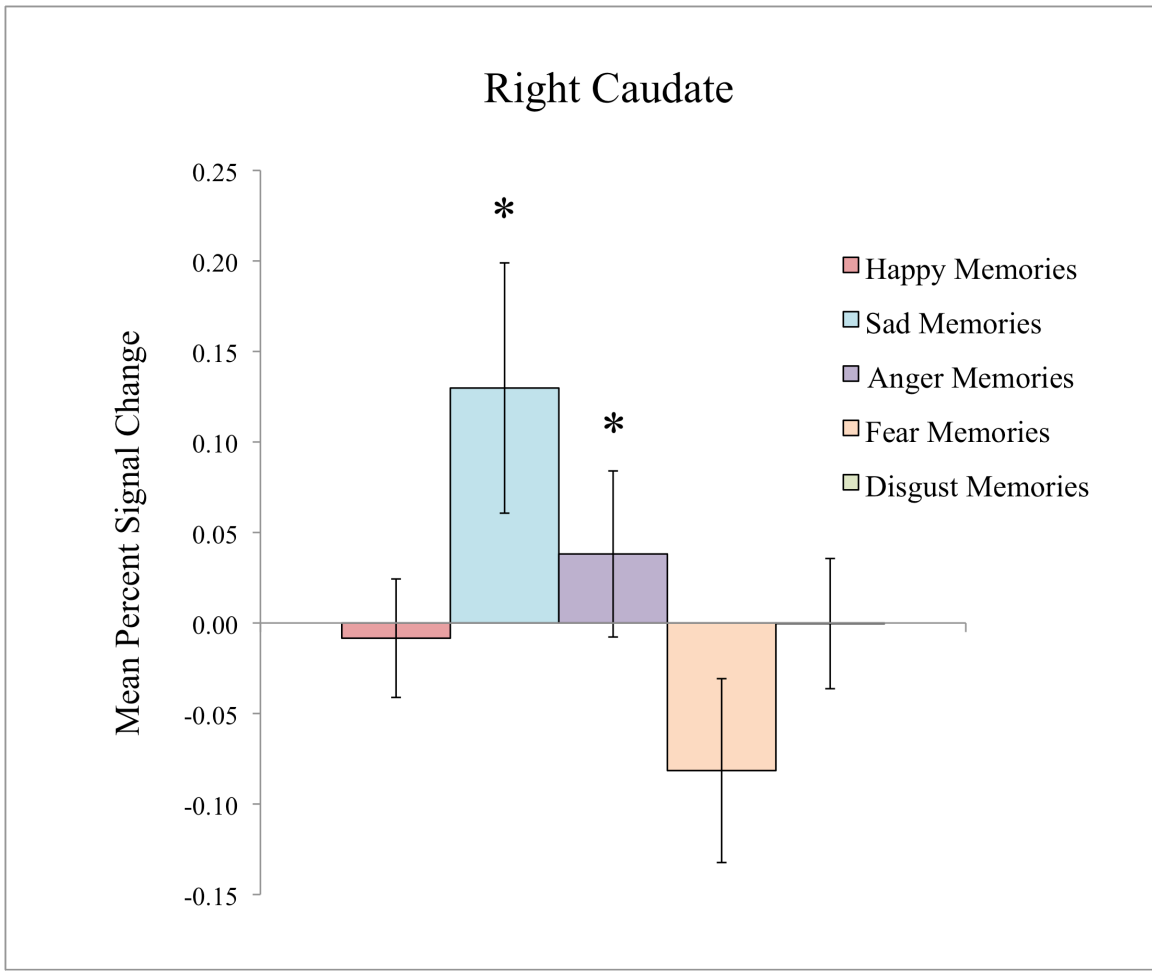
Figure 75. Mean percent signal change in the left anterior cingulate during film viewing



3.4.2.5.6.2 Memories

Similar to the left caudate ROI, mean percent signal change in the right caudate was greater during the recollection of sad and anger memories than during the recollection of fear memories (see Table 34 and Figure 76). These data partially support the hypothesis that sad-inducing stimuli would engage the caudate to a greater extent than all other emotion states.

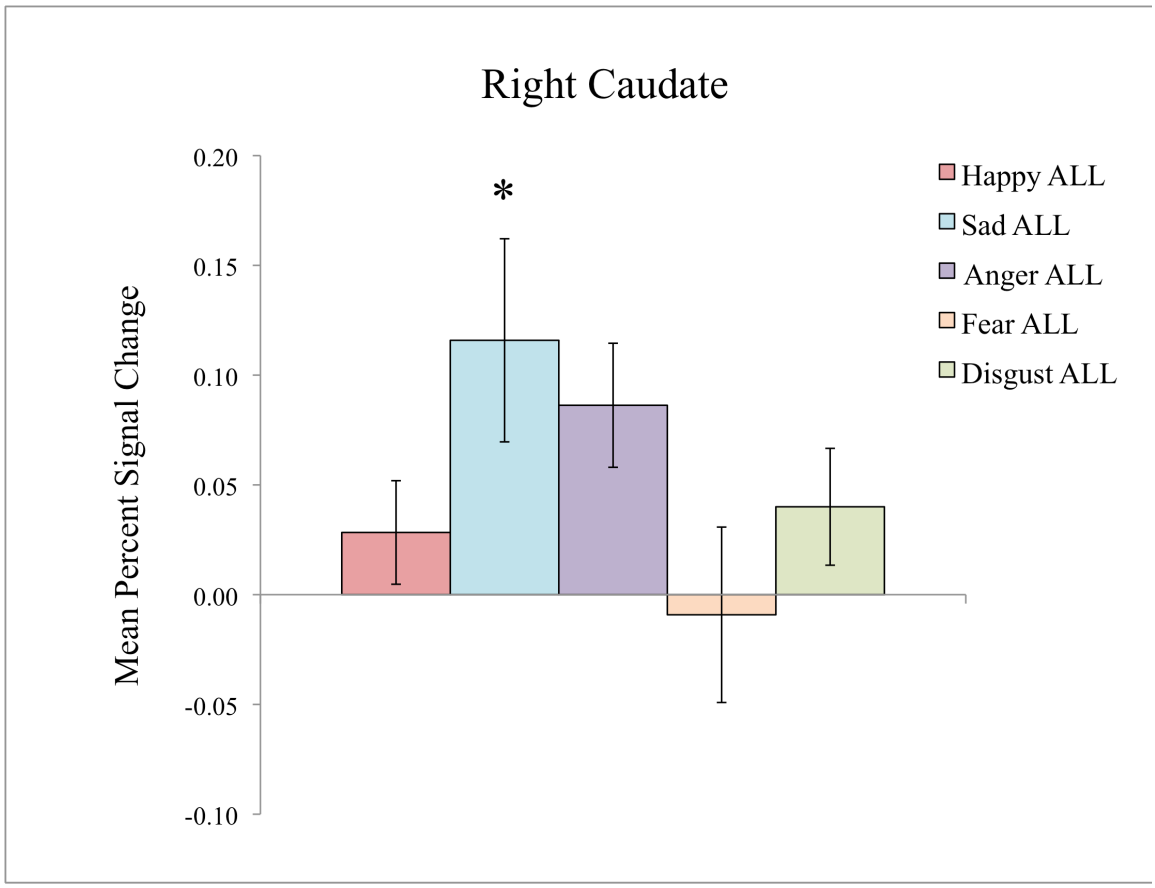
Figure 76. Mean percent signal change in the right caudate during memory recollection



3.4.2.5.6.3 Overall (Films and Memories)

Mean percent signal change in the right caudate was greater during the experience of sadness than during the experience of fear. Differences between sadness and other emotion conditions were not significant, but they were in the expected direction. during any other film condition (see Table 34 and Figure 77). These data partially support the hypothesis that sad-inducing stimuli would engage the caudate to a greater extent than all other emotion states.

Figure 77. Mean percent signal change in the right caudate across modalities

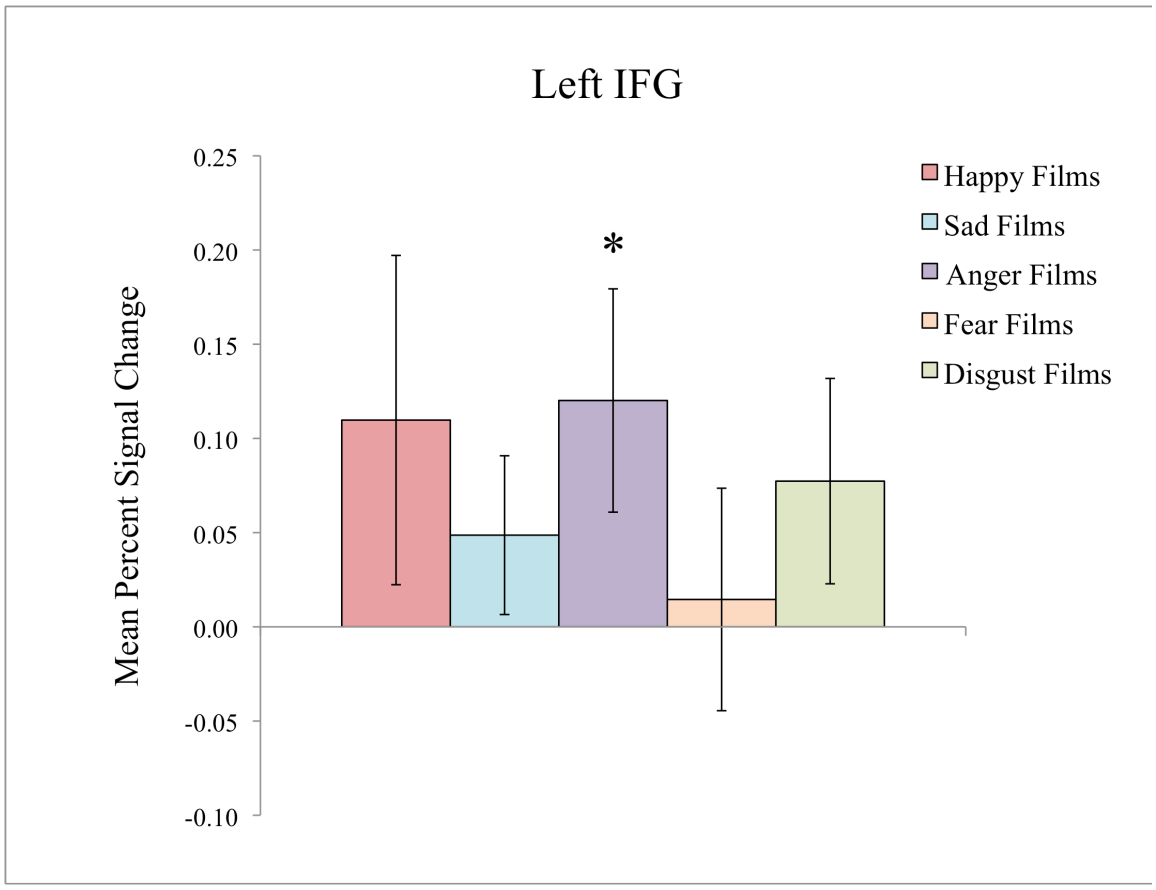


3.4.2.5.7 Left IFG

3.4.2.5.7.1 Films

Mean percent signal change in the right amygdala was greater during anger films than during fear films (see Table 34 and Figure 78). These data are consistent with the hypothesis that anger-inducing stimuli would engage the left IFG to a greater extent than other emotional stimuli.

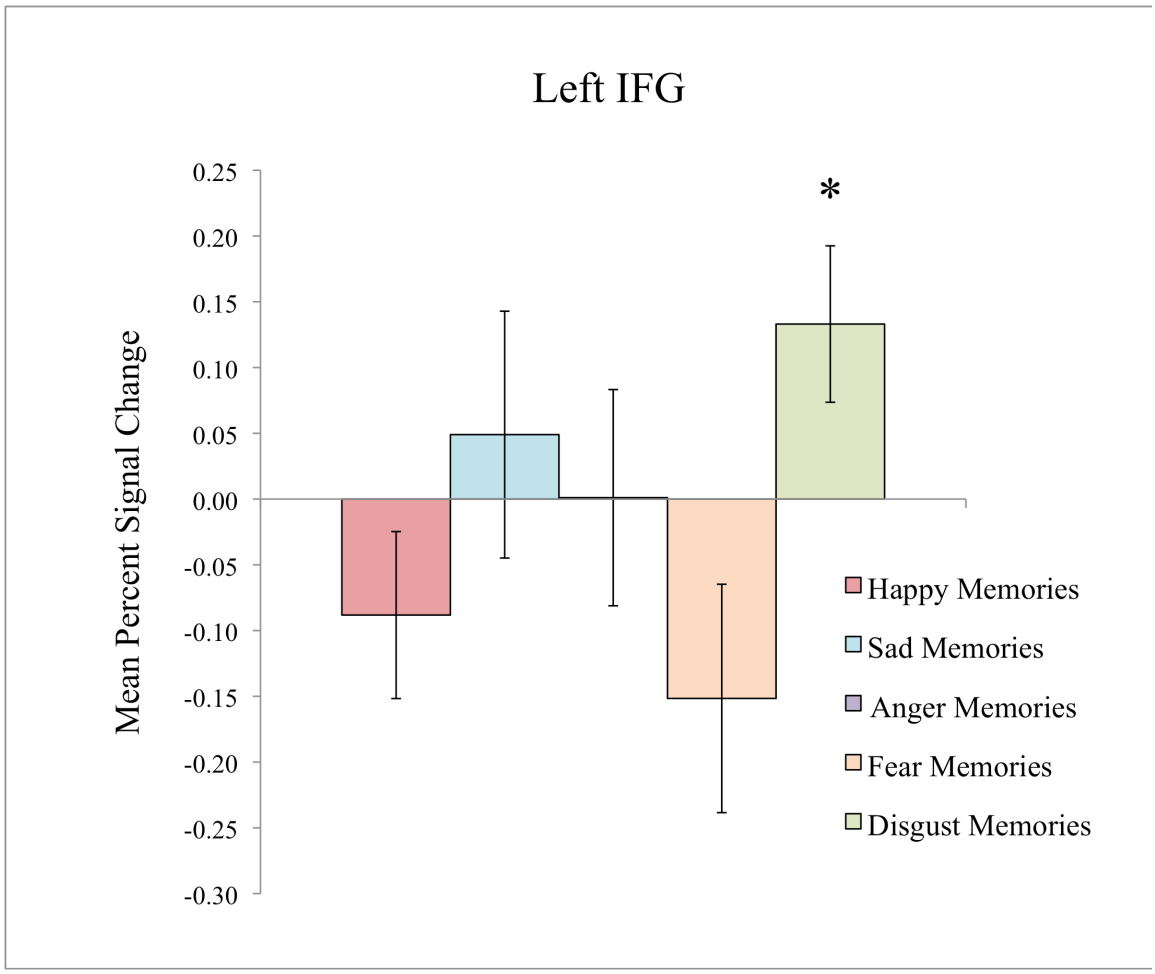
Figure 78. Mean percent signal change in the left inferior frontal gyrus during film viewing



3.4.2.5.7.2 Memories

Mean percent signal change in the left IFG was greater during recollection of disgust memories than during recollection of happy or fear memories, supporting the hypothesis that IFG plays a role in the experience of disgust (see Table 34 and Figure 79). Again, these data do not support the hypothesis that fear-inducing stimuli would engage the amygdala to a greater extent than all other emotion states.

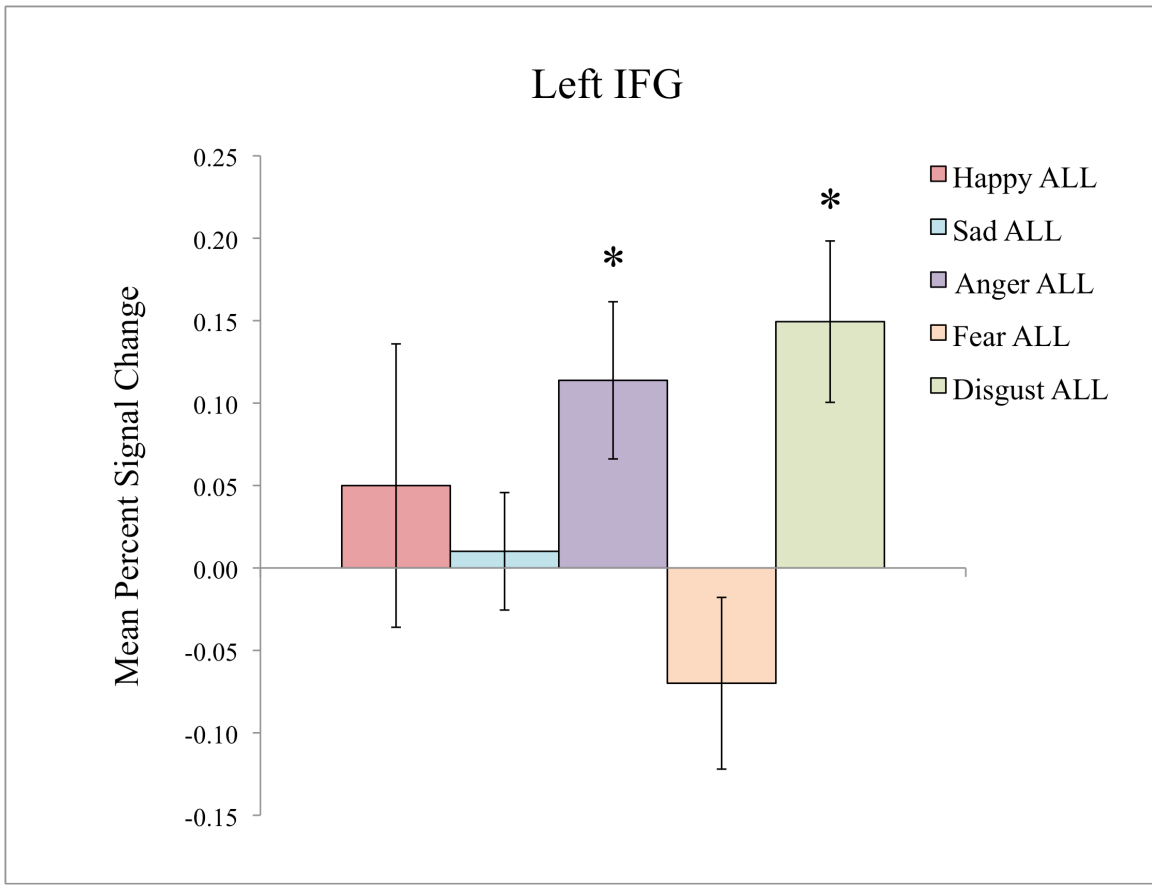
Figure 79. Mean percent signal change in the left inferior frontal gyrus during memory recollection



3.4.2.5.7.3 Overall (Films and Memories)

Mean percent signal change in the left IFG was greater during the experience of anger when compared with fear, and greater during the experience of disgust when compared with fear and sadness (see Table 34 and Figure 80). Mean percent signal change between the experience of disgust and anger did not differ. These results are consistent with our hypotheses and the findings of the Vytal et al. meta-analysis.

Figure 80. Mean percent signal change in the left inferior frontal gyrus across modalities

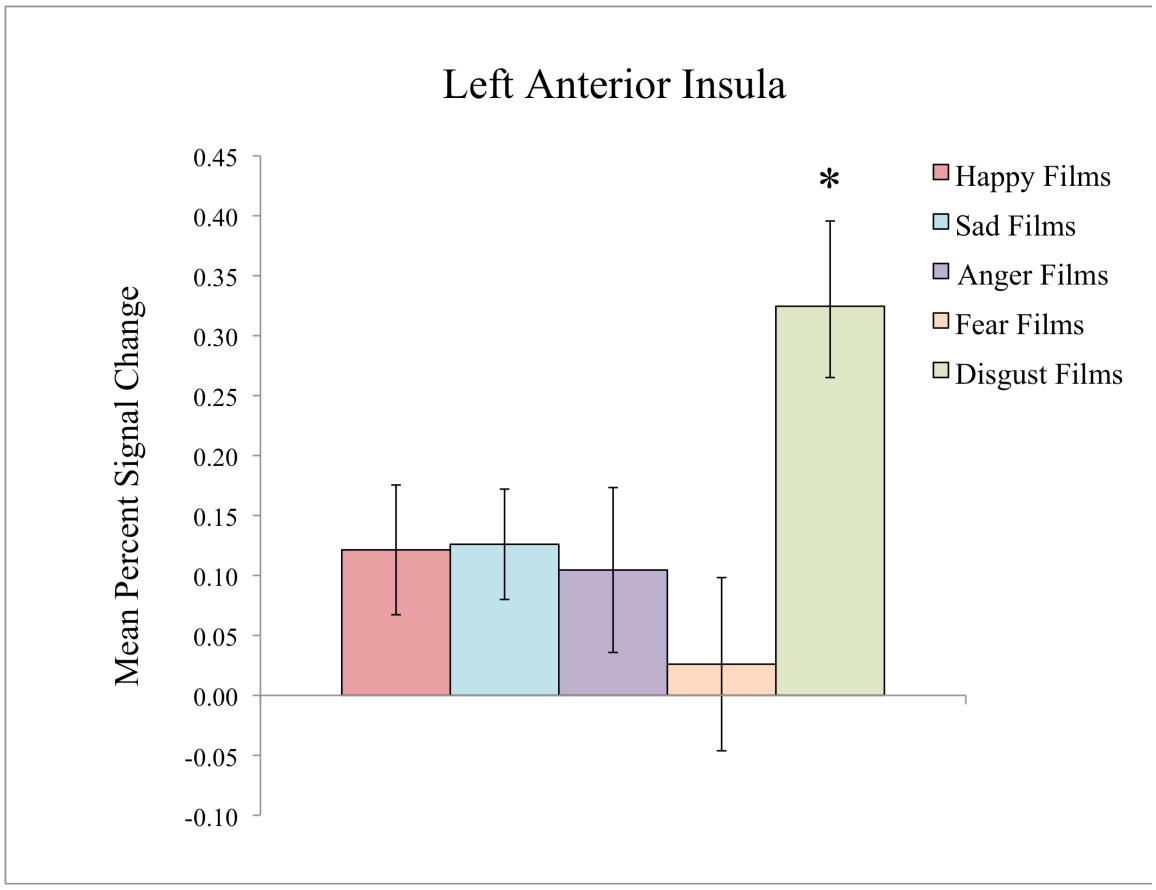


3.4.2.5.8 Left Anterior Insula

3.4.2.5.8.1 Films

Mean percent signal change in the left anterior insula was greater during disgust films than during any other emotional film (see Table 34 and Figure 81). These findings support the hypothesis that disgust-inducing stimuli would engage the anterior insula to a greater extent than all other emotion states.

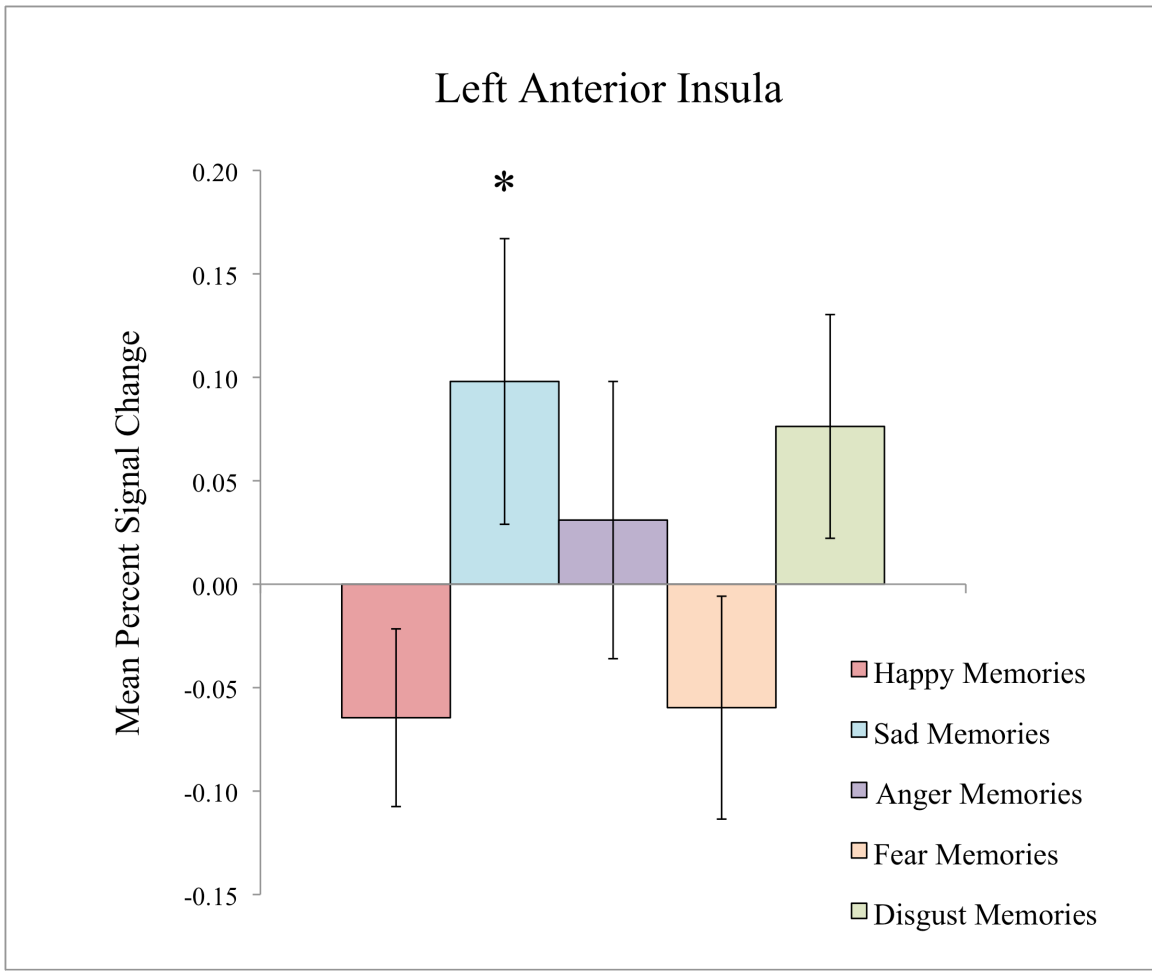
Figure 81. Mean percent signal change in the left anterior insula during film viewing



3.4.2.5.8.2 Memories

Mean percent signal change in the left anterior insula was greater during the recollection of sad memories than during the recollection of happy or fear memories (see Table 34 and Figure 82). These findings do not support the hypothesis that disgust-inducing stimuli engage the anterior insula to a greater extent than all other emotion states.

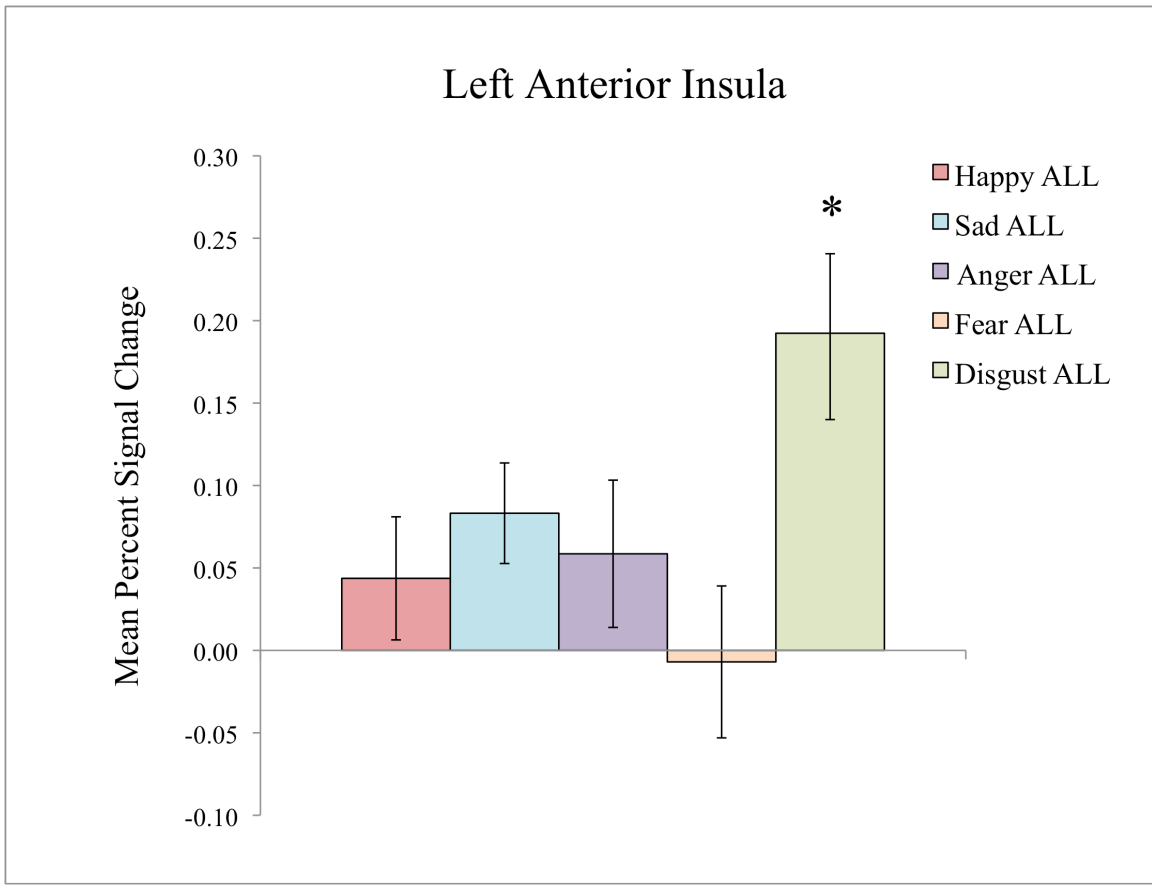
Figure 82. Mean percent signal change in the left anterior insula during memory recollection



3.4.2.5.8.3 Overall (Films and Memories)

Mean percent signal change in the left anterior insula was greater during recollection of disgust memories than during the recollection of any other emotional memory type (see Table 34 and Figure 83). These findings support the hypothesis that disgust-inducing stimuli engage the anterior insula to a greater extent than all other emotion states.

Figure 83. Mean percent signal change in the left anterior insula across modalities

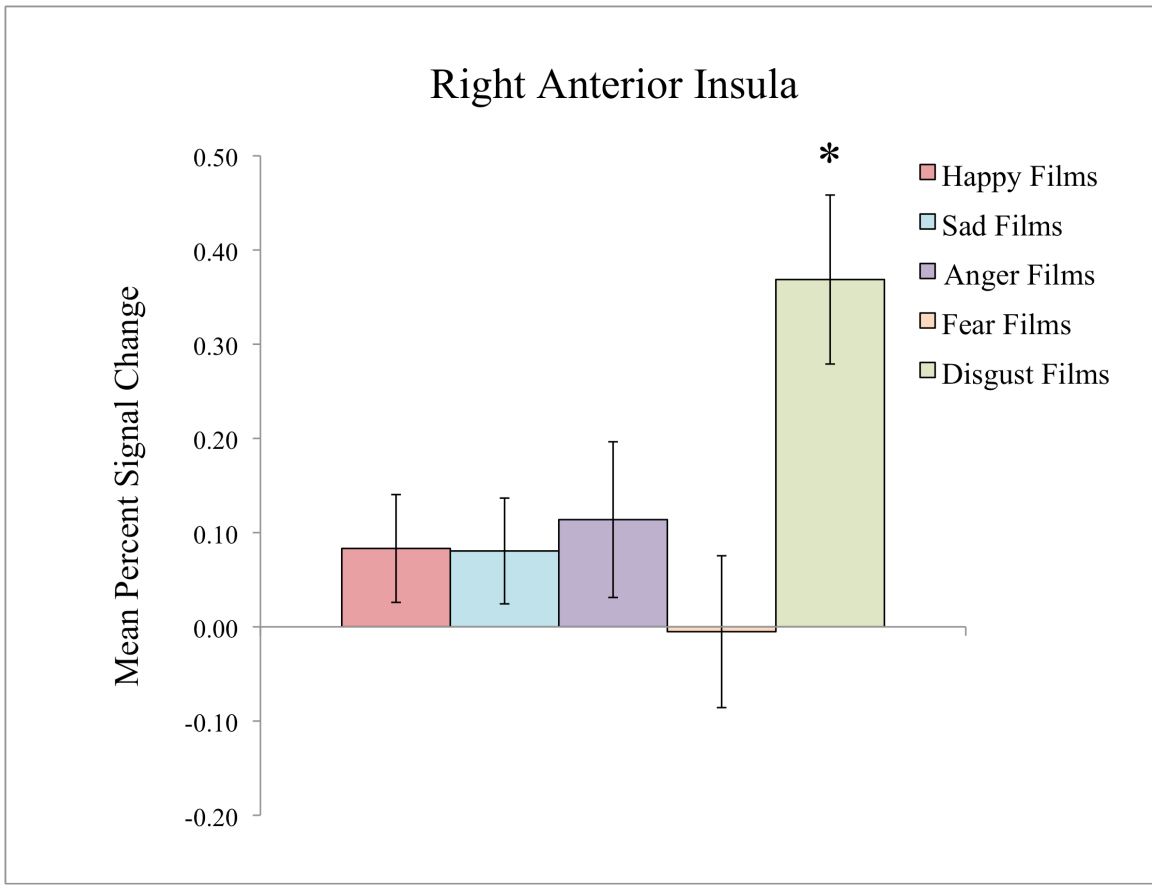


3.4.2.5.9 Right Anterior Insula

3.4.2.5.9.1 Films

Mean percent signal change in the right anterior insula was greater during disgust films than during any other film condition (see Table 34 and Figure 84). Again, these findings support the hypothesis that disgust-inducing stimuli engage the anterior insula to a greater extent than all other emotion states.

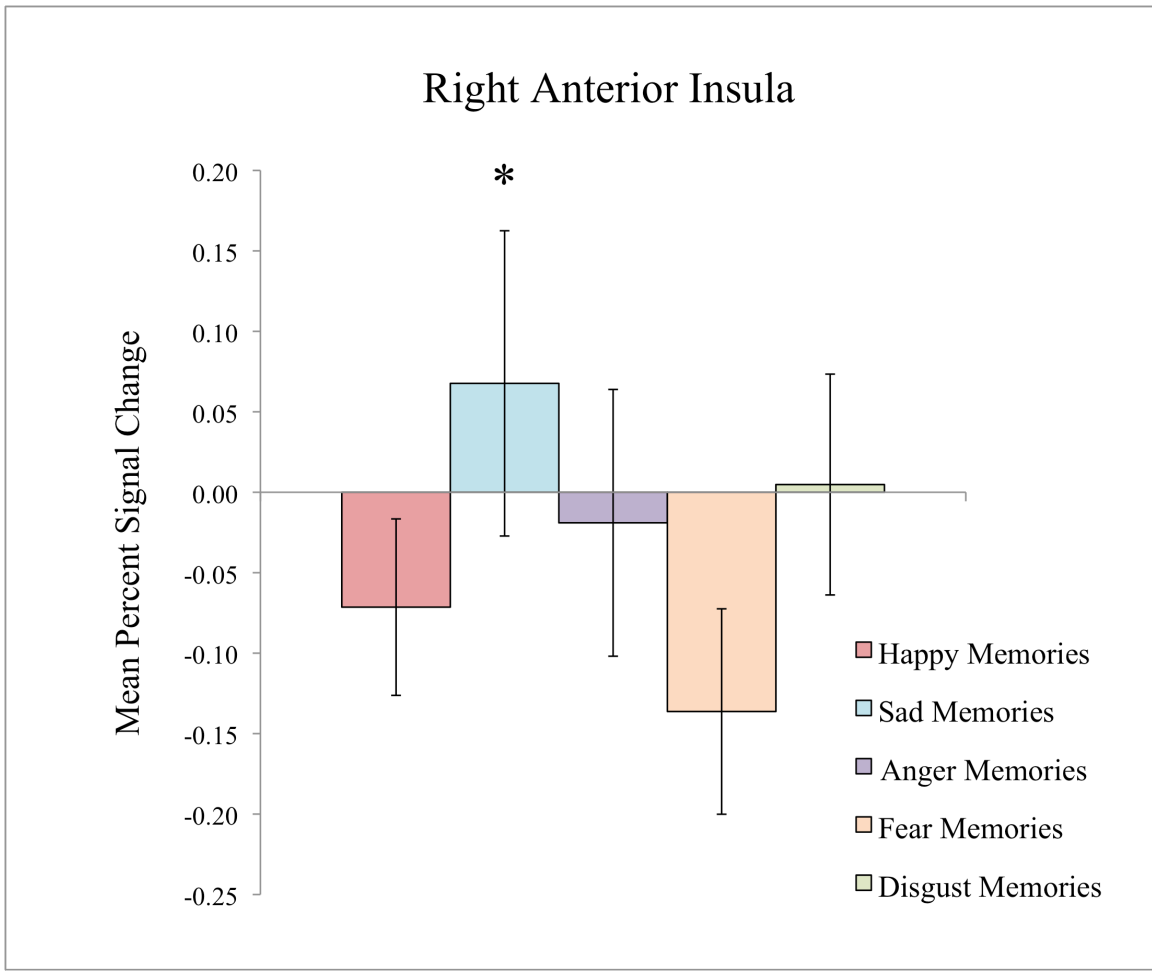
Figure 84. Mean percent signal change in the right anterior insula during film viewing



3.4.2.5.9.2 Memories

Similar to the left anterior insula ROI, mean percent signal change in the right anterior insula was greater during the recollection of sad memories than during the recollection of fear memories (see Table 34 and Figure 85). These findings do not support the hypothesis that disgust-inducing stimuli uniquely engage the anterior insula.

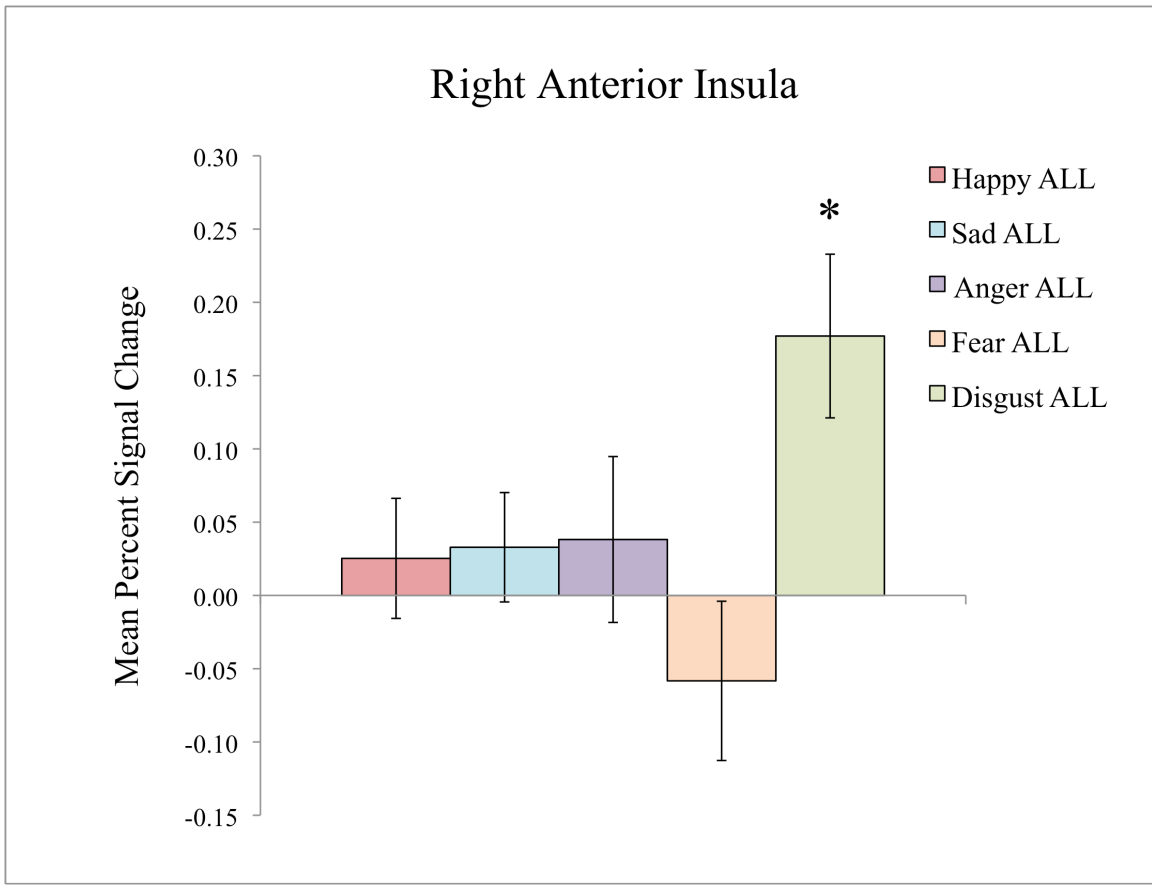
Figure 85. Mean percent signal change in the right anterior insula during memory recollection



3.4.2.5.9.3 Overall (Films and Memories)

Mean percent signal change in the right anterior insula was greater during the experience of disgust than during the experience of any other emotion state (see Table 34 and Figure 86). Again, these findings support the hypothesis that disgust-inducing stimuli engage the anterior insula to a greater extent than all other emotion states.

Figure 86. Mean percent signal change in the right anterior insula across modalities

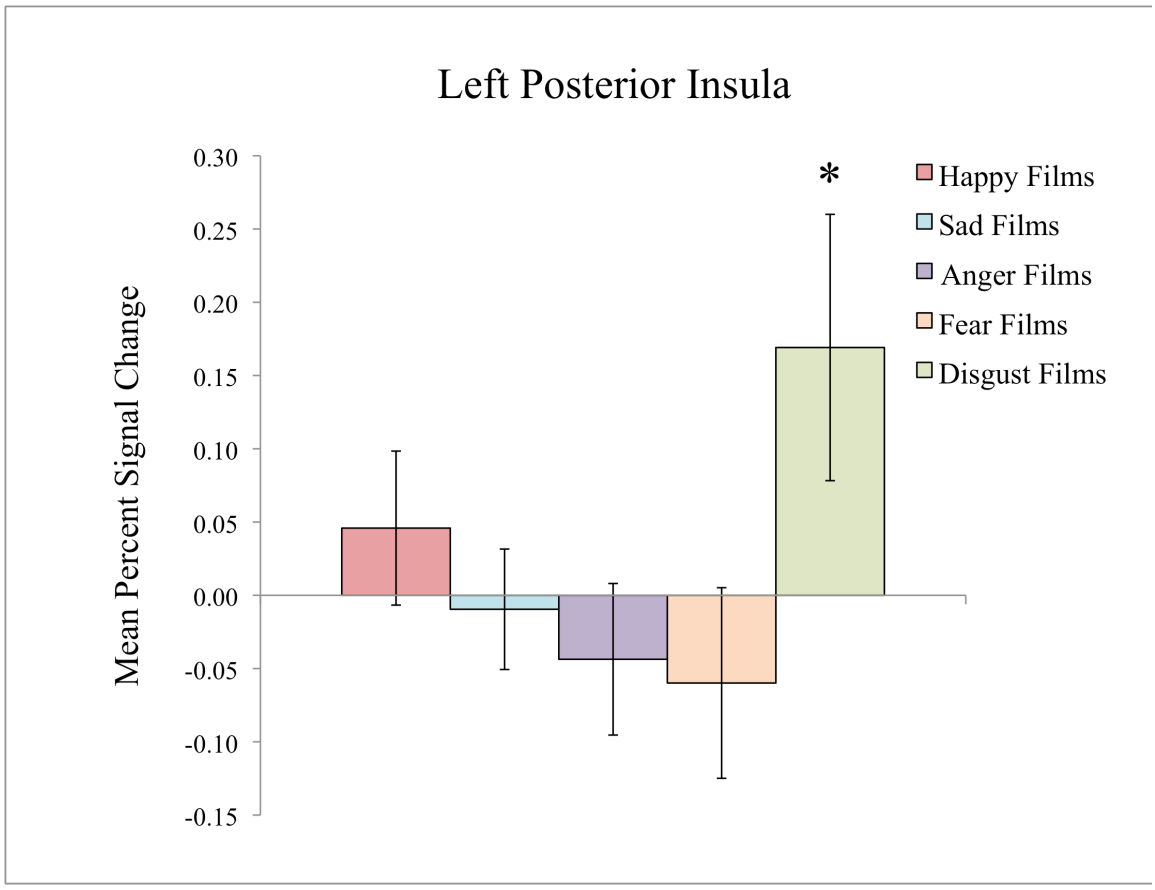


3.4.2.5.10 Left Posterior Insula

3.4.2.5.10.1 Films

Mean percent signal change in the left posterior insula was greater during disgust films than during sad, anger, or fear films (see Table 34 and Figure 87). These findings are consistent with the hypothesis that disgust-inducing stimuli engage the insula to a greater extent than all other emotion states. However, they are not consistent with the prediction that fear-inducing stimuli would engage posterior insula to a greater extent than other emotion states.

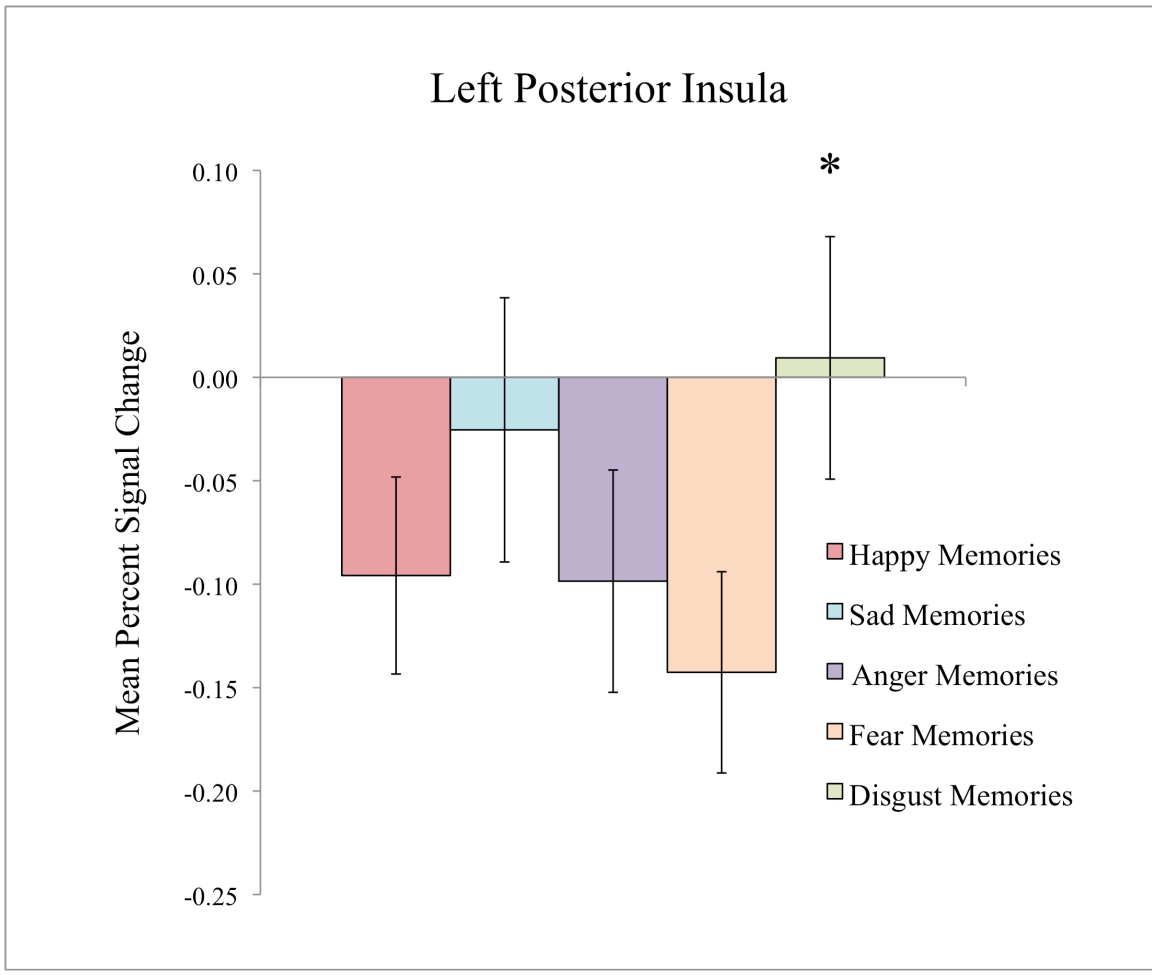
Figure 87. Mean percent signal change in the left posterior insula during film viewing



3.4.2.5.10.2Memories

Mean percent signal change in the left posterior insula was greater during the recollection of disgust memories than during the recollection of fear memories (see Table 34 and Figure 88). These findings are partially consistent with the hypothesis that disgust-inducing stimuli engage the insula to a greater extent than other emotion states. However, they are not consistent with the prediction that fear-inducing stimuli would engage posterior insula to a greater extent than other emotion states.

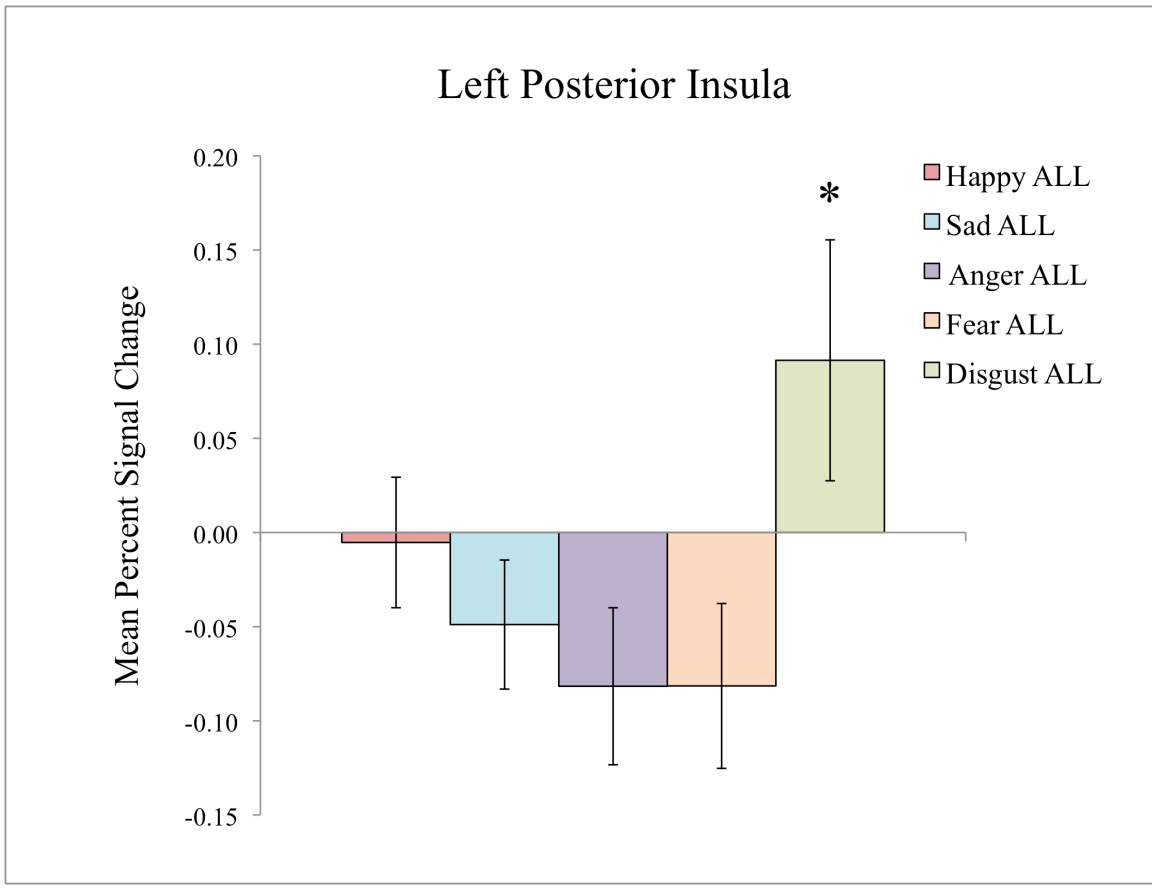
Figure 88. Mean percent signal change in the left posterior insula during memory recollection



3.4.2.5.10.3Overall (Films and Memories)

Mean percent signal change in the left posterior insula was greater during the experience of disgust than during the experience of sadness, anger, and fear (see Table 34 and Figure 89). These findings are consistent with the hypothesis that disgust-inducing stimuli engage the insula to a greater extent than all other emotion states. However, they are not consistent with the prediction that fear-inducing stimuli would engage posterior insula to a greater extent than other emotion states.

Figure 89. Mean percent signal change in the left posterior insula across modalities

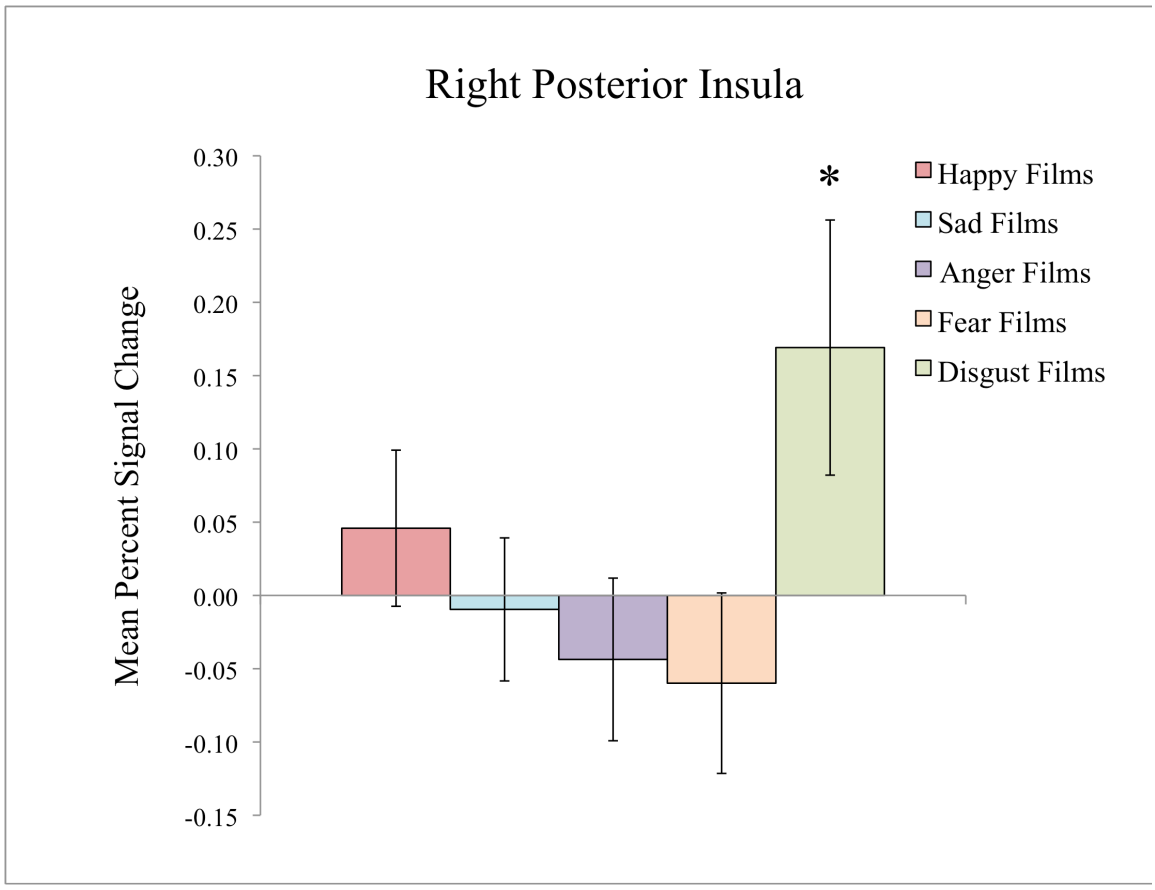


3.4.2.5.11 Right Posterior Insula

3.4.2.5.11.1Films

Mean percent signal change in the right posterior insula was significantly greater during disgust films than during any other emotional film condition (see Table 34 and Figure 90). These findings are consistent with the hypothesis that disgust-inducing stimuli engage the insula to a greater extent than all other emotion states. However, they are not consistent with the prediction that fear-inducing stimuli would engage posterior insula to a greater extent than other emotion states.

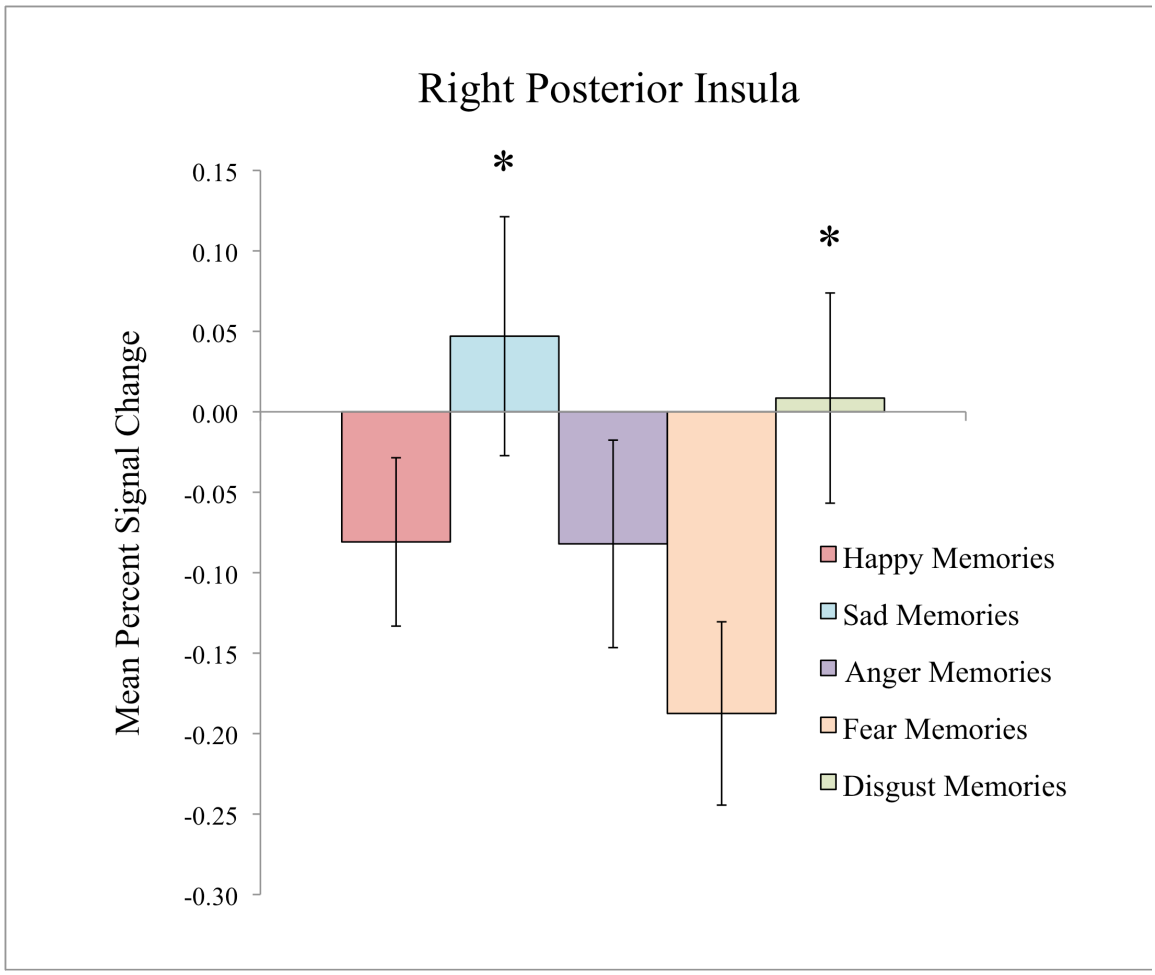
Figure 90. Mean percent signal change in the right posterior insula during film viewing



3.4.2.5.11.2Memories

Mean percent signal change in the right posterior insula was greater during the recollection of sad memories and disgust memories than fear memories (see Table 34 and Figure 91). These findings are partially consistent with the hypothesis that disgust-inducing stimuli engage the insula, but are they consistent with the hypothesis that fear-inducing stimuli specifically engage the posterior insula.

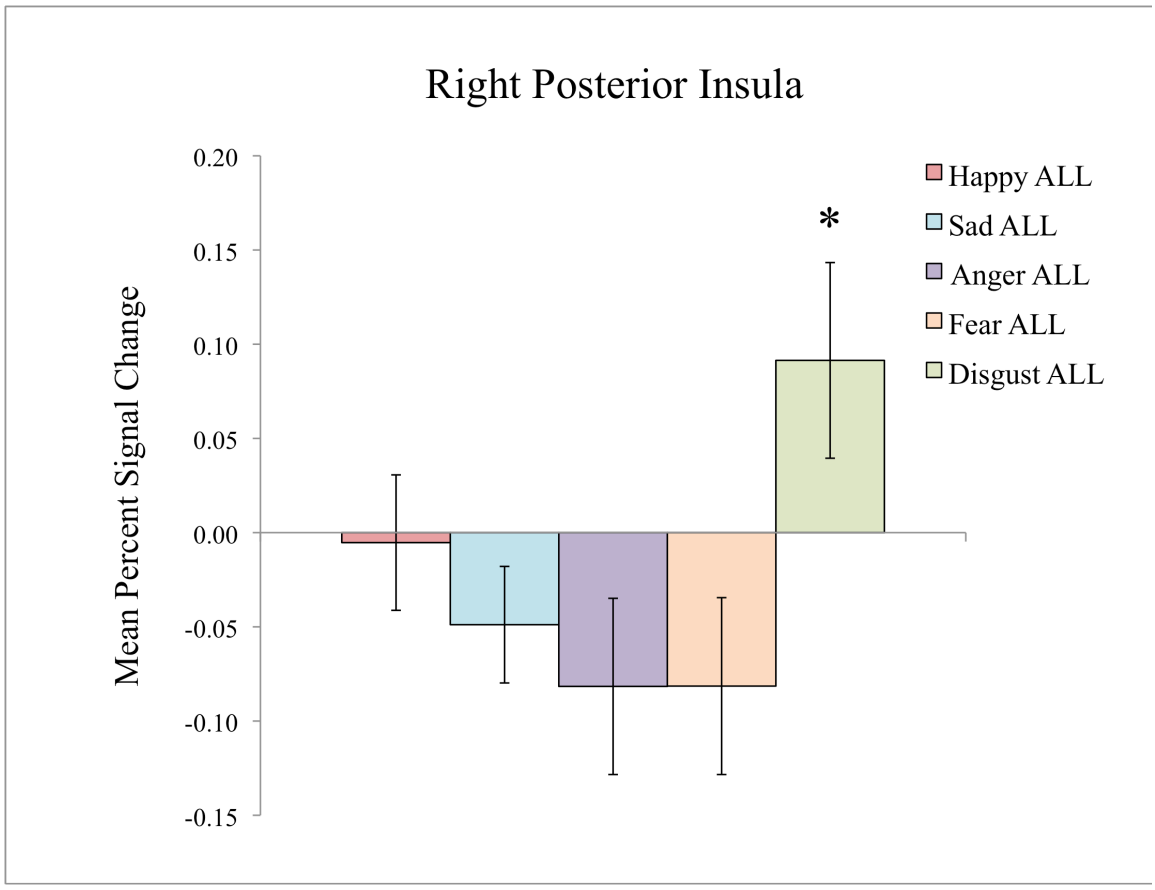
Figure 91. Mean percent signal change in the right posterior insula during memory recollection



3.4.2.5.11.3Overall (Films and Memories)

Mean percent signal change in the right posterior insula was greater during the experience of disgust than during the experience of any other emotional state (see Table 34 and Figure 92). These findings are consistent with the hypothesis that disgust-inducing stimuli engage the anterior insula to a greater extent than all other emotion states. However, they are not consistent with the hypothesis that fear-inducing stimuli specifically engage the posterior insula.

Figure 92. Mean percent signal change in the right posterior insula across modalities



3.4.2.5.12 Modality-specific activations (regions that are uniquely activated by emotional films versus emotional memories, both within and across emotion states)

Although the primary goal of the study was to investigate the core emotional responses associated with basic emotion states, we were also interested in investigating the effect of elicitation method on these neural representations. Pairwise contrasts were calculated between modalities (films and memories) within each emotion state and across all emotion states together. The following results present activations specific to emotion elicitation via film and via memory, respectively.

3.4.2.5.12.1 Films > Memories

3.4.2.5.12.1.1 Emotional Films > Emotional Memories

The comparison of emotional films to emotional memories revealed visual activations in occipital cortex, emotion-related activations in the amygdala (see Figure 93), thalamus, insula, and basal ganglia, as well as activations in fusiform gyrus (see Table 36 for all coordinates associated with the pairwise comparisons between memories and films).

Table 36. Whole brain activations associated with emotion elicitation via films

		Coordinate (MNI)				
Region	*HEM*	*x*	*y*	*z*	*k* (volume)	*Z*
FILMS – MEMORIES						
Emotional Films (ALL) > Emotional Memories (ALL)						
Mid. Occipital G.	L	-48	-73	7	5449	5.07
Fusiform G.	L	-45	-67	-8	LM	5.04
Fusiform G.	L	-33	-67	-11	LM	4.99
Inf. Frontal G.	R	42	11	31	270	4.64
Mid. Frontal G.	R	33	8	34	LM	4.50
Mid. Frontal G.	R	39	23	34	LM	3.35
Midbrain	L	-6	-25	-8	409	4.26
Midbrain/Thalamus	L	-6	-7	-8	LM	4.12
Thalamus	R	18	-7	10	LM	3.85
Sup. Temporal G.	L	-57	-25	7	191	3.92
Sup. Temporal G./Insula	L	-66	-31	16	LM	3.84
Sup. Temporal G.	L	-66	-28	7	LM	3.59
Mid. Frontal G.	R	33	11	58	85	3.71
Inf. Frontal G./Insula	R	48	29	-5	64	3.71
Globus Pallidus/Amygdala	R	21	-4	-11	53	3.52
Amygdala	R	33	-4	-14	LM	3.33
Amygdala	R	30	-13	-8	LM	3.18
Mid. Frontal g.	L	-24	14	49	24	3.44
Inf. Frontal G	L	-48	11	31	18	3.38
Inf. Frontal G.	L	-36	11	28	LM	3.29
Sup. Frontal G.	R	3	38	52	11	3.38
Putamen/Insula	L	-27	11	-5	8	3.37
Putamen/Caudate	L	-18	11	4	16	3.28
Thalamus	L	-15	-1	10	LM	3.14
Happy Films > Happy Memories						
Mid. Occipital G.	L	-45	-76	13	3699	5.17
Mid. Temporal G.	R	42	-58	4	LM	4.91
Pos. Cingulate	R	24	-61	10	LM	4.80
Thalamus	L	-12	-13	-2	145	4.69
Putamen	L	-18	-4	7	LM	3.95
Thalamus	R	3	-25	-2	LM	3.73
Mid. Frontal G.	R	33	14	49	83	4.28
Mid. Frontal G.	R	36	8	58	LM	3.70
Mid. Frontal G.	R	36	23	46	LM	3.51
Ant. Insula	R	51	2	-8	562	4.19
Sup. Temporal G.	R	66	-13	7	LM	4.15
Sup. Temporal G./Insula	R	42	-31	13	LM	4.04
Insula	L	-33	23	13	29	4.07
Mid. Frontal G.	L	-30	35	16	LM	3.41

Mid. Frontal G.	L	-33	44	19	LM	3.33
Sup. Temporal G./Insula	L	-48	-25	10	158	3.92
Sup. Temporal G.	L	-57	-7	7	LM	3.51
Pos. Insula	L	-45	-4	-5	LM	3.45
Mid. Frontal G.	R	45	38	10	20	3.64
Mid. Frontal G.	R	48	44	19	LM	3.55
Pons	L	-9	-22	-26	8	3.62
Precentral G.	R	54	2	40	10	3.57
Mid. Frontal G.	L	-51	29	25	10	3.56
Cerebellum	L	-3	-70	-32	6	3.54
Mid. Frontal G.	R	33	23	31	6	3.51
Pons	L	-6	-34	-35	10	3.45
Precuneus	R	21	-64	49	6	3.39
Caudate Body	L	-18	20	4	11	3.32

Sad Films > Sad Memories

Fusiform G.	R	42	-52	-14	42	3.98
Parahippocampal G.	R	39	-58	-2	LM	3.70
Cerebellum	R	3	-64	4	12	3.65
Precuneus	R	27	-55	52	6	3.52
Mid. Occipital G.	L	-39	-73	10	17	3.43

Anger Films > Anger Memories

Fusiform G.	L	-39	-46	-17	213	5.00
Amygdala	L	-24	-4	-26	LM	4.32
Parahippocampal G.	L	-36	-34	-20	LM	4.15
Mid. Temporal G.	R	57	-34	-10	1430	4.96
Sup. Temporal G.	R	63	-10	-5	LM	4.95
Sup. Temporal G./Insula	R	54	-28	1	LM	4.94
Mid. Temporal G.	L	-57	-52	10	1735	4.76
Mid. Temporal G.	L	-63	-55	1	LM	4.72
Inf. Temporal G.	L	-51	-40	4	LM	4.66
Sup. Frontal G.	R	21	29	49	481	4.63
Med. Frontal G.	R	12	53	34	LM	4.14
Sup. Frontal G.	R	9	47	46	LM	3.81
Inf. Frontal G.	R	54	35	7	258	4.38
Inf. Frontal G.	R	48	29	16	LM	4.27
Ant. Cingulate	R	6	20	16	LM	4.07
Fusiform G.	R	39	-46	-20	100	4.28
Fusiform G.	R	42	-61	-11	LM	3.53
Precuneus	R	3	-67	25	299	4.14
Posterior Cingulate	R	6	-58	19	LM	3.89
Cerebellum/Lingual G.	R	9	-52	4	LM	3.82
Inf. Frontal G.	L	-57	23	10	9	3.91
Midbrain/Thalamus	L	-12	-28	-5	48	3.63
Parahippocampal G.	L	-9	-40	1	LM	3.14
Pos. Cingulate	L	-15	-58	13	23	3.49
Lingual G.	L	-12	-61	4	LM	3.17

Parahippocampal G.	L	-42	-67	-23	9	3.35
Cerebellum	R	24	-70	-29	24	3.33
Cerebellum	R	21	-64	-14	LM	3.24
Fusiform G.	L	-30	-73	-17	10	3.33
Cuneus	L	0	-79	19	11	3.29
Fear Films > Fear Memories						
Thalamus	L	-6	-19	22	102	4.70
Pos. Cingulate	R	12	-25	22	LM	4.67
Thalamus	L	0	-28	19	LM	4.35
Disgust Films > Disgust Memories						
Fusiform G.	L	-45	-64	-5	261	4.62
Cerebellum	L	-3	-70	-8	LM	3.86
Fusiform G.	L	-39	-49	-17	LM	3.66
Mid. Temporal G.	R	51	-52	-2	159	4.61
Fusiform G.	R	36	-64	-11	LM	3.96
Precuneus	R	30	-55	46	394	4.55
Precuneus	R	30	-67	34	LM	4.42
Precuneus	R	18	-58	49	LM	4.42
Sup. Parietal Lobule	L	-27	-64	55	271	4.17
Inf. Parietal Lobule	L	-30	-55	52	LM	4.13
Inf. Parietal Lobule	L	-39	-43	58	LM	3.93
Postcentral G./Insula	R	60	-19	25	144	4.14
Inf. Frontal G./Insula	R	42	8	28	115	3.96
Inf. Frontal G.	R	48	14	19	LM	3.58
Ant. Insula	R	36	11	19	LM	3.45
Cerebellum	R	0	-73	-2	24	3.57
Precentral G.	L	-21	-10	52	13	3.56
Mid. Frontal G.	R	36	2	52	18	3.51
Pos. Insula	R	48	2	-8	33	3.35
Pos. Insula	R	35	-1	-14	LM	3.35
Pos. Insula	R	39	-7	-8	LM	3.12
Mid. Temporal G.	R	48	-55	10	7	3.34
Postcentral G./Insula	L	-60	-25	22	11	3.24
Lingual G.	R	33	-76	7	5	3.23
Lingual G.	R	27	-82	10	LM	3.21
Globus Pallidus	R	24	-7	-11	11	3.23

Figure 93. Emotional Films > Emotional Memories

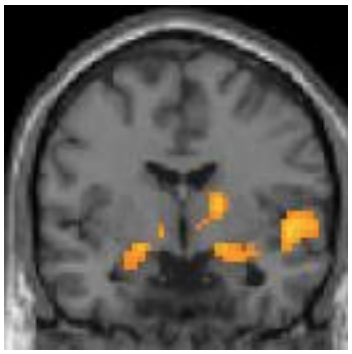


Figure Caption

Activation in bilateral amygdala and right insula associated with emotional films but not emotional memories. $p < 0.001$, uncorrected.

3.4.2.5.12.1.2 Happy Films > Happy Memories

When compared to happy memories, happy films were associated with activity in bilateral STG/insula, bilateral insula, posterior cingulate, precuneus, basal ganglia, and thalamus (see Table 36 for a full list of activation coordinates and associated statistics)

3.4.2.5.12.1.3 Sad Films > Sad Memories

When compared to sad memories, sad films were associated with activity in fusiform gyrus, PHG, precuneus, and middle occipital gyrus (see Table 36 for a full list of activation coordinates and associated statistics)

3.4.2.5.12.1.4 Anger Films > Anger Memories

When compared to anger memories, anger films were associated with activity in the amygdala, PHG, precuneus, insula, midbrain/thalamus, ACC, MTG, and STG (see Table 36 for a full list of activation coordinates and associated statistics)

3.4.2.5.12.1.5 Fear Films > Fear Memories

When compared to fear memories, fear films were associated with activity in the thalamus and posterior cingulate (see Table 36 for a full list of activation coordinates and associated statistics)

3.4.2.5.12.1.6 Disgust Films > Disgust Memories

When compared to disgust memories, disgust films were associated with activity in the bilateral insula, precuneus, fusiform gyrus, MTG, and basal ganglia (see Table 36 for a full list of activation coordinates and associated statistics)

3.4.2.5.12.2Films > Memories

3.4.2.5.12.2.1 Emotional Memories > Emotional Films

The comparison of emotional films and emotional memories revealed robust emotion-related activations in the caudate (head, body and tail), as well as activations in the thalamus, PHG, and medFG (potentially reflecting self-referential thought during cued autobiographical memory recall; Mitchell et al., 2007) (see Table 37 for a full list of activation coordinates and associated statistics, see Figure 94 for medFG activation).

Table 37. Whole brain activations associated with emotion elicitation via autobiographical memories

		Coordinate (MNI)				
Region	*HEM*	*x*	*y*	*z*	*k* (volume)	*Z*
MEMORIES - FILMS						
Emotional Memories (ALL) > Emotional Films (ALL)						
Thalamus	R	15	-34	19	80	4.26
Caudate Tail	R	27	-40	13	LM	3.61
Caudate Body	L	-9	-16	25	201	4.02
Caudate Tail	L	-15	-37	19	LM	3.95
Parahippocampal G.	L	-27	-49	13	LM	3.90
Caudate Head	R	12	29	-5	10	3.79
Med. Frontal G.	R	24	41	4	5	3.60
Caudate Body	L	-18	14	22	6	3.40
Happy Memories > Happy Films						
Pos. Cingulate	L	-24	-49	16	8	3.75
Sad Memories > Sad Films						
Caudate Head	L	-9	23	-2	5	3.30
Anger Memories > Anger Films						
Cingulate G./ACC	L	-6	19	22	102	4.70
Pos. Cingulate	R	12	-25	22	LM	4.67
Pos. Cingulate	L	0	-28	19	LM	4.35
Fear Memories > Fear Films						
Cingulate G.	R	18	-31	25	5	3.18
Disgust Memories > Disgust Films						
Caudate Tail	R	30	-40	13	64	4.26
Caudate Tail	R	18	-25	25	LM	3.72
Thalamus	R	24	-34	19	LM	3.68
Pos. Cingulate	L	-21	-46	16	52	3.82
Caudate Tail	L	-15	-34	22	LM	3.28
Caudate Body/Head	L	-9	26	1	13	3.78

Figure 94. Emotional Memories > Emotional Films

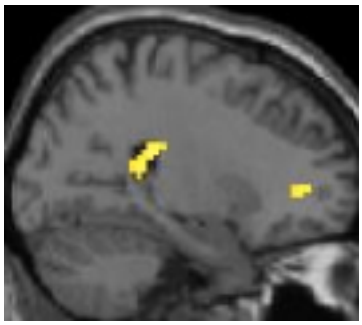


Figure Caption

Activation in the right medial frontal gyrus associated with emotional memories but not emotional films. $p < 0.001$, uncorrected.

3.4.2.5.12.2.2 Happy Memories > Happy Films

When compared to happy films, happy memories were associated with activity in the posterior cingulate (see Table 37 for associated statistics).

3.4.2.5.12.2.3 Sad Memories > Sad Films

When compared to sad films, sad memories were associated with activity in the left caudate head (see Table 37 for associated statistics).

3.4.2.5.12.2.4 Anger Memories > Anger Films

When compared to anger films, anger memories were associated with activity across different subsections of the cingulate gyrus (posterior, central, and anterior) (see Table 37 for a full list of activation coordinates and associated statistics).

3.4.2.5.12.2.5 Fear Memories > Fear Films

When compared to fear films, fear memories were associated with activity in the cingulate gyrus (see Table 37 for associated statistics).

3.4.2.5.12.2.6 Disgust Memories > Disgust Films

When compared to sad films, sad memories were associated with multiple activations within the caudate (head, body, and tail), as well as activity in the posterior cingulate and thalamus (see Table 37 for a full list of activation coordinates and associated statistics).

3.4.2.5.13 Individual differences in personality and mood

Individual differences in personality and mood were used to predict activity in the left and right amygdala (anatomically-defined ROIs, see methods section for additional details) during the experience of different basic emotions. Mean, SD, and range of scores for each of the questionnaires are listed in Table 38. Correlations between the measures are listed in the same table. As expected, there was a large negative correlation observed between the neuroticism and extraversion factors of the NEO-FFI, and a large positive correlation between state and trait anxiety. Large positive correlations were also observed between state anxiety and openness to experience, and positive and negative affect. Both of these findings seem counter-intuitive; yet it is possible that the first finding reflects subjects who are currently in an anxious state, but who perhaps typically enjoy being adventurous and trying new things, and may even seek out anxiety-evoking activities. However, previous research has found large negative correlations with between openness and harmavoidance (N = 1015; Tellegen & Waller, 2008), suggesting that our sample may be different than the general population regarding how they interpret the items related to openness to experience and avoidance of risky situations. We may have sampled a group of individuals who are open to experience but acutely aware of the risks associated with them. The second finding may be the result of selecting subjects that are highly emotionally aware and reactive, which would be reflected on both the positive and negative affect scales. We recruited subjects who were interested in sharing their emotional experiences with us and capable of producing many emotional memories form

their past. Therefore our sample is necessarily composed of individuals who are attuned to their different emotional states.

Table 38. Descriptive statistics of and correlations between scores on each psychological inventory

				Correlations between measures (Pearson's *r*)								
					NEO-FFI			PANAS		STAI		MPQ
Psychological Inventory	*M*	*SD*	Range	E	O	C	A	*Pos*	*Neg*	*State*	*Trait*	*HA*
NEO-FFI												
Neuroticism (N)	20.0	4.6	14-30	***-0.62***	*-0.20*	*-0.15*	0.08	*0.18*	*0.26*	0.06	0.07	*0.30*
Extraversion (E)	34.2	5.4	25-42		0.04	*0.22*	*0.16*	*0.15*	**-0.31**	*-0.12*	*-0.14*	0.01
Openness to experience (O)	28.9	8.0	18-43			*-0.11*	*0.13*	0.08	*0.21*	***0.50***	**0.48**	*0.25*
Conscientiousness (C)	33.2	6.6	21-44				*-0.10*	*0.28*	0.04	-0.02	-0.12	0.01
Agreeableness (A)	30.9	5.5	22-38					**0.33**	*-0.11*	*-0.21*	-0.17	***0.53***
PANAS												
Positive Affect (Pos)	24.6	8.7	12-36						**0.48**	**-0.32**	-0.47	*0.18*
Negative Affect (Neg)	13.1	3.6	10-21							*0.23*	0.16	-0.04
STAI												
State Anxiety	33.7	10.0	21-51								***.078***	0.04
Trait Anxiety	35.2	10.5	19-56									*-0.14*
MPQ												
Harmavoidance (HA)	16.8	5.6	7-25									

Figure Caption

On the left, mean, SD, and range of scores on each psychological inventory. On the right, Pearson's product moment correlation coefficients(*r*) between measures. Small correlations are italicized, medium correlations are in bold, and large correlations are italicized and in bold.

In general, subjects showed typical central tendency and variability in their responses. For example, the means (positive affect = 29.0; negative affect 15.8) and SDs (positive affect = 8.0; negative affect = 5.9) of PANAS scores for a large sample (n = 2,213) of undergraduates (Watson, 1988) is comparable to our sample (positive affect, M= 24.6, SD = 8.7; negative affect, M = 13.1, SD = 3.6). Similarly, Spielberger (1983) reported typical state anxiety scores (males, M = 35.72, SD = 10.4; female, M = 35.20, SD = 10.61) and trait anxiety scores (males, M = 34.89, SD = 9.19; female, M = 34.79, SD = 9.22) in close proximity to ours (state, M = 33.70, SD = 10.1; trait, M = 35.20, SD = 10.5).

3.4.2.5.13.1Left amygdala ROI

In order to investigate individual differences in emotional experience, Pearson product-moment correlation coefficients (r) were calculated between activity in the left amygdala and scores on the personality and mood questionnaires. Mean percent signal change in the left amygdala during each basic emotion state did not correlate with any factor (neuroticism, extraversion, openness to experience, agreeableness, conscientiousness, or harmavoidance) from either of the personality measures (NEO-FFI, MPQ). Additionally, positive and negative affect scores did not correlate with activity in the amygdala during the experience of any basic emotion state. However, both state and trait anxiety scores (as measure by the STAI) showed significant correlations with left amygdala activity during recollection of happy, sad, and anger memories. State anxiety was negatively correlated with mean percent signal change in the left amygdala during the recollection of happy memories ($r(14) = -.641$, $p = 0.018$) (see Figure 95). Thus,

subjects who reported higher levels of state anxiety exhibited lower activity in the left amygdala while they were recalling happy memories. Although this finding was not predicted based on previous research, it fits with the idea that individuals in a current state of anxiety might not engage the amygdala during the experience of happiness as much as those who report a lower state of anxiety. Experience of positive emotion has been linked to left amygdala activation (Hamann & Mao, 2002), and, like other internal emotion variables, anxiety may modulate this response. State anxiety was positively correlated with mean percent signal change in the left amygdala during the recollection of sad memories ($r(14) = .794, p = 0.001$) (see Figure 96). Thus, as we predicted, subjects who reported higher levels of state anxiety exhibited higher activity in the left amygdala while they were recalling sad memories. State anxiety was also positively correlated with mean percent signal change in the left amygdala during the recollection of anger memories ($r(14) = .573, p = 0.041$) (see Figure 97). Thus, as we predicted, subjects who reported higher levels of state anxiety exhibited higher activity in the left amygdala while they were recalling anger memories.

Figure 95. Correlation between percent signal change in the left amygdala and state anxiety scores during happy memory recollection

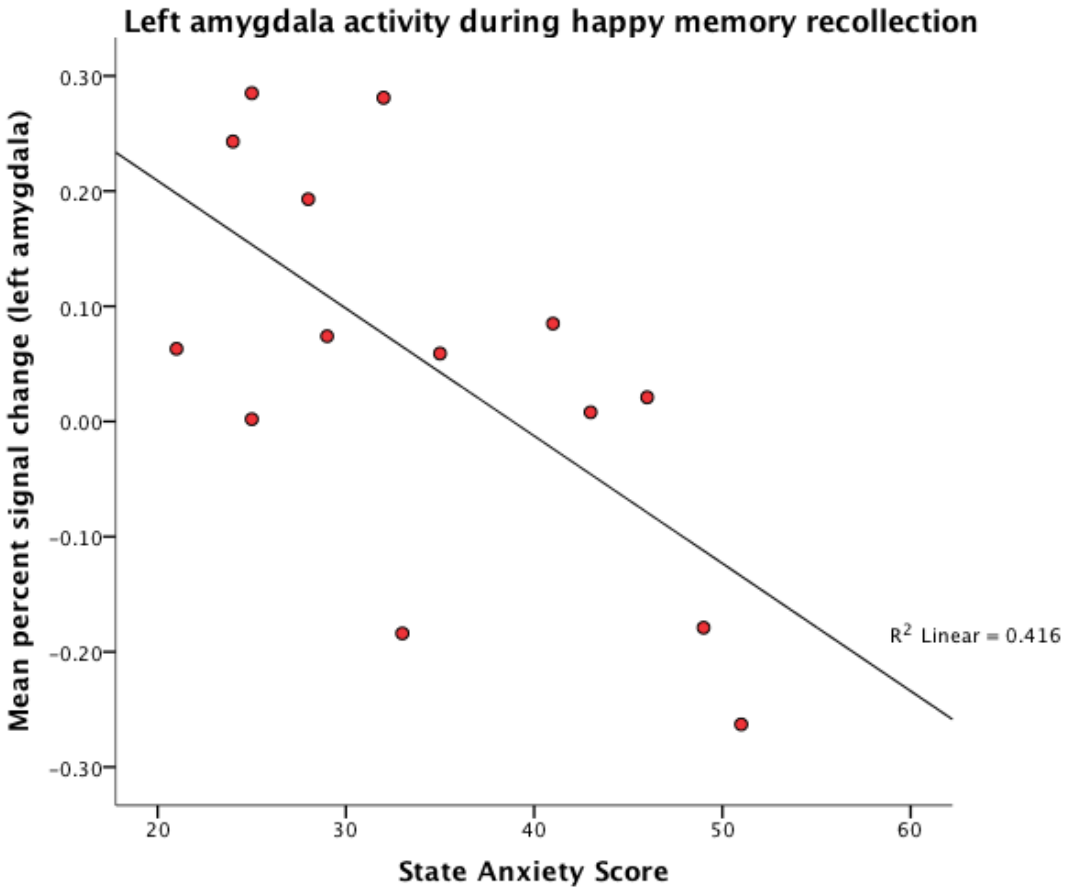


Figure Caption

Scatterplot of correlation between activity in the left amygdala and state anxiety during the recollection of happy memories. Mean percent signal change was negatively correlated with state anxiety scores on the STAI.

Figure 96. Correlation between percent signal change in the left amygdala and state anxiety scores during sad memory recollection

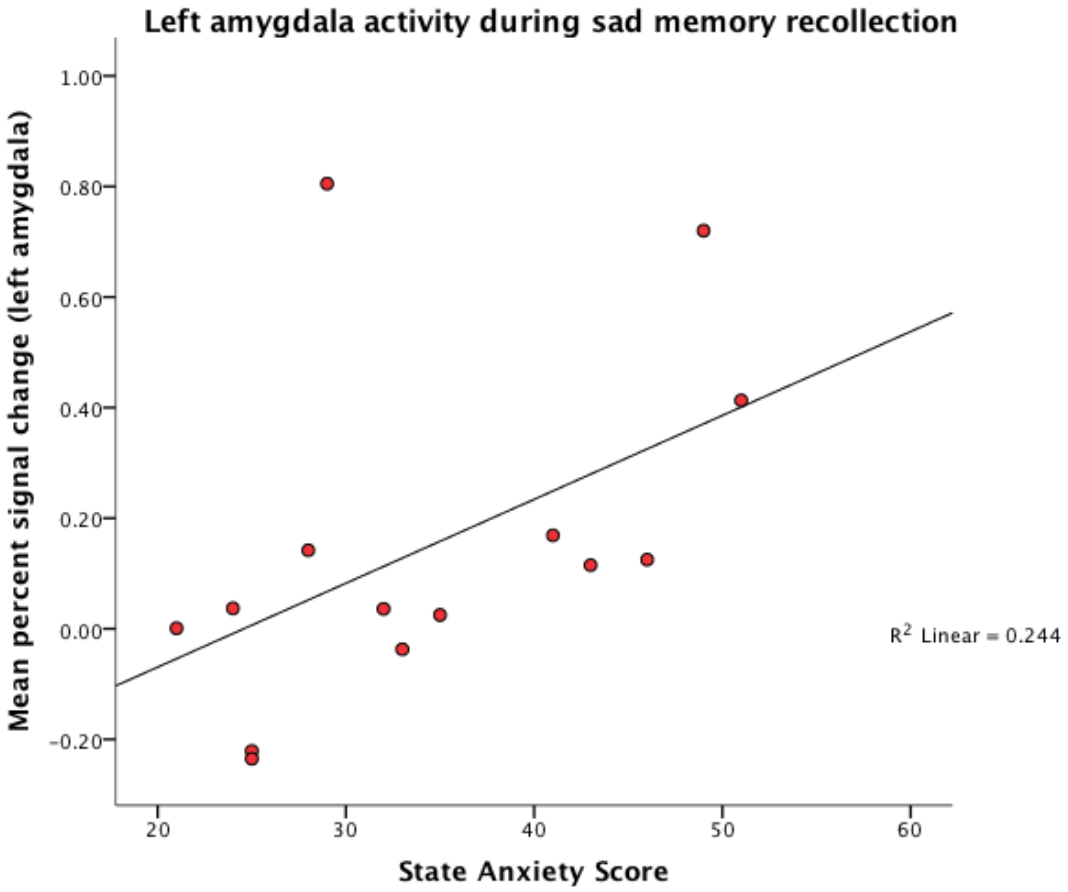


Figure Caption

Scatterplot of correlation between activity in the left amygdala and state anxiety during the recollection of sad memories. Mean percent signal change was positively correlated with state anxiety scores on the STAI.

Figure 97. Correlation between percent signal change in the left amygdala and state anxiety scores during anger memory recollection

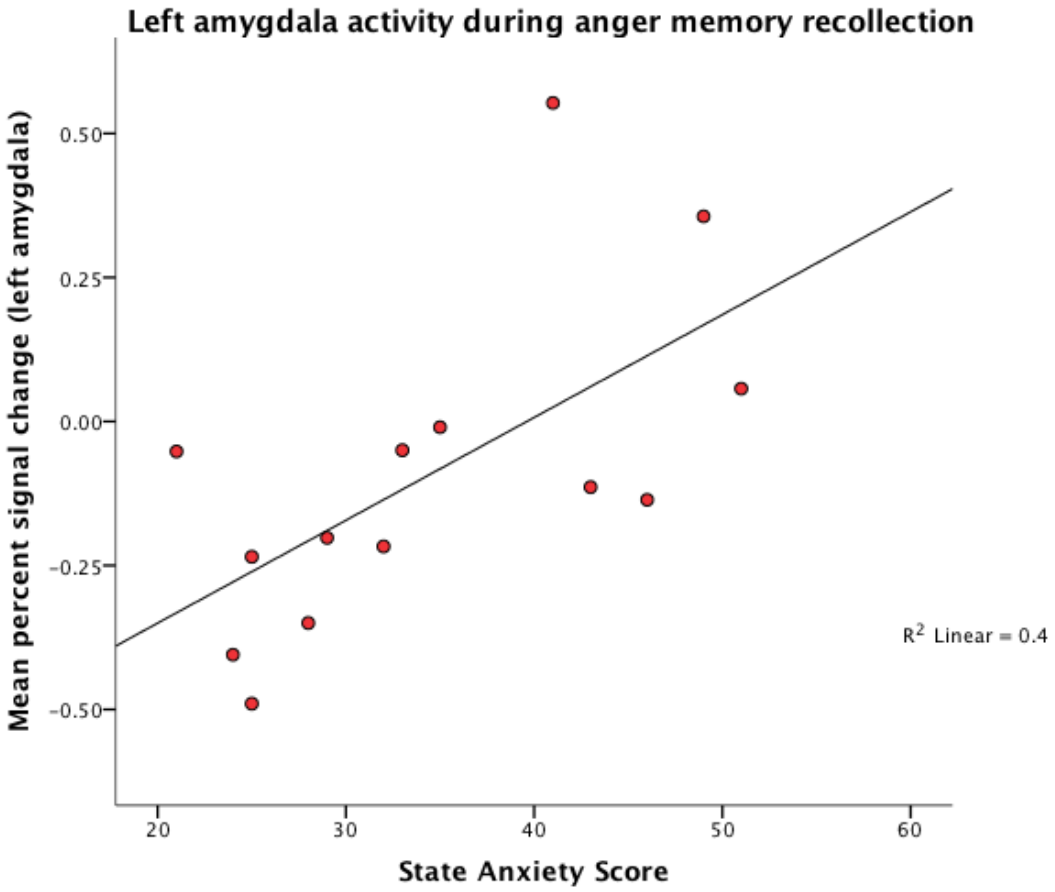


Figure Caption

Scatterplot of correlation between activity in the left amygdala and state anxiety during the recollection of anger memories. Mean percent signal change was positively correlated with state anxiety scores on the STAI.

Trait anxiety correlations paralleled state anxiety correlations: trait anxiety was negatively correlated with left amygdala activity during the recollection of happy memories, and positively correlated with amygdala activity during recollection of sad memories. Trait anxiety was negatively correlated with mean percent signal change in the left amygdala during the recollection of happy memories ($r(14) = -.677, p = 0.011$) (see Figure 98). Thus, subjects who reported higher levels of trait anxiety exhibited lower activity in the left amygdala while they were recalling happy memories. Trait anxiety was positively correlated with mean percent signal change in the left amygdala during the recollection of sad memories ($r(14) = .779, p=.002$) (see Figure 99). Thus, as we predicted, subjects who reported higher levels of trait anxiety exhibited higher activity in the left amygdala while they were recalling sad memories.

Figure 98.Correlation between percent signal change in the left amygdala and trait anxiety scores during happy memory recollection

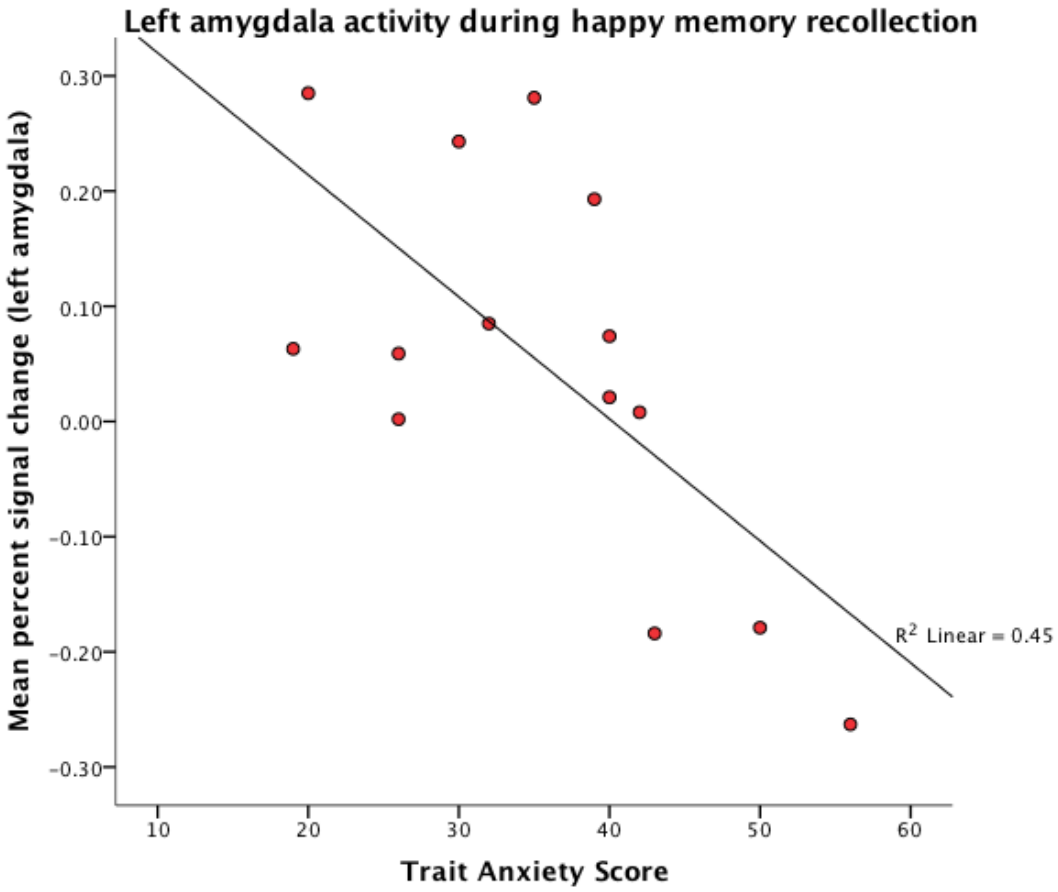


Figure Caption

Scatterplot of correlation between activity in the left amygdala and trait anxiety during the recollection of happy memories. Mean percent signal change was negatively correlated with trait anxiety scores on the STAI.

Figure 99. Correlation between percent signal change in the left amygdala and trait anxiety scores during sad memory recollection

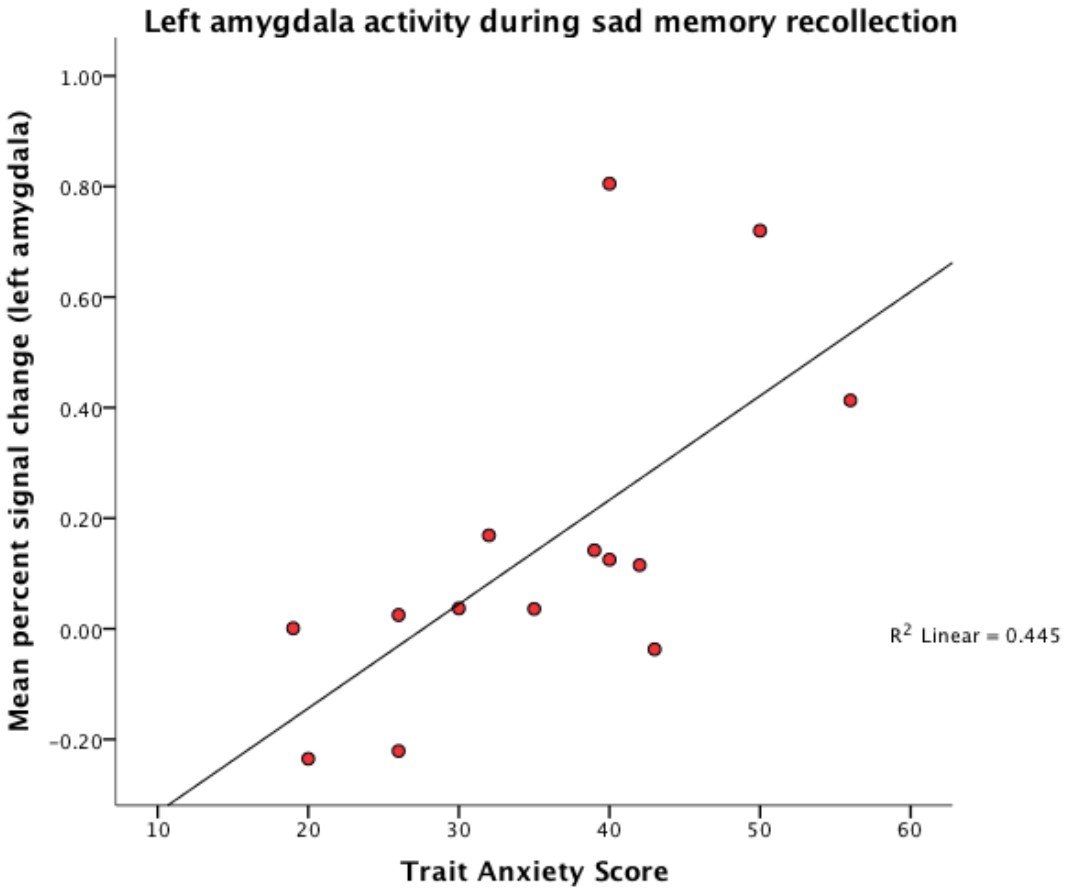


Figure Caption

Scatterplot of correlation between activity in the left amygdala and trait anxiety during the recollection of happy memories. Mean percent signal change was positively correlated with trait anxiety scores on the STAI.

3.4.2.5.13.2Right amygdala ROI

Pearson product-moment correlation coefficients (r) were also calculated between activity in the right amygdala and scores on the personality and mood questionnaires. As in the left amygdala ROI, mean percent signal change in the right amygdala during each basic emotion state did not correlate with factors from the personality measures (NEO-FFI, MPQ) or PANAS. Similarly, state and trait anxiety scores were shown to predict right amygdala activity during the presentation of happy films and sad films. Results followed the same pattern as those in the left amygdala: state anxiety was negatively correlated with mean percent signal change in the right amygdala during happy films ($r(15) = -.648, p = 0.009$), and positively correlated with mean percent signal change in the right amygdala during sad films ($r(15) = .524, p = 0.045$) (see Figure 100 and Figure 101). Trait anxiety scores predicted right amygdala activity in the way: trait anxiety was negatively correlated with mean percent signal change in the right amygdala during happy films ($r(15) = -.684, p = 0.005$), and positively correlated with mean percent signal change in the right amygdala during sad films ($r(15) = .638, p = 0.011$) (see Figure 102 and Figure 103). These findings fit with the idea that both transient and stable negative emotional states modulate activity in the amygdala during the experience of both positive and negative emotions.

Figure 100. Correlation between percent signal change in the right amygdala and state anxiety scores during happy memory recollection

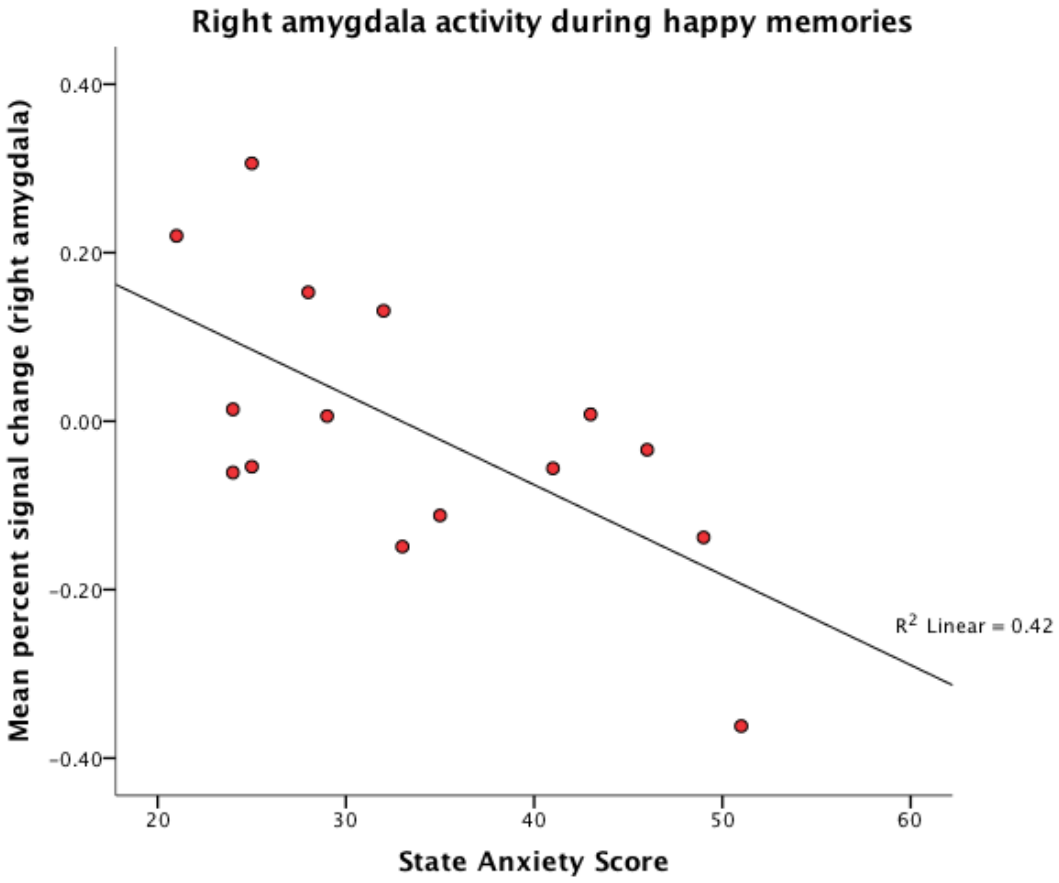


Figure Caption

Scatterplot of correlation between activity in the right amygdala and state anxiety during the recollection of happy memories. Mean percent signal change was negatively correlated with state anxiety scores on the STAI.

Figure 101. Correlation between percent signal change in the right amygdala and state anxiety scores during sad memory recollection

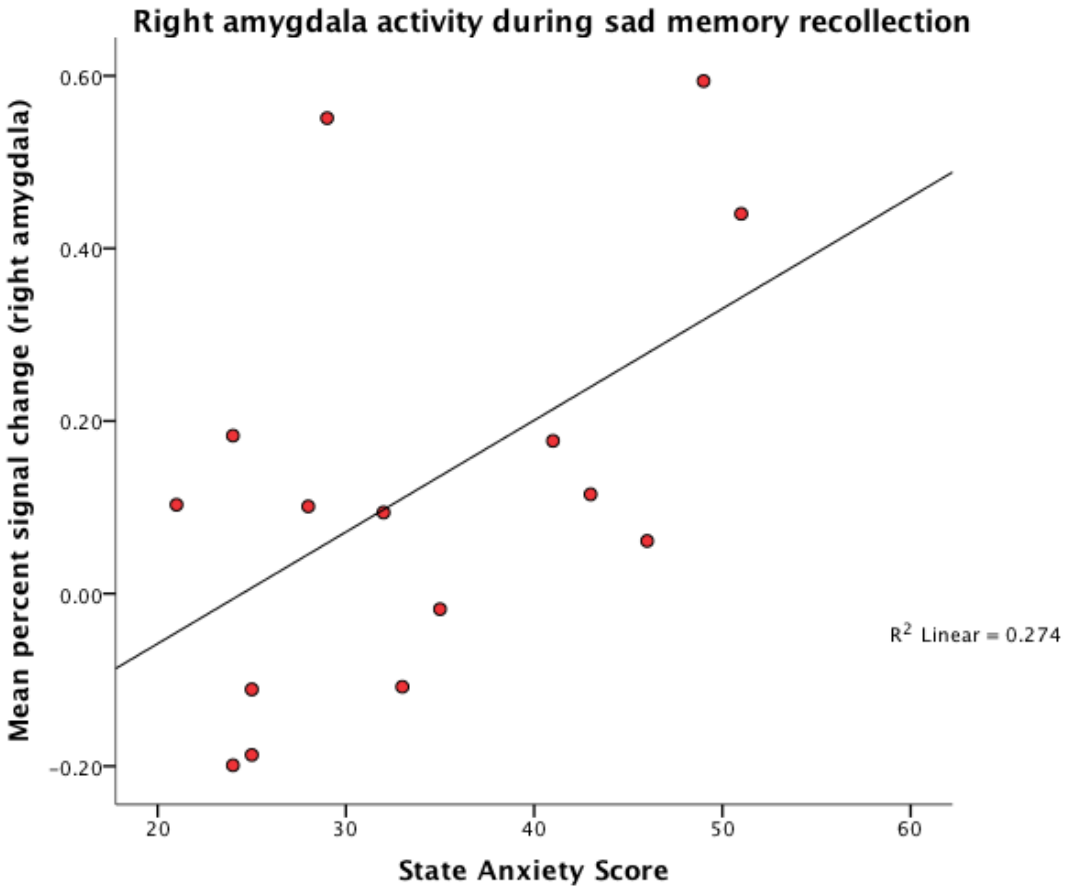


Figure Caption

Scatterplot of correlation between activity in the right amygdala and state anxiety during the recollection of sad memories. Mean percent signal change was positively correlated with state anxiety scores on the STAI.

Figure 102. Correlation between percent signal change in the right amygdala and trait anxiety scores during happy memory recollection

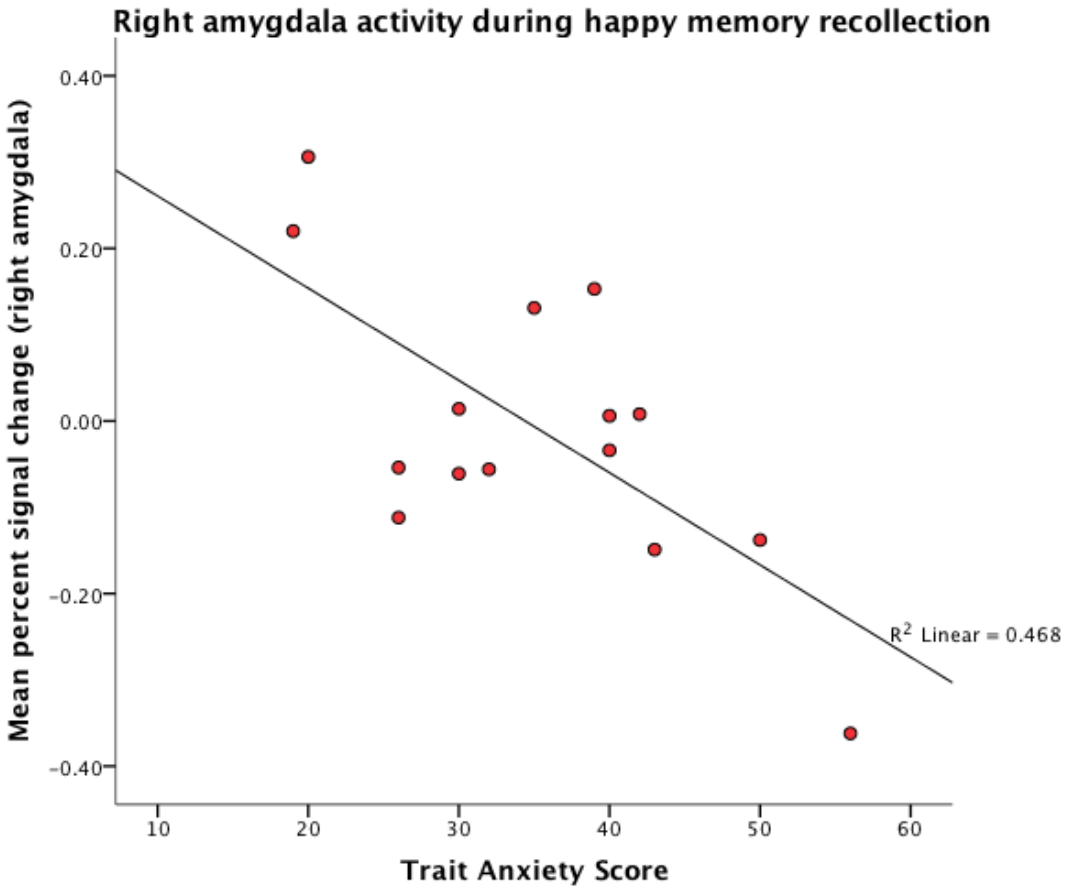


Figure Caption

Scatterplot of correlation between activity in the right amygdala and trait anxiety during the recollection of happy memories. Mean percent signal change was negatively correlated with trait anxiety scores on the STAI.

Figure 103. Correlation between percent signal change in the right amygdala and trait anxiety scores during sad memory recollection

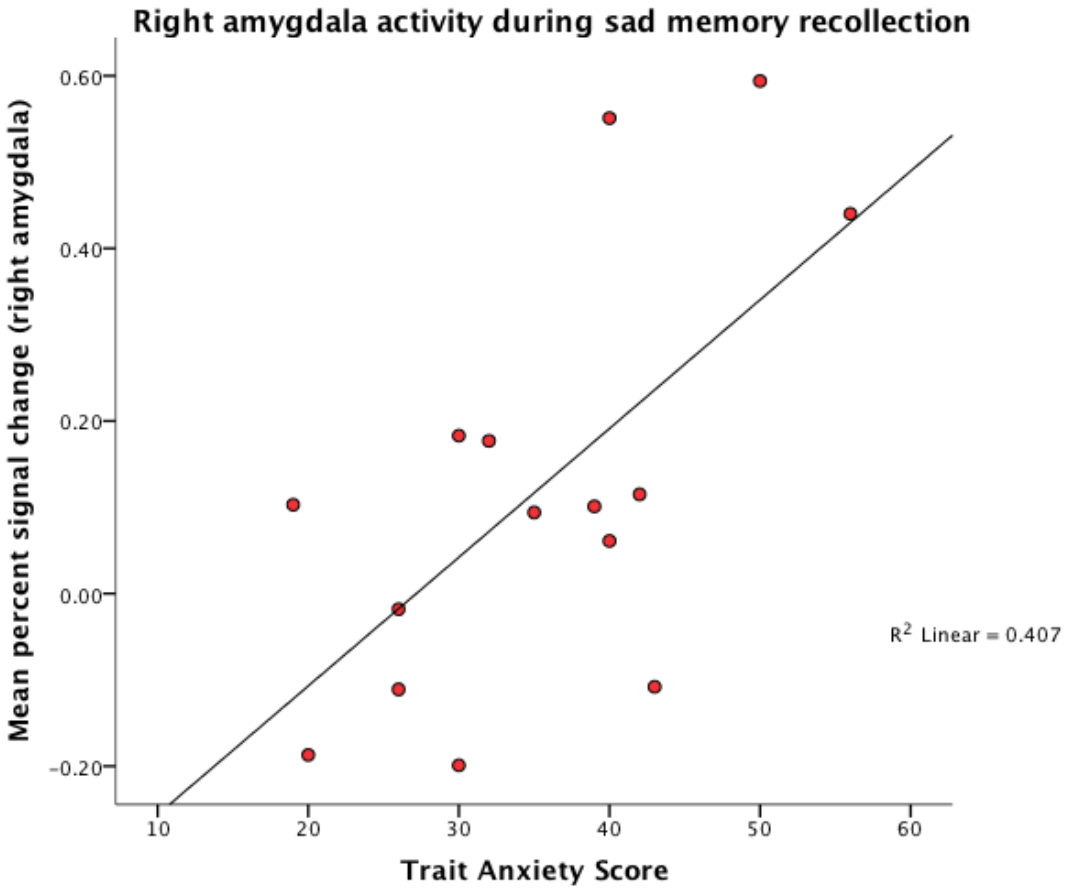


Figure Caption

Scatterplot of correlation between activity in the right amygdala and trait anxiety during the recollection of sad memories. Mean percent signal change was positively correlated with trait anxiety scores on the STAI.

3.4.2.6 Psychophysiology

3.4.2.6.1 Core emotion analyses (contrasts between emotional and neutral)

Table 39 presents the mean and SDs of physiological measures for each basic emotion state. Paired *t*-tests were performed on each dependent physiological measure to assess and verify differences between each basic emotion and the neutral condition (films only). Four of the 18 physiological variables differentiated at least one basic emotion state from neutral at a very lenient threshold ($p < 0.10$): SD R-R Interval, SD RSA, Mean Respiration Cycle Time, and Median Respiration Cycle Time (see Table 40). Happiness, sadness, anger, fear, and disgust were differentiated from neutral based on a decrease in median respiration cycle time (time between breath expirations). Anger was further differentiated from neutral based on an increase in mean respiration cycle time. Fear was further differentiated from neutral based on a decrease in variability (SD) of the R-R interval (inter-beat interval) and a decrease in variability (SD) of the respiratory sinus arrhythmia (variation in heart rate that occurs during a respiratory cycle). Disgust was further differentiated from neutral based on a decrease in mean respiration cycle time (i.e., shorter time between expirations). As a result of the fact that only four highly similar variables differentiated emotion states from neutral there was no motivation to reduce the number of variables using PCA or enter the variables into a MANOVA.

Table 39. Descriptive statistics of physiological variables

Physiological Measure	Happiness		Sadness		Anger		Fear		Disgust		Neutral	
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Mean R-R Interval	0.87	0.15	0.87	0.15	0.87	0.14	0.88	0.18	0.86	0.16	0.87	0.15
Median R-R Interval	0.87	0.16	0.87	0.16	0.88	0.16	0.89	0.19	0.87	0.18	0.88	0.16
SD R-R Interval	0.08	0.04	0.09	0.08	0.07	0.06	0.07	0.04	0.08	0.05	0.08	0.04
Mean RSA	0.23	0.31	0.23	0.33	0.20	0.29	0.20	0.22	0.20	0.21	0.21	0.29
Median RSA	0.20	0.29	0.24	0.43	0.19	0.31	0.20	0.24	0.20	0.23	0.19	0.28
SD RSA	0.13	0.17	0.12	0.17	0.11	0.15	0.09	0.12	0.09	0.10	0.12	0.16
Mean of Mean R-R per Resp Cycle	0.70	0.44	0.69	0.43	0.71	0.42	0.71	0.46	0.69	0.44	0.70	0.42
Median of Mean R-R per Resp Cycle	0.70	0.45	0.70	0.45	0.71	0.41	0.72	0.46	0.70	0.45	0.71	0.43
SD of Mean R-R per Resp Cycle	0.15	0.27	0.09	0.10	0.06	0.06	0.16	0.24	0.13	0.25	0.09	0.10
Mean of SD R-R per Resp Cycle	0.34	0.65	0.278	0.48	0.19	0.27	0.33	0.64	0.34	0.71	0.22	0.32
Median of SD R-R per Resp Cycle	0.30	0.55	0.27	0.48	0.19	0.28	0.35	0.76	0.31	0.64	0.18	0.26
SD of SD R-R per Resp Cycle	0.15	0.30	0.07	0.09	0.04	0.04	0.12	0.22	0.09	0.18	0.11	0.17
Mean Respiration Cycle Time	-4.25	1.20	-5.42	3.67	-5.04	3.65	-5.68	3.85	-6.40	5.41	-5.33	3.91
Median Respiration Cycle Time	-4.21	1.24	-5.15	3.75	-5.09	3.78	-5.72	4.00	-6.49	5.52	1.82	1.20
SD Respiration Cycle Time	0.83	0.40	1.13	0.77	0.86	0.81	1.05	0.65	1.00	0.66	0.96	0.51
Mean Respiration Amplitude	2.02	1.19	1.73	1.38	1.65	1.49	1.65	1.30	1.93	1.58	1.81	1.17
Median Respiration Amplitude	1.94	1.10	1.77	1.52	1.57	1.52	1.51	1.36	1.94	1.65	1.82	1.20
SD Respiration Amplitude	0.62	0.40	0.55	0.36	0.50	0.51	0.60	0.55	0.72	0.60	0.72	0.41

Note: Table includes means and standard deviations of raw values for all physiological measures across conditions.

Table 40. Differences between emotion states and neutral states on physiological measures

	H > N		S > N		A > N		F > N		D > N	
Physiological measure	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
SD R-R Interval	0.888	0.400	0.430	0.679	-0.513	0.622	***-1.942***	***0.088***	0.605	0.562
SD RSA	0.838	0.426	0.174	0.866	-0.825	0.433	***-1.939***	***0.088***	-1.338	0.218
Mean Resp Cycle Time	1.169	0.276	-0.258	0.803	***2.092***	***0.070***	-0.729	0.487	***-1.594***	***0.150***
Median Resp Cycle Time	***-12.897***	***0.001***	***-5.494***	***0.001***	***-5.316***	***0.001***	***-5.464***	***0.001***	***-4.540***	***0.002***

Note: Table includes physiological measures on which a significant difference was observed between a basic emotion condition and the neutral condition. A lenient threshold ($p < 0.10$) was used for this exploratory analysis. Significant differences are listed in bold and italics. Resp = respiration; H = happy; S = sad; A = anger; F = fear; D = disgust.

3.4.2.6.2 Pairwise contrasts of physiological variables between emotions (univariate analyses between emotion states on each dependent measure)

In order to reduce variability introduced by individual differences in physiological responding, cardiovascular and respiratory measures were first log transformed using the ratio of the emotion condition over the neutral condition [log(Emotion) / Neutral]. The application of this transformation reduces skew, based calculations used by Rainville et al. (2006). Pairwise contrasts of each emotion condition are presented in Table 41. Significant differences were observed between anger and happiness, disgust and happiness, anger and sadness, anger and disgust. Anger and disgust were differentiated from happiness based on a decrease in variability of the SD of R-R intervals per respiratory cycle (i.e., anger and decrease were associated with less variability across trials, of the variability of inter-beat intervals between breaths within each trial). Anger was differentiated from sadness based on a decrease in both the mean and median RSA (i.e., anger was associated with less of an increase in HR during inspiration and less of a decrease in HR during expiration). Anger was differentiated from disgust based on a decrease in median RSA and mean respiration cycle time. Further, mean respiration cycle time was the only variable found to differentiate between emotion states that also differentiated emotion states from neutral: anger showed an increase in mean respiration cycle time compared to neutral, and disgust showed a decrease in mean respiration cycle time compared to neutral.

Table 41. Pairwise contrasts between each emotion condition on each physiological variable

	Paired comparisons									
Physiological variable	H vs. S		H vs. A		H vs. F		H vs. D		S vs. A	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Mean R-R Interval	0.193	-0.852	-0.476	0.646	-0.402	0.698	0.917	0.386	-1.166	0.277
Median R-R Interval	0.028	0.978	-0.555	0.594	-0.400	0.700	0.540	0.604	-1.188	0.269
SD R-R Interval	1.031	0.333	1.810	0.108	1.681	0.131	0.636	0.542	1.029	0.334
Mean RSA	0.137	0.894	1.619	0.144	0.449	0.665	-0.005	0.996	***2.704***	***0.027***
Median RSA	-0.035	0.973	2.209	0.058	-0.387	0.709	-1.562	0.157	***2.746***	***0.025***
SD RSA	0.210	0.839	0.614	0.556	1.131	0.291	0.646	0.536	0.816	0.438
Mean of Mean R-R per Resp Cycle	-0.546	0.602	0.328	0.754	-0.768	0.472	0.705	0.507	-1.096	0.315
Median of Mean R-R per Resp Cycle	0.047	0.964	1.037	0.334	1.047	0.326	-1.012	0.345	1.091	0.311
SD of Mean R-R per Resp Cycle	1.116	0.297	1.864	0.099	-0.185	0.858	0.739	0.481	1.555	0.158
Mean of SD R-R per Resp Cycle	0.472	0.649	1.524	0.166	1.152	0.282	0.074	0.943	1.857	0.100
Median of SD R-R per Resp Cycle	-0.282	0.785	1.025	0.335	0.445	0.668	-0.502	0.629	1.574	0.154
SD of SD R-R per Resp Cycle	*2.260*	*0.054*	***2.507***	***0.037***	1.732	0.121	***2.623***	***0.031***	1.418	0.194
Mean Respiration Cycle Time	-1.468	0.180	-0.503	0.629	-1.334	0.219	-1.883	0.096	1.088	0.308
Median Respiration Cycle Time	-0.937	0.376	-0.563	0.589	-1.321	0.223	-1.707	0.126	0.450	0.664
SD Respiration Cycle Time	-1.062	0.319	0.521	0.616	-0.701	0.503	-0.001	0.999	1.537	0.163
Mean Respiration Amplitude	1.049	0.325	1.372	0.207	1.282	0.236	1.018	0.339	1.539	0.162
Median Respiration Amplitude	0.987	0.353	1.481	0.177	1.617	0.144	0.998	0.348	1.298	0.230
SD Respiration Amplitude	0.426	0.681	1.366	0.209	1.102	0.302	0.133	0.897	1.341	0.217

	Paired comparisons (cont'd)									
Physiological variable	S vs. F		S vs. D		A vs. F		A vs. D		H vs. S	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Mean R-R Interval	-0.462	0.656	0.748	0.476	-0.095	0.927	1.356	0.212	-1.568	0.156
Median R-R Interval	-0.512	0.622	0.511	0.623	-0.049	0.962	0.970	0.361	-1.074	0.314
SD R-R Interval	0.447	0.666	-0.515	0.620	-0.415	0.689	-1.354	0.213	1.043	0.327
Mean RSA	0.430	0.679	-0.166	0.872	-1.677	0.132	*-2.195*	*0.059*	0.674	0.519
Median RSA	-0.283	0.784	-0.989	0.352	-1.735	0.121	***-2.786***	***0.024***	0.948	0.371
SD RSA	1.008	0.343	0.665	0.525	0.395	0.703	-0.121	0.907	0.588	0.572
Mean of Mean R-R per Resp Cycle	-1.336	0.230	-0.518	0.623	-0.983	0.364	0.343	0.743	-1.461	0.194
Median of Mean R-R per Resp Cycle	0.414	0.690	-0.978	0.361	-1.134	0.294	-0.868	0.419	0.924	0.386
SD of Mean R-R per Resp Cycle	-0.996	0.349	-0.116	0.910	-1.878	0.097	-0.969	0.361	-0.666	0.524
Mean of SD R-R per Resp Cycle	0.586	0.574	-0.213	0.837	-0.752	0.474	-1.459	0.183	0.754	0.472
Median of SD R-R per Resp Cycle	0.449	0.665	-0.416	0.688	-0.260	0.801	-1.423	0.193	0.814	0.439
SD of SD R-R per Resp Cycle	-0.522	0.616	0.208	0.840	-1.536	0.163	-0.964	0.363	-0.567	0.586
Mean Respiration Cycle Time	-0.223	0.829	-1.016	0.339	-1.347	0.215	***-2.075***	***0.072***	0.552	0.596
Median Respiration Cycle Time	-0.630	0.546	-1.611	0.146	-1.039	0.329	-1.889	0.096	0.558	0.592
SD Respiration Cycle Time	0.177	0.864	0.790	0.452	-1.264	0.242	-0.412	0.691	-0.740	0.481
Mean Respiration Amplitude	0.981	0.355	-0.540	0.604	-0.492	0.636	-1.219	0.258	0.794	0.450
Median Respiration Amplitude	1.050	0.325	-0.648	0.535	-0.307	0.767	-1.566	0.156	1.706	0.126
SD Respiration Amplitude	0.833	0.429	-0.384	0.711	-0.383	0.712	-1.767	0.115	0.998	0.347

Note: Table presents pairwise contrasts between all emotion conditions for each physiological measure (log-transformed values). Significant differences ($p < 0.05$) are in bold and italics. Differences approaching significance ($p < 0.08$) are italicized only. *df*(9).

3.4.3 Discussion

The primary aim of the current study was to examine the consistency and differentiability of neural activity associated with basic emotion states. In general, our results are consistent with basic emotion theory: all five basic emotion states engaged consistent neural correlates in comparison with the neutral condition, and each basic emotion state was differentiated from all other basic emotion states on the basis of at least one measure (e.g., whole-brain consistency analyses). However, it would be inaccurate to conclude that the emotion states we elicited were cleanly separated across measures, by the same pattern of activations we predicted in our hypotheses. Although there is notable overlap with the Vytal et al. meta-analysis (e.g., sadness was associated with activity in caudate head, disgust was associated with activity in posterior insula), as well as with previous research in other domains (e.g., parahippocampal gyrus is associated with fear in our study; Burwell et al., 2004 has shown that lesions to this area lead to fear-learning deficits in rats), the results were not entirely consistent with previous basic emotion research. There were notable inconsistencies between the experimental results and the meta-analysis (e.g., amygdala activity was associated with fear in the meta-analysis and previous research, but not in the experiment), suggesting that our paradigm and small sample may capture only one facet of patterns associated with basic emotion states. There was also overlap in activations across all emotion states, composing a general emotional processing network. Further, the stability of basic emotion neural correlates differed between different states and these neural correlates also varied based on how the emotion was elicited. Our findings suggest that a hybrid approach is best suited for characterizing

emotions, where both core emotion experience and contextual experience (external and internal) play an important part in modulating aspects of the biological response.

Core emotion experience was reflected most robustly in the inclusive whole brain analyses where emotion states were considered both within and across elicitation modality. As expected, the consistency and differentiability profiles of basic emotion states corresponded with previous research, including the results of the Vytal et al. meta-analysis. In both studies, happiness was associated with activity in STG and ACC and activity in these regions differentiated happiness from sadness and fear (STG) and anger and disgust (ACC) respectively. Similarly, Vytal et al. demonstrated a role for caudate in the experience of sadness, and we found that sadness was both characterized by and differentiated from other emotions on the basis of caudate activity. This finding was reinforced by ROI analyses that demonstrated bilateral caudate activity was associated with sadness (memories only, and across stimuli). Anger was associated with IFG activity in both studies, and activity in this region also differentiated it from all other emotion states. This finding was reinforced by ROI analyses that demonstrated left IFG activity was associated with anger (films only, and across stimuli). Fear was associated with activity in parahippocampal gyrus (for discussion of fear and the amygdala see below), and activity in this region differentiated fear from sadness and anger in the meta-analysis, and fear from sadness, anger and disgust in this study (activity in posterior cingulate differentiated fear from happiness). Disgust was characterized by activity in anterior insula and activity in this region differentiated disgust from all other emotions (both studies). This finding was reinforced by ROI analyses that demonstrated bilateral anterior

amygdala activity was associated with disgust (films only, and across stimuli). Together, these findings suggest reliability in core activation both within and across studies.

Conjunction analyses also demonstrated characteristic and unique neural correlates of basic emotion states: the conjunction of happy films and memories was associated with activity in posterior insula and hippocampus and these regions differentiated happiness from anger and disgust. The conjunction of sad films and memories was associated with medFG activity and activity in this region differentiated sadness from happiness, fear, and disgust (activity in ACC differentiated sadness from anger). The conjunction of anger films and memories was associated with activity in SFG and cerebellum and activity in these regions differentiated anger from happiness (cerebellum), fear (both), and disgust (SFG). The conjunction of disgust films and memories was associated with activity in IFG and basal ganglia, and activity in IFG differentiated disgust from sadness and fear (activity in postcentral gyrus differentiated disgust from happiness and activity in insula differentiated disgust from anger). Overall, these findings suggest that the overlap in activation between emotions elicited by films and emotions elicited by memories can be used to characterize and differentiate emotion states. The one exception to this conclusion is fear.

Notably, fear was not reliably associated with commonly activated activations across elicitation modality (reflected in the consistency and differentiability analyses). However, this finding does not necessarily preclude the existence of core fear activity in the brain, particularly in light of the whole brain findings here, the results of the Vytal et al. meta-analysis, and a large body of research suggesting that fear is critically tied to particular brain structures like the amygdala (for a review of this research see Davis,

1994). Possible explanations for this null finding lie in the nature of the analysis and the behavioral and neural manifestation of the emotion state. The difficulty with detecting activations in the conjunction between fear films and fear memories is threefold: 1) the conjunction itself is statistically stringent in that it requires 1:1 voxel overlap in order to reveal an effect (a criterion that we would not necessarily expect to meet when considering emotion states elicited by different methods across different functional runs), 2) the experience of fear may be more temporally transient, and 3) activity in the primary region associated with fear experience (the amygdala) habituates both within and across trials making it more difficult to detect (Breiter et al., 1996;Phelps et al., 2001). Searching for direct overlap across runs and between states elicited by highly dynamic and highly different stimuli is necessarily difficult, and by definition, fear states are phasic and transient in nature (Davis et al., 2004). Although our analysis of one subject's continuous emotion ratings suggests that fear is not experienced over a period too brief to detect in a block design, nevertheless activity in the amygdala may have been diluted across a 20-second epoch (in addition to the expected habituation of amygdala activity - activity has been shown to drastically decline over 18-seconds). Future analysis of the behavioral and neural responses associated with fear could potentially lend clarity to this null finding.

3.4.3.1 Psychophysiology Results

The second part of our approach to characterizing basic emotion states involved the measurement of cardiovascular and respiratory activity while subjects viewed emotional film clips. Overall, physiological results were inconsistent with the functional

imaging data because they did not explicitly characterize each basic emotion state with a reliable and unique profile. Of the 18 dependent measures we used, only four differentiated basic emotion states from neutral, and only three were unique in their direction of differentiation (e.g., mean respiration cycle time increased relative to neutral during the experience of anger, whereas mean respiration cycle time decreased relative to neutral during the experience of disgust). Happiness, sadness, anger, fear and disgust were all associated with a decrease in median respiratory cycle time, which is consistent with both Rainville et al. and Wilson et al., who found decreases on that variable relative to neutral during happiness, anger and fear; and anger and fear, respectively. Although anger was associated with increased respiratory cycle time in our study, Rainville at al. (2006) and Wilson et al. (2010) found that anger was associated with a decrease in respiratory cycle time when compared with neutral. We found that disgust was associated with a decrease in respiratory cycle time, which is consistent with findings from Wilson et al. although the contrast was not significant (disgust was not included in the Rainville et al. analyses). Fear was associated with a decrease in standard deviation of the R-R interval and standard deviation of RSA in our study, which parallels the findings of Rainville et al. (2006). However, Wilson et al. did not find any significant differences between fear and neutral on either of those measures (sadness was associated with a decrease in standard deviation of the R-R interval in Wilson et al.). On the whole, the physiological profiles of basic emotion states have not been consistently defined across studies.

In general, physiological profiles looked very similar between emotional and neutral states, indicating that physiology was not a viable method for characterizing

emotion states in our paradigm. Fourteen of our physiological measures failed to differentiate between any emotional state and neutral. However, it is important to note that we did find minimal differences from neutral using such measures, moderate consistency with previous findings, and a more robust profile of neural activations using fMRI. These results underscore the importance of investigating patterns at different levels of analysis in order to best characterize emotional experience. By honing in on more central changes in physiology (i.e., neural activity), we have successfully characterized and differentiated basic emotion states.

Similar to the core emotion analyses, pairwise contrasts between emotions did not reveal clear patterns associated with basic emotion states. Although previous research has determined clusters of physiological variables that differentiate basic emotion states, our findings did not support this conclusion. Pairwise contrasts between emotions indicate that anger can be differentiated from certain emotion states (i.e., happiness, sadness, and disgust), and that happiness and disgust can be differentiated as well. However, all of these effects are based on differences in only one or two variables, derived from only three measures (standard deviation of R-R per respiratory cycle, RSA, and respiratory cycle time). Interestingly, we did find some overlap with our emotion consistency analyses. Differences in mean respiration cycle time, which characterized anger (increase relative to neutral) and disgust (decrease relative to neutral) also differentiated anger from disgust in the same direction. This correspondence lends interpretability and theoretical importance to the findings, demonstrating the importance of respiration frequency in differentiating emotion states.

However, these findings do not fit with the current literature: Wilson and Hamann (2010) could not differentiate between anger and disgust based on any of their measures, and Rainville et al. did not include disgust as one of their basic emotions so we cannot make any claims regarding correspondences for that particular contrast. Despite finding very few differences between emotion states on our physiological measures and little convergence between our findings and previous findings, this does not preclude the possibility that physiology can be used to differentiate basic emotions with an approach optimized for psychophysiological data acquisition. Although we were interested in exploring physiological patters associated with basic emotion states, our primary objective was to differentiate basic emotion states using fMRI. The transient nature of the fMRI signal and the slow drift of the magnetic field motivate a design with shorter events. In addition, the high cost of fMRI, and the aim to parallel fMRI results with those of psychophysiology in the same group of participants necessitated a small number of subjects (15 total, 9 with viable physiological data). Previous studies (e.g., Rainville et al.; Wilson et al.) that have used psychophysiological measures to differentiate basic emotion states have extracted data from 90-second epochs (almost 5 times the duration of our films), which are still considered short for optimal physiological recording. In addition, these studies have collected data from 50 and 24 participants, respectively, which is significantly more than our sample size of 9. Further, both of these studies found robust effects when autobiographical memories were used to elicit emotion, and we were unable to collect data during memory recall due to session length. Clear differences such as these, and likely more subtle ones as well, could easily account for our null effects. Importantly, Rainville et al. and Wilson et al. were successful in differentiating basic

emotion states using physiological measures, suggesting that basic emotions may be differentiable at the level of the ANS as well as the brain when more optimal paradigms are used.

3.4.3.2 Variability and commonality in emotional responses

Behavioral verification was necessary for us to make any inferences regarding the physiological profiles associated with basic emotion states. In general, behavioral responses indicated that subjects experienced discrete emotion states when they were expected to, and they did not experience an emotional response when they were expected to be emotionally neutral. Subjects rated happy stimuli as highly positive, and emotionally arousing, and all other negative states (sadness, anger, fear, and disgust) as highly negative and emotionally arousing. Target emotion and basic emotion ratings (those that asked subjects to evaluate how well a particular emotion state was elicited in them) demonstrated that our stimuli uniquely elicited each basic emotion state. Further, there was very little variability in how subjects rated each event (all SDs were less than .5), suggesting that they consciously experienced emotions in similar ways.

Despite the consistency subjective evaluation of emotion, we were able to predict variability in neural responses based on state and trait measures of anxiety. Previous research (e.g., Canli et al., 2001; Haas et al., 2007; Hariri et al., 2002) has shown that personality factors related to emotional experience, like neuroticism and extraversion modulate amygdala response to negative and positive stimuli, respectively. Canli et al. demonstrated that individuals high on neuroticism exhibit increased amygdala activity in response to negative pictures and individuals high on extraversion exhibit increased

amygdala response to positive pictures. Interestingly, we did not find an association between personality factors (e.g., neuroticism, extraversion, harmavoidance) and amygdala activity, or between affect (positive or negative) and amygdala activity. However we did find that state and trait anxiety was negatively correlated with amygdala activity during the experience of happiness and positively correlated with amygdala activity during the experience of sadness. Thus individuals who exhibited high levels of anxiety (state or trait) exhibited less activity in the amygdala in associated with positive emotion states and greater amygdala activity in association with negative states. From a measurement perspective, it makes sense that state and trait anxiety predict amygdala responses in similar way because they are highly correlated with one another (r = .78). Individuals with trait anxiety tended to report current anxious feelings. Together these findings demonstrate that both stable (trait) and transient (state) internal emotional milieu can modulate emotion-related brain activity.

In addition to investigating the variability in neural responses at the level of the individual, we also explored group-level differences related to elicited method. The examination of whole brain activity patterns associated with films but not memories revealed robust modality-specific activation in visual areas within the middle occipital gyrus, and activity in areas implicated in attention and somatovisceral experience (e.g., amygdala, basal ganglia, insula, pons and thalamus). ROI analysis of activations associated with films demonstrated robust activation of the insula and moderate activation of the amygdala in response to disgust films, and robust activation of STG to in response to anger films. Emotion-specific STG activity was unique to the film modality, and activation differences associated with films were, in general, more robust across both

ROI and whole brain analyses than the activation differences associated with memories. Further, films elicited activity that accounted for the majority of regions identified with basic emotions in the consistency and differentiation analyses. The sensory experience of films is highly similar across stimuli, whereas autobiographical memories are unbounded in the sensory simulations they access and thus will be highly variable across stimuli as well as individuals. Thus it makes sense that films would be associated with more stable activation patterns, making them easier to detect.

Like films, memories tended to activate somatovisceral areas (thalamus, caudate) when contrasted with films, as well as subregions of the cingulate cortex (posterior and midcingulate gyrus) and medial frontal gyrus. Posterior cingulate has been implicated in memory monitoring and sensory evaluation (Vogt et al., 1992), and medial frontal gyrus has been implicated in self-referential processing (Mitchell et al, 2005). Activation of these regions fits with the subjects' task in the scanner: they were asked to engage in episodic recollection (i.e., mental time travel) (Tulving, 2002) and simulate the external environment while experiencing the related emotional state. This type of recollection would necessarily elicit activations in areas involved in memory, sensory experience, and self-monitoring.

In addition to the modality-specific differences identified by these analyses, we were able to identify regions commonly activated by both memories and films. Across all contrasts and analytical approaches we found overlapping regions involved in organizing and regulating visceral responses. Regions like the midbrain, pons, thalamus, caudate, and insula exhibited varying degrees of activity across emotional states. These findings fit with previous research that has demonstrated a common somatovisceral network

shared by basic emotion states (Damasio et al., 2000), emphasizing the importance of considering both the core profiles of basic emotions and the core profiles of emotional experience. Somatovisceral mappings in the brain represent a direct connect between our two approaches to characterizing basic emotion states. Brain regions in this network exert control over the internal organs, and we measure the activity associated with this ANS response. By exploring different levels and patterns of activation associated with basic emotions states, a more comprehensive biological profile can be established.

Future research exploring basic emotions should continue to characterize and explain differences as well as commonalities in emotional experience. In addition, experimental designs should be optimized separately to measure neural and cardiorespiratory activity in the most accurate manner possible. By acknowledging and subsequently describing variability in experience a comprehensive way, we will be better equipped to inform clinical theory as well as basic theories of emotional organization.

Taken together, the findings of this study suggest that basic emotion states elicit common core neural patterns, supporting basic emotion theory. However, these patterns only explain one aspect of emotional experience. Our data also suggest that the neural patterns associated with experiential context, the common somatovisceral mappings of emotions, and the variability introduced by the internal evaluation of the response all play important roles in the unfolding of an emotional response. Ultimately, it is the combination all such elements that provides us with the rich resonant experience we call emotion.

Chapter 4

General Discussion

4.1 General Discussion

Emotional experience has long been defined by the bodily states that accompany it. James (1890) described emotions by their physiological profiles, by claiming that an emotion like fear is the experience of a change in heart rate, respiration, and eccrine response. To James, "the emotion is nothing but the feeling of a bodily state, and it has a purely bodily cause." (James, 1890, pp. 459). This interest in the visceral experience of emotion eventually led to the development of basic emotion theory, which proposes that basic emotions (i.e., those coarser, more evolutionarily linked: happiness, sadness, anger, fear disgust) are characterized and differentiated by unique physiological patterns (Ekman, 1999). When we experience these emotions, it is difficult to describe them and impossible to separate them from the visceral activity that awakens the body. We would not say we feel angry unless we truly felt the boiling under our skin and fire in our chest. Without that response, we could not call the experience anger, because it is devoid of emotion.

It follows that a theory would develop to describe emotion states in such a way, grounded in embodiment. Basic emotion theory is consistent with how we describe and respond to emotional experience in categorical ways: we experience disgust when we see excrement, and we respond by avoiding contact. We are afraid of a snake we see in the woods and we respond with increased vigilance and cautious steps. If these emotion states are veridical concepts, the utility of describing them is clear. They explain the structure of emotional experience and can be readily applied to explain behavior and used to inform clinical theory of emotional disorders like anxiety or depression, that share correspondences with healthy sadness and fear, respectively.

This project was motivated by critiques of the evidence supporting basic emotion theory (Barrett & Wager 2006; Cacioppo et al., 2002), and by an assessment of the literature that led to the following conclusion: the biological proposals of basic emotion theory have not been previously examined in a systematic, sophisticated, and naturalistic way. Thus, we sought to evaluate the current corpus of neuroimaging data to capture regularities across many studies (Study 1) and investigate the core neural correlates of basic emotions using personally meaningful and dynamic stimuli (Study 2). The following sections will briefly review the findings in support consistent and discrete basic emotions across studies.

4.1.1 Status of the support for basic emotions

4.1.2 Neuroimaging

4.1.2.1 Meta-analyses

Previous meta-analyses of neuroimaging evidence in support of basic emotions (e.g., Murphy et al., 2003; Phan et al., 2004) have yielded mixed and inconclusive findings. The neuroimaging literature cannot be used to cleanly characterize basic emotion states. However, our meta-analysis of the neuroimaging literature suggests that this interpretation may not be an accurate characterization of the data. A reanalysis of the data included in other meta-analyses, along with the data published since the last review, indicates that robust emotion-specific patterns of neural activation emerge only when the special information present in the raw data is preserved. Study 1 demonstrated that all five basic emotion states examined elicited differentiable patterns of regional brain activation. Further, activation patterns that reliably characterized a given emotion also

tended to differentiate that emotion from other emotions (e.g., disgust was associated with insula activation, and the insula was prominent among several regions reliably differentiating disgust from anger). These results clarify earlier meta-analysis results and converge with recent multivariate psychophysiological studies that suggest basic emotions can be reliably differentiated.

The findings are consistent with animal models (e.g., Davis, 1994) and human lesion studies (e.g., Adolphs, Tranel, Damasio, and Damasio, 1994) that have previously sought to identify the role(s) of these regions in emotional experience. For example, amygdala lesions in both nonhuman animals and humans result in fear deficits, suggesting a critical role for the amygdala in fear. Converging evidence across animal models, human lesion research, and functional imaging suggests that these findings are not in error and that basic emotion states may be differentiable at the level of the brain.

Specifically, Study 1 found that discrete patterns of activation differentiated between all pairwise comparisons of emotion states; each basic emotion state was reliably distinguished from other basic emotion states based on neural activity. Furthermore, the patterns of neural activation that characterized each emotion also tended to differentiate it from other emotions. Happiness consistently activated ACC and basal ganglia, and ACC was one of several regions that differentiated happiness from anger, fear and disgust (happiness and sadness activation patterns differed based on other regions). Sadness consistently activated caudate head and MFG, and activations in both regions reliably differentiated sadness from anger, fear, and disgust. Anger consistently activated IFG and PHG, and both regions differentiated anger from all other emotion states. Fear reliably activated the amygdala and right insula, and these regions differentiated fear from

happiness (amygdala only), sadness, anger, and disgust. Disgust consistently activated IFG/insula, and these regions reliably differentiated disgust from all other emotion states. Together, these findings support a discrete model of affective space and indicate that basic emotion states are processed as qualitatively different phenomena in the brain.

4.1.2.2 Experimental evidence

Study 1 identified regions that were consistently activated across studies. In study 2, we sought to identify regions that characterize five basic emotions (happiness, sadness anger, fear, and disgust) within a single experiment. We found that basic emotions elicited by films and memories were associated with consistent core activity both within and across elicitation modality. As predicted, the neural signatures of basic emotion states corresponded with previous research, including the results of the Study 1. In both studies, happiness was associated with activity in STG and ACC and activity in these regions differentiated happiness from sadness and fear (STG) and anger and disgust (ACC) respectively. Sadness was associated with caudate activity and activity in this region differentiated it from all other emotions. Anger was associated with IFG activity in both studies, and activity in this region also differentiated it from all other emotion states. Fear was associated with activity in parahippocampal gyrus and activity in this region differentiated fear from sadness and anger in Study 1 and fear from sadness, anger and disgust in Study 2. Finally, disgust was characterized by activity in anterior insula and activity in this region differentiated disgust from all other emotions (both studies). The correspondences between Study 1 and Study 2 suggest reliability in core activation both within and across studies.

Further, these findings fit with previous research, lending meaning to these long lists of activations. For example, caudate activity was associated with the experience of sadness, and research has shown the caudate is engaged during crying episodes (Gordon et al 2002). Activity in ACC (BA24; subgenual cingulate) associated with sadness has been targeted by clinical interventions as a site of dysregulation in depression; with deep brain stimulation to this area, subjects report an improvement in depressive symptoms. Fear was associated with parahippocampal gyrus activity and Burwell et al. (2004) demonstrated that lesions to this area lead to fear-learning deficits in rats, implicating a critical role for this area in fear.

Despite the observed correspondences between studies, it is important to note that the comparison of certain emotion states (e.g., happiness and sadness, fear and all other emotions) did not reveal differences that were as robust as other comparisons (e.g., disgust and anger). Future research should explore the degree to which these states are related in order to characterize their proximity in affective space. In addition, it is essential to explore the link between the amygdala and fear further using naturalistic stimuli. The unexpected lack of a connection between amygdala activity and fear in the current study does not fit with the results of Study 1 or the results of a wide range of previous research, necessitating further attention.

4.1.3 Psychophysiology

Study 2 used psychophysiology measures to parallel the neuroimaging results associated with basic emotion states. Previous research has demonstrated that cardiorespiratory variables can be used in a multivariate approach to differentiate basic

emotions (Nyklíček et al., 2002; Rainville et al., 2006; Wilson et al., 2010). However, we were unable to find significant differences between emotional and neutral conditions across any of our measures (using a *p* threshold of 0.05) and we were also unable to differentiate basic emotion states in a meaningful way using pairwise comparisons. Our sample size ($N = 9$) and short physiological recording epochs (optimized for neuroimaging) likely contributed to the inability to detect effects. Of the few differences we observed, we found one instance of correspondence between emotion consistency analyses (emotion > neutral) and pairwise contrasts. Differences in mean respiration period characterized anger (increase relative to neutral) and disgust (decrease relative to neutral), and differentiated anger from disgust in the same direction (mean respiration period was greater for anger than for disgust). This correspondence between analyses lends interpretability to the findings, demonstrating the importance of respiration frequency in differentiating emotion states. Future research should explore this connection in a larger sample.

4.1.4 Variability in Emotional Responses

It is clear from the current and previous findings that basic emotions are best approached using naturalistic stimuli. Experiments that have successfully characterized discrete profiles of basic emotion states (e.g., Damasio et al., 2000; Rainville et al., 2006; Wilson et al., 2010) have used self generation of emotions and other ecologically valid stimuli to elicit emotions. Emotional states are powerful responses to dynamic and often personally meaningful events. In the laboratory, they should be explored in a way that is as close to their naturally occurring form as possible. This necessarily includes exploring

the differences in emotional experience that occur depending on how emotions are elicited and how they are experienced internally (which can be studied indirectly using measures of personality and mood).

In Study 2 we collected personality, trait, mood, and state data so that we could investigate what types of internal emotional states predict emotional responses in the brain. In addition, we used two different types of naturalistic stimuli, emotionally evocative films and autobiographical memories, to explore the variability in how people respond to emotions elicited in different ways. In line with previous research demonstrating that personality modulates emotional brain activity (e.g., Canli et al., 2001), we found that state and trait anxiety predict amygdala activity during the experience of happiness and sadness. State and trait anxiety were positively associated with activity in the left and right amygdala during the experience of happiness and negatively associated with right and left amygdala activity during the experience of sadness. These findings suggest that both transient and stable differences in anxiety modulate brain activity.

In addition, we found that emotional films tended to elicit more robust activations in the brain than emotional memories, in areas associated with visceral responses (e.g., insula, thalamus) as well as areas involved in the processing of emotionally arousing stimuli (e.g., amygdala). In contrast, emotional memory recollection tended to activate posterior cingulate regions and medFG (in addition to subcortical structures associated with emotion; e.g., caudate). Posterior cingulate has been implicated in memory and sensory evaluation (Vogt et al., 1992) and medFG has been implicated in self-referential

processing (Mitchell et al, 2005), so it is likely that subjects were engaging these regions in order to simulate the events they were recalling.

4.1.3 Conclusions

Our goal was to evaluate support for basic emotion theory within the context of a meta-analysis and experiment. Results from both studies indicate that discrete patterns of neural activity are associated with basic emotion states, supporting the utility of conceptualizing emotions in a categorical manner.

Despite our focus on a categorical approach to emotional experience, we thought it was important to describe variability in emotional responses as well as core networks engaged to an extent by all emotion states. It is intuitive that emotional states change according to conditions in the environment: you would not experience the same type of anger in response to losing the most recent version of an important document as you would in response to discovering that your spouse has been unfaithful. Although the core feelings may be similar, the gestalt of the emotional response is represented differently based on internal and external environmental variables. In other words, the manifestation of the state is different throughout the body, despite a common core response.

Both the categorical and variability approach provided us with interesting patterns of neural activity associated with emotions, allowing us to capture more than just the core responses most robustly associated with basic emotion states. By examining the transient and subtle as well as the fundamental aspects of how these emotions unfold in the body, we have a more comprehensive understanding of emotional experience.

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Appendix A. Experiment pilot study

In order to determine the set of film clips that optimally elicit each of the basic emotion states, 10 pilot subjects were asked to rate 60 film clips on five emotion elicitation dimensions (one for each emotion condition) and 3 additional scales (arousal, valence, and approach/withdrawal). Subjects were tested in groups of two to five, and each group rated half of the film clips (30) in a single session so that fatigue effects were minimized.

Sixty potential clips were extracted from DVDs and high-resolution YouTube (http://www.youtube.com) videos. Clips were selected to include high social content (e.g., interactions among people), clear audio, and complex visual scenes. Pilot study ratings were used to reduce the number of clips to three clips that uniquely elicited each basic emotion state (15 emotional clips total) and 20 clips that were emotionally neutral (based on both valence and arousal ratings). Pilot subjects rated how well each basic emotion state was elicited by the clip (e.g., "How much SADNESS does the clip elicit in you?") on a 7-point Likert scale, where 1 corresponded to "no (sadness)" and 7 corresponded to "a lot (of sadness)". They also rated the arousal level of the clip from 1 (representing "not at all arousing") to 7 (representing "highly arousing"), and the valence of the clip (how negative or positive the clip was) on a scale from 1 (representing "highly negative") to 7 (representing "highly positive"). Finally, they rated their emotional response to the clip in terms of a dimension called approach/withdrawal. Subjects were explained that some emotional responses elicit a desire to approach a person or situation (e.g., anger may cause a person to want to confront or fight someone) and other emotional responses elicit a desire to withdraw from a person or situation (e.g., sadness

may cause a person to want to isolate themselves or socially withdraw from a situation). Subjects were instructed to rate the clip from 1 (representing "high withdrawal") to 7 (representing "high approach"), depending on the type of motivation the clip elicited.

For each basic emotion state, the three clips that were rated highest on emotional arousal, highest on how well the target emotion state (e.g. sadness) was elicited, lowest on non-target emotion states, and appropriately on valence (i.e., low for negative emotions, high for happiness) were selected. Neutral clips were selected based on those rated lowest on emotional arousal, low on all emotion ratings, and closest to neutral (i.e., the middle of the scale = 4) on valence.

Appendix B. Detailed experiment stimuli

Film clips consisted of short (20s) videos in audio video interleave (AVI) format that were selected based on results form a pilot study (see below for details). All clips were presented using Psyscope X (http://psy.ck.sissa.it/) on an Apple Macbook 13" laptop (2.4GHz Intel Core 2 Duo processor), with MacOSX 10.6.3. The program displayed each clip in its entirety, in a standardized size that optimized size and resolution (3:2 aspect ratio). Words were presented in white uppercase Arial font (size 48) against a black background. Rating scales (4-point, Likert style) were displayed as figures that consisted of a horizontal line with 4 vertical tick marks, with the first and last anchored by labels. Responses were made using an in-line button box with four buttons. Film clip trials began with an initial fixation of 500ms, followed by a 20-second emotional or neutral film clip, and then two ratings (valence and arousal). Valence and arousal were rated on 4-point scales (for valence: 1- highly negative to 4- highly positive, for arousal: 1- low to 4- high)). Trials were separated by a three-second inter-trial interval (see Figure 1 for an example film trial). During the film clip presentation, subjects were asked to indicate when they first began feeling an emotional response of any type by pressing a button. Similar to film trials, memory trials began with an initial fixation of 500ms, followed by a 3-second emotional or neutral memory cue. After the cue left the screen, subjects continued to recall the memory for another 27s (30s total) and then rated the valence, arousal, and target emotion success on 4-point scales that were anchored in the same way as the film clip trials. In addition, subjects rated how well the basic emotion of interest was elicited by the memory (e.g., target emotion ratings asked subjects: "How much ANGER does the event elicit in you?" from 1- no/a little anger to 4- a lot of

anger). Trials were separated by a three-second inter-trial interval (see Figure 2 for an example film trial). During the period of memory recall, subjects were asked to indicate when they first began feeling an emotional response of any type by pressing a button.

Appendix C. Detailed experiment procedure

Subjects were recruited via electronic and paper flyers posted on the Emory University campus. All potential subjects were screened for any contraindications to fMRI (e.g., ferromagnetic metal implants) and for the ability to recollect three highly emotionally evocative for each target emotion as well as 20 events for the neutral condition. Subjects who met pre-screening criteria were invited to participate in the first of three sessions (see Figure 3 for a description of the three sessions).

During the first session, subjects read and signed a consent form, indicating their willful participation in the study. Following informed consent, subjects were asked to recount the 35 autobiographical memories they prepared on a worksheet prior to the first session. Subjects were guided to reflect for a minute upon each experience, taking time to imagine the details of the event. Then subjects were instructed to describe each memory aloud, recounting details of the event as they unfolded in time. They were asked to talk about the event as if they were walking through a scene, while focusing on the emotionally evocative aspect of the experience. Memory descriptions were screened to ensure that they provided enough detail, identified specific time and place information, and uniquely elicited the specified target emotion. Subjects rated each memory on vividness (from 1- not at all vivid, to 5- extremely vivid) and arousal (from 1- not arousing, to 4- very arousing) to verify emotionally arousing episodic recollection for emotional memories and emotionally neutral episodic recollection for neutral memories. Finally, subjects selected a unique cue (1-3 words) to refer to each memory. Cues were presented in the scanner at the beginning of each memory trial as a reminder of which memory the subject should recall.

After reviewing all of their memories, subjects were presented with 4 trials (two neutral - one film and one memory, and two emotional - one film and one memory). The practice trials reduced the effects of a learning curve that could result from increased familiarity with program and task format. For the first part of the practice component, subjects were told that they would be viewing an emotionally arousing and an emotionally neutral film, and that they should attentively watch each film and feel whatever feelings the film may elicit in them. Subjects were instructed to make a button press response on the keyboard when they first began to feel an emotional response. They were also told that they would rate the arousal level of the clip from 1 (representing "not at all arousing") to 4 (representing "highly arousing"), as well as the valence of the clip (how negative or positive the clip was) on a scale from 1 (representing "highly negative") to 4 (representing "highly positive"). They were explicitly instructed that their responses should be based on their actual emotional reaction to the film clip, not simply on the emotional reaction of the people in the film clip.

For the second part of the practice component, subjects were told that they would be viewing an emotionally arousing and an emotionally neutral fake memory cue and that they should attend to the cue, try to associate it with an event in their past and feel whatever feelings the memory may elicit in them. Subjects were instructed to become acclimated with using the full 30s to recall a memory and to try and prevent their mind from wandering. In addition to the ratings made in response to the film clips, subjects were asked to rate how well the memory elicited a specific emotional response (e.g., 'How well did the event elicit sadness in you?') from 1 (representing "not at all") to 4 (representing "very well") using a button press response. All other instructions were

identical to those given prior to the film clip practice. After the subjects completed the four practice trials, they were asked if they understood all instructions and clarifications were given if necessary. Their responses were evaluated online for any anomalies, and subjects were corrected if they made any mistakes or atypical responses. After subjects successfully finished the practice trials, they completed three inventories: two personality measures (the NEO-FFI and MPQ harmavoidance scale) and two indices of current and typical mood states (the state-trait anxiety inventory [STAI] and the positive and negative affective schedule [PANAS]). Eligible subjects were then scheduled for their scanning session within one week of their first session.

On the day of scanning, subjects were greeted at the Emory University Hospital and administered the STAI and PANAS inventories. Following the questionnaires, subjects were prepared for the scanner (i.e., subjects were inspected for any metal on their clothing/body, situated on the scanner bed, taped across the head to limit movement, and introduced to the button box and its operation). Prior to the experimental scans, a short 6-minute T1-weighted scan imaged each subject's neuroanatomy. Subjects were instructed to relax, keep their head still, and not talk during the scan. During the anatomical scan, subjects practiced the experimental tasks using the memory cue practice trials from the first session. After the anatomical scan, subjects were scanned with the EPI scout to orient the scanner and check for adequate coverage and signal dropout. During the scout, subjects practiced the film clip trials so that the sound could be adjusted according to the noise interference from the functional scan (functional sequences are typically much louder). After the scout, the task instructions were reviewed and subjects were told that the experimental trials were about to begin and would last approximately

60 minutes. During the experimental trials, subjects were scanned with the functional EPI T2*-weighted sequence.

Each trial began with a film clip/autobiographical memory script followed by a series of behavioral ratings (made with the button box) and a rest period. In order to reduce event time in order to minimize the effects of slow drifts in the fMRI signal while providing our subjects with ample time to get into an emotional state, each run included neutral stimuli and stimuli intended to elicit one basic emotion only (e.g. only fear films and neutral films were presented in the same run). Each run began with a neutral stimulus, and consisted of seven interleaved trials: four neutral and three emotional (see Figure 4). The interleaved neutral states were used to control for artifacts that are specific to that run. Ten runs alternated between film clips and autobiographical memories, and a reverse ordering of the stimuli was used for half of the subjects in order to reduce ordering effects. Runs were also counterbalanced in a pseudo-random manner to reduce ordering effects and prevent the same emotion state from being presented in successive runs. This counterbalancing technique created six different run orders, resulting in 12 total run orders, with the second half presenting a reversed ordering of the stimuli within each run. The first run alternated between film and memory runs every subject.

After the experimental session, subjects were taken out of the scanner, debriefed, and escorted to the Psychology building for a short rating session. During the rating session, we monitored subjects' respiration and ECG while they watched all of the emotional film clips and a subset (10) of the neutral clips from the scanning session. Subjects were instructed that they would be viewing a subset of the clips they just saw while we tracked their breathing and heart rate. They were also told that instead of

making a button press when they began to feel an emotion, they should continuously track their emotional response on a 30-point scale from 1 (no emotional response) to 30 (high emotional response). Subjects were given practice using left and right arrow buttons to move a red cursor across the scale. The scale was created using Presentation software (http://www.neurobs.com/), and was presented using WindowsXP in Bootcamp on same Macbook as previously described. All film stimuli were presented on an iMac 21.5" desktop computer running MacOSX 10.5.1. The laptop was situated directly below the desktop monitor so that the emotional response scale was presented as close as possible to the film stimuli. Subjects did not report having any difficulty tracking their responses on a different monitor.

Rating session trials began with the presentation of a film, followed by a 10-second period where subjects reset their cursor to the starting point of the scale. After the scale was reset, subjects rated the valence and arousal of the clip using the same scales as they used in the scanner. Finally, in a series of five ratings, subjects indicated how much each of the emotion states was elicited by the film using the same scales they used during the scanning session (e.g., "How well does the clip elicit ANGER?"). Film clip order was reversed for half of the subjects. After all 25 clips were presented, the psychophysiological recording equipment was removed and subjects were debriefed. At the end of the rating session, subjects were thanked and compensated for their participation.

Appendix D. Measures

NEO-FFI (Costa & McRae, 1992)

The NEO-FFI is a self-report that measures the 'big five' personality factors: Neuroticism (N), Extraversion (E), Openness to Experience (O), Agreeableness (A), and Conscientiousness (C). Previous research has demonstrated that neuroticism is associated with negative mood states and is associated with positive mood states (Costa & McRae, 1980). The NEO-FFI served primarily as an index of neuroticism and extraversion, and these variables were used to explore a potential correlation with amygdala activity during the experience of positive (e.g., happiness) and negative (e.g., fear) emotions. Canli et al. (2001) found that subjects who were high on neuroticism tended to exhibit a greater response in the amygdala while viewing negative pictures, and those who were high on extraversion tended to exhibit a similar response when viewing positive pictures. This effect was expected to replicate in the current study, and consequently the NEO-FFI was selected as a reliable measure of these two personality factors.

The NEO-FFI is a short version of the NEO-PI-R (NEO Personality Inventory - Revised) and consists of 60 items, with 12 items addressing each trait. Items are rated on a five point Likert-type scale (ranging from 'disagree strongly' to 'agree strongly'). Some examples of items on the questionnaire are: 'I seldom feel blue' (Neuroticism, reverse scored), 'I am skilled in handling social situations' (Extraversion), 'I tend to vote for conservative political candidates' (Openness to Experience, reverse scored), 'I accept people as they are' (Agreeableness), and 'I strive for excellence in everything I do' (Conscientiousness). The NEO-PI-R has empirically validated internal consistency (ranging from .68 to .89, alpha coefficient) and test retest reliability (ranging from .79

to.83, alpha coefficient). The NEO-FFI scales show correlations of .75 to .89 with the NEO-PI validimax factors, indicating good convergent and discriminant validity.

State-Trait Anxiety Inventory (Spielberger, 1983)

The State-Trait Anxiety Inventory (STAI) is a self-report assessment that includes separate measures of state and trait anxiety. The inventory measures anxiety based on feelings of nervousness, apprehension, tension, and worry. Similar to high scores on the neuroticism scale in the NEO, high scores on both the state and trait anxiety scales index negative mood state, which has been shown to correlate with amygdala activity when subjects are exposed to aversive stimuli (Canli et al., 2001). The STAI was used in a similar manner to the neuroticism scale of the NEO, as both a predictor of amygdala activity and as a covariate of the neuroticism factor. The STAI is a widely used inventory that is both consistent and valid, and thus was chosen as a measure for the study.

The STAI consists of 40 items, with half of the items addressing the trait scale (referring to how a subject feels 'generally') and the other half addressing the state scale (referring to how a subject feels 'right now, at this moment'). The items on the trait scale are rate on four-point Likert-type scale (ranging from 'almost never' to 'almost always'), and some representative items are as follows: 'I am a steady person' and 'I lack self confidence'. The items on the state scale are rated on four-point Likert-type scale (ranging from 'not at all' to 'very much so'), and some representative items are as follows: 'I feel at ease' and 'I feel upset'. The STAI has empirically validated internal consistency (ranging from .68 to .89, alpha coefficient) and test retest reliability for the trait scale (ranging from .65 to.86, alpha coefficient) and state scale (ranging from .16 to

.62). The state scale test retest reliability range is large because it indexes a fluctuating mood state that varies depending on internal and external contextual factors. Convergent validity between trait scale and other measures of trait-anxiety (Taylor Manifest Anxiety Scale, IPAT Anxiety Scale, and Multiple Affect Adjective Check List) is moderate to high (correlations are .80, .75, and .52, respectively).

PANAS: Positive and Negative Affect Schedule (Watson et al., 1988)

The PANAS measures positive and negative mood. It consists of 20 items, with 10 items addressing positive mood and 10 items addressing negative mood. These scales, which index positive and negative mood, were selected as equivalent 'state' scales of the personality factors extraversion and neuroticism, respectively. The scales were used in a similar way to predict amygdala activity following positive or negative emotion elicitation. Like the STAI state scale, the PANAS scales were used as covariates of the more stable NEO factors.

PANAS items are rated on a five-point Likert-type scale (ranging from 'very slightly' to 'extremely') and some example items are: interested (positive), excited (positive), irritable (negative), and ashamed (negative). Depending on the instruction, the scales can be used to assess general mood (e.g., I generally feel this way), or mood at certain times (e.g., I felt this way during the past week, I feel this way now). Empirical evidence indicates that the scales are internally consistent (.84 and .90, alpha coefficients), they are shown to exhibit good test retest reliability (.39 and .71), and they are largely uncorrelated (-.12 and -.23).

Multidimensional Personality Questionnaire (MPQ) Harmavoidance Scale (Tellegen, 1982)

The MPQ is a personality questionnaire that measures 11 primary trait dimensions. Our interest was in the harmavoidance (fearful) dimension (27 items), which falls under the higher order constraint dimension and consistent of two subscales: 1) dislikes dangerous adventures, and 2) dislikes dangerous predicaments. The MPQ harmavoidance dimension has high internal validity (alpha coefficients ranging from .82 to .84), with an estimated mean inter-item correlation of $r = .15$. Test retest reliability is also high ($r = .88$) and external correlations of ($r = .56$) with trait ratings. Individuals who score high on the harmavoidance dimension describe themselves as avoidant of situations or activities that put them at risk (e.g., being in a forest fire, skydiving, being in a hold-up, handling poisonous snakes, attempting to beat a railroad train at a crossing). As such, when given an option between a potentially harmful situation and a mundane or tedious task (e.g., walking a mile when it is 15 degrees below zero), they would choose the safer alternative.

Items consist of two-alternative forced choice statements and true or false statements. Example items include: “It might be fun and exciting to experience an earthquake”, with the response choices: “Yes” and “No”; “Of the following two situations I would like the least: a) Having a pilot announce that the plane has engine trouble and he may have to make an emergency landing, b) Working in the fields digging potatoes”. The second choice on both items would be scored as “harmavoidant”. Scores on the harmavoidance dimension were used to reflect a fearful trait that supplemented the factors identified by the NEO-FFI.