Title	Distinct parietal sites mediate the influences of mood, arousal, and their interaction on human recognition memory
Authors(s)	Greene, Ciara M., Flannery, Oliver, Soto, David
Publication date	2014-12
Publication information	Greene, Ciara M., Oliver Flannery, and David Soto. “Distinct Parietal Sites Mediate the Influences of Mood, Arousal, and Their Interaction on Human Recognition Memory.” Springer, December 2014. https://doi.org/10.3758/s13415-014-0266-y.
Publisher	Springer
Item record/more information	http://hdl.handle.net/10197/6124
Publisher's statement	The final publication is available at www.springerlink.com
Publisher's version (DOI)	10.3758/s13415-014-0266-y

Distinct parietal sites mediate the influence of mood, arousal and their interaction on human recognition memory

Ciara M. Greene[1,2], Oliver Flannery[1] and David Soto[1]

[1]Imperial College London, Department of Medicine, Division of Brain Sciences, St. Dunstan's Road, London, W6 8RP (UK)

[2]University College Cork, School of Applied Psychology, Cork, Ireland

Corresponding author: Ciara Greene, School of Applied Psychology, University College Cork, Cork, Ireland. Tel: +353 (021) 4904520. Email: c.greene@ucc.ie

Running title: Mood, arousal and parietal recognition memory

Full citation: Greene, C.M., Flannery, O. & Soto, D. (2014). Distinct parietal sites mediate the influences of mood, arousal, and their interaction on human recognition memory. Cognitive, Affective and Behavioural Neuroscience.

Abstract

The two dimensions of emotion, mood valence and arousal, have independent effects on recognition memory. At present, however, it is not clear how those effects are reflected in the human brain. Previous research in this area has generally dealt with memory for emotionally valenced or arousing stimuli but the manner in which interacting mood and arousal states modulate responses in memory substrates remains poorly understood. We investigated memory for emotionally neutral items while independently manipulating mood valence and arousal state by means of music exposure. There were four emotional conditions: positive mood/high arousal, positive mood/low arousal, negative mood/high arousal and negative mood/low arousal. We observed distinct effects of mood valence and arousal in parietal substrates of recognition memory. Positive mood increased activity in ventral posterior parietal cortex (PPC) and orbitofrontal cortex, while arousal condition modulated activity in dorsal PPC and the posterior cingulate. An interaction between valence and arousal was observed in left ventral PPC, notably in a distinct parietal area from the main effects, with a stronger effect of mood on recognition memory responses here under conditions of relative high vs. low arousal. We interpret the PPC activations in terms of the attention to memory hypothesis: increased arousal may lead to increased top-down control of memory, and hence dorsal PPC activation, while positive mood valence may result in increased activity in ventral PPC regions associated with bottom-up attention to memory. The findings indicate that distinct parietal sites mediate the influence of mood, arousal and their interplay during recognition memory.

Introduction

Emotional influences on memory are clearly demonstrable; most people will have experienced a ‘flashbulb’ memory of a dramatic or highly emotional event, such as the birth of their first child or the events of September 11th, 2001. A variety of studies have demonstrated that memories for emotional events are more persistent and vivid than their neutral counterparts (Ochsner, 2000; Sharot & Yonelinas, 2008; Todd, Talmi, Schmitz, Susskind, & Anderson, 2012), suggesting that emotional aspects of stimuli influence memory encoding and hence subsequent recollection.

Emotion may be measured both in terms of its valence (i.e. happy/sad) and the degree of physiological arousal elicited. Both of these dimensions appear to influence memory processes. For example, the degree of arousal associated with the to-be-remembered items appears to be critical for feature binding in working memory (Mather, 2007) and for long-term memory (Judde & Rickard, 2010), while mood valence has been shown to influence associative memory (Isen, Johnson, Mertz, & Robinson, 1985). Corson and Verrier (2007) report that high levels of arousal induced prior to a recognition test increased false alarm rates for novel stimuli, though variations in mood valence had no effect. This evidence points to an effect of the emotional content and context of stimuli on the efficiency of memory encoding, and several imaging studies have examined the neural regions that mediate this process. For instance, the amygdala, medial temporal lobe and prefrontal cortex have been shown to be involved in successful encoding of emotional stimuli such as arousing pictures or scenes (Dolcos, LaBar, & Cabeza, 2004; Kalpouzos, Fischer, Rieckmann, Macdonald, & Backman, 2012; Kensinger & Corkin, 2004; Mickley Steinmetz & Kensinger, 2009), and inferior frontal cortex has been implicated in enhanced retrieval of emotionally valenced autobiographical memories (Denkova, Dolcos, & Dolcos, 2013a). Memory for emotionally valenced but non-arousing stimuli have been shown to elicit activation in a network encompassing the hippocampus and prefrontal cortex, while improved memory for highly arousing stimuli is dependent on response in the hippocampus and amygdala (Kensinger & Corkin, 2004). Response in the amygdala and hippocampus during retrieval has also been linked to the emotional valence of autobiographical memories (Denkova, Dolcos, & Dolcos, 2013b).

To understand the role of emotion in memory it is fundamental to distinguish effects operating during memory encoding from other emotional influences operating after stimulus encoding has taken place. In this vein, previous research has shown that post-encoding manipulation of the individual's emotional state may also influence memory for otherwise neutral events and stimuli (Anderson, Wais, & Gabrieli, 2006; Finn & Roediger, 2011; Greene, Bahri, & Soto, 2010; Kuhbandner & Pekrun, 2013; Liu, Graham, & Zorawski, 2008; Nielson & Arentsen, 2012; Nielson & Lorber, 2009). However many of these studies have either conflated valence and arousal effects or focused on one dimension to the exclusion of the other. Recent research indicates that neither mood valence nor arousal alone is sufficient to explain emotional effects on memory performance; rather, it is their interaction that appears most critical (Greene, et al., 2010). In this study, increasing arousal after initial encoding but prior to memory testing was found to improve subsequent recognition of neutral stimuli when participants were in a positive mood, but impair performance when combined with a negative mood state.

The present study aims to characterise the neurocognitive mechanisms that mediate the influence of mood valence and arousal on post-encoding memory processes such as retrieval and recognition, following our prior behavioural work (Greene, et al., 2010). One possibility is that emotional influences on recognition memory may be mediated by attention control mechanisms, of which the posterior parietal cortex is a key substrate (Ciavarro et al., 2013; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Han et al., 2004; Lane, Smith, Schenk, & Ellison, 2011; Yin et al., 2012). The posterior parietal cortex (PPC) is also one of the most commonly activated regions in fMRI studies of episodic memory and recognition (Kim, 2011; Wagner, Shannon, Kahn, & Buckner, 2005). Surprisingly, then, parietal lesions appear to cause only subtle impairments in recognition (Davidson et al., 2008; Haramati, Soroker, Dudai, & Levy, 2008; Rossi et al., 2006; though see Simons, Peers, Mazuz, Berryhill, & Olson, 2010). Despite its recurring role in memory retrieval studies, it has been suggested that the PPC's role is not mnemonic per se, but may instead reflect attentional control processes in the service of recognition memory (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010). To our knowledge, no studies to date have investigated the influence of emotional context on posterior parietal response during memory retrieval. Evidence that positive moods lead to greater incidence of global, rather than local, processing (Basso, Schefft, Ris, & Dember, 1996; Gasper & Clore, 2002) and to reduced attentional control (Jefferies, Smilek, Eich, & Enns, 2008) suggests that emotional state influences attentional selection processes. We hypothesise that if the attentional control aspects of recognition memory operate via the posterior parietal cortex, activity in the PPC during memory retrieval may be modulated by emotional state and by the interplay between mood valence and arousal.

Functional MRI studies of emotional effects on retrieval are lacking in comparison to the number of studies assessing the mechanisms underlying emotional influences on memory encoding. To redress this balance, we manipulated emotional state following the presentation of neutral, abstract stimuli and used fMRI to assess recognition signals in a subsequent memory test. Music listening is an extremely effective method of inducing specific emotions in an experimental setting (Blood, Zatorre, Bermudez, & Evans, 1999; Greene, et al., 2010; Rowe, Hirsh, & Anderson, 2007). Using the same method we successfully employed in an earlier study (Greene, et al., 2010), we carefully selected musical excerpts to vary post-encoding emotional state in an orthogonal manner, and hence evoked different combinations of mood valence and arousal in our participants (positive mood/high arousal; positive mood/low arousal; negative mood/high arousal; negative mood/low arousal). This allowed us to assess recognition memory responses driven by mood valence, arousal and their interaction, and critically to determine whether any interaction effect reflects a quantitative change in responses in the same substrates that respond to mood or arousal, or a distinct effect in the operation of a different neural substrate. This is a critical aspect of our design since, to the best of our knowledge, no previous fMRI studies, even those assessing the effects of emotion on memory encoding, have included independent manipulations of mood and arousal in a factorial design.

Methods

Participants

24 healthy participants (14 male) aged between 20 and 24 were recruited for this study and were paid £30 for their involvement. All participants were right handed and had normal or corrected to normal vision with no past history of head trauma or neurological problems. Each provided informed consent and ethics approval was granted by the West London Research Ethics Committee.

Music selection

Participants attended a training session one to two days prior to the scanning session, during which the pieces of music that would be used to induce the emotional states were selected. A series of short musical excerpts were played to the participants who were asked to indicate how each piece made them feel by placing a mark on a chart representing the dimensions of valence and arousal. The chart took the form of a large cross in which the vertical line denoted arousal, on a scale going from high (‘alert/energised’) to low (‘relaxed’) while the horizontal line represented mood valence on a continuum from ‘positive mood’ to ‘negative mood’. The pieces of music were drawn from a wide variety of genres (e.g. classical, jazz, blues, rock, heavy metal, electronica) with the sole restriction that they be instrumental pieces. The music selection process continued until participants had assigned at least one piece of music to each of the 4 quadrants, representing the 4 mood/arousal conditions.

During this session, participants also practiced the behavioural task described below to ensure their familiarity with it. The stimuli used during the training session were not presented during the scanning session.

Behavioural task

Participants underwent functional magnetic resonance imaging while performing a recognition memory experiment. Stimuli for this experiment were monochrome abstract shapes, generated from bitmap images by custom software programmed in MATLAB. Four blocks of the experiment, one for each emotional condition, were performed in counterbalanced order. Each block began with a study phase, in which twenty stimuli were presented sequentially for 3 seconds each, with a 500ms inter-trial interval. Participants were instructed to study these shapes and attempt to remember them for a subsequent recognition test. The study phase was followed by 3 minutes of music exposure. In order to enhance the emotional induction, participants were asked to focus on thoughts and memories consonant with the emotions evoked by the music. Participants rated their subjective mood (from ‘very negative’ to ‘very positive’) and level of arousal (from ‘very relaxed’ to ’very alert’) before and after the presentation of each musical selection.[1] Visual Analogue Scales (VAS), consisting of a horizontal line anchored at either end by the extremes of the dimension, were presented onscreen for 6 seconds each. Participants used the button box to move a cursor along the horizontal line to indicate their emotional state. The final position of the cursor was converted to a numerical score between 0 and 100. Following the second mood valence and arousal rating, participants performed a recognition memory test. Twenty old shapes (viewed during the study phase) and twenty completely new shapes were presented centre screen, one at a time. Each shape remained onscreen for 2 seconds before the presentation of the response cue, and remained onscreen throughout the response period. Participants were first asked to indicate whether the shape was old or new and then to rate their confidence in that decision (‘not sure’, ‘quite sure’ or ‘very sure’). A two second window was provided for each response.

Image acquisition/scanning parameters

MRI scanning was conducted using a Siemens Avanto 1.5 Tesla MRI scanner with a 32-channel head coil. Following a brief localizer scan to determine the orientation of the subject’s head within the field, 176 high-resolution T1 weighted anatomical sagittal images were acquired with a field of view of 224 x 224mm, TR of 2000 ms, TE of 2.48 ms and slice thickness of 1mm with a resulting voxel resolution of 1x1x1 mm. Four functional runs of 2* weighted echo planar imaging (EPI) were then conducted to obtain 29 contiguous sagittal slices covering the whole brain. Each run contained 262 volumes which were acquired with a field of view of 224x224mm, TR of 2500 ms, TE of 44 ms and slice thickness of 3.2 mm. Music was presented using Sensimetrics S14 MR Conditional headphones at a consistent volume across participants.

Imaging data analysis

fMRI data processing was carried out using FEAT (fMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). The following pre-statistics processing was applied: non-brain removal using BET (S. M. Smith, 2002); motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002); grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor; high-pass temporal filtering above 100s (Gaussian-weighted least-squares straight line fitting) and spatial smoothing using a Gaussian kernel of FWHM 6.0mm.

Time-series statistical analysis was carried out using FILM (FMRIB's Improved Linear Model) with local autocorrelation correction for each run (M. W. Woolrich, Ripley, Brady, & Smith, 2001). Recognition test trials were modelled separately for old and new shapes. Each event had a duration of 2 seconds corresponding to the presentation of the memory probe and was modelled as a boxcar function from the onset of the stimulus convolved with the hemodynamic response function. Additional explanatory variables (EVs) included the onset of each stimulus within the study phase (duration = 3 seconds), the VAS rating sessions (duration = 6 seconds) and the music listening phase (duration = 180 seconds). Error trials and realignment parameters from the motion correction were added to the model as regressors of no interest and the temporal derivative of the haemodynamic response function was added for each explanatory variable in order to account for latency differences between slice acquisitions. Contrasts to test for simple effects of old and new trials, and for the difference between old and new trials were conducted.

Mean effects of trial type (old or new), irrespective of emotional condition, were assessed by means of cross-run individual analyses. Contrast parameter estimates from the four experimental runs were analysed using fixed effects to derive Z statistic images for each participant. These were then added into a group-level analysis using FLAME (FMRIB's Local Analysis of Mixed Effects) stage 1+2 as implemented in FEAT (Beckmann, Jenkinson, & Smith, 2003; M. Woolrich, 2008; M. W. Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004). In all cases, we report maps of BOLD responses thresholded using clusters determined by a voxelwise Z threshold of 2.3 and a corrected cluster significance threshold of p=0.05. Each individual's EPI scans were registered to high-resolution structural images using FLIRT (Jenkinson, et al., 2002; Jenkinson & Smith, 2001), and were then co-registered and transformed to standard (Montreal Neurological Institute) space.

As each emotional condition was assessed in a separate scanning run, effects of the emotional variables (valence and arousal) were computed via a quadrupled two-group difference ('quadrupled t-test') design, a natural extension of the paired t-test and 'tripled' t-test procedures implemented in FSL (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT/UserGuide. See Demeter *et al.* (2011), Warbrick, Reske, & Shah (2013) and Zhu *et al.* (2010) for published examples of the tripled t-test design). These tests were performed on the lower-level contrast of parameter estimates for the old vs. new differences from each of the four emotional conditions. In this method, the four conditions (positive mood/high arousal; positive mood/low arousal; negative mood/high arousal; negative mood/low arousal) are represented by different combinations of three EVs. EV1 models the difference between condition 1 and condition 2 for each subject, EV2 models condition 1 - condition 3 and EV3 models condition 1 - condition 4. 24 additional regressors were included to model the mean effect for each subject. The mean of condition 1 is therefore given by EV1 + EV2 + EV3, the mean of condition 2 is given by –EV1, the mean of condition 3 is given by –EV2 and the mean of condition 4 is given by –EV3. These contrast specifications were extended to test for main effects and interactions between the emotional variables (see Supplementary Data for further information). The resulting z statistic images were then thresholded and co-registered as above.

Results

Emotional Induction

VAS ratings of mood valence and arousal provided prior to the participants' exposure to music were compared across the four experimental blocks using one-way repeated measures ANOVAs. These revealed no significant differences in preliminary mood valence ($F_{3,69} = 0.55$, $p>0.05$, $\eta_p^2 = 0.024$) or arousal ($F_{3,69} = 0.42$, $p>0.05$, $\eta_p^2 = 0.018$) ratings across the conditions, indicating that participant's emotional state returned to a baseline level between experimental blocks (see Figure 1).

A 2x2x2 repeated measures ANOVA was conducted to assess the effect of the mood dimension of the selected music (positive/negative), arousal dimension (high/low) and time (before music/after music) on the mean mood VAS ratings. A main effect of the mood dimension was noted ($F_{1,23} = 66.44$, $p<0.05$, $\eta_p^2 = 0.74$), indicating that mood was rated as more positive in positive mood conditions (M = 67.88, SD = 14.95) than in negative mood conditions (M = 46.6, SD = 18.45). A significant interaction between the mood dimension of the music and time was also observed ($F_{1,23} = 60.31$, $p<0.001$, $\eta_p^2 =0.72$), such that ratings of mood valence increased after exposure to music rated as positive, and decreased after music rated as negative (Figure 1A). Importantly there was no main effect of the arousal dimension of the music on mood valence ratings (High arousal: M = 57.08, SD = 17.65; low arousal: M = 57.4, SD = 15.76. $F_{1,23} = 0.02$, $p>0.05$, $\eta_p^2 =0.001$).

Mean arousal scores were then entered in to a separate 2x2x2 repeated measures ANOVA involving the same factors. High arousal conditions led to increased ratings of arousal whilst low arousal conditions resulted in lower ratings of arousal, as evidenced by a main effect of arousal ($F_{1,23} = 78.64$, $p<0.05$, $\eta_p^2 = 0.77$). A significant interaction between the arousal dimension of the music and time ($F_{1,23} = 68.86$, $p<0.001$, $\eta_p^2 = 0.75$) was also noted: subjective arousal ratings increased following music rated as highly arousing but decreased following music rated as less arousing (Figure 1B). There was no main effect of the mood dimension of the music on arousal ratings ($F_{1,23} = 0.27$, $p>0.05$, $\eta_p^2 = 0.012$). These results indicate that music listening successfully induced different mood valence and arousal states.

Recognition Test

Recognition test performance was assessed in terms of three variables: sensitivity to old/new differences, mean reaction time and mean confidence rating. Sensitivity (d') was calculated using signal detection theory with a hit defined as an 'old' response to a previously viewed shape and a false alarm defined as an 'old' response to a novel shape (Stanislaw & Todorov, 1999). A 2(mood: positive/negative) x 2(arousal: high/low) ANOVA was used to investigate the effects of emotional variables on sensitivity. Confidence ratings and reaction time data were assessed using a 2x2x2 ANOVA in which trial type (i.e. old/new) was added as an additional factor. Descriptive statistics for each of these measures may be found in Table 1.

Initial analyses indicated no significant effect of mood valence ($F_{1,23} = 0.005$, $p>0.05$, $\eta_p^2 = 0$) or arousal ($F_{1,23} = 0.12$, $p>0.05$, $\eta_p^2 = 0.005$) on measures of sensitivity to old/new differences (d'). Similarly, there were no significant effects of mood valence ($F_{1,23} = 0.045$, $p>0.05$, $\eta_p^2 =0.002$) or arousal ($F_{1,23} = 0.31$, $p>0.05$, $\eta_p^2 =0.013$) on confidence ratings, though participants rated their confidence as higher when responding to old (M = 2.27, SD = 0.33) rather than new shapes (M = 1.84, SD = 0.31), a difference which was statistically significant ($F_{1,23} = 169.07$, $p<0.001$, $\eta_p^2 = 0.88$). In accordance with the pattern observed in the confidence ratings, mean reaction time was found to be shorter in old trials than in new trials ($F_{1,23} = 27.37$, $p<0.001$, $\eta_p^2 = 0.54$), however no main effects of mood or arousal condition were observed ($F_{1,23} = 0.78$, $p>0.05$, $\eta_p^2 = 0.033$; $F_{1,23} = 1.67$, $p>0.05$, $\eta_p^2 = 0.068$).

A hypothesis that the emotional induction effect may not have persisted throughout the recognition test period led us to re-examine measures of sensitivity, confidence and reaction time during the first half of the recognition test only. The numerical means of d’ in the first half of the trials were similar to those observed in our original behavioural experiment (Greene, et al., 2010), such that sensitivity appeared to increase during positive mood/high arousal and negative mood/low arousal conditions (Figure 2A), but the interaction was not statistically significant ($F_{1,23} = 0.44$, $p>0.05$, $\eta_p^2 = 0.02$). No effect of emotional condition on confidence ratings was observed. A significant 3-way interaction between mood valence, arousal and trial type was however observed in the reaction time data during the first half of the recognition test ($F_{1,23} = 8.865$, $p<0.05$, $\eta_p^2 = 0.28$).

Further investigation of the mood valence x arousal x trial type interaction within the first half of the trials indicated that the effects of mood and arousal on mean reaction time differed in the presence of new and old shapes. In order to test these effects in more detail we performed post hoc analysis by splitting this 3-way interaction into two separate 2-way interactions. This allowed us to assess the effect of a mood valence x arousal interaction on mean reaction times independently for old and new shapes. No main effects of valence or arousal were observed, but we found a significant interaction between valence and arousal in the presence of new shapes ($F_{1,23} = 4.32$, $p<0.05$, $\eta_p^2 = 0.16$; see Figure 2B). Post-hoc paired samples t-tests indicated that negative mood led to speeded reactions relative to positive mood under conditions of high arousal ($t_{23} = -2.662$, $p<0.05$) but not low arousal ($t_{23} = 0.395$, $p>0.05$). The interaction effect in the presence of old shapes did not reach statistical significance ($p = 0.277$, Figure 2C). This finding suggests that emotional effects on recognition memory performance in the present study may have depended on the relative novelty of the stimuli.

fMRI Results

The presentation of old trials relative to new trials (i.e. a contrast of old > new) during the recognition test activated a network of regions typically observed in memory retrieval studies, including the posterior parietal cortex (PPC), precuneus and hippocampus (see Figure 3). Further analyses assessed the effects of emotional state on old/new responses. Here we analysed the effect of mood valence and arousal conditions on the contrast parameter estimates for old vs. new differences.

A main effect of mood valence on old/new responses was observed such that recognition memory response (i.e. BOLD response detected using a contrast of old > new) increased during positive mood conditions in the left frontal cortex, including the inferior frontal gyrus and orbitofrontal cortex and bilateral posterior parietal cortex. The bilateral PPC clusters encompassed the angular gyrus, inferior parietal lobule and supramarginal gyrus, just encroaching on the anterior intraparietal sulcus (see Table 2 for peak coordinates). No clusters displayed the opposite pattern of response (negative > positive).

A main effect of arousal on old/new responses was observed in the left superior and posterior parietal cortices, covering the superior parietal lobule and the intraparietal and in a large medial cluster covering the posterior cingulate, the precuneus and the visual cortex. These regions displayed increased response to old relative to new trials under conditions of high arousal.

We next tested for interactions between the mood and arousal variables. A cluster in the left PPC – specifically the inferior parietal lobule and angular gyrus – displayed increased response during the positive mood/high arousal and negative mood/low arousal conditions, but reduced response during the positive mood/low arousal and negative mood/high arousal conditions (see Figure 4). Paired samples t-tests indicated that there was a significant difference in BOLD signal in the activated voxels between the positive mood/high arousal and negative mood/high arousal conditions ($t_{23} = 2.75$, $p < 0.05$), though not between the positive mood/low arousal and negative mood/low arousal conditions. There was also a significant difference between the negative mood/high arousal and negative mood/low arousal conditions ($t_{23} = -2.37$, $p < 0.05$). Note that this is the same interaction effect between mood valence and arousal that we have previously shown to influence recognition memory performance in our behavioural work (Greene, et al., 2010). Both main effects and the interaction described here resulted in heightened recognition (old > new) response in the left PPC. The interaction effect was observed in a section of the PPC inferior and lateral to the regions displaying main effects of mood valence and arousal, which also encompass the superior parietal lobule (see Figure 4).

To further investigate the effects in the posterior parietal cortex, we conducted region of interest (ROI) analyses in dorsal and ventral regions of the PPC. Coordinates for the ROIs were taken from Ciaramelli et al.'s (2008) review of the Attention to Memory hypothesis. The dorsal ROI was centred on the coordinates -36 -57 42 in the intraparietal sulcus, while the ventral ROI centred on the coordinates -50 -57 38 in the supramarginal gyrus. These regions have been shown to underlie top-down and bottom-up attention to memory, respectively. Spherical masks with a radius of 10mm were drawn around these coordinates. Mood valence and arousal effects on recognition memory (old trials > new trials) were investigated within the masked regions, and small volume cluster-based correction was applied (voxelwise $Z = 2.3$, $p < 0.05$, corrected).

Within the dorsal PPC ROI, a main effect of mood (positive > negative) and arousal (high > low) was observed; there was no significant interaction effect. A main effect of mood (positive > negative) was also observed in the ventral PPC ROI, although there was no main effect of arousal. An interaction effect was however observed in the ventral PPC, such that there was increased BOLD signal during positive mood states relative to negative mood states, but only under conditions of high arousal. Paired t-tests confirmed this interpretation, indicating that there was a significant difference in BOLD signal within the voxels displaying the interaction effect between the positive mood/high arousal and negative mood/high arousal conditions ($t_{23} = 2.69$, $p < 0.05$), but not between the positive mood/low arousal and negative mood/low arousal conditions (see Figure 5 and Table 3).

In order to investigate the hypothesis that the emotional induction may have worn off during the recognition test, we repeated our analysis examining the first and second halves of the experiment separately. Whole brain analyses revealed that the main effects of mood valence and arousal were stronger and more widespread during the first half of the recognition test trials than in the analysis of the full experiment, but covered similar regions (see Table 4). This interaction effect was not initially observed during the first half of trials, however, a significant interaction effect was observed in the ventral PPC ROI, following small volume correction. This suggests that the interaction effect, which was somewhat weaker than the main effects, could not be detected with the reduced statistical power caused by discarding half of the data. Analysis of the second half of the experiment revealed a main effect of arousal in the left dorsal PPC, including the postcentral gyrus, supramarginal gyrus, superior parietal lobule and inferior parietal lobule. No main effect of mood valence or significant interaction effect was observed in the second half of the experiment, even when analysis was restricted to ROIs in the PPC. We interpret these results as indicating that the induced level of arousal persisted longer than the changes in valence, which appear to have worn off by the second half of the experiment.

Discussion

The two dimensions of emotional state – mood valence and arousal – were independently manipulated and their effects on the neural substrates of recognition memory were assessed. Distinct effects of valence, arousal and their interaction were observed in a number of regions, most interestingly in the posterior parietal cortex. We begin this section by summarising our findings with respect to the neural correlates of recognition memory, and then elaborate on the effects of the emotional manipulation.

The expected neural response to previously viewed shapes was seen in a network of cortical and subcortical areas, including the PPC, precuneus and hippocampus, regions that are traditionally associated with recognition memory. Increased neural response to old/new differences was observed under conditions of positive mood (relative to negative mood) in bilateral posterior parietal cortex, and, interestingly, in the left orbitofrontal cortex. The left OFC has been reported to be involved in reward and pleasure, memory formation and retrieval of emotionally valenced information (Grabenhorst & Rolls, 2011; Petrides, 2007; Shigemune et al., 2010; A. P. Smith, Henson, Dolan, & Rugg, 2004; Tsukiura & Cabeza, 2011; Young & Shapiro, 2011). Our results indicate that the OFC (Brodmann's area 47) may benefit processing of previously experienced neutral information that is subsequently re-encountered under positive mood states. A main effect of arousal on old/new responses was also evident, with increased responses under conditions of high arousal in the bilateral posterior cingulate gyrus, left superior and posterior parietal cortex and the precuneus. The posterior cingulate cortex is tightly linked with arousal systems in the brainstem and has been posited to play a key role in the relationship between levels of alertness and levels of awareness (Vogt & Laureys, 2005). In addition the posterior cingulate and precuneus cortex are well-established nodes within a broader parietal network for the control of memory retrieval (Wagner, et al., 2005).

Interestingly, neural response in the posterior parietal cortex during memory retrieval was modulated by both mood valence and arousal, and by the interaction of those two factors. While there was considerable overlap between the valence and arousal activations – specifically, in the inferior parietal lobule and around the intraparietal sulcus – the two main effects show a clear dorsal/ventral distinction. Arousal condition modulated recognition memory responses in regions of the dorsal PPC including the intraparietal sulcus and superior parietal lobe. In contrast, variation in mood valence (positive/negative) modulated recognition memory response in ventral PPC, in the angular gyrus and inferior parietal lobe. The interaction between valence and arousal condition activated a PPC cluster that was both ventral and lateral to the regions modulated by mood or arousal alone. These findings demonstrate that neural activity underlying recognition memory retrieval is sensitive to relatively small fluctuations in both mood valence and arousal which also influence memory performance. Some previous studies have described an effect of stimulus valence on activity in the inferior parietal lobule (Kensinger & Corkin, 2004; Mickley Steinmetz & Kensinger, 2009), corresponding to the ventral PPC activations reported here, but these studies assessed the influence of the emotional characteristics of the items on memory encoding. To our knowledge, however, no previous studies have investigated the influence of arousal on parietal contributions to post-encoding memory processes (i.e. retrieval) for otherwise neutral items.

Despite its frequent appearance in memory retrieval studies, it has been suggested that the PPC's role is not mnemonic, but rather relates to the salience or 'target-value' of the recognised items (Vilberg & Rugg, 2008). According to this theory, the PPC may play a role in categorising items according to their relevance to on-going tasks. The attention to memory hypothesis (Cabeza, et al., 2008; Ciaramelli, et al., 2010) proposes a functional segregation of the PPC for this purpose, positing that dorsal PPC regions (including the superior parietal lobule and intraparietal sulcus) underlie top-down, voluntary allocation of attention to memory while ventral PPC (including the supramarginal gyrus and angular gyrus) is recruited during bottom-up attentional processes such as those involved in the in automatic guidance of attention to memory contents.

To investigate the parietal attention-to-memory hypothesis in the context of our emotional manipulation, we conducted region of interest analyses in dorsal and ventral regions of the PPC that have been previously shown to underlie top-down and bottom-up attention to memory, respectively (Ciaramelli, et al., 2008). These analyses confirmed that arousal effects were observed only in the dorsal PPC, while effects of mood valence were observed dorsally and ventrally. The interaction between mood valence and arousal was only observed in the ventral ROI. Together, these findings demonstrate the parcellation of posterior parietal areas for recognition memory as a function of emotional state.

The finding that increased levels of arousal during recognition memory recruits dorsal posterior parietal regions suggests that arousal exerts top-down control over recognition memory, perhaps directing more attentional resources towards the memory task. This thesis is supported by research demonstrating that similar dorsal parietal regions are recruited when participants voluntarily shift their attention during performance of a memory task (Tamber-Rosenau, Esterman, Chiu, & Yantis, 2011), and by recent work showing that emotional arousal (irrespective of mood valence) enhances top-down prioritisation of goal-relevant memory traces (Sakaki, Fryer, & Mather, 2013). The effects of mood valence may be more passive; positive emotion has been associated with a broadening of spatial attention and increased susceptibility to peripheral stimuli and distractors (Basso, et al., 1996; Gasper & Clore, 2002; Jefferies, et al., 2008; Vanlessen, Rossi, De Raedt, & Pourtois, 2013). The ventral parietal regions that are reported here to be modulated by mood valence have previously been linked with bottom-up attentional processes during memory tasks (Cabeza, et al., 2008; Ciaramelli, et al., 2010), whereby attention is automatically captured by old stimuli, leading to retrieval of those items from memory. That recognition responses in ventral PPC were modulated by an interaction between mood valence and arousal is noteworthy, and indicates that response in ventral parietal regions is not merely modulated by changes in arousal but also dependent on the specific mood state experienced by the participants. In particular, the effect of mood on recognition responses in ventral PPC was enhanced under relative high (vs. low) levels of arousal. On these grounds, future studies ought to avoid conflating levels of positive and negative arousal while controlling for the valence dimension.

The behavioural data reported here indicate an interaction between mood valence and arousal on recognition performance, such that identification of novel items was faster during the negative mood/high arousal and positive mood/low arousal conditions. There was also a non-significant trend towards increased sensitivity to old/new differences during the positive mood/high arousal and negative mood/low arousal conditions. The pattern of results described here is consonant with the emotional effects on recognition performance that we observed in our original behavioural study (Greene, et al., 2010). The effects reported here were however weaker than those described in that study, and only manifested in the first half of the experiment, suggesting that the behavioural effects of the emotional induction wore off relatively quickly. The fMRI analyses supported this hypothesis, showing that the neural effects of emotion on recognition memory were stronger in the first half of the experiment. Despite the weak behavioural effects, the pattern of subjective ratings of mood valence and arousal indicated that the desired emotional states were successfully induced, and we observed clear effects of the emotional conditions on BOLD activation associated with memory recognition.

In sum, we describe for the first time a neural circuitry involving the posterior parietal cortex and orbitofrontal cortex that is sensitive to the modulation of memory responses by emotion. This novel delineation of distinct and overlapping networks mediating the effect of mood valence and arousal on recognition of emotionally neutral stimuli indicates that the neural substrates of human memory can be fractionated based on internal emotional state.

References

Anderson, A., Wais, P., & Gabrieli, J. (2006). Emotion Enhances Remembrance of Neutral Events Past. *Proceedings of the National Academy of Sciences of the United States of America, 103*(5), 1599-1604.

Basso, M. R., Schefft, B. K., Ris, M. D., & Dember, W. N. (1996). Mood and global-local visual processing. *Journal of the International Neuropsychological Society, 2*(3), 249-255.

Beckmann, C. F., Jenkinson, M., & Smith, S. M. (2003). General multilevel linear modeling for group analysis in FMRI. *Neuroimage, 20*(2), 1052-1063.

Blood, A. J., Zatorre, R. J., Bermudez, P., & Evans, A. C. (1999). Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nature Neuroscience, 2*(4), 382-387.

Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: an attentional account. *Nat Rev Neurosci, 9*(8), 613-625.

Ciaramelli, E., Grady, C., Levine, B., Ween, J., & Moscovitch, M. (2010). Top-down and bottom-up attention to memory are dissociated in posterior parietal cortex: neuroimagingand and neuropsychological evidence. *Journal of Neuroscience, 30*(14), 4943-4956.

Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: a hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia, 46*(7), 1828-1851.

Ciavarro, M., Ambrosini, E., Tosoni, A., Committeri, G., Fattori, P., & Galletti, C. (2013). rTMS of Medial Parieto-occipital Cortex Interferes with Attentional Reorienting during Attention and Reaching Tasks. *Journal of Cognitive Neuroscience, 25*(9), 1453-1462.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature*

Neuroscience, 3(3), 292-297.

Corson, Y., & Verrier, N. (2007). Emotions and false memories: valence or arousal? *Psychol Sci, 18*(3), 208-211.

Davidson, P. S., Anaki, D., Ciaramelli, E., Cohn, M., Kim, A. S., Murphy, K. J., et al. (2008). Does lateral parietal cortex support episodic memory? Evidence from focal lesion patients. *Neuropsychologia, 46*(7), 1743-1755.

Demeter, E., Hernandez-Garcia, L., Sarter, M., & Lustig, C. (2011). Challenges to attention: A continuous arterial spin labeling (ASL) study of the effects of distraction on sustained attention. *NeuroImage, 54*(2), 1518-1529.

Denkova, E., Dolcos, S., & Dolcos, F. (2013a). The Effect of Retrieval Focus and Emotional Valence on the Inferior Frontal Cortex Activity during Autobiographical Recollection. *Front Behav Neurosci, 7*, 192.

Denkova, E., Dolcos, S., & Dolcos, F. (2013b). The Effect of Retrieval Focus and Emotional Valence on the Medial Temporal Lobe Activity during Autobiographical Recollection. *Front Behav Neurosci, 7*, 109.

Dolcos, F., LaBar, K. S., & Cabeza, R. (2004). Dissociable effects of arousal and valence on prefrontal activity indexing emotional evaluation and subsequent memory: an event-related fMRI study. [doi: DOI: 10.1016/j.neuroimage.2004.05.015]. *Neuroimage, 23*(1), 64-74.

Finn, B., & Roediger, H. L., 3rd. (2011). Enhancing retention through reconsolidation: negative emotional arousal following retrieval enhances later recall. *Psychol Sci, 22*(6), 781-786.

Gasper, K., & Clore, G. L. (2002). Attending to the big picture: mood and global versus local processing of visual information. *Psychological Science, 13*(1), 34-40.

Grabenhorst, F., & Rolls, E. T. (2011). Value, pleasure and choice in the ventral prefrontal cortex.

Trends Cogn Sci, 15(2), 56-67.

Greene, C. M., Bahri, P., & Soto, D. (2010). Interplay between affect and arousal in recognition memory. [10.1371/journal.pone.0011739]. *PLoS One, 5*(7), e11739.

Han, S., Jiang, Y., Gu, H., Rao, H., Mao, L., Cui, Y., et al. (2004). The role of human parietal cortex in attention networks. *Brain, 127*(Pt 3), 650-659.

Haramati, S., Soroker, N., Dudai, Y., & Levy, D. A. (2008). The posterior parietal cortex in recognition memory: a neuropsychological study. *Neuropsychologia, 46*(7), 1756-1766.

Isen, A. M., Johnson, M. M., Mertz, E., & Robinson, G. F. (1985). The influence of positive affect on the unusualness of word associations. *J Pers Soc Psychol, 48*(6), 1413-1426.

Jefferies, L. N., Smilek, D., Eich, E., & Enns, J. T. (2008). Emotional valence and arousal interact in attentional control. *Psychological Science, 19*(3), 290-295.

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. *Neuroimage, 17*(2), 825-841.

Jenkinson, M., & Smith, S. (2001). A global optimisation method for robust affine registration of brain images. *Med Image Anal, 5*(2), 143-156.

Judde, S., & Rickard, N. (2010). The effect of post-learning presentation of music on long-term word-list retention. *Neurobiology of Learning and Memory*.

Kalpouzos, G., Fischer, H., Rieckmann, A., Macdonald, S. W., & Backman, L. (2012). Impact of negative emotion on the neural correlates of long-term recognition in younger and older adults. *Front Integr Neurosci, 6*, 74.

Kensinger, E. A., & Corkin, S. (2004). Two routes to emotional memory: distinct neural processes for valence and arousal. *Proceedings of the National Academy of Sciences of the*

United States of America, 101(9), 3310-3315.

Kim, H. (2011). Neural activity that predicts subsequent memory and forgetting: a meta-analysis of 74 fMRI studies. *Neuroimage, 54*(3), 2446-2461.

Kuhbandner, C., & Pekrun, R. (2013). Affective state influences retrieval-induced forgetting for integrated knowledge. *PLoS One, 8*(2), e56617.

Lane, A. R., Smith, D. T., Schenk, T., & Ellison, A. (2011). The involvement of posterior parietal cortex in feature and conjunction visuomotor search. *J Cogn Neurosci, 23*(8), 1964-1972.

Liu, D. L., Graham, S., & Zorawski, M. (2008). Enhanced selective memory consolidation following post-learning pleasant and aversive arousal. *Neurobiology of Learning and Memory, 89*(1), 36-46.

Mather, M. (2007). Emotional Arousal and Memory Binding: An Object-Based Framework. *Perspectives on Psychological Science, 2*, 33-52.

Mickley Steinmetz, K. R., & Kensinger, E. A. (2009). The effects of valence and arousal on the neural activity leading to subsequent memory. *Psychophysiology, 46*(6), 1190-1199.

Nielson, K. A., & Arentsen, T. J. (2012). Memory modulation in the classroom: selective enhancement of college examination performance by arousal induced after lecture. *Neurobiol Learn Mem, 98*(1), 12-16.

Nielson, K. A., & Lorber, W. (2009). Enhanced post-learning memory consolidation is influenced by arousal predisposition and emotion regulation but not by stimulus valence or arousal. *Neurobiol Learn Mem, 92*(1), 70-79.

Ochsner, K. N. (2000). Are affective events richly recollected or simply familiar? The experience and process of recognizing feelings past. [Article]. *Journal of Experimental Psychology-General, 129*(2), 242-261.

Petrides, M. (2007). The orbitofrontal cortex: novelty, deviation from expectation, and memory. *Ann N Y Acad Sci, 1121*, 33-53.

Rossi, S., Pasqualetti, P., Zito, G., Vecchio, F., Cappa, S. F., Miniussi, C., et al. (2006). Prefrontal and parietal cortex in human episodic memory: an interference study by repetitive transcranial magnetic stimulation. *Eur J Neurosci, 23*(3), 793-800.

Rowe, G., Hirsh, J. B., & Anderson, A. K. (2007). Positive affect increases the breadth of attentional selection. *Proceedings of the National Academy of Sciences of the United States of America, 104*(1), 383-388.

Sakaki, M., Fryer, K., & Mather, M. (2013). Emotion Strengthens High-Priority Memory Traces but Weakens Low-Priority Memory Traces. *Psychol Sci*.

Sharot, T., & Yonelinas, A. P. (2008). Differential time-dependent effects of emotion on recollective experience and memory for contextual information. *Cognition, 106*(1), 538-547.

Shigemune, Y., Abe, N., Suzuki, M., Ueno, A., Mori, E., Tashiro, M., et al. (2010). Effects of emotion and reward motivation on neural correlates of episodic memory encoding: a PET study. *Neurosci Res, 67*(1), 72-79.

Simons, J. S., Peers, P. V., Mazuz, Y. S., Berryhill, M. E., & Olson, I. R. (2010). Dissociation between memory accuracy and memory confidence following bilateral parietal lesions. *Cereb Cortex, 20*(2), 479-485.

Smith, A. P., Henson, R. N., Dolan, R. J., & Rugg, M. D. (2004). fMRI correlates of the episodic retrieval of emotional contexts. *Neuroimage, 22*(2), 868-878.

Smith, S. M. (2002). Fast robust automated brain extraction. *Hum Brain Mapp, 17*(3), 143-155.

Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behav Res Methods Instrum Comput, 31*(1), 137-149.

Tamber-Rosenau, B. J., Esterman, M., Chiu, Y. C., & Yantis, S. (2011). Cortical mechanisms of cognitive control for shifting attention in vision and working memory. *J Cogn Neurosci, 23*(10), 2905-2919.

Todd, R. M., Talmi, D., Schmitz, T. W., Susskind, J., & Anderson, A. K. (2012). Psychophysical and Neural Evidence for Emotion-Enhanced Perceptual Vividness. *The Journal of Neuroscience, 32*(33), 11201-11212.

Tsukiura, T., & Cabeza, R. (2011). Remembering beauty: roles of orbitofrontal and hippocampal regions in successful memory encoding of attractive faces. *Neuroimage, 54*(1), 653-660.

Vanlessen, N., Rossi, V., De Raedt, R., & Pourtois, G. (2013). Positive emotion broadens attention focus through decreased position-specific spatial encoding in early visual cortex: evidence from ERPs. *Cogn Affect Behav Neurosci, 13*(1), 60-79.

Vilberg, K. L., & Rugg, M. D. (2008). Memory retrieval and the parietal cortex: a review of evidence from a dual-process perspective. *Neuropsychologia, 46*(7), 1787-1799.

Vogt, B. A., & Laureys, S. (2005). Posterior cingulate, precuneal and retrosplenial cortices: cytology and components of the neural network correlates of consciousness. *Prog Brain Res, 150*, 205-217.

Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. [doi: DOI: 10.1016/j.tics.2005.07.001]. *Trends in Cognitive Sciences, 9*(9), 445-453.

Warbrick, T., Reske, M., & Shah, N. J. (2013). Do EEG paradigms work in fMRI? Varying task demands in the visual oddball paradigm: Implications for task design and results interpretation. *NeuroImage, 77*(0), 177-185.

Woolrich, M. (2008). Robust group analysis using outlier inference. *Neuroimage, 41*(2), 286-301.

Woolrich, M. W., Behrens, T. E., Beckmann, C. F., Jenkinson, M., & Smith, S. M. (2004). Multilevel linear modelling for FMRI group analysis using Bayesian inference. *Neuroimage, 21*(4), 1732-1747.

Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of FMRI data. *Neuroimage, 14*(6), 1370-1386.

Yin, X., Zhao, L., Xu, J., Evans, A. C., Fan, L., Ge, H., et al. (2012). Anatomical substrates of the alerting, orienting and executive control components of attention: focus on the posterior parietal lobe. *PLoS One, 7*(11), e50590.

Young, J. J., & Shapiro, M. L. (2011). The orbitofrontal cortex and response selection. *Ann N Y Acad Sci, 1239*, 25-32.

Zhu, X., Wang, X., Parkinson, C., Cai, C., Gao, S., & Hu, P. (2010). Brain activation evoked by erotic films varies with different menstrual phases: An fMRI study. *Behavioural Brain Research, 206*(2), 279-285.

Footnotes

[1] The selection of appropriate musical excerpts took place up to two days before the testing phase. It is therefore unlikely that participants will have retained a clear memory of the rating assigned to each piece during the selection phase.

[2] This result would not survive correction for multiple comparisons if a Bonferroni correction was applied to account for separate analyses of d’, confidence and reaction time data.

Tables

Table 1. Mean values for proportion of hits, proportion of false alarms, d' and confidence ratings across all four emotional conditions (standard deviations in parentheses).

	Positive Mood High Arousal	*Positive Mood Low Arousal*	*Negative Mood High Arousal*	*Negative Mood Low Arousal*
		All trials		
Hits	0.72 (0.18)	0.71 (0.15)	0.74 (0.14)	0.73 (0.14)
False Alarms	0.28 (0.12)	0.28 (0.15)	0.26 (0.12)	0.28 (0.1)
d'	1.38 (1.03)	1.35 (1)	1.40 (0.74)	1.32 (0.56)
RT: old trials (ms)	702.04 (139.8)	724.77 (121.07)	692.06 (173.65)	719.40 (159.47)
RT: new trials (ms)	855.73 (120.07)	833.23 (155.97)	787.62 (184.39)	853.70 (151.13)
Confidence rating	2.05 (0.31)	2.06 (0.29)	2.04 (0.31)	2.06 (0.27)
		First half of trials		
Hits	0.76 (0.18)	0.75 (0.21)	0.74 (0.14)	0.75 (0.18)
False Alarms	0.23 (0.15)	0.26 (0.16)	0.23 (0.19)	0.23 (0.16)
d'	2.22 (1.66)	1.90 (1.57)	1.96 (1.51)	2.11 (1.57)
RT: old trials (ms)	699.72 (162)	728.74 (155.6)	722.93 (228.9)	685.88 (140.7)
RT: new trials (ms)	883.25 (151.6)	846.44 (159.9)	772.96 (217. 3)	865.13 (222.4)
Confidence rating	2.13 (0.32)	2.13 (0.29)	2.11 (0.31)	2.11 (0.3)
		Second half of trials		
Hits	0.68 (0.2)	0.70 (0.2)	0.74 (0.21)	0.72 (0.17)
False Alarms	0.32 (0.19)	0.3 (0.2)	0.28 (0.12)	0.3 (0.17)
d'	1.26 (1.74)	1.51 (2.1)	1.98 (2.38)	1.63 (2)
RT: old trials (ms)	713.72 (174.2)	720.05 (177.4)	673.26 (178.1)	742.09 (216.3)
RT: new trials (ms)	844.15 (164.6)	811.14 (191.9)	799.26 (219.5)	828.28 (182.5)
Confidence rating	1.97 (0.33)	1.98 (0.33)	1.95 (0.33)	20.1 (0.27)

Table 2. Peak coordinates of significantly activated clusters from whole-brain analysis

Region	*Hemisphere*	*Cluster size (voxels)*	*max Z*	*MNI Coordinates*
Mood: positive > negative				
Frontal pole, inferior frontal gyrus, middle frontal gyrus, orbitofrontal cortex, insula, caudate	Left	3294	3.79	-40 36 0
Angular gyrus, superior parietal lobule, supramarginal gyrus, anterior intraparietal sulcus	Right	1566	3.77	36 -50 38
Superior parietal lobule, angular gyrus, supramarginal gyrus, anterior intraparietal sulcus	Left	891	4.04	-30 -44 40
Arousal: high > low				
Precentral gyrus, postcentral gyrus, superior parietal lobule, inferior parietal lobule	Left	2236	4.26	-36 -24 58
Anterior cingulate, posterior cingulate, cuneus, precuneus, intracalcarine cortex	Bilateral	2160	3.71	-2 -42 36
Interaction				
Angular gyrus, inferior parietal lobule, supramarginal gyrus	Left	1125	3.73	-56 -56 24

Table 3. Peak coordinates of significantly activated clusters from ROI analysis in dorsal and ventral PPC.

Region	*Hemisphere*	*Cluster size (voxels)*	*Max Z*	*MNI coordinates*
Dorsal PPC ROI				
Mood: positive > negative				
Inferior parietal lobule; intraparietal sulcus	Left	107	3.21	-32 -66 40
Arousal: high > low				
Inferior parietal lobule; intraparietal sulcus	Left	260	3.05	-38 -64 44
Ventral PPC ROI				
Mood: positive > negative				
Angular gyrus; inferior parietal lobule	Left	124	3.22	-52 -52 40
Interaction				
Angular gyrus; inferior parietal lobule	Left	224	3.41	-54 -56 32

Table 4. Peak coordinates of significantly activated clusters during the first and second half of the recognition test.

Region	*Hemisphere*	*Cluster size (voxels)*	*Max Z*	*MNI coordinates*
First half of recognition test				
Mood: positive > negative				
Inferior and middle frontal gyrus, anterior and posterior cingulate, inferior and superior parietal lobule, supramarginal gyrus, postcentral gyrus, precuneus and cuneus	Bilateral	39527	5.19	-36 36 4
Arousal: high > low				
Precentral gyrus, supplementary motor area, anterior and posterior cingulate, left precuneus, left postcentral gyrus.	Bilateral	3482	4.28	-40 -36 60
Thalamus	Bilateral	1297	3.69	-4 -22 10
Frontal operculum, sub-callosal cortex.	Left	901	3.47	-4 10 -4
Interaction (small volume correction, ventral PPC ROI)				
Angular gyrus	Left	72	3.13	-58 -56 36
Second half of recognition test				
Arousal: high > low				
Postcentral gyrus, supramarginal gyrus, superior parietal lobule, inferior parietal lobule.	Left	801	3.62	-50 -30 52

Figures

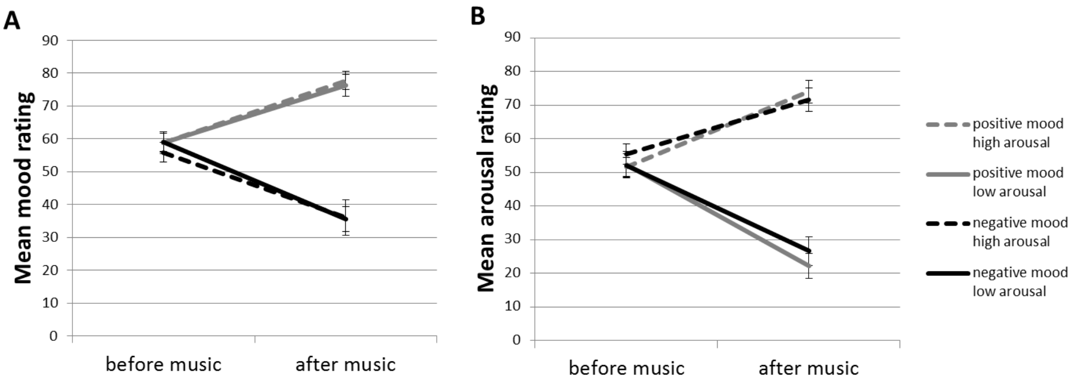


Figure 1. Subjective mood and arousal ratings before and after music exposure. Panel A: ratings of mood increased following presentation of music rated as positive and decreased following music rated as negative. Panel B: subjective arousal ratings increased following highly arousing music and decreased following non-arousing, or calming, music. Error bars represent standard errors of the mean.

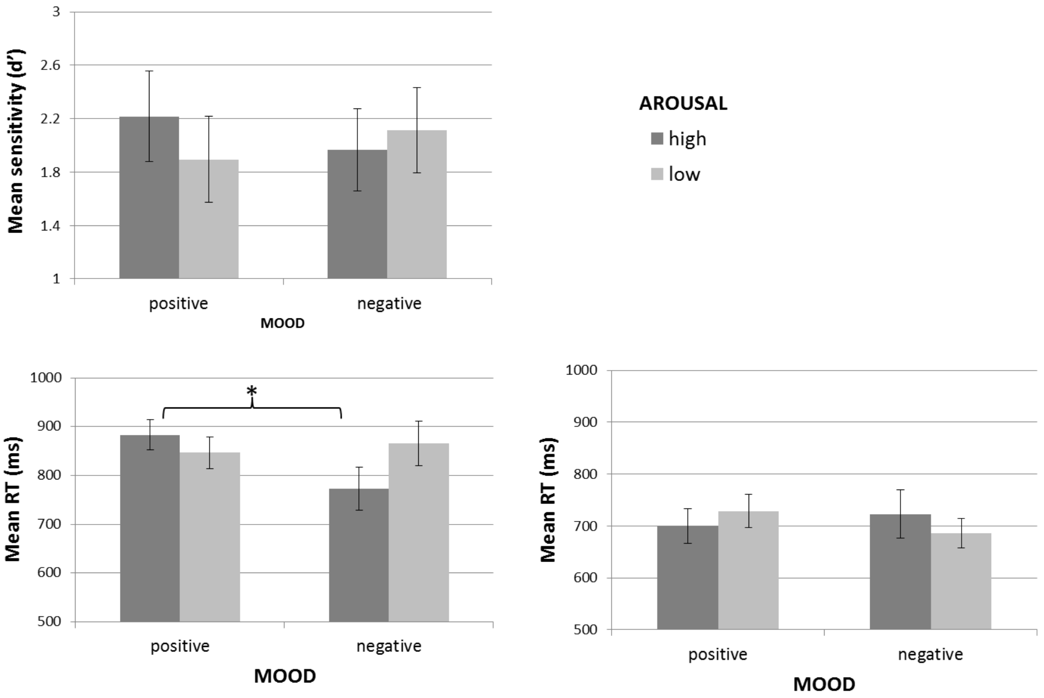


Figure 2. Influence of mood and arousal on recognition memory during the first half of the recognition test. (A) Mean sensitivity; (B) Mean RT during new trials; (C) mean RT during old trials. Error bars represent standard errors of the mean.

* Significant difference between conditions (p < .05)

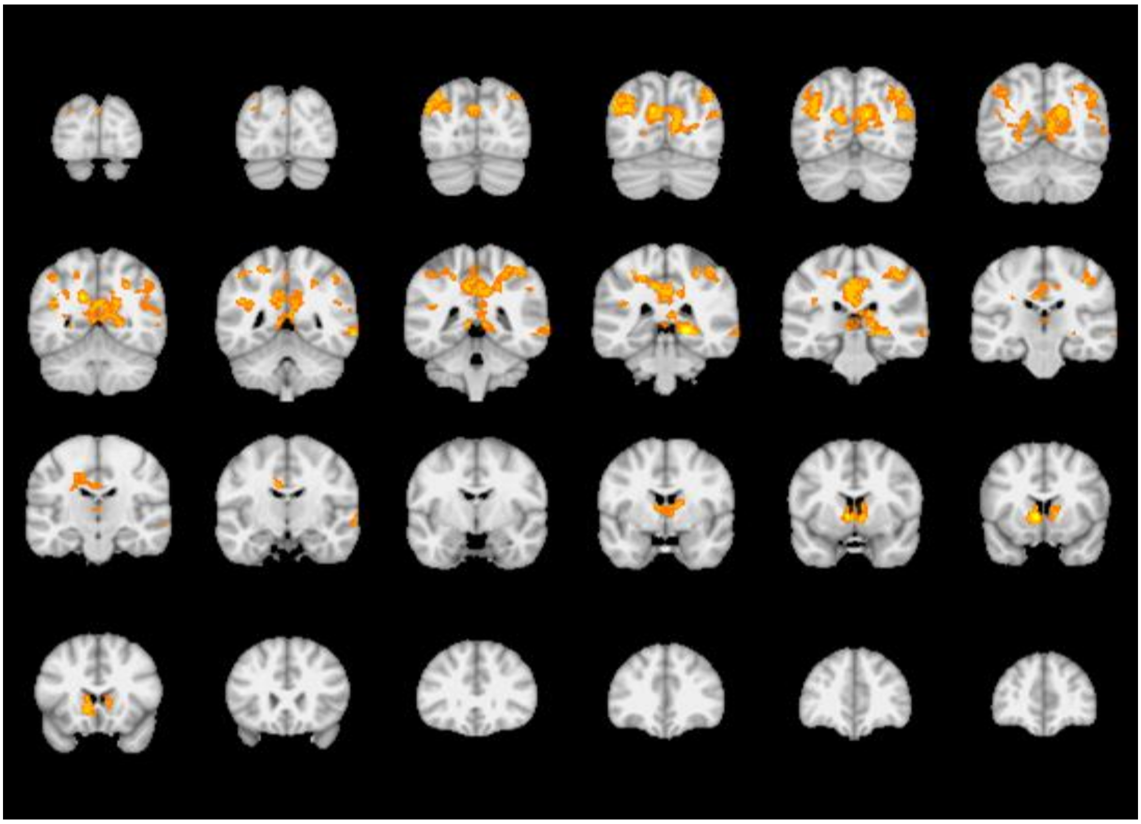


Figure 3. Regions showing increased BOLD response during presentation of old shapes relative to new shapes in recognition test.

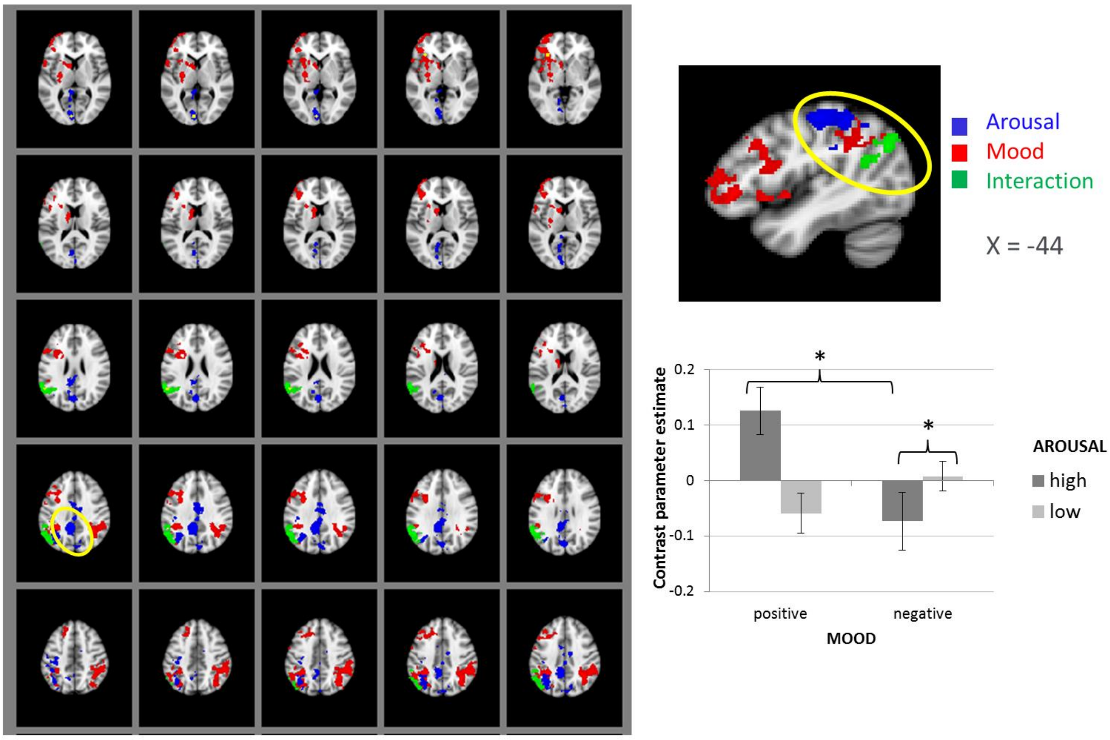


Figure 4. Main effects of mood condition (red voxels), arousal condition (blue voxels) and the interaction between the two variables (green voxels). Top right panel depicts the relative location of activations in left posterior parietal cortex from the three contrasts. Bottom right panel depicts parameter estimates from the interaction contrast, indicating that BOLD response in the inferior PPC increased with arousal during positive mood but decreased with arousal during negative mood.

* Significant difference between conditions, p < .05

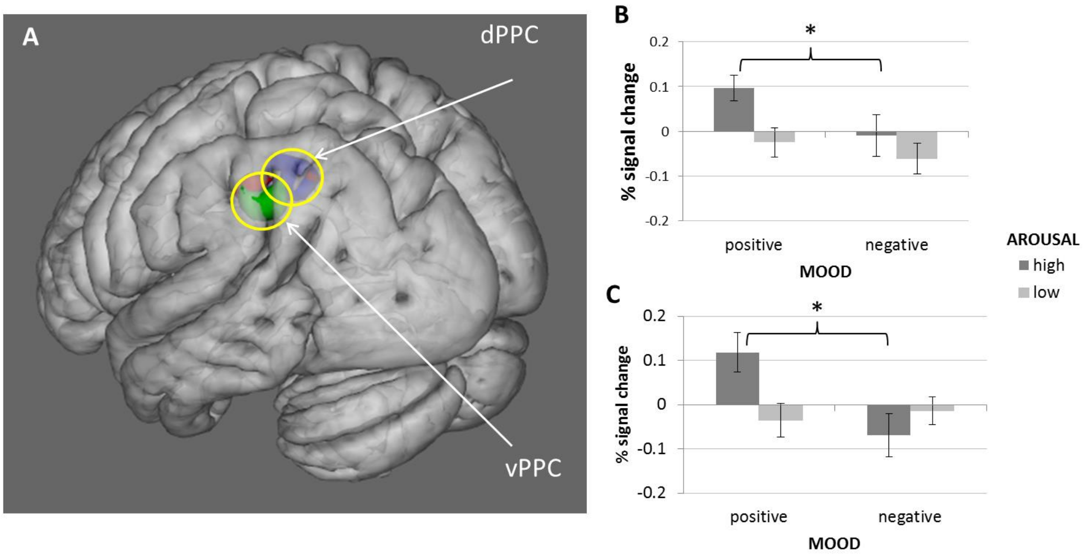
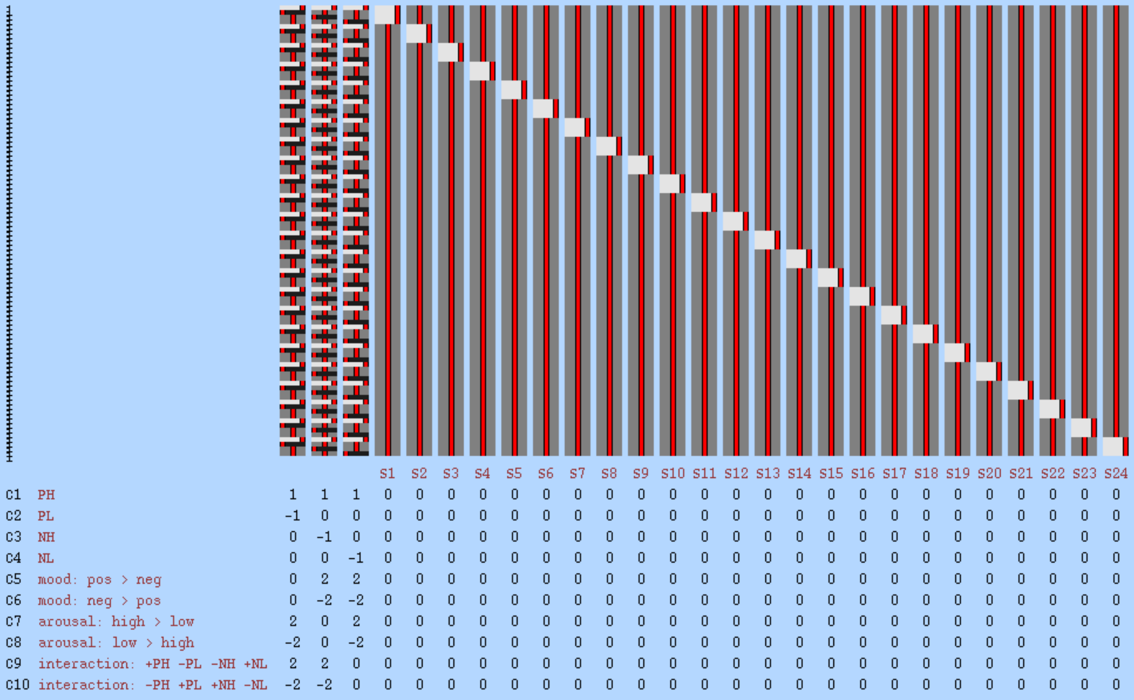


Figure 5. Results of ROI analysis. (A) Regions of interest in dorsal and ventral PPC. Red voxels = main effect of mood valence; blue voxels = main effect of arousal; green voxels = interaction effect. (B) Contrast parameter estimates from dorsal PPC ROI. (C) Contrast parameter estimates from ventral PPC ROI.

* Significant difference between conditions, p < .05



					S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24
C1	PH	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C2	PL	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C3	NH	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C4	NL	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C5	mood: pos > neg	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C6	mood: neg > pos	0	-2	-2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C7	arousal: high > low	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C8	arousal: low > high	-2	0	-2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C9	interaction: +PH -PL -NH +NL	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C10	interaction: -PH +PL +NH -NL	-2	-2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary Figure 1. FEAT model and contrast specification for quadrupled t-test design.