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Elizabeth G. Kehoe
Trinity College Dublin

John M. Toomey
Technological University Dublin

Joshua H. Balsters
Trinity College Dublin

Arun L.W. Bokde
Technological University Dublin

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Personality modulates the effects of emotional arousal and valence on brain activation

Elizabeth G. Kehoe,[1] John M. Toomey,[2] Joshua H. Balsters,[3] and Arun L. W. Bokde[1]

[1]Cognitive Systems Group, Discipline of Psychiatry, School of Medicine and the Trinity College Institute of Neuroscience (TCIN), Trinity College Dublin, [2]School of Computing, Dublin Institute of Technology and [3]The School of Psychology and The Trinity College Institute of Neuroscience (TCIN), Trinity College Dublin, Dublin, Ireland.

The influence of personality on the neural correlates of emotional processing is still not well characterized. We investigated the relationship between extraversion and neuroticism and emotional perception using functional magnetic resonance imaging (fMRI) in a group of 23 young, healthy women. Using a parametric modulation approach, we examined how the blood oxygenation level dependent (BOLD) signal varied with the participants' ratings of arousal and valence, and whether levels of extraversion and neuroticism were related to these modulations. In particular, we wished to test Eysenck's biological theory of personality, which links high extraversion to lower levels of reticulothalamic–cortical arousal, and neuroticism to increased reactivity of the limbic system and stronger reactions to emotional arousal. Individuals high in neuroticism demonstrated reduced sustained activation in the orbitofrontal cortex (OFC) and attenuated valence processing in the right temporal lobe while viewing emotional images, but an increased BOLD response to emotional arousal in the right medial prefrontal cortex (mPFC). These results support Eysenck's theory, as well as our hypothesis that high levels of neuroticism are associated with attenuated reward processing. Extraversion was inversely related to arousal processing in the right cerebellum, but positively associated with arousal processing in the right insula, indicating that the relationship between extraversion and arousal is not as simple as that proposed by Eysenck.

Keywords: arousal; extraversion; fMRI; neuroticism; valence

INTRODUCTION

Extraversion and neuroticism are two of the most widely studied personality traits (Canli *et al.*, 2001; Hamann and Canli, 2004) and they are common to several dominant theories of personality including Costa and McCrae's Big Five model (2003) and Eysenck's biological approach (1967, 1994). Extraversion and neuroticism have been found to correlate robustly with positive and negative emotionality, respectively (Costa and McCrae, 1980; Rusting and Larsen, 1997), a relationship which seems to remain stable across the lifespan (Wilson and Gullone, 1999); and differences in these traits are known to influence emotional and cognitive processing (Bradley and Mogg, 1994; Amin *et al.*, 2004; Canli, 2004; Kumari *et al.*, 2004, 2007).

Although neuroticism describes differences in a personality dimension rather than a clinical disorder, it can be of high clinical relevance as it is a risk factor for developing anxiety and depression disorders (Derryberry and Reed, 1994; Kendler *et al.*, 2004). Several neuroimaging studies have found that this trait is most notably associated with biases towards negative emotional processing (Canli *et al.*, 2001; Haas *et al.*, 2007, 2008; Chan *et al.*, 2008, 2009; Cremers *et al.*, 2010). However, there has been little focus to date on the relationship between neuroticism and positive emotional perception. There is evidence that depressed patients demonstrate reduced neural responding to positive emotional stimuli (Shestyuk *et al.*, 2005), and given that neuroticism is a risk factor for depression, we were interested in investigating whether high levels of this trait are associated with an attenuated neural response to positive valence.

According to Eysenck's biological theory of personality (Eysenck and Eysenck, 1991; Eysenck, 1994), the neuroticism dimension is also posited to affect how individuals respond to emotional arousal. Whereas extraversion is considered to be linked to differences in the functioning of the reticulothalamic–cortical arousal system, high levels of neuroticism are theorized to reflect increased reactivity of the limbic system, which predisposes individuals high in neuroticism to react strongly to emotionally arousing experiences and take longer to return to pre-arousal states. In spite of these predictions about the relationship between personality and reactivity to emotional arousal, the neural bases of these relationships have never been investigated using functional magnetic resonance imaging (fMRI). Therefore, we were interested in examining whether differences in this trait are related to how emotional arousal is processed in the brain.

Eysenck's biological theory of extraversion (1967, 1994) proposes that differences in this personality dimension are reflective of differences in a reticulothalamic–cortical arousal system, with extraverts experiencing both lower baseline

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Correspondence should be addressed to Elizabeth G. Kehoe, Lloyd Institute, Trinity College Institute of Neuroscience, Trinity College Dublin, Dublin 2, Ireland. E-mail: elkehoe@tcd.ie

levels of cortical arousal, as well as low arousability of the cortex, i.e. they show a smaller change in cortical activity in response to arousing stimuli than introverts (Eysenck, 1967; Eysenck and Eysenck; 1991; Hagemann *et al.*, 2009). It is this chronic intrinsic under-arousal which is thought to drive highly extraverted people to engage in typically extraverted behaviours in order to enhance their low arousal states (Eysenck, 1994). Furthermore, this under-arousability enables extraverts to tolerate much higher levels of arousal than introverts, who withdraw to avoid further increases in arousal which they find difficult to withstand (Eysenck, 1967, 1994).

Several neuroimaging studies have supported this theory of extraversion (Kumari *et al.*, 2004; O'Gorman *et al.*, 2006; Hagemann *et al.*, 2009); for example, Hagemann and colleagues (2009) found that alpha activity as measured by resting-state electroencephalography (EEG), which is indicative of lower arousal states (Barry *et al.*, 2011; De Cesarei and Codispoti, 2011) was positively associated with extraversion levels in left and right frontal sites, indicating that extraverted individuals had lower baseline levels of cortical arousal; while Kumari *et al.* (2004) found that levels of extraversion were negatively associated with resting fMRI signals in the thalamus and in Broca's area extending to Wernicke's area. Given the predictions of Eysenck's arousal hypothesis, one might expect that in the context of emotional processing, extraversion levels would have a pervasive influence on the perception of emotional arousal; however, the relationship between extraversion and the neural substrates of emotional arousal processing are unknown. Therefore, we sought to investigate this question using fMRI.

In the present study, we used fMRI to examine how levels of extraversion and neuroticism are related to the neural substrates of emotional arousal and valence processing in a group of 23 young healthy women. We utilized an amplitude modulation approach to dissociate the effects of arousal and valence on the blood oxygenation level-dependent (BOLD) signal during an emotional image viewing task. We examined single trial dynamics, whereby the subject's valence and arousal ratings for each stimulus image were included as a parametric weight in our model. We then examined how these effects varied as a function of neuroticism and extraversion levels.

We used the Eysenck personality questionnaire to measure levels of neuroticism and extraversion (Eysenck and Eysenck, 1991). The primary reason we used Eysenck's scale and theoretical framework is that this personality theory has a strong biological component and causal explanation, with individual differences in personality thought to arise from differences in brain function. Specifically, Eysenck proposed that differences in the extraversion dimension are reflective of differences in the functioning of the reticular arousal system, while neuroticism reflects differences in the limbic system's emotional responses (Eysenck, 1967, 1994). Gray's (1982, 1990, 1997) theory proposes that there are two basic motivational systems in the brain which drive behavioural responses, an approach and an inhibition system, which differ between individuals, representing differences in sensitivity to environmental cues of reward and punishment. This theory also has a strong biological component, however, due to the focus on behavioural inhibition in the avoidance of punishment cues, we choose Eysenck's model as having potentially more predictive power in the context of our experimental questions, namely concerning the processing of rewarding stimuli, and arousal in particular. Finally, the Big Five model of Costa and McCrae (McCrae and Costa, 2003), although very popular in the field of personality has been criticized for being more of a descriptive model, with less scope for explanation as it contains no specific predictions about the biological basis of personality (Block, 2010).

In particular, we were interested in testing the relationship between extraversion and the perception of emotional arousal, and predicted that individuals high in this trait would experience less brain activation in response to increasing levels of arousal, in accord with the predictions of Eysenck's arousal hypothesis (Eysenck, 1994). Second, we wished to examine the relationship between neuroticism and positive valence and arousal processing. We predicted that high levels of neuroticism would be associated with reduced neural activation in response to positive valence, but an increased response to emotional arousal.

MATERIALS AND METHODS

Participants

Twenty-three young (mean age = 23.04 ± 3.46 years, age range = 19–29 years), healthy, right-handed women took part in the study. Only women were included as there have been considerable differences found between genders in emotional reactivity (Bradley *et al.*, 2001b) in the neural representation of emotion (Beck *et al.*, 1996; Cahill *et al.*, 2001; Wager *et al.*, 2003; Wrase *et al.*, 2003) and in levels of neuroticism (Lynn and Martin, 1997). They had no history of psychiatric or neurological illness and were not depressed [Beck Depression Inventory scores: 4.83 ± 3.38; cut-off score for mild depression = 14 (Beck *et al.*, 1996)]. The study had full ethical approval from the St James Hospital and the Adelaide and Meath Hospital, incorporating the National Children's Hospital Research Ethics Committee. All of the participants gave written informed consent and were paid €40 for taking part.

Personality measurement

The participants completed the Eysenck personality questionnaire, revised edition short scale (EPQ-R, Eysenck and Eysenck, 1991), a self-report questionnaire which measures levels of extraversion, neuroticism and psychoticism on scales ranging from 0 to 12, with 0 indicating the lowest level of the trait and 12 the highest level of the trait. We focused our analyses on neuroticism and extraversion.

Stimuli

The stimuli consisted of 190 coloured photographs. They were a combination of 98 images from the International Affective Picture System (IAPS, Lang *et al.*, 2007) and 92 images gathered by the experimenter from various sources. They were either positive or neutral in valence and they varied in arousal levels. The stimuli were limited to neutral and positive valence only for several reasons. First, although arousal and valence tend to be highly correlated (Bradley *et al.*, 1992; Ribeiro *et al.*, 2005), we included images which were positive or neutral in valence and which varied in arousal level, allowing us to match the stimuli along one dimension while varying along the other and so investigate their effect on the BOLD signal separately. However, the co-variation of arousal with valence is particularly strong in the case of negative images, which tend to be rated as more arousing than positive images (Lang *et al.*, 2008). Therefore, it was not possible to have enough negative low arousal exemplars. Second, we were particularly interested in examining the relationship between neuroticism and positive valence. Third, we wanted to be sure that any linear associations with valence in the imaging paradigm could be interpreted clearly as being associated with increasing valence from neutral to positive, and not confounded by the inclusion of negative stimuli.

The IAPS was supplemented to increase the number of positive, low arousal and neutral, higher arousal images. None of the images we used were of a sexual nature. The new images were chosen to be as similar as possible to the IAPS images and so, included very similar content and a mixture of objects, scenes, animals and people as does the IAPS.

As far as was possible the images of different valence and arousal levels were chosen to contain the same number of people, animals, scenes and objects. Before the experiment, all of the images were rated by 15 age-matched controls, of which 8 were women, along the dimensions of valence, arousal and dominance. These ratings were collected to both devise approximate ratings for the new images and also to assess the level of agreement between the IAPS standard ratings, which are devised from a US sample, and the ratings of a group of young Irish adults. Further details of the ratings of the new images and the IAPS images, as well as examples of images from our stimulus set can be found in the Supplementary Data. The stimuli were delivered using Presentation v. 13.0 (Neurobehavioral Systems, Albany, CA, USA).

Experimental design

Functional MRI paradigm

The participants viewed 190 coloured images as they underwent fMRI. To avoid long-lasting mood states, the images were pseudo-randomized so that no more than three images of the same valence or arousal type were presented in a row. The task consisted of two experimental runs, each containing 95 trials and lasting ~20 min. In each trial, an image was presented in the centre of a white background for 3000 ms, and after a delay of 1000–3000 ms (pseudo-random jitter), a prompt appeared on screen for 2000 ms asking the participants to classify the image they had just seen as 'Living' or 'Non-living'. The participants were instructed to make their response by pressing either the left or right button on a MR-compatible button response box held in their right hand, to correspond with the left/right position of the 'Living/Non-living' word on the screen. This shallow encoding task was intended to maintain the participants' focus for the duration of the task, without explicitly drawing their attention to the emotional content of the stimuli (Kensinger *et al.*, 2007). The onset of both the images and the prompts were jittered to ensure optimal sampling of the haemodynamic response (Josephs and Henson, 1999).

Post-scanning image rating

The participants did not rate the images while in the scanner as emotional evaluation has been found to result in attenuation of the neural response to emotional stimuli, thought to be due to the top–down influences of cognitive re-evaluation and judgement (Hariri *et al.*, 2000; Taylor *et al.*, 2003). Instead, they returned 2–3 days later and rated all of the images they had seen during the scanning session, as well as 48 negative images from the IAPS along the dimensions of valence, arousal and dominance. (The 2–3 days gap was to facilitate the collection of memory recall information that is not part of this report). The negative images were included in the rating task to provide contrast to the others, to ensure that the participants understood the full remit of the valence dimension. A computerized version of the Self-Assessment Manikin (SAM, Lang *et al.*, 2008) was used to operationalize valence, arousal and dominance.

MRI scanning protocol

Imaging data were acquired using a Philips Intera Achieva 3.0 T MR system (Best, The Netherlands). The BOLD signal changes were measured using a T2*-weighted echo-planar imaging sequence with $TR = 2000$ ms and $TE = 30$ ms. Each volume of data covered the entire brain with 39 slices, and the slices were acquired in interleaved sequence from inferior to superior direction. In total 598 volumes were acquired during each of the two runs, with voxel dimensions of $3.5 \times 3.5 \times 3.85$ mm and a 0.35 mm gap between the slices. A T1W/IR sequence was used to collect a 3D high-resolution anatomical image with voxel dimensions equal to $0.9 \times 0.9 \times 0.9$ mm for structural localization.

Analysis

Behavioural data

The experimental log files were parsed using python scripts (version 2.6.2, http://www.python.org/) to extract performance and rating information. These data were then used to create individually tailored regressors for each participant

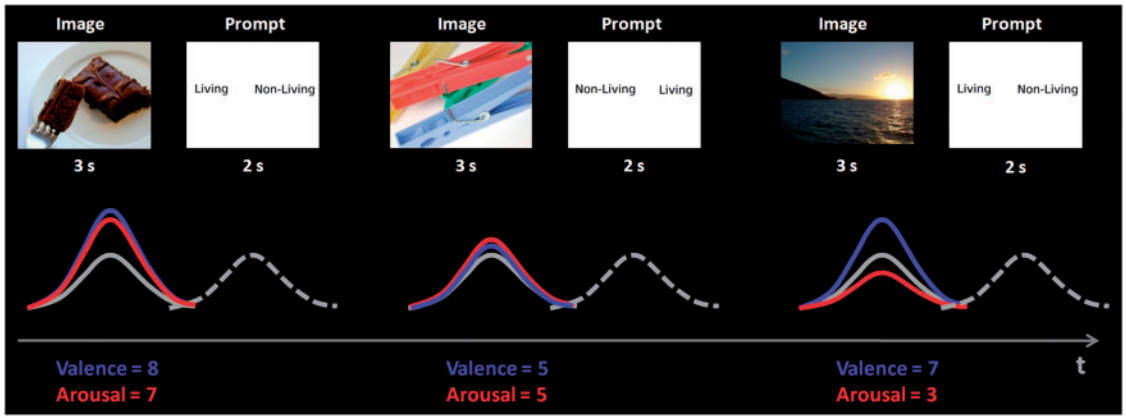

Fig. 1 Illustration showing a schema of the fMRI analysis and parametric modelling of the haemodynamic response function. Each trial consisted of an image presented for 3000 ms, a pseudo-random jitter of 1000–3000 ms before the onset of the prompt for 2000 ms, followed by an inter-trial interval of between 5000 ms and 8000 ms. The valence and arousal ratings were included in the GLM as amplitude modulators and are shown in blue and red, respectively, whereas the constant or average BOLD response is represented by the solid grey response. The BOLD response to the prompts is shown as a dashed grey line.

based on their subjective ratings of the images. Statistical analyses of the behavioural results were conducted using Minitab (version 15, Coventry, UK).

MRI data analysis

The MRI data were analysed using Analysis of Functional NeuroImaging (AFNI) (Cox, 1996) (http://afni.nimh.nih.gov/afni/) and FSL (FMRIB Software Library- http://www.fmrib.ox.ac.uk/fsl/). The first four dynamics were obtained to correct for T1 equilibration effects and were subsequently discarded. The data were motion-corrected by realignment to the first volume of the first run, concatenated into a single run, global mean adjusted by proportional scaling and smoothed with a 6-mm full-width-at-half-maximum Gaussian kernel.

A general linear model (GLM) analysis was conducted in AFNI. Figure 1 shows a schema of the experimental design. Two regressors of interest were included to model the variance due to the image and prompt trials—these two regressors modelled the mean BOLD signal change from baseline across all trials. To model the additional effects of arousal and valence on the BOLD response during the image trials, subjective ratings of arousal and valence for each image were included as single trial parametric weights. This resulted in three image regressors: a constant unmodulated regressor describing the mean BOLD response during the image presentations, regardless of the arousal or valence of the image (this will be referred to in this manuscript as the constant BOLD response), BOLD activation during the image trials modulated by arousal, and BOLD activation during the image trials modulated by valence. A separate regressor was included for all of the images rated as negative, so that these trials were not included in the amplitude modulation analysis. Several regressors of no interest were also included in the GLM to model the following sources of variance: (i) six motion parameters, (ii) eight regressors to model low frequency noise and (iii) two regressors to model the mean differences between the two runs.

All statistical analyses were calculated in the participants' native space, then the regressor coefficients maps were normalized into standard stereotactic space by warping them to the MNI brain template (Montreal Neurological Institute/International Consortium for Brain Mapping 152 standard atlas as provided in the FSL software package) using FSL's linear registration tool, FLIRT. The transformation matrix (12 parameter affine) from native space to MNI space was calculated using the high resolution structural images from each subject.

The group statistical analyses were based on a random-effects model, and activation maps of the constant and modulated responses were calculated with a series of independent *t*-tests. The relationship between personality and brain activation was examined with a series of whole brain correlations using AFNI's tool 3dRegAna. The participants' levels of extraversion and neuroticism were separately regressed against the constant BOLD response, the arousal-modulated response and the positive valence-modulated response. In order to control for the near inverse correlation between extraversion and neuroticism, when examining the relationship between extraversion and the BOLD signal, neuroticism was included as a covariate of no interest in the model, while extraversion was included as a covariate of no interest when examining the effects of neuroticism on brain activation.

Significant voxels passed a voxel-wise statistical threshold of $P \leq 0.01$. To correct for multiple comparisons across the brain, each cluster had to have a minimum size of 708 μl of contiguous statistically significant voxels to be considered statistically significant. This minimum cluster size was calculated using a Monte Carlo simulation (in AFNI) to obtain a (familywise error) corrected $P < 0.05$ statistical significance in the *t*-tests. The SPM anatomy toolbox

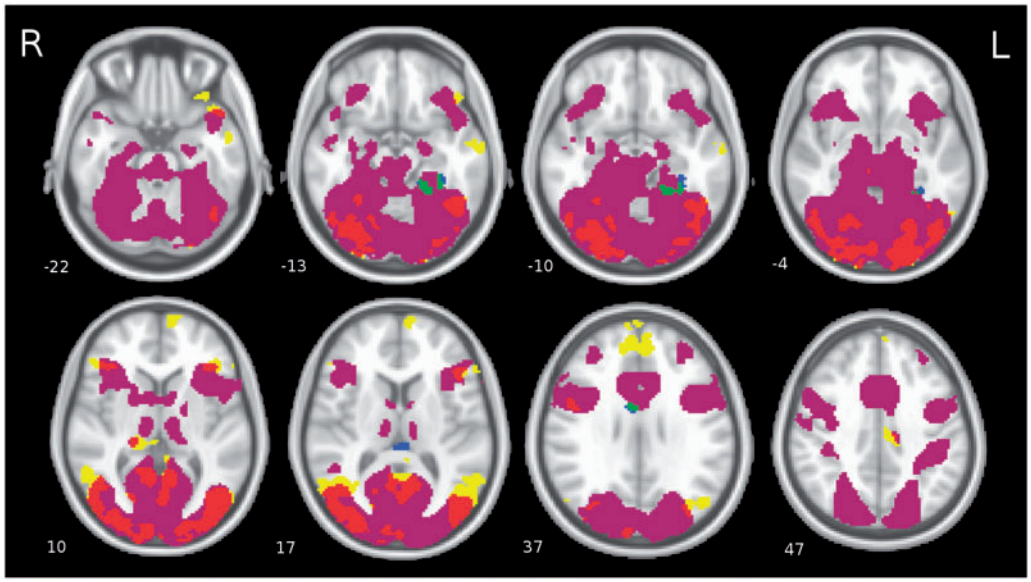

Fig. 2 The group level results independent of the personality traits. A conjunction map was created to show the brain regions with a statistically significant constant BOLD signal not modulated by the emotional content of images, and brain regions where the BOLD signal was modulated by the arousal and valence characteristics of the stimuli. The colours represent the following: Purple = Constant BOLD response; yellow = regions modulated by arousal; red = regions activated in both the constant response and the arousal-dependent response; blue = regions modulated by valence; green = regions activated in both the constant response and the valence-dependent response. The numbers of the slices indicate the direction along the inferior–superior axis in millimetres in standard MNI space (−LPI).

(V1.7b, Eicknoff *et al.*, 2005) was used to localize activation clusters; however, where there were no probabilistic cyto-architectonic labels available, a Brodmann area (BA) is given in the results table instead.

RESULTS

Behavioural results

Image ratings

The participants' individual arousal and valence ratings of the stimuli were used to create regressors which were unique for each subject. Average ratings were calculated to give an idea of the distribution of the scores; however, they are included here for guidance only. On average, 53.87 (±26.91) images were rated as positive (i.e. having a valence of 7, 8 or 9), 113.04 (±37.19) as neutral (i.e. having a valence of 4, 5 or 6), and 18.43 (±13.96) as negative (i.e. having a valence of 1, 2 or 3). The participants rated 99.57 (±13.76) images as having an arousal level of between 1 and 5, while 67.35 were rated as having an arousal level of 6 or more. All negative images were excluded from the parametric modulation analysis and were included in the GLM as a regressor of no interest.

EPQ scores

The mean and standard deviation of the neuroticism and extraversion scores were 4.8 ± 2.6 and 8.0 ± 3.6, respectively. These scores were not correlated, although there was a trend towards an inverse correlation (Pearson's $r = -0.397$, $P = 0.061$). In order to investigate whether there was a linear relationship between the emotional ratings and levels of neuroticism and extraversion, each subject's neuroticism and extraversion scores were correlated against the number of images they rated as positive and negative, and high and low in arousal. In all cases, the results were not statistically significant ($P \geq 0.38$ in all cases), indicating that personality scores were not associated with the ratings of the images.

fMRI results

The constant and modulated BOLD responses independent of personality variables

The constant BOLD response during image viewing, as well as the modulations due to arousal and positive valence were first examined independent of neuroticism and extraversion levels. A conjunction analysis was performed to examine which regions of the brain were activated in the constant response only, which regions were modulated only by increasing levels of arousal and positive valence and whether there were regions which were active in both the constant response and which were also modulated by the arousal and valence of the stimuli. The results of this conjunction analysis are shown in Figure 2, and the interested reader can find a table summarizing the significant activation clusters in Supplementary Table S3 in the Supplementary Data.

Regions which were significantly active compared with baseline in the constant response only, and which were not modulated by the arousal or valence level of the stimuli are shown in purple in Figure 2. They include a very large cluster spanning widespread areas of the occipital and temporal lobes and which included the hippocampus, and clusters in the right superior temporal gyrus, the left middle frontal

gyrus, the left and right cerebellum and the right middle occipital gyrus.

Overlap between the constant and arousal-dependent BOLD responses

There was a large degree of overlap between regions which were activated in the constant BOLD response and also modulated by increasing levels of emotional arousal, especially in the occipital and temporal visual processing areas. These regions are shown in red in Figure 2 and include a large cluster that spans the fusiform gyrus and primary and secondary visual cortex (BA 17 and 18) bilaterally, and further clusters in the left temporal pole, the right superior temporal gyrus, the right and left inferior frontal gyrus, the right thalamus and the right precentral gyrus.

The arousal-dependent BOLD response

Several brain regions in the temporal and frontal lobes were not activated in the constant BOLD response but only preferentially responded to increasing levels of arousal. These are shown in yellow in Figure 2, and included clusters in the middle temporal gyri bilaterally, the left inferior temporal gyrus, the right superior temporal gyrus, the left superior medial frontal gyrus, the left and right inferior frontal gyrus, the precuneus, the left middle cingulate cortex, the right thalamus and the left middle occipital gyrus.

The valence-dependent BOLD response

The valence-dependent BOLD response was much less extensive than the arousal-dependent response. There was a single cluster located in the left inferior temporal gyrus which was not activated in the constant BOLD response but whose BOLD signal was significantly modulated by increasing levels of positive valence. This cluster is shown in blue in Figure 2. There was also a cluster in the left fusiform gyrus that was both activated in the constant BOLD response and which also showed a positive modulation of the BOLD signal in response to increasingly positive valence. This is shown in green in Figure 2.

The influence of personality on emotional processing

The relationship between neuroticism and the BOLD signal

There was a strong negative linear association between neuroticism and the constant BOLD response in the middle orbitofrontal cortex (OFC). There was a negative linear association between neuroticism and the valence-dependent BOLD modulation in the right middle temporal gyrus and the right rolandic operculum. There was a positive linear association between neuroticism and the degree of arousal-dependent BOLD modulation in the right medial prefrontal cortex (mPFC; Table 1 and Figure 3).

Table 1 Linear associations between neuroticism levels and the BOLD signal during image viewing

	Voxels	*t*-value[a]	MNI co-ordinates	Area: prob or BA
Constant BOLD response				
Frontal lobe				
Left rectal gyrus	161	−4.96	−4, 38, −26	BA 11
Left rectal gyrus		−3.62	−6, 30, −22	BA 11
Arousal modulation				
Frontal Lobe				
Right middle orbital gyrus	211	5.65	12, 52, −8	BA 11
Right middle orbital gyrus		4.72	2, 48, −6	BA 10
Right middle orbital gyrus		3.47	2, 58, −14	BA 11
Valence modulation				
Temporal Lobe				
Right middle temporal gyrus	102	−4.43	70, −38, −14	BA 21
Right middle temporal gyrus		−4.3	70, −34, −16	BA 21
Right inferior temporal gyrus		−4.16	64, −26, −18	BA 21
Right rolandic operculum	98	−3.92	54, −18, 18	OP 1: 50%; OP 4: 30%

[a] $t \geq 2.82$, $P < 0.01$; $t \geq 3.79$, $P < 0.001$, corrected. OP = opercular cortex. Labels were generated using SPM's anatomy toolbox; however, where there was no cytoarchitectonic information available, a Brodmann area is given. MNI co-ordinates are—LPI (i.e. negative indicates left, posterior and inferior directions).

The relationship between extraversion and the BOLD signal

Extraversion was negatively associated with the constant BOLD response in a region of BA 6 spanning the middle cingulate cortex and supplemental motor area (SMA). There was a negative linear relationship between extraversion and the arousal-dependent BOLD response in the right cerebellum and a positive linear association between extraversion and the arousal-dependent BOLD response in the right insula. Extraversion was negatively associated with the valence-dependent BOLD signal in the right superior parietal lobule, the right postcentral gyrus and the left posterior hippocampus (Table 2 and Figure 4).

DISCUSSION

The results of the present study demonstrate several relationships between personality and emotional processing that are novel findings, in particular the relationships between neuroticism and three different elements of emotional processing. First, neuroticism levels were negatively associated with the constant BOLD signal in the OFC, regardless of the valence or arousal level of the stimuli. Although this relationship was not valence specific as the images included both neutral and positive exemplars, it is of particular interest given that the OFC is known to play a pivotal role in the processing of emotion and reward (Schultz *et al.*, 2000; O'Doherty, 2004; Rolls, 2004; Kringelbach, 2005), and in also in the successful down-regulation of negative emotional states (Ochsner *et al.*, 2004; Eippert *et al.*, 2007).

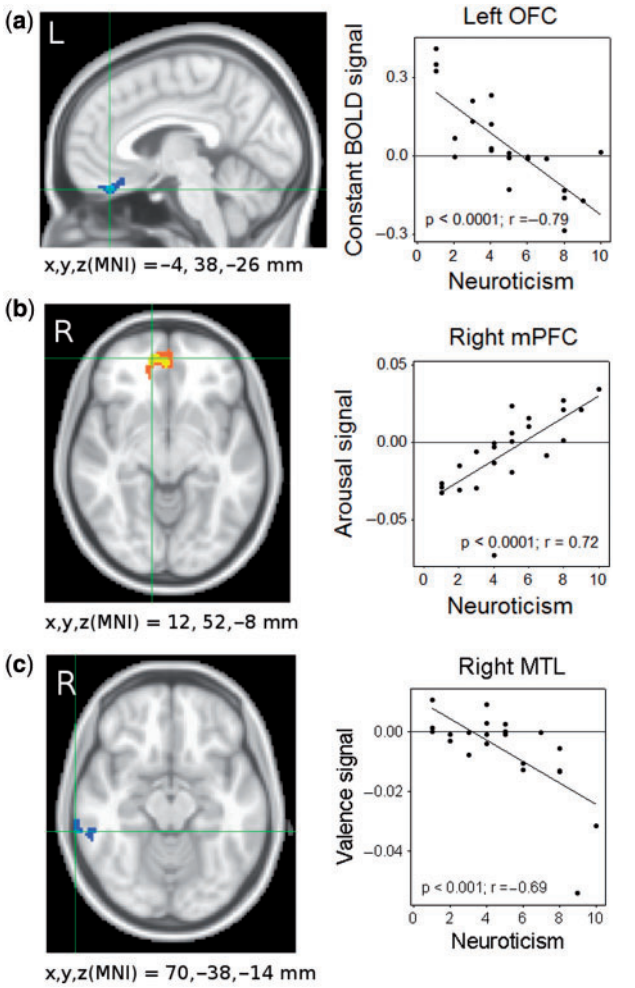

Fig. 3 Neuroticism levels were negatively associated with the constant BOLD signal in the (**a**) orbitofrontal cortex (OFC), positively associated with the arousal-dependent BOLD signal in the (**b**) medial prefrontal cortex (mPFC) and negatively associated with the valence-dependent BOLD signal in the (**c**) right middle temporal gyrus.

Second, we found that in accordance with our prediction, neuroticism was negatively associated with valence processing, in two regions of the right temporal lobe. It has previously been reported that patients with major depression show reduced brain activation in response to positive emotional words on an emotional working memory task (Shestyuk *et al.*, 2005). Given that higher levels of neuroticism are associated with an increased risk of developing affective disorders such as depression and anxiety (Kendler *et al.*, 2004), we hypothesized that a similar pattern may be evident in the case of high neuroticism individuals. Indeed, we found a negative relationship between neuroticism and the neural response to positive valence in the right middle temporal gyrus and the right rolandic operculum. The right middle temporal gyrus has been found to be activated in both emotional processing and encoding tasks (Critchley *et al.*, 2000; Dolcos *et al.*, 2004; Olson *et al.*, 2007), and the group results from the current study also indicate widespread activation in the temporal lobes associated with emotional image viewing. Previous neuroimaging studies have identified this trait to be strongly associated with negative, rather than positive emotional processing (Canli *et al.*, 2001; Haas *et al.*, 2007, 2008; Chan *et al.*, 2008, 2009; Cremers *et al.*, 2010). We found in the current study that the converse is also apparent—neuroticism is associated with a tendency for several regions in the brain to be less responsive to positive emotional stimuli.

The attenuated neural response to the stimuli in the OFC and reduced activation to positive emotional valence in the right middle temporal gyrus might tentatively be interpreted as a predisposition in cases of high neuroticism for under activation in reward-processing or emotional regulation. We believe that this is the first demonstration of such a finding in a non-clinical population, and it may represent a biological vulnerability marker or putative phenotypic characteristic at a neural network level (Lesch *et al.*, 1996; Sen *et al.*, 2003; Strobel *et al.*, 2003), which may help to further explain the relationship between this trait and the increased risk of developing depression and anxiety disorders. However, further elucidation of these types of functional phenotypes will be needed to understand the complex relationship between personality, emotional processing and the risk for affective disorders.

Last, we found that neuroticism was associated with an increased BOLD response to emotional arousal in the left mPFC. This is the first time, to our knowledge, that a link has been identified between neuroticism and increased reactivity to emotional arousal, rather than valence, in the brain. Eysenck (1967, 1994) proposed in his biological theory of personality that high neuroticism is associated with increased reactivity of the limbic system, which predisposes individuals high in neuroticism to react strongly to emotionally arousing experiences and take longer to return to pre-arousal states. This suggests that neuroticism influences emotional processing by enhancing neural sensitivity to high levels of emotional arousal, making high neuroticism individuals predisposed or primed to react strongly to arousing experiences (Eysenck, 1967). Indeed this trait is associated with greater sensitivity to negative mood inductions (Larsen and Ketelaar, 1991); and it has been found to correlate with larger electrodermal responses (EDR) to both arousing negative and positive emotional images, as well as with a longer period of recovery in the EDR signal (Norris *et al.*, 2007). The results of the present study support Eysenck's theory, with individuals high in neuroticism showing an enhanced response to emotional arousal in the left mPFC. This cortical region has previously been implicated to play a central role in self-referential processing and emotional attribution and appraisal (Eysenck, 1967; Fossati *et al.*, 2003; Mitchell *et al.*, 2005, 2006; Ochsner *et al.*, 2005). Furthermore, constant activation in the mPFC in response to sad faces has been found to correlate with neuroticism (Haas *et al.*, 2008). Thus, the enhancement of activation in

Table 2 Linear associations between extraversion levels and the BOLD signal during image viewing.

	Voxels	*t*-value[a]	MNI Co-ordinates	Area: prob or BA
Constant BOLD response				
Frontal Lobe				
Left middle cingulate cortex	189	−4.01	−6, −0, 40	Area 6: 10%
Right SMA		−3.79	10, 0, 46	Area 6: 40%
Arousal modulation				
Cerebellum				
Right cerebellum	96	−4.17	24, −68, −26	Lobule VI: 75%
Right cerebellum		−3.85	26, −72, −38	Lobule VIIa Crus I: 57%
Right cerebellum	91	−3.85	30, −84, −42	Lobule VIIa Crus II: 98%
Right cerebellum		−3.84	22, −86, −38	Lobule VIIa Crus II: 93%
Frontal Lobe				
Right insula Lobe	130	5.46	34, 14, 2	BA 13
Right insula Lobe		4.23	32, 10, 14	BA 13
Valence modulation				
Parietal Lobe				
Right superior parietal lobule	102	−4.72	24, −58, 72	SPL (7A): 50%
Right postcentral gyrus		−3.99	30, −48, 74	BA 2
Right superior parietal lobule		−3.68	14, −56, 68	SPL (5L): 60%
Right postcentral gyrus	132	−3.2	30, −32, 42	Area 3a: 40%
Temporal Lobe				
Left hippocampus	109	−4.47	−18, −36, 8	Hipp (CA): 50%
Left hippocampus		−4.19	−24, −34, 2	Hipp (CA): 20%

[a]$t \geq 2.82$, $P < 0.01$; $t \geq 3.79$, $P < 0.001$, corrected. SPL = superior parietal lobule. Refer to Table 1 legend.

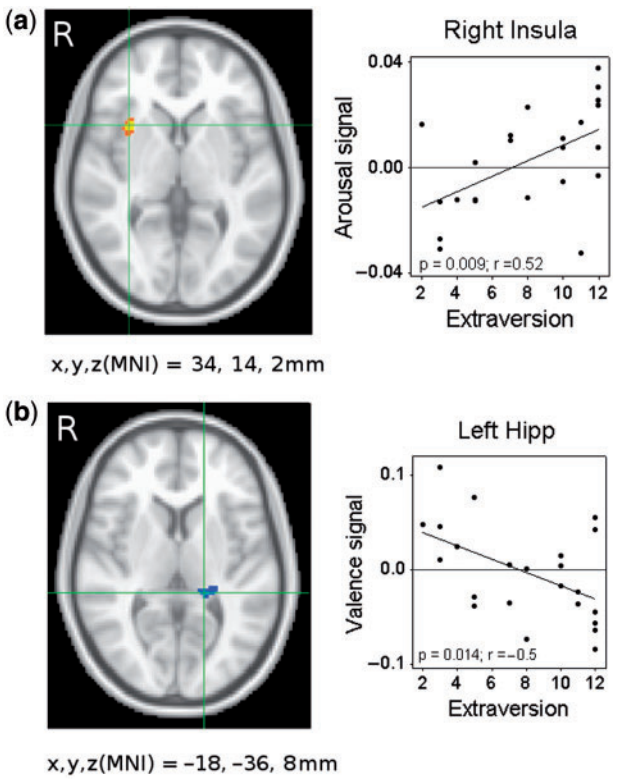

Fig. 4 Extraversion levels were positively associated with the arousal-dependent BOLD signal in the (**a**) right insula lobe and negatively associated with the valence-dependent BOLD signal in the (**b**) left hippocampus.

this key emotional appraisal area in high neuroticism individuals suggests a heightened response to high levels of emotional arousal which may go some way to explaining why arousing experiences might have a more intense and lasting effect.

The relationship we identified between extraversion and the neural response to emotional arousal in the right cerebellum is consistent with Eysenck's arousal hypothesis of extraversion (1967, 1994), which proposes that extraverts demonstrate both lower baseline levels of cortical arousal and under-arousability of the cortex, and can tolerate higher levels of arousal better than introverts (Eysenck, 1967; Kumari *et al.*, 2004; O'Gorman *et al.*, 2006; Hagemann *et al.*, 2009). This is postulated to explain why extraverts typically engage in more risk-taking and impulsive behaviours (Costa and McCrae, 1980; Eysenck, 1994), as they endeavour to enhance their intrinsic low arousal levels. Our results provide some supporting evidence for the under-arousability component of this hypothesis, with individuals high in extraversion showing less activation in response to increasing levels of arousal in areas Crus I and Crus II in the right cerebellum.

Although once considered a purely motor region, it is now known that outputs from the cerebellum influence more widespread regions of the cerebral cortex than previously recognized, and there is converging evidence from primate connectivity studies and human resting-state fMRI data that there are several anatomical circuits between the cerebellum and PFC (Kelly and Strick, 2003; Habas *et al.*, 2009;

O'Reilly *et al.*, 2010). For example, there are reciprocal connections between Crus II and BA 46 (Strick *et al.*, 2009), supporting the idea that the cerebellum may play an important role in attention and working memory among other diverse cognitive and emotional functions (Dolan, 1998; Rapoport *et al.*, 2000; Stoodley and Schamahmann, 2009; Leiner, 2010). Therefore, it is not entirely surprising to find a relationship between personality and arousal processing in these regions, and in a review of neuroimaging studies which have reported cerebellar activations, Stoodley and Schamahmann (2009) localized the topography of emotion-related activation to Crus I in particular. In the context of our study, the fact that highly extraverted individuals showed less arousal modulation in Crus I and II may indicate under-sensitivity to the effects of emotional arousal.

However, we also found there to be a strong positive linear association between extraversion and arousal processing in the right insula lobe, which contradicts Eysenck's predictions about this trait. The insula is thought to play a central role in the perception of bodily sensations and in particular the perception of pain (Bornhovd *et al.*, 2002); and there is also evidence that this structure has a role in the maintenance of drug addiction (Naqvi and Bechara, 2009; Garavan, 2010), as well as more general evidence for its involvement in a myriad different tasks involving emotional processing (Lamm and Singer, 2010) and attention (Nelson *et al.*, 2010). The fact that highly extraverted individuals in our study displayed increased insula activity to high levels of arousal does not support the notion that extraverts are less sensitive to the effects of arousal. However, Kumari and colleagues (2004) found that high extraversion was associated with increased activation in the dorsolateral PFC and anterior cingulate in response to increasing levels of cognitive demand on an *n*-back working memory task, indicating that extraverts were more sensitive to the effects of cognitive arousal. It may well be the case that the relationship between extraversion and arousal is a more complex story than that originally proposed by Eysenck, with further research required to elucidate if and how arousal processing differences are a central feature of this personality trait, and whether there are effects related to emotional arousal, cognitive arousal or both.

The negative relationship we identified between extraversion and activation due to positive valence was somewhat unexpected, as previous studies have found this trait to be associated with increased activation in response to positive emotional stimuli (Canli *et al.*, 2001; Haas *et al.*, 2006). It may be, however, that our results contrast with previous neuroimaging studies of personality (e.g. Canli *et al.*, 2001; Haas *et al.*, 2006; Chan *et al.*, 2008) due to the slightly different design of our study. For example, we used only neutral and positive stimuli, whereas the other studies also employed negative stimuli (Canli *et al.*, 2001; Canli, 2004), which have been found to activate the key emotional processing centres such as the amygdala more substantially than either neutral or positive stimuli (For a review, see Carretie *et al.*, 2009). The contrast between positive versus negative image viewing may also reveal greater differences in brain activation than the contrast between positive and neutral image viewing. Further, our positive stimuli had only moderately high arousal levels (few were rated as 8 or 9 on a 9-point scale) as we did not include any erotic stimuli. This may indicate that high extraversion is associated with greater neural sensitivity to highly arousing, highly positive stimuli rather than all positive stimuli. The amplitude modulation analysis and use of subjective rather than group ratings may also have contributed to these different results as previous neuroimaging studies have tended to rely on standard ratings and compare across image categories rather than using a parametric modulation approach.

A general observation of our results is that, whereas the linear associations between neuroticism and the neural response to the emotional stimuli were found in areas which have previously been linked to emotional processing, e.g. the OFC and the mPFC (Phan *et al.*, 2002; O'Doherty, 2004), the relationships we found between extraversion and the fMRI results were in regions which would not be considered purely 'emotional', e.g. the SMA, cerebellum and parietal cortex. The evidence for a link between extraversion levels and emotional processing is not as strong as the body of literature supporting the influence of neuroticism on emotional processing at a behavioural (Bolger and Schilling, 1991; Rusting and Larsen, 1997; Kendler *et al.*, 2004; Denissen and Penke, 2008) and neural level (Canli, 2004; Haas *et al.*, 2007, 2008; Kumari *et al.*, 2007; Cremers *et al.*, 2010). It may well be the case that extraversion does not play a large modulatory role in affective processing, which is why we do not see strong evidence for variation in this trait being related to neural activation in emotional processing regions. Given that the associations we observed were mostly in motor and parietal regions, it seems likely that extraversion may not play a prominent mediating role in the experience of emotion, but rather may affect other elements of the task performance captured by these differences in the BOLD signal. The negative association between extraversion and the mean BOLD signal for example may indicate that those low in this trait were more susceptible to motor priming effects in readiness to press the button to respond to the prompt following the image. It is known, for example, that highly emotional stimuli capture attention faster than neutral stimuli (Bradley, 2009); therefore, it is possible that the associations with arousal and/or valence are due to attentional differences, e.g. high extraversion may be linked to increased susceptibly to the effects of attention. Obviously, there is no way using the current data to disentangle the effects of emotion and other factors such as attention, however, it would be interesting in future studies to investigate whether extraversion levels influence cognitive rather than affective aspects of emotional perception.

The amplitude modulation analysis we employed in this study has been used in other neuroimaging studies to examine single trial dynamics, such as in motor learning (Friston *et al.*, 1992) and stimulus–response pairings (Buchel *et al.*, 1998); however, it has only been used to examine how emotional judgements modulate the BOLD signal in a few studies (Phan *et al.*, 2004; Heinzel *et al.*, 2005; Anders *et al.*, 2008; Northoff *et al.*, 2009), and has not been applied in the study of personality and emotional processing. It proved highly effective at disentangling the effects of emotional arousal and valence on the BOLD signal, and the results are broadly similar to studies which have used different analysis methods, such as contrasting the activation maps associated with viewing emotional versus neutral images (Lang *et al.*, 1998; Bradley *et al.*, 2001a, Mourao-Miranda *et al.*, 2003; Anders *et al.*, 2004). The extensive modulations in the occipital and temporal lobes associated with increasing arousal corroborate many neuroimaging studies which have found increases in neural activation associated with increasing emotional arousal in the occipital cortex and inferotemporal regions of the ventral visual pathway (Bradley *et al.*, 2003; Sabatinelli *et al.*, 2005; Junghofer *et al.*, 2006; Sabatinelli *et al.*, 2007). Furthermore, the arousal-associated increases in the BOLD signal that we observed in the prefrontal gyrus have been found in others' studies of emotional processing and evaluation (Grimm *et al.*, 2006). The amplitude modulation due to valence during image viewing revealed a less extensive and distinct different pattern of neural activation, including significant clusters in the visual processing regions noticeably concentrated around the fusiform gyrus. Mourao-Miranda *et al.* (2003) also reported increased activation in the occipitotemporal visual processing areas when they compared responses with positive versus neutral images with the same arousal level. Lang *et al.* (1998) found that only positive images, not neutral or negative valences, increased the BOLD signal in the left fusiform gyrus. These patterns of activation are very similar to the modulation due to valence in the current study, and suggest that arousal and valence are represented by quite distinct neural networks.

The analysis of the fMRI results with respect to the subject's individual ratings is also a relatively novel approach, having been used only rarely (Anders *et al.*, 2008) and we are confident that this is preferable to using standard or group average ratings as actual emotional ratings are quite variable. We believe that this design approach allowed us the opportunity to explore the interaction of personality with emotional processing in ways that have not yet been examined. Although beyond the scope of the current study, it may be interesting in future studies to compare this approach with the standard approach of using average emotional ratings, in order to see what effect this has on the fMRI results. It would also be interesting to investigate whether there are any interactions between mood, personality and emotional perception, with the administration of a mood scale such as the PANAS (Positive and Negative Affective Scales; Watson *et al.*, 1988) or POMS (Profile of Mood States; McNair *et al.*, 1971).

There has been some discussion and controversy in the past few years about the reliability of studies in social and personality neuroscience which correlate brain activations as measured by fMRI with measures of personality (Vul *et al.*, 2009; Yarkoni, 2009). Some authors have argued that the results of such studies may be inflated due to lack of statistical power in small sample sizes (Vul *et al.*, 2009; Yarkoni, 2009), while others have criticized the methods they claim are used by certain experimenters, whereby, region of interest analyses are carried out on the basis of whole-brain correlations, giving exaggeratedly high correlation coefficients (Vul *et al.*, 2009). We are confident, however, that the results of the current study are reflective of real differences in brain function related to personality, and are not spurious results or inflated correlations. First, we employed a whole-brain correlation approach which has been validated as a reliable, independent measure to detect brain–behaviour relationships (Lieberman *et al.*, 2009; Poldrack and Mumford, 2009). Second, we employed a robust multiple comparison procedure which protects against the possibility of false positives. Furthermore, given the anatomical specificity of our results, for example, reduced activation in the OFC associated with neuroticism, we are confident that our results are not simply spurious correlations in random brain regions. Finally, by including only women in the current study, we greatly reduced the heterogeneity of our sample given that there have been considerable differences found between genders in emotional reactivity (Bradley *et al.*, 2001b), in the neural representation of emotion (Beck *et al.*, 1996; Cahill *et al.*, 2001; Wager *et al.*, 2003; Wrase *et al.*, 2003) and in levels of neuroticism (Lynn and Martin, 1997).

In summary, our findings offer a unique insight into how extraversion and neuroticism interact with the neural representation of emotional arousal and valence, two critical components of emotional processing. We identified several novel relationships between personality and the emotional processing, notably reduced sustained activation in the OFC and attenuated valence processing associated with high levels of neuroticism. These results provide further evidence for the important role that this trait plays in individual responses to affective stimuli, and they also suggest similarities between emotional processing in individuals with high levels of neuroticism and in depressed patients which may help to elucidate the role that this trait plays in the development of depression and other affective disorders. Furthering our understanding of individual differences in neural reactivity to emotional stimuli is pivotal to increasing our understanding of the role that personality plays in emotional processing, and may help to elucidate how personality influences the development of affective disorders.

SUPPLEMENTARY DATA

Supplementary data are available at *SCAN* online.

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Conflict of Interest

None declared.

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