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The Effect of Arousal on the Emotional Memory Network Depends on Valence

Katherine R. Mickley Steinmetz[1],[2], **Donna Rose Addis**[2],[3], and **Elizabeth A. Kensinger**[1],[2]

[1] Department of Psychology, Boston College, Chestnut Hill, MA [2] Athinoula A. Martinos Center for Biomedical Imaging, Charlestown, MA [3] Department of Psychology, University of Auckland

Abstract

Some suggest that arousal is the essential element in order to engage the amygdala. However, the role of arousal in the larger emotional memory network may differ depending on the valence (positive, negative) of the to-be-remembered information. The goal of the current study was to determine the influence of arousal-based changes in amygdalar connectivity for positive and negative items. Participants were shown emotional and neutral pictures while they underwent a functional magnetic resonance imaging (fMRI) scan. The emotional pictures varied by valence (positive or negative), and arousal (high or low). Approximately 45 minutes later, outside of the scanner, participants took a surprise recognition test. Effective connectivity analysis examined how arousal affected successful encoding activity. For negative information, arousal increased the strength of amygdala connections to the inferior frontal gyrus and the middle occipital gyrus, while for positive information arousal decreased the strength of these amygdala efferents. Further, while the effect of arousal on memory for positive information was restricted to amygdalar efferents, arousal had a more widespread effect for negative items, enhancing connectivity between other nodes of the emotional memory network. These findings emphasize that the effect of arousal on the connectivity within the emotional memory network depends on item valence.

The amygdala has long been cited as an important part of the neural circuitry for processing emotion. Its importance in emotion processing has been found in studies that have focused on the processing of a variety of stimuli, including emotional faces (e.g., Morris et al., 1998), pictures (e.g., Glascher & Adolphs, 2003), and words (e.g., Hamann & Mao, 2002; Isenberg et al., 1999). When processing these emotional stimuli, the amygdala activation has been linked to modulation of other brain areas, including the fusiform gyrus, the middle occipital gyrus, and the parahippocampal gyrus (e.g., Kilpatrick & Cahill, 2003; Tabert et al., 2001; Vuilleumier et al., 2001), leading to enhancements in attention directed towards the emotional stimuli (Phan, Wager, Taylor, & Liberzon, 2002; Stein, et al., 2007). The amygdala's modulation of these networks during emotion processing also has been shown to be important in the retention of emotional information over time (Cahill et al., 1996; Kilpatrick & Cahill, 2003; Richardson, Strange, & Dolan, 2004).

It has been debated whether the amygdala's role in information processing and retention is modulated by arousal (the stimulating or calming nature of a stimulus) or valence (the positive or negative nature of a stimulus). Initial studies suggested that the amygdala primarily responded to threatening stimuli (Kluver & Bucy, 1937; Weiskrantz, 1956;

Address correspondence to: Katherine R. Mickley, Steinmetz Boston College, McGuinn Hall, 140 Commonwealth Ave., Chestnut Hill, MA 02467, Phone: 617-552-3108, Fax: 617-552-0523, mickley@bc.edu.

Whalen, 1998), and there has been some evidence from lesion studies that the amygdala may be more involved in the recognition of negative stimuli than of positive stimuli (Adolphs, Russell, & Tranel, 2001; Tranel, Gullickson, Koch, & Adolphs, 2006). However, recent neuroimaging and lesion evidence has suggested that arousal may be the key factor; the amygdala may respond to any arousing stimulus regardless of valence. Further, the arousal response might be essential in order for the amygdala to modulate memory (Adolphs, Russell, & Tranel, 1999; Anderson, 2005; Anderson, Wais, & Gabrieli, 2006; Kensinger, 2004; Cahill & McGaugh, 1995; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Cahill et al., 2003).

The focus of the current study is to examine how arousal affects connectivity within an amygdala-modulated emotional memory network, and to examine whether the influence of arousal varies depending on whether stimuli are of positive or negative valence. As reviewed above, the link between amygdala activity and subsequent memory may not differ based upon item valence (Hamann & Mao, 2002; Kensinger & Schacter, 2006), yet this does not mean that the effect of arousal on the amygdala's role in guiding memory must be identical for positive and negative stimuli. Based on prior research, we hypothesized that increasing stimulus intensity would have a greater impact on amygdala connectivity with regions of the emotional memory network when stimuli were negative than when they were positive. This hypothesis stemmed from a few lines of prior research. First, the effect of arousal may differ based on valence. Garavan, Pendergrass, Ross, Stein, & Risinger (2001) found that when processing emotional pictures, arousal modulated amygdala increases for negative stimuli, while the amygdala response remained high across positive stimuli. In addition, Bernsten, Bechara, Damasil, Tranel & Cacioppo (2007) found that people with amygdalar lesions did not show a typical behavioral gradient in arousal ratings to negative pictures, while the gradient in ratings for positive pictures was preserved. These findings suggest that the amygdala is particularly important for processing the arousal tied to negative stimuli. Second, amygdala damage disrupts the ability to re-experience the negative affect that accompanied prior events (Buchanan, Ezel, Adolphs, & Tranel, 2006), corroborating a strong link between amygdala function and the experience of arousal during a negative event. Third, amygdala damage has a detrimental impact on the ability to recall negative arousing life experiences, whereas it does not have as large an effect on the recall of positive arousing experiences (Buchanan et al., 2006), suggesting that the amygdala may play a particularly central role in the emotional memory network when information is both arousing and also of negative valence. These studies suggest that arousal may affect amygdala activity differently depending on the valence of the item. This differential effect of arousal may have implications for the amygdala-based processes that guide emotional memory (see McGaugh, 2004).

Arousal seems to affect memory by leading to amygdala-related modulation of other areas, including other regions of the medial temporal lobe (McGaugh, 2004; Kilpatrick & Cahill, 2003), regions with the temporo-occipital cortex (Lane, Chua, & Dolan, 1999; Dolan & Vuilleumier, 2003), and regions within the prefrontal cortex (Zald et al., 1998). Yet these studies have primarily focused on the role of arousal when information is negative in valence, leaving open the possibility that the ability for arousal to modulate the strength of connections between the amygdala and other peripheral areas may depend of the valence of the to-be-remembered item. Because negative and arousing information is often recollected with a sense of strong visual detail, and has been associated with encoding activity in the middle occipital gyrus and fusiform gyrus (Kensinger & Corkin, 2003; Mickley & Kensinger, 2008; Mickley Steinmetz & Kensinger, 2009), it is possible that for negative information, arousal may be especially likely to increase connections between the amygdala and these areas associated with visual processing for negative information. By contrast, for positive information, arousal may not elicit the same magnitude of strengthened

connections. Thus, differences in arousal based memory for positive and negative items might be due to changes in the way in which arousal influences the *connections* between the amygdala and a broader emotional memory network. To address this hypothesis, the present study employed effective connectivity analyses using structural equation modeling (SEM).

Methods

Participants

Participants included the same nineteen right-handed young adults, aged 19 – 35, reported in Mickley Steinmetz and Kensinger (2009). All participants were native English speakers and had normal or corrected to normal vision. Participants with a history of psychiatric or neurological disorders or participants taking medication that would affect the central nervous system were excluded from the study. Informed consent was obtained in a method approved by the Institutional Review Boards at Massachusetts General Hospital and Boston College.

Materials and Procedure

The materials and procedure were identical to those described in Mickley Steinmetz and Kensinger (2009). Behavioral data can also be found in that publication. To briefly reiterate those parameters, stimuli were 350 pictures: 70 negative arousing, 70 negative nonarousing, 70 positive arousing, 70 positive nonarousing and 70 neutral pictures taken from the International Affective Picture System database (Lang et al., 1999). Positive and negative pictures were matched on visual complexity, brightness [as indicated in Adobe Photoshop (Adobe Systems, San Jose, CA)], and number pictures that included animals, people, buildings or landscapes (normative data from Kensinger & Schacter, 2006b). Positive and negative pictures were equated for arousal and for absolute valence (i.e., distance form neutral valence). High and low arousal images were equated for valence ratings.

Participants viewed 175 pictures (35 from each emotion category) for 2 sec each while undergoing a functional magnetic resonance imaging (fMRI) scan. Interstimulus intervals were jittered, ranging from 2 to 14 s (Dale, 1999). About an hour and a half later and outside of the MRI scanner, participants performed a recognition memory task. During the delay interval, all participants completed a verbal attention task. On the recognition memory task, participants were shown the 175 pictures that they had viewed in the scanner intermixed with 175 new pictures. The studied pictures varied across participants, counterbalancing whether an image appeared on the recognition test as a studied item or as a novel foil. Each picture was shown for 2 sec, and participants were asked to indicate if they recognized the picture as “old” or if it was “new.” If the participant recognized the picture as “old,” they were asked to complete a modified version of the Memory Characteristics Questionnaire (Johnson, Foley, Suengas, & Raye, 1988), rating their memory for confidence, remembered thoughts, feelings, intensity of feelings, associations, visual details, and temporal information they remembered about the item’s presentation. There were no significant valence x arousal interactions for any of the ratings. Therefore, these memory characteristic data will not be discussed further.

Image Acquisition and Preprocessing

Data were acquired on a 1.5 Tesla Siemens Avanto whole body MRI system (Erlangen, Germany) with a standard birdcage head coil. Stimuli were projected from a Macintosh iBook G4 using a Sharp200 color LCD projector with a collimating lens (Buhl Optical). The image was shown on a screen that was mounted at the end of the magnet bore. The screen was viewed via mirrors placed on the head coil.

Anatomic images were acquired with a multi-planar rapidly acquired gradient echo (MP-RAGE) sequence with a repetition time (TR) of 2730 ms, an echo time (TE) of 3.31 ms, a flip angle of 40°, a field of view of 256 x 256 mm, an acquisition matrix of 256 x 256, slice thickness of 1.33 mm, no gap, and a 1x1x1.33 mm resolution. Co-planar and high-resolution T1 weighted localizer images were acquired. In addition, a T1 weighted inversion recovery echo planar image was acquired for auto alignment.

Functional images were acquired via at T2* weighted echo planar imaging sequence sensitive to blood oxygenation dependant contrast (BOLD). The TR was 3000 ms, the effective TE was 40 ms, and the flip angle was 90°. The slices were taken in an interleaved fashion, at an axial-oblique angel (parallel to the AC-PC line). Twenty-nine slices were acquired in a 3.125 mm x 3.125 mm x 3.72 mm matrix. The slices were 3.12 mm thick and had a 0.6 mm skip between slices.

Preprocessing and data analysis were completed using SPM2 (Wellcome Department of Cognitive Neurology, London, UK). Preprocessing included: slice time correction, motion correction (which used a six parameter, rigid body transformation algorism from SPM2), normalization (to the Montreal Neurological Institute template, with resampling at 3mm isotropic resolution), and spatial smoothing (at a 7.6 mm isotropic Gaussian kernel).

Region Selection

Regions were selected *a priori* based on those areas known to be an important part of the emotional memory network (e.g., LaBar & Cabeza, 2006; Mickley & Kensinger, 2008). Five regions were included in our model: left amygdala, left hippocampus, left inferior frontal gyrus, left middle occipital gyrus, and left fusiform gyrus (see Table 1). We defined these ROIs using coordinates selected from a contrast that examined the regions whose encoding-related activity corresponded parametrically with a more confident response during retrieval. At the first level, the parametric modulation function was used, entering the corresponding confidence ratings for each trial in each of the five emotion conditions. Contrast images of the parametric effect of confidence (collapsed across emotion condition) were entered into a second level (group) one sample t-test to identify a network of regions involved in the encoding of confident emotional memories. This analysis collapsed across emotion types, so that regions were not biased with regard to how they processed the emotional content of the items. Further, there were no statistically significant differences in confidence ratings across the five emotion categories (F (4,72) = 1.145, $p > .05$, partial eta squared = 0.06). Our model included left-lateralized ROIs because the amygdalar activity revealed in the parametric analysis was left-lateralized, and because evidence suggests that the strongest amygdalar connections were likely to be ipsilateral (Amaral, Behniea, & Kelly, 2003; Kilpatrick & Cahill, 2003; Vuilleumier, Richardson, Armony, Driver & Dolan, 2004). A significance threshold of $p < .001$ (uncorrected for multiple comparisons), and an extent threshold of five contiguously active voxels (3x3x3mm) was applied to this parametric analysis. MNI coordinates were converted to Talairach space and regions of activation were localized in reference to a standard stereotaxic atlas (Talairach & Tournoux, 1988).

From each region in our model, we then extracted BOLD signal from a 5 mm sphere centered on the local maximum coordinate. Using the Marsbar toolbox in SPM2 (Brett, Anton, Valabregue, & Poline, 2002), a hemodynamic response function was calculated for each individual subject and for each emotion type (positive arousing, positive non-arousing, negative arousing, and negative non-arousing) relative to baseline (fixation). Note that signal was only extracted from encoding trials of items that were subsequently remembered, so that differences in connectivity between the two item types would not be due to differences in later memory accuracy given that more arousing than non-arousing items were later remembered. Thus, if signal from all trials (remembered and forgotten) was entered into the

analysis, differential connectivity between arousing and non-arousing conditions could have nothing to do with arousal-based processing but rather to changes in the proportion of processes that were associated with successful vs. unsuccessful encoding. We then computed the average of the signal change within peristimulus times 4-6 seconds, and these values were used to construct the functional models for the SEM analyses, as described below.

Effective Connectivity Analysis—We investigated the effective connectivity of the regions within the emotional memory network using structural equation modeling (SEM; McIntosh & Gonzalez-Lima, 1994). This is a multivariate technique that uses the neuroanotomical model of connections and assesses its fit with the interregional covariances associated with the BOLD signal. SEM provides information about the strength of the connections in the model, and how these connections vary under different conditions. Moreover, unlike correlations, SEM analysis can also determine the directionality of the connections between different regions given that path coefficients can be asymmetric (e.g., the influence of region A upon region B can be greater than the influence of region B upon region A). The anatomical model specified the location and potential direction of the connections to ensure that the significant functional differences were anatomically viable. The connections in this model were based on known primate and rodent anatomy (Amaral, Behniea, & Kelly, 2003; Burman, Palmer, Gamberini & Rosa, 2006; Petrides & Pandya, 1999; Rosene & Van Hoesen, 1977) and were further refined to ensure stability of the model. First a model was made in which all connections were reciprocal connections. This model did not have good stability (i.e., stability estimates were above 1, indicating an unstable model) and so it was necessary to revise that model. Because the amygdala efferents were the dominant connections, and because of our theoretical motivation for studying the amygdala's modulation of other brain areas, we revised the model to include only amygdalar efferents, leaving the bidirectional connections between the hippocampus and fusiform and the fusiform and the middle occipital gyrus. This model revealed beta weights that were greater than 1 for the hippocampus to fusiform connection. Beta weights that are greater than 1 are theoretically impossible and indicate the presence of an inappropriate reciprocal connection. Replacing the reciprocal connection between the fusiform and hippocampus with a unidirectional connection eliminated these inflated beta weights. This model also had good stability, and so it was this anatomical model that we used in the present study. Once the anatomical model was set, a functional model was then constructed for each emotion category condition (positive arousing, positive nonarousing, negative arousing, and negative nonarousing) by correlating the percent signal change for that condition across the regions in the anatomical model.

All SEM calculations were performed using Lisrel 8.30 (Joreskog & Sorbom, 1993). Two separate SEM analyses were computed. One compared negative arousing to negative nonarousing items. The other compared positive arousing to positive nonarousing items[1]. These two SEM analyses were therefore designed to reveal whether there were arousal-dependent changes in connectivity for (1) negative items or for (2) positive items. For each of the two SEM analyses, estimates of path coefficients were calculated based on the correlation matrices (i.e., the functional models).

To determine whether there were significant differences in connectivity between the conditions (i.e., between negative arousing and negative nonarousing, or between positive arousing and positive nonarousing), we used a stacked-model approach (McIntosh &

[1]Models that compared positive to negative items (collapsing across arousal types) were also created and compared. However, the null and the alternate model in this analysis did not differ significantly. Thus, there does not appear to be an overall effect of valence on the connectivity within the network examined here, but rather a difference in the way that arousal modulates that network.

Gonzalez-Lima, 1994). Using an omnibus test, a null model was constructed in which the path coefficients from both conditions were assumed to be equal. The fit of this model was determined using a goodness-of-fit χ2 test. The fit of the null model was compared to the fit of an alternative model in which the path coefficients were allowed to vary. The fit of the alternate model was also determined using a goodness-of-fit χ2 test, and the differences between the models were calculated by comparing these goodness-of-fit χ^2 values to obtain a $\chi^2_{diff.}$ If the χ^2_{diff} was significantly lower for the alternate model relative to the null model (significance being determined by taking into account the difference in degrees of freedom between the two models), it indicated that at least some connections within the emotional memory network differed as a function of stimulus arousal ($p < .05$).

Thus, the next step was to determine *which* connections contributed significantly to the omnibus difference between the null and the alternate model. To do so, the amygdalar efferents and then the other connections were allowed to vary in a stepwise manner (following the methods of Gilboa et al., 2004). First, an alternate model was created in which only the amygdalar efferents were allowed to vary, and the significance of the decrease in the goodness-of-fit χ^2 value relative to the null model was assessed (i.e., a χ^2_{diff} was computed as described above for the omnibus analysis). If the χ^2_{diff} was not significant ($p > .05$), then the strength of the amygdalar efferents were permanently set as equivalent for the two conditions (e.g., between negative arousing and negative nonarousing) in all subsequent alternate models. If the χ^2_{diff} was significant ($p < .05$), then the amygdalar efferents were permanently allowed to vary between the two conditions (e.g., between negative arousing and negative nonarousing) for all subsequent models. Then a second alternate model was created, in which the extra-amygdalar connections were now allowed to vary, and if this caused a further reduction in the goodness-of-fit χ^2 value, then those connections also were set to vary between the conditions in the final model; otherwise the strength of these connections were fixed to be equivalent.

Results

Effects of Arousal on the Connectivity for Negative Items

The first SEM analysis compared the connectivity among regions in the emotional memory network for subsequently remembered negative items that were either arousing or non-arousing. The omnibus SEM analysis revealed that the goodness-of-fit was significantly better for the alternate model relative to the null model fit ($\chi^2_{diff} = 16.48$, df = 7, $p < .05$), indicating there was a significant effect of condition on the effective connectivity of the emotional memory network. A stepwise assessment of connections was conducted to determine which connections differed significantly across conditions. This assessment revealed that the networks differed in both the amygdalar efferents ($p < .01$) and also the extra-amygdalar connections ($p < .01$; See Figure 1). The encoding of subsequently remembered negative arousing items was associated with stronger connections from the amygdala to the left inferior frontal gyrus and left middle occipital gyrus than was the successful encoding of negative nonarousing items. Connectivity between the fusiform and middle occipital gyrus was also stronger when encoding negative arousing versus non-arousing items. Finally, there was evidence that when successfully encoding negative low arousing items relative to negative arousing items, amygdala influences on the hippocampus became weakly negative, while positive influences of the fusiform upon the hippocampus became stronger.

Effects of Arousal on the Connectivity for Positive Items

An omnibus SEM analysis comparing the connectivity within the emotional memory network during the successful encoding of positive arousing versus nonarousing items

revealed that the goodness-of-fit was significantly better for the alternate model relative to the null model fit ($\chi^2_{diff} = 14.68$, df = 7, $p < .05$), indicating there was a significant effect of condition ($p < .05$). A stepwise assessment of connections was revealed that the networks differed in terms of the connectivity of amygdalar efferents ($p < .01$) but not extra-amygdalar connections (See Figure 2). The encoding of subsequently remembered positive nonarousing items was associated with stronger connections from the amygdala to left inferior frontal gyrus, left hippocampus, and left middle occipital gyrus (See Figure 2) than was the successful encoding of positive arousing items.

DISCUSSION

The current study demonstrates that the level of arousal of successfully encoded items modulates the connectivity between the amygdala and other regions of the emotional memory network. Although past studies have suggested that the amygdala may play a particularly important role during the encoding of high-arousal stimuli, this study adds the important caveat that the effect of arousal may critically depend on the valence of the stimuli. To briefly summarize the results, for both positive and negative items, arousal modulated the strength of amygdalar efferents. However, the effects of arousal on those efferents differed for negative and for positive items. For negative items, there were stronger amygdalar efferents when encoding arousing items as compared to nonarousing items, both to the left middle occipital gyrus and the left inferior frontal gyrus. For positive items, on the other hand, it was nonarousing items that resulted in stronger amygdala connectivity to the left middle occipital gyrus, the left inferior frontal gyrus and the left hippocampus. Furthermore, only for negative items did arousal modulate the connections among regions aside from the amygdala, with arousal modulating connections between the middle occipital gyrus and the fusiform gyrus, as well as from the fusiform to the hippocampus.

Only a small number of studies have assessed the encoding of low-arousal positive and negative stimuli as well as high-arousal positive and negative stimuli, and this is the first study to examine changes in the neural connectivity of the emotional memory while using this broader range of stimuli. Therefore, this study opens a number of questions for future research. The most notable question is why amygdala connectivity would strengthen as arousal increases for negative stimuli but weaken as arousal increases for positive stimuli, a point which we will return to later in this discussion.

The finding for the negative stimuli is generally consistent with prior proposals regarding the role of the amygdala in encoding: It makes sense that amygdala connectivity would strengthen with increasing arousal if the amygdala plays a particularly important role in the encoding of negative, high-arousal stimuli (e.g., Adolphs, Russell, & Tranel, 1999; Kensinger & Cokrin, 2004; Cahill & McGaugh, 1995). It also makes sense that if this enhanced connectivity were disrupted – such as by damage to the amygdala – then this could disrupt the perception of negative arousal, or the preferential retention of negatively arousing memories (e.g., Bernsten et al., 2007; Buchanan et al., 2006).

A particularly interesting finding for the negative items was that arousal seemed to change the way in which valence modulated the neural connectivity that would be tied to sensory processing. For the encoding of negative items that are low in arousal, the amygdala exerted its influence on the hippocampus via the fusiform gyrus. Thus, even when negative items did not elicit high arousal, there was a pathway through which the amygdala could influence the amount of sensory input being received by the hippocampus. This finding may explain why negative events are sometimes remembered vividly, and with sensory detail, even when they are not high in arousal (e.g., Kensinger & Corkin, 2003) although it is important to note that in the present study, subjective perceptual memory vividness was not greater for

negative pictures than it was for positive or neutral pictures. Because differences in connectivity are evident despite a lack of difference in the subjective vividness ratings, this connectivity does not seem to *necessitate* that a perceptually vivid memory will be maintained. However, previous studies using neutral and emotional stimuli have suggested that differences in fusiform-hippocampal connections may be associated with differences in memory for perceptual details (Dickerson et al. 2007; Kensinger & Schacter, 2007). Thus, in general these changes in connectivity may increase the likelihood that perceptual information is retained, thereby explaining why it is more common to find perceptual enhancements in memory for negative low-arousal stimuli than for other types of low-arousal information.

For negative items that were high in arousal, the connection through the fusiform gyrus was not as strong, and instead the middle occipital gyrus played a significant role, forming a loop from the amygdala to the middle occipital gyrus and the fusiform and then on to the hippocampus. Numerous studies have found amygdala activity to be coupled with activity in the visual cortex when processing negative information (Hamann, Ely, Hoffman & Kilts, 2002; Morris et al., 1998; Tabert et al., 2001; Vuilleumier, Armony, Driver, & Dolan, 2001; Vuilleumier, et al., 2004), and studies have revealed that the encoding of negative information that is high in arousal is specifically associated with activity in the middle occipital gyrus (Mickley & Kensinger, 2008; Mickley Steinmetz & Kensinger, 2009). It therefore makes sense that the connectivity between the amygdala and these occipital regions would be enhanced during the encoding of negative information that is arousing. This finding may also help to explain why there is such perceptual vividness associated with memories for items that are negative and high in arousal (Dewhurst & Parry, 2000; Doerksen & Shimamura, 2001; Kensinger & Schacter, 2006a; Kensinger, Garoff-Eaton, & Schacter, 2007). The perceptual quality associated with negative information that is high in arousal may be due to the overall strength of connections through the occipital cortex, or it may be due to the alternate pathway through the occipital gyrus, or a combination of the two. Future research will be necessary to directly examine whether these changes in connectivity modulates the specific phenomenological qualities of a memory.

Although the findings for the negative stimuli can be interpreted within existing frameworks regarding the role of the amygdala in emotional memory, the findings for the positive stimuli are not consistent with existing frameworks and suggest that the link between high-arousal and amygdala engagement may be more nuanced than previously discussed. The finding that high arousal *decreases* the strength of most amygdala efferents when stimuli are positive cannot be accounted for by the hypothesis that it is the high arousal level of stimuli that strengthens the amygdala's role in memory encoding, nor can it be accounted for by any hypothesis that suggests that the amygdala only is engaged for negative stimuli and not for positive stimuli. The present data suggest that amygdala efferents can be strong for both positive and negative stimuli, and that the strength of those efferents can be modulated by arousal for both valences of stimuli, yet the direction of that modulation is opposite depending on the item valence.

As indicated in the introduction, studies have shown that arousal may have different effects depending on the valence of the item. For example, Bernsten, et al. (2007) found that people with amygdalar lesions did not show a typical behavioral gradient in arousal ratings to negative pictures, while the gradient in ratings for positive pictures was preserved. In addition, Garavan et al. (2001) found that arousal modulated amygdala activity for processing negative information, but amygdala activity remained constant for the processing of all positive stimuli, regardless of arousal. The present study extends these prior findings, revealing that arousal can have fundamentally different effects on amygdala connectivity with other regions of the emotion memory network, depending upon the valence of the

information. Although arousal enhances amygdala connectivity for negative items, it does not do so for positive items. The present study cannot explain the basis for the enhanced connectivity for positive items that are low in arousal, but one interesting possibility is that the amygdala efferents for positive stimuli could be tied to more controlled or elaborative processes, which may be particularly likely to occur for low-arousal stimuli, whereas the amygdala efferents for negative stimuli may be linked to a different type of processing, perhaps one that is more automatic in nature, and thus that is more likely to occur for high-arousal stimuli. Although speculative, this proposal is consistent with the fact that amygdala efferents to the prefrontal cortex were particularly strong for positive, low-arousal items, whereas bottom-up inputs from sensory cortices to the amygdala were particularly strong for negative, high-arousal items.

Positive information has often been associated with a more global, heuristic, and elaborative processing than negative information (Fredrickson, 2004; Gasper & Clore, 2002), and the engagement of these types of processes seems to lead to the successful encoding of positive information (reviewed by Kensinger, 2009). Because elaborative processes have been proposed to be particularly important for the encoding of low-arousal information (e.g., Kensinger & Corkin, 2004), it is possible that these elaborative processes are most likely to be implicated in successful encoding when information is positive and of low arousal, whereas they may be less likely to correspond with successful encoding when arousal level is increased. Although the tie to elaborative processing is a speculative one at this point, the present results clearly demonstrate that arousal influences amygdala connectivity differently for negative and positive items.

A final point of interest is that, while the effect of arousal on memory for positive information was restricted to the amygdalar efferents, arousal had a more widespread effect for negative items. It was only for negative stimuli that arousal modulated connections among regions beyond the amygdala, between the fusiform and the hippocampus and the fusiform and the middle occipital gyrus. Thus, it seems that for the encoding of negative items, arousal has a more global effect, while the effect of arousal on positive items is more focused upon the amygdala efferents. The reason for this difference across valences is an open question for further research but it emphasizes that the power for arousal to enhance neural connectivity may be exaggerated for items that are of negative valence.

In summary, the current study is the first to reveal that the effect of arousal on the connectivity within the emotional memory network differs depending on the valence of the to-be-remembered item: while amygdala efferents ramp up in strength as arousal increases for negative items, this is not the case for positive items. This finding sheds light on previous findings which indicate that amygdalar involvement and encoding processes may differ depending on valence (Berntson et al., 2007; Dolcos, LaBar, & Cabeza, 2004; Mickley & Kensinger, 2008; Mickley Steinmetz & Kensinger, 2009), revealing that the way in which arousal influences how the amygdala is incorporated into the emotional memory network depends critically upon the valence of the information. These results underscore the importance of considering how the effects of arousal may be qualified by the valence of the item.

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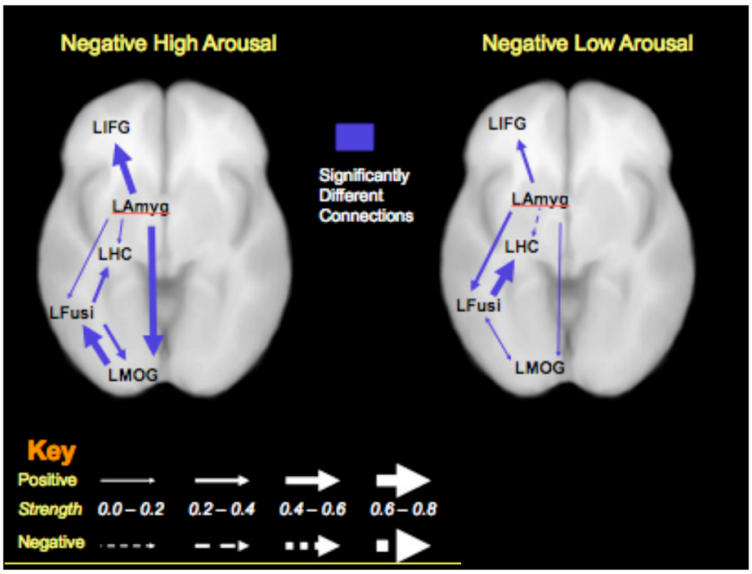

Figure 1.

Anatomical model for the effective connectivity analysis of negative items. Arrows represent anatomical connections used in the model based on known primate and rodent neuroanatomy. Connections that are significantly different between the two arousal conditions are in blue. All connections were significantly different in this model. For Talairach coordinates of peak voxels see Table 1. L=Left, IFG = Inferior Frontal Gyrus, Amyg = Amygdala, HC = Hippocampus, Fusi = Fusiform, MOG = Middle Occipital Gyrus.

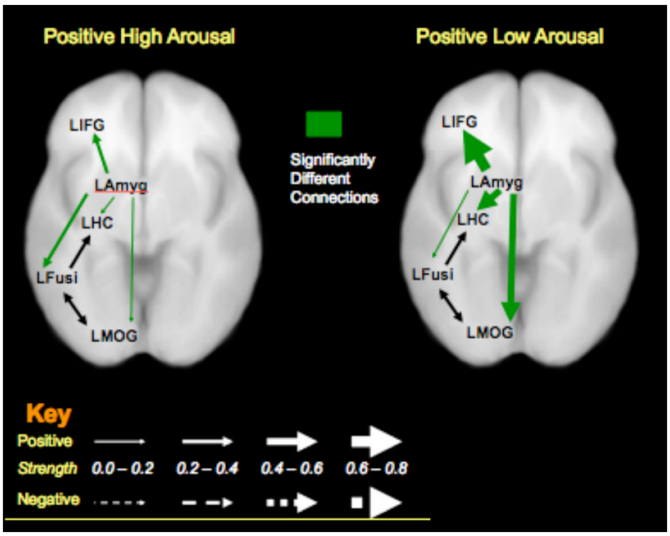

Figure 2.

Anatomical model for the effective connectivity analysis of positive items. Arrows represent anatomical connections used in the model based on known primate and rodent neuroanatomy. Connections that are significantly different between the two arousal conditions are in green. For Talairach coordinates of peak voxels see Table 1. L=Left, IFG = Inferior Frontal Gyrus, Amyg = Amygdala, HC = Hippocampus, Fusi = Fusiform, MOG = Middle Occipital Gyrus.

Table 1

Brain Area	Talairach Coordinates	Brodmann Area
Left Inferior Frontal Gyrus (OFC)	−40, 24, −18	47
Left Amygdala	−24, −1, −13	
Left Hippocampus	−34, −9, −12	
Left Fusiform Gyrus	−30, −45, − 18	37
Left Middle Occipital Gyrus	−26, −86, −1	18