The influence of personality on neural mechanisms of observational fear and reward learning

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ABSTRACT

Fear and reward learning can occur through direct experience or observation. Both channels can enhance survival or create maladaptive behavior. We used fMRI to isolate neural mechanisms of observational fear and reward learning and investigate whether neural response varied according to individual differences in neuroticism and extraversion. Participants learned object-emotion associations by observing a woman respond with fearful (or neutral) and happy (or neutral) facial expressions to novel objects. The amygdala–hippocampal complex was active when learning the object-fear association, and the hippocampus was active when learning the object-happy association. After learning, objects were presented alone; amygdala activity was greater for the fear (vs. neutral) and happy (vs. neutral) associated object. Importantly, greater amygdala–hippocampal activity during fear (vs. neutral) learning predicted better recognition of learned objects on a subsequent memory test. Furthermore, personality modulated neural mechanisms of learning. Neuroticism positively correlated with neural activity in the amygdala and hippocampus during fear (vs. neutral) learning. Low extraversion/high introversion was related to faster behavioral predictions of the fearful and neutral expressions during fear learning. In addition, low extraversion/high introversion was related to greater amygdala activity during happy (vs. neutral) learning, happy (vs. neutral) object recognition, and faster reaction times for predicting happy and neutral expressions during reward learning. These findings suggest that neuroticism is associated with an increased sensitivity in the neural mechanism for fear learning which leads to enhanced encoding of fear associations, and that low extraversion/high introversion is related to enhanced conditionability for both fear and reward learning.

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1. Introduction

Learning to avoid danger and approach reward is crucial for survival, yet an exaggerated response to perceived danger can lead to maladaptive fear, including anxiety disorders (Mineka & Ohman, 2002), and an exaggerated response to reward can lead to maladaptive reward-seeking behaviors, including addiction disorders (LaLumiere & Kalivas, 2007). Adaptive and maladaptive emotional learning can occur through direct experience with punishment or reward, as in *classical conditioning*, or through observation of another person's experience of punishment or reward as in *observational learning* (Merckelbach, Arntz, & de Jong, 1991; Ost, 1991; Rachman, 1977).

Although the mechanisms of classical conditioning are well defined, little is known about the mechanisms of observational learning.

In addition, personality traits, such as neuroticism and extraversion, are associated with the vulnerability to develop maladaptive stimulus-reinforcement behaviors. Neuroticism is characterized by an increased sensitivity to punishment and a tendency to feel negative affect (Costa & McCrae, 1980; John & Srivastava, 1999). Individuals with high levels of neuroticism have greater risk for developing anxiety disorders (Bienvenu, Hettema, Neale, Prescott, & Kendler, 2007; Clark, Watson, & Mineka, 1994). Extraversion is associated with an outgoing and sociable nature (Costa & McCrae, 1980; John & Srivastava, 1999). One proposal is that high extraversion is characterized by an increased sensitivity to reward (Depue & Collins, 1999; Lucas, Diener, Grob, Suh, & Shao, 2000), resulting in a greater risk of developing addiction disorders (Munafo & Black, 2007; Munafo, Zetteler, & Clark, 2007; ter

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Bogt, Engels, & Dubas, 2006). However, the mechanism by which personality creates this vulnerability is not understood. We use a classical conditioning framework to identify the neural mechanisms of observational learning and then investigate whether these neural mechanisms vary according to individual differences in personality.

1.1. Basic models of classical conditioning and observational learning

In classical conditioning, a neutral stimulus, (e.g. tone), is directly followed by an aversive (e.g. shock) or appetitive (e.g. food) outcome. Participants learn the predictive association and subsequently show a conditioned response (CR), such as fear in anticipation of shock or saliva in anticipation of food, to the conditioned stimulus (CS+) when that stimulus is presented without reinforcement. Adaptive emotional learning depends on the healthy functioning of the amygdala–hippocampal complex (LeDoux, 1992; Phelps, 2004; Schoenbaum, Chiba, & Gallagher, 1998). The amygdala–hippocampal complex is active for the acquisition of stimulus-reinforcement contingencies (LaBar, LeDoux, Spencer, & Phelps, 1995; Schoenbaum, Setlow, Nugent, Saddoris, & Gallagher, 2003). When the CS+ is presented alone after learning, the amygdala is more active to the CS+ than to a conditioned stimulus with a learned neutral (i.e. non-reinforced) outcome (CS−). Thus amygdala activity to the CS+ is a reflection of the learned punishment and reward value and mediates expression of the CR (Buchel & Dolan, 2000; Gottfried, O'Doherty, & Dolan, 2002). Furthermore, amygdala activity related to arousal in response to the aversive or appetitive outcome during learning enhances encoding and consolidation of learned associations in the hippocampus (Phelps, 2004).

Observational learning occurs when the causal relationship between a neutral stimulus (CS+) and an affective outcome is learned through the observation of someone else's emotional experience. There is no doubt that people learn the emotional value of objects and situations through observation, but the exact mechanism is not clear. The primary theory is that observational learning occurs through a classical (i.e. Pavlovian) conditioning process in which the emotional expression of the person being observed acts as an unconditioned stimulus (UCS) for the observer and the object eliciting the emotional response is the conditioned stimulus (CS+) (Mineka & Cook, 1993; Olsson & Phelps, 2007). However, most studies have not adequately isolated this mechanism because the emotional facial expression is not the only UCS in the learning experience (Merckelbach et al., 1991; Mineka & Cook, 1993; Mineka, Davidson, Cook, & Keir, 1984; Olsson & Phelps, 2004). For example, an individual with no prior fear can develop a fear of snakes after observing someone else's fearful reaction (Mineka & Cook, 1993). However, snakes have inherent emotional value which primates are biologically prepared to fear (Mineka & Ohman, 2002), and thus it is difficult to identify whether learning occurred solely as a result of the fearful expression.

An additional challenge is that observation of the emotional expression is a necessary element of observational learning, yet the amygdala responds to emotional facial expressions outside of the learning context. Therefore, it is difficult to identify whether amygdala activity reflects neural response to facial expression perception or association learning. We addressed this issue in a prior study; using an observational reversal learning paradigm, we found that the amygdala–hippocampal complex is more active when learning object-emotion associations from happy and fearful facial expressions as compared to perceiving happy and fearful facial expressions without learning (Hooker, Germine, Knight, & D'Esposito, 2006).

1.1.1. Observational learning paradigm and predictions for the current study

Here we build on our prior findings, and test the hypothesis that amygdala–hippocampal complex is involved in *acquisition* of object-emotion associations, subsequent *expression* of learned emotional value, and enhanced *memory* for emotion associated objects. Our paradigm maintains the necessary elements of observational learning while controlling for potential confounds. Participants view a display in which there are two unidentifiable, neutral objects on either side of a woman's face and are instructed to learn the emotional value of these objects by observing the woman's fearful (or neutral) and happy (or neutral) facial expressions when she looks at them. Thus, the emotional facial expression is the only UCS, the object associated with an emotional response is the CS+ and the object associated with a neutral response is the CS−. We verify learning with three measures: (1) reaction time, which should be faster for the emotion association; (2) subsequent memory, which should be better for the emotion associated object; and (3) amygdala–hippocampal activity, which should be greater for learning the emotion association as well as recognizing the emotion associated object when it is presented alone.

1.2. The influence of personality on emotional learning

1.2.1. Neuroticism

Although it has been proposed that increased sensitivity to punishment in people with high levels of neuroticism causes enhanced fear learning (Eysenck, 1967; Gray, 1982), behavioral studies have had surprisingly little success showing this predicted outcome (Matthews & Gilliland, 1999). Here, we test the idea that the effect of neuroticism on fear learning is mediated by neural response to punishment. In other words, self-reported neuroticism may be the consequence of increased sensitivity of the amygdala in response to negative information (Eysenck, 1967; Gray, 1982), and it is this neural activity in the context of a fearful experience that contributes to the development of maladaptive fear responses.

1.2.2. Extraversion

There are several competing models regarding the core component of extraversion and how it influences emotional learning. One view proposes that extraversion is related to baseline arousal level, which is mediated by reticulo-cortical neural pathways (Eysenck, 1967; Matthews & Gilliland, 1999). Theoretically, people with low extraversion (i.e. high introversion) have higher baseline arousal, resulting in more rapid learning for both fear and reward conditioning, particularly when the unconditioned stimuli (UCS) is relatively 'weak' (i.e. non-arousing). This rapid learning has been demonstrated for aversive outcomes (Eysenck, 1967; Matthews & Gilliland, 1999) but not for appetitive outcomes.

More recent models claim that high extraversion is characterized by increased sensitivity to reward and/or reward incentives (Depue & Collins, 1999; Lucas et al., 2000). This view is compatible with Gray's model (1982) which proposes that people vary according to individual differences in punishment sensitivity, associated with high neuroticism and low extraversion, and reward sensitivity, associated with high extraversion and impulsivity. Consistent with this model, people with high extraversion have more amygdala activity to rewarding stimuli such as happy faces (Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002), pleasant scenes (Canli et al., 2001), and monetary gains in a gambling task (Cohen, Young, Baek, Kessler, & Ranganath, 2005). However, high extraversion might, instead, be better characterized by increased sensitivity to the rewarding value of certain experiences, such as social interactions (Diener, Larsen, & Emmons, 1984; McCrae & Costa, 1987), social

attention (Ashton, Lee, & Paunonen, 2002) or novelty (Ebstein, 2006; Munafo et al., 2007).

1.2.3. Personality predictions in the current study

Our observational learning paradigm is uniquely suited to test these unresolved issues. The face stimuli used for learning consist of three emotional expressions (happy, fearful, and neutral) from the same woman. This controls for confounding effects of novelty and emotion intensity differences inherent in viewing different face identities on every trial.

Our primary prediction is that neuroticism will be associated with increased amygdala–hippocampal complex activity during fear learning but not reward learning. We test 3 competing models of extraversion. First, if extraversion is an index of reward sensitivity then those with high extraversion will have greater amygdala–hippocampal activity during observational reward learning but not observational fear learning. Second, if extraversion is more related to baseline arousal then low extraversion/high introversion should be related to enhanced learning and therefore greater amygdala activity during both fear and reward learning. Finally, if extraversion is better characterized by the reward value of social attention, socializing, or novelty-seeking then we would expect no relationship between extraversion and amygdala activity in our task, since we control for the effects of these variables by using the same face identity on every trial.

2. Methods

2.1. Participants

Twelve healthy, right-handed, English speaking adults (7 females; mean age 21 y/o) volunteered and were paid for their participation. All participants gave written, informed consent before participation in accordance with the guidelines of the Committee for Protection of Human Subjects at the University of California, Berkeley. Participants were screened for MR compatibility, neurological, and psychiatric illness.

2.2. Task and stimuli

Participants completed a self-report questionnaire assessing neuroticism and extraversion [Big Five Inventory (BFI) (John & Srivastava, 1999)], an event-related functional magnetic resonance imaging (fMRI) scan in which they completed two experiments: observational fear learning and observational reward learning (Fig. 1). After scanning, participants completed a surprise, subsequent memory post-test.

Within each fMRI observational learning experiment, there were two tasks, learning and recognition. In the learning task, participants learned object-emotion associations by observing whether a woman reacted with a fearful or neutral expression to a neutral object or with a happy or neutral expression to a neutral object. At the beginning of the trial, participants saw a visual display of a woman's neutral face, looking straight ahead, with an object on either side. A fixation cross indicated one of the objects, and participants predicted whether the woman would be afraid of this object or not in the fear learning runs or whether the woman would be happy in response to this object or not in the reward learning runs. This initial stimulus containing the neutral face and the participant's prediction was the cue phase (stimulus presentation = 2 s). After the prediction, the woman turned, looked at the object, and displayed either an emotional expression (fearful in fear learning runs or happy in the reward learning runs) or neutral expression. The emotional or neutral expression is the outcome phase (stimulus presentation time = 2 s), and this is the information that participants use to form the object-emotion association. Participants learned the object-emotion associations over 8 learning trials (4 Learn Fear; 4 Learn Neutral and 4 Learn Happy; 4 Learn Neutral).

Immediately after learning, participants performed the recognition task, in which a series of 8 isolated objects were sequentially presented (2 s each), including the just learned fear (or happy) object and neutral object as well as 6 new distracter objects. Participants were asked whether or not the object had been presented to the woman in the learning trials (i.e. "Is this an object that was presented before?").

Thus, participants acquired the object-emotion association over the 8 trials of learning. Recognition of the emotion object (CS+) and neutral object (CS−) presented alone provided the opportunity to test whether the CS had acquired neurally represented emotional value. The association (fear vs. neutral or happy vs. neutral) of each object remained constant within the 16 trial learning/recognition set and a new group of novel objects was used for each new learning/recognition set. Presentation order of trials within each block of task trials was randomized.

After scanning, participants completed a surprise memory post-test in which they viewed objects seen in the experiment and identified whether or not the object had been presented to the woman.

The face stimuli consisted of three different expressions (fearful, happy, and neutral) from one woman. To create the stimuli, a rapid series of photographs were taken while a professional actor turned and responded to a neutral object (to her right and left) with a fearful, happy, and neutral expression. In the task, the outcome portion of the trial consisted of 10 photographs, presented for 200 ms each, of the head turn and emotional response, such that it seemed like a short (2 s) video to the participant. Each facial expression was coded by a trained psychologist using the Facial Action Coding System (FACS) in order to verify the authenticity of the fearful and happy emotional expressions and the lack of emotion in the neutral expression. In addition, an independent group of participants (N = 19) rated the facial expressions according to intensity of valence and arousal on a 5-point scale (1 = not at all; 5 = extremely). The neutral expression was uniformly perceived as 'not at all' intense or arousing. The fearful and happy expressions were rated as 'extremely' intense [fear intensity = 4.6; happy intensity = 3.9] and 'very' arousing [fear arousal = 4.1; happy arousal = 3.5]. The fearful expression was rated significantly more intense and arousing than the happy expression [intensity: $t(18)$ = 4.4, $p < .01$; arousal: $t(18)$ = 2.9, $p < .05$].

The objects were made with Strata 3DCX by Corastar Inc., (George, UT). Objects consisted of neutral, arbitrary visual patterns, letters, numbers, color patches, and geometric shapes and were thematically grouped by learning/recognition block. Objects were randomly assigned as fear associated objects, happy associated objects, and neutral associated objects. An independent group of participants (N = 15) rated "pleasantness" of all the objects on a 1–4 scale. Paired t-tests show that there is no significant difference in the inherent "pleasantness" of objects assigned to the fearful as compared to neutral or happy as compared to neutral association learning conditions.

2.3. Scanning procedure

Prior to scanning, participants completed the BFI (John & Srivastava, 1999) which is a 44-item self-report questionnaire assessing five personality traits: openness, conscientiousness, agreeableness, neuroticism, and extraversion. Participants identified the degree to which each item applied to them on a scale from 1 to 5 (1 = disagree strongly and 5 = agree strongly). BFI neuroticism and BFI extraversion have 8 items each. Participants also completed 2 practice sets of learning and recognition blocks.

fMRI scanning consisted of eight event-related observational fear learning runs. There were four runs of fear leaning and four runs of reward learning. Each run consisted of 4 sets of learning/recognition task blocks. Each task block consisted of 8 trials each (i.e. each run consisted of 32, 4 s learning trials and 32, 2 s recognition trials). These observational learning runs yielded a total of 64 trials for each of the four learning condition and 16 trials of each of the four object conditions. Each trial throughout the experiment was separated by a 2, 4, or 6 s jittered ITI, so that each trial type could be analyzed separately.

The subsequent memory post-test contained 128 objects which included all learned objects (fear, neutral (in fear runs); happy, neutral (in happy runs)), as well as two distracter objects from each recognition block. Objects in the post-test were presented in a self-paced, random order. Participants identified whether or not the object had been presented to the woman (i.e. whether it had been associated with a fearful, happy or neutral expression) in the course of the experiment.

2.4. Image acquisition

All images were acquired at 4 Tesla using a Varian INOVA MR scanner (Palo Alto, CA) that was equipped with echo-planar imaging. E-Prime software (PST, Pittsburgh, PA) controlled the stimulus display and recorded participant responses via a magnetic-compatible fiber-optic keypad. An LCD projector (Epson, Long Beach, CA) projected stimuli onto a backlit projection screen (Stewart, Torrance, CA).

Functional images were acquired during eight fMRI runs, which included 209 whole brain volumes per run, and 1672 whole brain volumes total for each participant. Images were acquired with specific parameters to optimize signal in regions susceptible to drop-out due to magnetic field inhomogeneity. Each acquisition included 40, 3.5 mm thick coronal slices with a 0.5 mm inter-slice gap, with a phase encode direction oriented in the superior-inferior direction. A one-shot T2*weighted EPI sequence (TR = 2000 ms, TE = 28 ms, FOV = 22.4 cm^2, matrix size = 64 × 64) was used to acquire blood-oxygenated dependent (BOLD) signal. A high-resolution 3D T1-weighted structural scan (MPFLASH sequence) and an in-plane low-resolution T2-weighted structural scan (GEMS) were acquired for anatomical localization.

2.5. Data processing and analysis

MRI data was processed and analyzed using SPM2 software. Each EPI volume was realigned in space to the first scan (participants with more than 3 mm of movement were excluded), and smoothed 8 mm (FWHM). We then created and estimated a general linear model (GLM) and created contrast images of the difference between neural activity for each comparison of interest. Contrast images were coregistered to
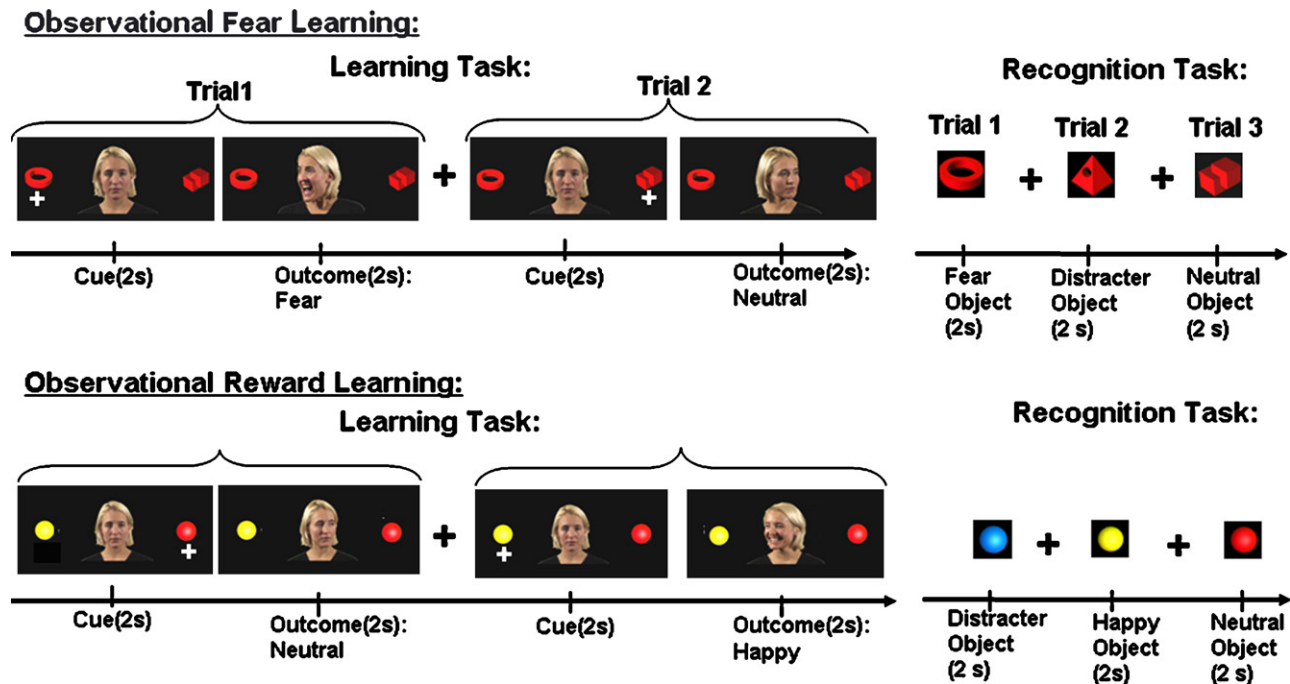
Fig. 1. In the experiment there were two different run types: observational fear learning and observational reward learning. Within each run there are two different tasks, learning and recognition, which alternated in groups of 8 trials each throughout the fMRI run. During learning trials, a fixation cross appeared under one of the objects and participants made a prediction about the association This is the cue period of the trial and the prediction choice was fearful or neutral during fear learning and happy or neutral during reward learning. Participants learned the true association at the outcome. The association of the object remained constant for 8 learning trials, then recognition trials started, and participants identified whether the object had been shown to the woman before (yes or no). After 8 recognition trials, a new set of learning trials started with two new objects. All trials are separated by a 2, 4, or 6 s jittered ITI.

the individual participant's anatomical images, resliced to $2 \times 2 \times 2$ isotropic voxels, skull-stripped to better match the template brain and then normalized using the Montreal Neurological Institute (MNI) template.

In the creation of the GLM, the hemodynamic response for learning trials was modeled from the onset of the outcome portion of the trial. (The cue portion of the trial remains constant throughout the experiment.) The hemodynamic response for the objects during recognition trials was modeled from the stimulus onset of the object. We defined individual movement parameters as a covariate of no interest. We defined each trial type as a covariate of interest: (1) Learn Fear; (2) Learn Neutral (fear runs); (3) Learn Happy; (4) Learn Neutral (happy runs); (5) Fear Object; (6) Neutral Object (fear runs); (7) Happy Object; (8) Neutral Object (happy runs); (9) Distracter Object (fear runs); (10) Distracter Object (happy runs).

The canonical hemodynamic response function (hrf) was convolved with brain activity at the onset of the trial type. Data was high-pass filtered at 200 s, scaled by the global mean, and corrected for serial autocorrelation. We computed the difference in neural activity between two trial types and computed whether this difference was significant across participants by entering the contrast value into a one-sample t-test. This whole brain random effects analysis was thresholded at $T(11) = 4.0$, $p < .001$ (uncorrected for whole brain comparisons). In the whole brain correlation analysis, we entered the BFI neuroticism or extraversion sum score in a simple regression with the contrast value between two trial types of interest (e.g. the contrast between Learn Fear vs. Learn Neutral). The correlation analysis was thresholded at $T(11) = 4.14$, $p < .001$ (uncorrected). After the whole brain analysis, significant neural activity in the amygdala–hippocampal complex was corrected for multiple comparisons using the Small Volume Correction (SVC) tool in SPM2. Volume of the amygdala–hippocampal complex was estimated by using an anatomical mask (AAL template) that incorporated the amygdala, hippocampus, and parahippocampal gyrus for the right and left hemisphere. SVC was done on each hemisphere separately. In addition, due to our a priori hypothesis concerning neural activity in the amygdala–hippocampus for emotional learning, we report activity significant at $p < .005$ (uncorrected) in these regions and note the lower threshold with an asterix in the tables.

3. Results

3.1. Behavioral results

We compared accuracy and reaction time of predicting the emotional association as compared to the neutral association and recognizing the emotional object as compared to the neutral object. We tested four main hypotheses: (1) emotional associations will be learned more efficiently (i.e. show faster reaction times) than neutral associations; (2) acquisition of the object-emotion association will continue throughout the learning block, resulting in faster reaction time with successive learning trials; (3) emotional associations will persist over time, resulting in better behavioral performance for emotional associations on the post-test; and (4) personality traits will predict learning efficiency such that both high neuroticism and low extraversion will be (independently) related to faster reaction times during fear learning.

Behavioral responses for the observational fear learning and observational reward learning experiments were analyzed separately (e.g. fear learning trials are compared with the neutral learning trials that occur within the fear learning experiment). Behavioral predictions to the first learning trial were not included in the behavioral analyses, since it was impossible to predict the association on the first trial (i.e. the association in each learning block was revealed at the outcome of the first trial). Reaction time analyses included correct trials only. 2-Tailed paired sample t-tests were used to test the difference between conditions. Data is reported for each variable as mean (standard deviation). It appeared that one participant responded randomly on the post-test; data from this participant was not used for analyses of the post-test.

3.1.1. Observational fear learning: learning, recognition, and post-test performance

Participants performed at a high level of accuracy. There was no significant difference in accuracy between predicting the fearful expression and predicting the neutral expression during learning trials [Learn Fear = 96% (4); Learn Neutral = 96% (4); $t(11) = 0.008$, ns]. There was no difference in accuracy for recognizing the fear associated object versus the neutral associated object when

these objects were presented alone during recognition trials [Fear Object = 97% (4); Neutral Object = 90% (14); $t(11) = 1.7$, ns].

As expected, participants responded significantly faster when predicting the fearful expression as compared to predicting the neutral expression [Learn Fear = 963 ms (99); Learn Neutral = 1000 ms (105); $t(11) = 2.7$, $p < .05$].

To identify whether acquisition of the emotional association continued throughout the learning block, we compared reaction time for behavioral predictions of early learning trials versus late learning trials. Early learning trials were defined as the first trial of that condition when it was presented as the second trial in the learning block (e.g. the first Learn Fear trial when it was presented as the second trial in the set of 8 learning trials). Late learning trials were defined as the 4th learning trial for that condition (i.e. the 4th Learn Fear trial and the 4th Learn Neutral trial). The 4th presentation of each learning condition could occur on the 5th, 6th, 7th, or 8th trial of the 8 trial learning block.

We found that behavioral predictions were significantly faster for late learning trials as compared to early learning trials for the fear association but not the neutral association [Early Learn Fear = 1078 ms (146) vs. Late Learn Fear = 943 ms (122); $t(11) = 3.5$, $p < .01$; Early Learn Neutral = 1033 ms (177) vs. Late Learn Neutral = 989 ms (100); $t(11) = 1.2$, ns]. There was no significant difference in the speed of behavioral prediction between Learn Fear and Learn Neutral at the early trials [Early Learn Fear vs. Early Learn Neutral; $t(11) = 0.8$, ns]. However, participants were significantly faster to predict the fear response as compared to the neutral response for the late trials [Late Learn Fear vs. Late Learn Neutral; $t(11) = 2.6$, $p < .05$]. This suggests that acquisition of the object-fear association continued throughout the 8 learning trials.

On the post-test, participants showed better recognition accuracy for the Fear Objects than the Neutral Objects presented in the fear learning runs [Post-test recognition accuracy: Fear Objects = 79% (17); Neutral Objects = 68% (18); $t(10) = 3.4$, $p < .01$]. Participants were quicker to correctly identify Fear Objects as compared to Neutral Objects [Fear Objects = 1190 ms (282); Neutral Objects = 1350 ms (357); $t(10) = 2.2$, $p = .05$].

3.1.2. Observational reward learning: learning, recognition, and post-test performance

During the reward learning runs, there was no significant difference in accuracy for predicting the happy expression as compared to neutral expression [Learn Happy = 96% (3); Learn Neutral = 96% (5)]. There was no significant difference in accuracy between recognizing the happy object as compared to the neutral object when these objects were presented alone during the recognition trials [Happy Object = 96% (5); Neutral Object = 90% (14); $t(11) = 1.6$, ns].

As expected, during learning, participants responded significantly faster when predicting the woman's happy expression as compared to the neutral expression [Learn Happy = 955 ms (120); Learn Neutral = 1002 ms (121); $t(11) = 2.1$, $p = .05$]. During recognition, participants responded significantly faster when recognizing the happy object as compared to the neutral object [Happy Object = 908 ms (103); Neutral Object = 1027 ms (127); $t(11) = 5.1$, $p < .05$].

There was no significant difference in reaction time between early and late learning trials for the prediction of a happy expression [Early Learn Happy = 1005 ms (117) vs. Late Learn Happy = 960 ms (151); $t(11) = 1.4$, ns] or for the neutral expression [Early Learn Neutral = 943 ms (164) vs. Late Learn Neutral = 993 ms (152); $t(11) = 1.4$, ns]. There was no significant difference between reaction times for the prediction of a happy expression versus neutral expression in the early learning trials [$t(11) = 1.2$, ns] or the late learning trials [$t(11) = 1.0$, ns].

On the post-test, there was no significant difference in accuracy between recognition of the Happy Objects versus the Neutral Objects that were presented in the reward learning runs [Happy Object = 74% (17); Neutral Object = 69% (16); $t(10) = 1.2$, ns], and there was no difference in reaction time when participants correctly identified Happy Objects and Neutral Objects on the post-test [Happy Objects = 1273 ms (368); Neutral Objects = 1335 ms (263); $t(10) = 0.8$, ns].

3.1.3. Correlation between personality variables and behavioral performance during observational fear learning—learning, recognition, and post-test

First, we identified the relationships between the five personality variables. Importantly, BFI neuroticism and BFI extraversion were not correlated with each other ($r = .0$). This suggests that these two factors are independent. BFI openness was negatively correlated with BFI neuroticism ($r = -.67$, $p < .05$). There were no other significant correlations between the big five personality variables.

To investigate whether high neuroticism predicted more efficient fear learning, we looked at the correlation between each participant's sum score on the BFI neuroticism scale and their behavioral accuracy and reaction time during fear learning. There was no statistically significant relationship between neuroticism and behavioral responses; however, the relationship was consistently in the predicted direction, such that a high level of neuroticism was related to better accuracy and faster reaction times during fear learning [Correlation coefficients for neuroticism and task accuracy: Learn Fear, $r = .54$, $p = .07$; Learn Neutral, $r = .38$, ns; Fear Object, $r = .25$, ns; Neutral Object, $r = .53$, $p = .08$. Correlation coefficients for neuroticism and RT: Learn Fear, $r = -.34$, ns; Learn Neutral, $r = -.24$, ns; Fear Object, $r = -.3$, ns; Neutral Object, $r = -.55$, $p = .06$].

On the post-test, neuroticism was not significantly related to accuracy for objects that were presented during the observational fear learning runs. However, the correlation was in the expected direction such that higher neuroticism was related to better accuracy [Fear Object, $r = .38$, ns; Neutral Object, $r = .57$, $p = .06$] and faster reaction times [Fear Object, $r = -.54$, $p = .09$; Neutral Object, $r = -.51$, ns].

In addition, we hypothesized that low BFI extraversion (i.e. high introversion) would be related to better accuracy and faster reaction times for fear learning. We found evidence to support this hypothesis, particularly in the analysis of reaction time. Extraversion was negatively correlated with accuracy (i.e. low extraversion predicted better accuracy) for prediction of the fear expression at the trend level ($r = -.55$, $p = .06$); extraversion was not related to accuracy for the prediction of the neutral expression ($r = -.48$, ns).

As expected, during learning, extraversion showed a significant positive correlation with reaction times when predicting the fear expression ($r = .72$, $p < .01$) as well as the neutral expression ($r = .8$, $p < .01$). During recognition, extraversion was positively correlated with reaction time for recognition of the Fear Object at the trend level ($r = .52$, $p = .08$) and was significantly positively correlated with reaction time for recognition of the Neutral Object ($r = .59$, $p < .05$). Thus low extraversion/high introversion was related to faster reaction times when predicting fear and neutral associations and recognizing fearful and neutral objects during observational fear learning.

On the post-test, extraversion was not related to recognition accuracy of the fear objects ($r = -.4$, ns) or neutral objects ($r = -.37$, ns) presented during the fear learning runs. Extraversion was not related to reaction time for the fear objects ($r = .19$, ns) or neutral object ($r = -.3$, ns).

There were no significant correlations between behavior during observational fear learning and the other big five personality traits:

conscientiousness, openness, and agreeableness. On the post-test, openness was significantly negatively correlated with accuracy for the Fear Object ($r = -.76$, $p < .01$) and Neutral Object ($r = -.66$, $p < .05$). Conscientiousness and agreeableness were not related to accuracy or reaction time on the post-test.

In summary, our main finding is that low extraversion/high introversion is strongly related to faster behavioral performance for all conditions in the observational fear learning experiment.

3.1.4. Correlation between personality variables and behavioral performance during observational reward learning—learning, recognition, and post-test

Consistent with the hypothesis that low extraversion is related to enhanced conditionability, we found that low extraversion/high introversion was significantly related to faster reaction times during reward learning. There was no relationship between extraversion and accuracy for the prediction of a happy expression ($r = -.2$, ns) or the neutral expression ($r = -.2$, ns). There was no relationship between extraversion and accuracy on recognition of the happy object ($r = -.1$, ns) or the neutral object ($r = -.2$, ns). However, extraversion was significantly positively correlated with reaction time for prediction of the happy expression ($r = .59$, $p < .05$) and neutral expression ($r = .78$, $p < .01$) during learning trials. Extraversion was not significantly related to reaction time for recognition of the Happy Object ($r = .5$, $p = .09$) or Neutral Object ($r = .44$, ns).

For the post-test, we found no significant relationships between extraversion and accuracy or reaction time for objects presented in the reward learning runs. The correlation coefficients are as follows: extraversion and Happy Object accuracy ($r = -.5$, ns); Neutral Object accuracy: ($r = -.17$, ns); Happy Object reaction time ($r = -.02$, ns) and Neutral Object reaction time ($r = .38$, ns).

During the reward learning experiment, neuroticism was related to better accuracy and faster reaction time when recognizing the Neutral Object on recognition trials [accuracy, $r = .7$; RT, $r = -.61$, p's $< .05$], but it was not related to any of the other reward learning variables.

On the post-test, there was no significant relationship between neuroticism and accuracy or reaction time for objects presented in the reward learning runs [Correlation coefficients: neuroticism and Happy Object accuracy ($r = .12$, ns); Neutral Object accuracy ($r = .57$, $p = .07$); Happy Object RT ($r = -.47$, ns); Neutral Object RT ($r = -.45$, ns)].

The other big five personality traits (conscientiousness, openness, and agreeableness) showed no significant correlations for behavior during the reward learning experiment. On the post-test, openness was related to worse accuracy ($r = -.8$, $p < .01$) and slower reaction time for neutral objects ($r = .73$, $p < .05$) but there was no relationship with performance for happy objects. Conscientiousness was related to worse accuracy for neutral objects ($r = -.67$, $p < .05$) but was not related to performance for happy objects. There were no other significant correlations.

In summary, the main finding is that low extraversion/high introversion is strongly related to faster behavioral performance for happy and neutral learning trials in the observational reward learning experiment.

3.2. fMRI results

3.2.1. Main effects: observational fear learning

3.2.1.1. Learn Fear versus Learn Neutral. To investigate brain mechanisms involved in learning the aversive value of an object through observation of another person's facial expression, we compared neural activity during fear learning and neutral learning. Across the group of participants, we found right amygdala–hippocampal activity when learning fear associations as compared to neutral

Table 1
Brain regions that have significantly more neural activity when learning the fear association as compared to the neutral association (Learn Fear vs. Learn Neutral) during observational fear learning

Brain region	R/L	BA	T-Value	MNI x, y, z coordinates
Learn Fear > Learn Neutral				
	R	28	4.74	28, 8, −24
Amygdala–parahippocampal gyrus				
Hippocampus	R	20	3.8[*]	42, −20, −18
Inferior frontal gyrus: triangularis	R	45	5.26	50, 32, 16
Inferior frontal gyrus: triangularis	L	45	4.3	−52, 32, 4
Inferior frontal gyrus: triangularis (superior portion)	L	44	4.1	−56, 18, 26
Intraparietal sulcus	L	7	4.0	−26, −76, 46
Middle temporal gyrus—superior temporal sulcus	R	21	11.0	66, −52, 2
Middle temporal gyrus—superior temporal sulcus	L	37	5.3	−62, −54, 4
Lingual gyrus	R	19	5.3	38, −84, −20
Fusiform gyrus	R	37	4.7	44, −46, −26

[*] $p = .002$, uncorrected.

associations (Learn Fear vs. Learn Neutral). Activations and coordinates for this contrast are listed in Table 1. Data is shown in Fig. 2A.

3.2.1.2. Fear Object versus Neutral Object. To identify whether the observation of a fear reaction would imbue the object with a neural representation of aversive value, we looked at the neural activity to the fear associated object (Fear Object) as compared to the neutral associated object (Neutral Object) during the object recognition trials. Across the group, we found greater right amygdala activity as well as bilateral parahippocampal gyrus activity in response to the Fear Object versus the Neutral Object when these objects were presented alone (see Fig. 2B). Activations listed in Table 2.

3.2.2. Correlation between personality variables and neural activity during observational fear learning

3.2.2.1. Learn Fear versus Learn Neutral. To investigate whether a higher level of neuroticism was related to greater activity in the amygdala during observational fear learning, we correlated each individual's BFI neuroticism sum score with neural activity during Learn Fear versus Learn Neutral. We found that individual level of neuroticism was significantly correlated with neural activity in the left and right amygdala; participants with higher neu-

Table 2
Brain regions that have significantly more neural activity for the fear associated object as compared to the neutral associated object (Fear Object vs. Neutral Object) on recognition trials during observational fear learning

| Brain region	R/L	BA	T-Value	MNI x, y, z coordinates
Fear Object > Neutral Object				
Amygdala	R	34	4.15	30, 2, −16
Parahippocampal gyrus	R	30	3.31[*]	26, −20, −20
Parahippocampal gyrus	L	30	4.22	−26, −24, −20
Superior frontal gyrus	R	6	3.9	24, −2, 62
Postcentral gyrus: superior	L	3, 2	7.9	−30, −38, 64
Supramarginal gyrus	L	48, 2, 1	7.3	−54, −26, 44
Middle temporal gyrus	L	19, 37	6.8	−46, −68, 6
Fusiform	R	19, 37	6.9	44, −60, −18
Posterior cingulate gyrus	L	23	5.1	−8, −50, 22

[*] $p = .003$, uncorrected.
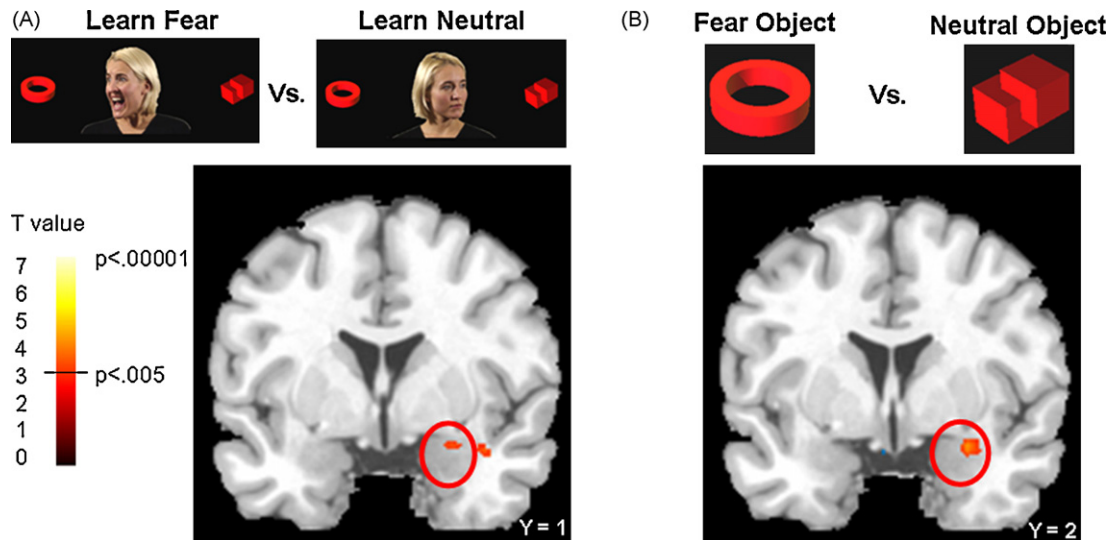
Fig. 2. Neural activity during observational fear learning. (A) During learning trials, there was greater right amygdala activity during fear learning relative to neutral learning (Learn Fear vs. Learn Neutral). (B) During recognition trials after learning, there was greater amygdala activity for the fear associated object than the neutral associated object (Fear Object vs. Neutral Object). Data shown at the threshold $t(11) = 3.11$, $p < .005$.

roticism scores had more activity in the amygdala–hippocampus complex when creating fearful as compared to neutral associations (see Fig. 3). In the left hemisphere, the amygdala activity extended to the anterior hippocampus. In the right hemisphere, there were two separate clusters in the medial temporal lobe, one cluster in the right amygdala and a separate cluster in the anterior hippocampus. Neural data extracted from the significant clusters

showed the following correlation coefficients with neuroticism: right amygdala, $r = .78$, $p < .01$; right hippocampus, $r = .88$, $p < .01$; left amygdala–hippocampus, $r = .85$, $p < .01$. Neuroticism was also correlated with other brain regions during fear learning (listed in Table 3).

BFI extraversion was not significantly related to neural activity in the amygdala–hippocampal complex during Learn Fear ver-
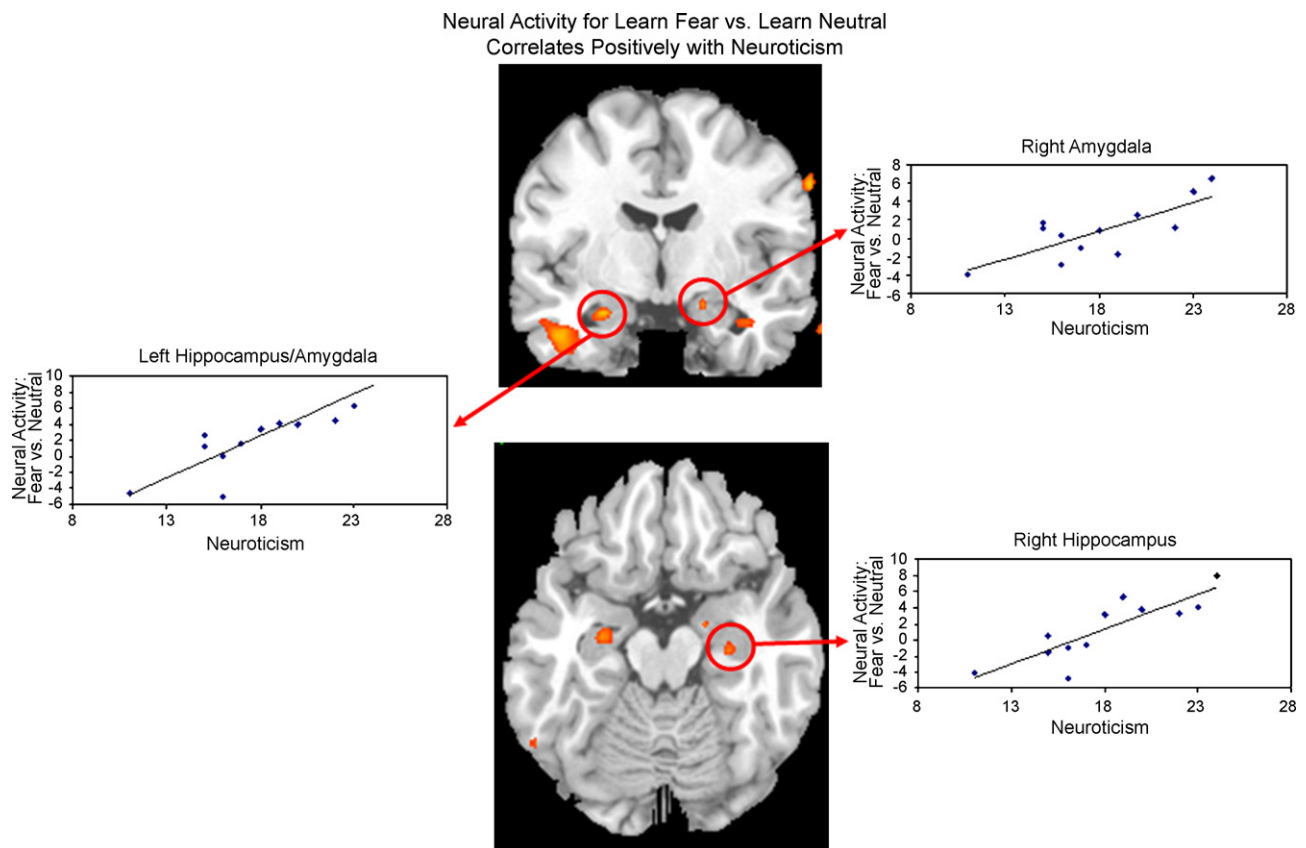
Fig. 3. Correlation of amygdala and hippocampal activity during fear versus neutral learning with individual sum score on BFI neuroticism scale. Data shown on coronal slice $y = -6$ and axial slice $z = -12$.

Table 3
Brain regions in which neural activity during fear learning as compared to neutral learning showed a significant positive correlation with individual differences in neuroticism

Brain region	R/L	BA	T-Value	MNI x, y, z coordinates
Learn Fear > Learn Neutral positive correlation with neuroticism				
Amygdala	R	34, 35	4.2	20, −6, −16
Hippocampus	R	20	5.8	32, −18, −20
Amygdala–hippocampus complex	L	20	6.0	−26, −10, −20
Superior parietal lobule	R	40	4.0	38, −52, 60
Middle occipital gyrus	R	39	4.0	44, −70, 28
Middle occipital gyrus	L	7	4.6	−36, −76, 42

sus Learn Neutral in either the positive or negative direction. There was no significant correlation between neural activity in the amygdala–hippocampal complex and the other big five personality traits: openness, agreeableness, and conscientiousness. Other brain regions in which neural activity for Learn Fear versus Learn Neutral correlated with BFI variables are listed in Table 5.

To determine the specificity of the relationship between neuroticism and amygdala–hippocampal activity during Learn Fear versus Learn Neutral, we performed a factor analysis of the four BFI personality traits other than neuroticism (extraversion, openness, agreeableness, and conscientiousness), took the factor that explained the most variance (factor one = 30% of the variance), and performed a multiple regression in SPM2. This analysis identified regions in which neural activity during Learn Fear versus Learn Neutral correlated with neuroticism while controlling for common variance associated with the four other BFI traits. Neural activity during Learn Fear versus Learn Neutral in the regions of interest remained significantly correlated with neuroticism in this analysis: right amygdala (peak value = 4.6, MNI coordinates = 20, −6, 16), right hippocampus (peak value = 4.7, MNI coordinates = 32, −18, −20) and left hippocampus (peak value = 5.5, MNI coordinates = −26, −12, −20).

3.2.2.2. Fear Object versus Neutral Object. To identify whether individual levels of neuroticism were related to neural activity when viewing the fear object alone, we correlated each individual's BFI neuroticism sum score with neural activity in the comparison of Fear Object versus Neutral Object in the recognition trials. We found no significant correlation between neuroticism and amygdala activity in response to the fear object. However, neuroticism was related to neural activity in response to the fear object in other brain regions (listed in Table 4).

Table 4
Brain regions in which neural activity during Fear Object versus Neutral Object showed a significant positive correlation with individual differences in neuroticism

Brain region	R/L	BA	T-Value	MNI x, y, z coordinates
Fear Object > Neutral Object positive correlation with neuroticism				
Superior frontal gyrus—inferior/anterior portion	R	11	4.3	26, 62, −6
Middle frontal gyrus	R	46	4.2	52, 50, 10
Middle frontal gyrus	L	46	5.5	−36, 50, 32
Middle cingulate gyrus	R	32	4.2	6, 20, 40
Supramarginal gyrus	R	48	4.7	60, −46, 30
Intraparietal sulcus	R	40	4.2	44, −44, 58
Thalamus	R		6.2	18, −4, 8
Thalamus	L		5.3	−14, 0, −8

Table 5
Brain regions in which neural activity for the main contrasts of the observational fear learning experiment (Learn Neutral and Fear Object vs. Neutral Object) showed a significant positive correlation with the BFI personality traits extraversion, openness, agreeableness, and conscientiousness

Brain region	R/L	BA	T-Value	MNI x, y, z coordinates
Learn Fear > Learn Neutral positive correlation with extraversion				
Middle temporal gyrus (anterior)	L	21	4.93	−44, −6, −18
Middle frontal gyrus	L	46	4.57	−40, 34, 36
Fear Object > Neutral Object positive correlation with extraversion				
Intraparietal sulcus	R	7	5.64	16, −78, 40
Posterior cingulate	R	23	5.37	8, −44, 44
Superior medial PFC/SMA	R	6, 8	7.68	6, 18, 50
Middle occipital gyrus	L	19	6.19	−22, −86, 30
Middle occipital gyrus	R	19	5.2	38, −86, 20
Angular gyrus/TPJ	L	39	5.89	−36, −50, 36
Precuneus	L	27	4.92	−10, −44, 4
Superior temporal sulcus	R	21, 22	4.36	52, −30, 4
Inferior temporal gyrus	L	20	4.8	−52, −42, −20
Inferior temporal gyrus	R	20	4.52	58, −42, −22
Learn Fear > Learn Neutral positive correlation with agreeableness				
Posterior insula	R	48	7.69	36, −10, 12
Superior frontal gyrus	L	8	7.47	−8, 20, 68
Middle cingulate gyrus	L	32	6.62	−12, 12, 44
Middle temporal gyrus (posterior)	L	37	6	−40, −76, 12
Superior temporal sulcus	L	21, 22	5.99	−54, −34, 4
Thalamus	L		5.92	−16, −22, 4
Posterior insula	L	48	5.34	−34, −30, 12
Intraparietal sulcus	R	7	5.3	26, −54, 42
Thalamus	R		5.23	22, −20, −2
Middle frontal gyrus	L	9	5.2	−36, 6, 58
Middle temporal gyrus	L	37	4.98	−52, −62, 2
Precentral gyrus	L	6	4.96	−52, 0, 28
Intraparietal sulcus	R	7	4.8	36, −50, 48
Fear Object > Neutral Object positive correlation with agreeableness				
Superior frontal gyrus	R	9	5.68	26, 32, 42
Superior temporal sulcus	L	21	5.67	−46, −36, 12
Cerebellum	L		5.16	−36, −80, −28
Temporoparietal junction	R		5.04	46, −50, 34
Middle temporal gyrus (posterior)	L	37	4.89	−56, −62, 0
OFC	R	11	4.62	30, 34, −22
OFC	L	12	4.59	−20, 60, −8
Middle frontal gyrus	R	46	4.56	36, 44, 4
Superior frontal gyrus	R	8	4.54	8, 32, 48
Lateral orbital gyrus	R	47	4.51	26, 26, −14
Precuneus	R	7	13.46	12, −54, 40
Precuneus	L	7	5.71	−12, −64, 28
Cerebellum	R/L		12.07	2, −44, −10
Superior temporal sulcus (posterior)	R	39	5.6	46, −56, 16
Learn Fear > Learn Neutral positive correlation with conscientiousness				
Medial OFC	R	11	6.18	10, 56, −8
Superior temporal gyrus	R	22	4.51	58, −16, −6
Learn Fear > Learn Neutral positive correlation with openness				
Inferior temporal gyrus	L	21	5.1	−44, 2, −10
Cerebellum	L	11	4.7	−36, −46, −44

Both positive and negative correlations were investigated for extraversion; however, there were no brain regions that showed a negative correlation with extraversion. Only those contrasts with significant correlations are listed.

Amygdala activity in response to the fear object was not related to BFI extraversion, conscientiousness, agreeableness, or openness (see Table 5).

3.2.3. Correlation of neural activity during fear learning and post-test behavioral performance

To identify whether greater neural activity in the amygdala–hippocampal complex during observational fear learning was related to better memory of the learned objects, we correlated neural activity in the amygdala and hippocampus during

Learn Fear trials with the accuracy and speed that participants identified the Fear and Neutral Objects in the post-test. Because the amygdala and hippocampus may have different roles in emotional memory (Phelps, 2004), we looked at each region separately. Specifically, in the contrast Learn Fear versus Learn Neutral, we divided the area of activation in the medial temporal lobe into separate clusters in the amygdala and hippocampus. To do this, we isolated amygdala activity (i.e. separated amygdala activity from the hippocampus) by masking the SPM correlation output with an anatomical mask of the left and right amygdala (MNI AAL). We then extracted the contrast values in the four regions (i.e. R amygdala, R hippocampus, L amygdala, L hippocampus) and investigated the relationship between this neural activity and behavior on the post-test.

In our initial analyses, we found that neural activity during Fear versus Neutral Learning in all four regions (R amygdala, R hippocampus, L amygdala, L hippocampus) was correlated (significantly or at the trend level) with faster and more accurate recognition of both the Fear Object and the Neutral Object. However, neural activity in these regions was not related to post-test behavior for the Distracter Objects. Therefore, because neural activity was modestly related to both the Fear Object and the Neutral Object, we created two new variables which were the average accuracy (Learned Objects-Accuracy) and average speed (Learned Objects-Reaction Time) of recognizing a learned object.

3.2.3.1. Post-test learned objects—accuracy. Neural activity in the right amygdala and left hippocampus during observational fear learning was significantly related to Learned Object-Accuracy on the subsequent memory post-test (correlation coefficients with post-test accuracy: right amygdala, $r = .59$, $p = .05$; left hippocampus, $r = .63$, $p < .05$). Individuals with greater activity in the right amygdala and left hippocampus during Learn Fear versus Learn Neutral showed enhanced memory for learned objects. There was also a positive correlation between neural activity in the left amygdala and right hippocampus and Learned Object-Accuracy though it was not statistically significant (left amygdala, $r = .5$; right hippocampus, $r = .36$). Neural activity in these regions during fear learning was not related to accuracy in identifying Distracter Objects in the subsequent memory post-test. See Fig. 4.

3.2.3.2. Post-test learned objects—reaction time. Neural activity in the right hippocampus during observational fear learning was significantly related to Learned Object-Reaction Time on the subsequent memory post-test ($r = -.71$, $p < .01$). Individuals with greater activity in the right hippocampus during Learn Fear versus Learn Neutral correctly identified learned objects faster in the post-test. The relationship was in the predicted direction for the other regions, though the correlation was not statistically significant (right amygdala, $r = -.47$, left amygdala, $r = -.53$, left hippocampus, $r = -.53$). Neural activity in these regions during fear learning was not related to reaction time when correctly identifying Distracter Objects in the subsequent memory post-test. See Fig. 4.

3.2.3.3. Correlation between neural activity and task performance. There was no significant relationship between amygdala–hippocampal activity during Learn Fear versus Learn Neutral and behavioral accuracy and reaction time for prediction of the fearful expression or prediction of the neutral expression during the task.

3.2.4. Main effects: observational reward learning
3.2.4.1. Learn Happy versus Learn Neutral. To investigate brain mechanisms involved in learning the reward valence of an object

through observation of another person's facial expression, we compared neural activity for Learn Happy versus Learn Neutral. Across the group of participants, we found greater right hippocampal and ventromedial prefrontal cortex (VMPFC) activity for Learn Happy versus Learn Neutral. VMPFC activity extended from the superior portion of VMPFC in Brodmann's area 10 to the medial orbitofrontal cortex in Brodmann's area 11 (see Fig. 5). All activations are listed in Table 6.

3.2.4.2. Happy Object versus Neutral Object. To identify whether the observation of a happy reaction would ascribe the object with a neural representation of reward value, we looked at the neural activity to the reward associated object (Happy Object) as compared to the neutral associated object (Neutral Object) during the object recognition trials. Across the group, we found greater activity in the left amygdala, left hippocampus, and right anterior hippocampus in the contrast Happy Object versus Neutral Object (see Fig. 5). Activations listed in Table 7.

Table 6
Brain regions that have significantly more neural activity when learning the happy association as compared to the neutral association (Learn Happy vs. Learn Neutral) during observational reward learning

Brain region	R/L	BA	T-Value	MNI x, y, z coordinates
Learn Happy > Learn Neutral				
Hippocampus	R	20	4.09	28, −22, −14
Ventromedial PFC	R/L	10	13.34	2, 66, 2
Ventromedial PFC	R/L	11	11.63	−10, 66, −4
Ventromedial PFC	R/L	11	7.42	0, 58, −8
Superior frontal gyrus	R	9	4.45	20, 32, 32
Middle frontal gyrus	L	9	4.2	−28, 24, 46
Rolandic operculum	R	48	5.72	44, −18, 18
Rolandic operculum	L	48	4.7	−32, −26, 20
Supplementary motor area	R/L	4	6.06	8, −22, 52
Precentral sulcus	R	4	4.77	32, −26, 52
Postcentral gyrus	L	48	5.67	−46, −12, 22
Paracentral lobule	L	4	5.55	−10, −30, 70
Superior temporal sulcus (anterior)	R	21	4.69	54, −22, −6
Superior temporal gyrus	R	42	6.3	60, −38, 18
Middle temporal gyrus	L	37	4.85	−44, −54, −2
Middle temporal gyrus	L	39	4.71	−40, −64, 24
Fusiform gyrus	L	30	4.37	−18, −36, −16
Posterior cingulate	R/L	23	6.71	−10, −56, 22

Table 7
Brain regions that have significantly more neural activity for the happy associated object as compared to the neutral associated object (Happy Object vs. Neutral Object) on recognition trials during observational reward learning

Brain region	R/L	BA	T-Value	MNI x, y, z coordinates
Happy Object > Neutral Object				
Hippocampus–parahippocampal gyrus	L	35	4.95	−18, −14, −22
Amygdala	L	34	3.85	−22, 2, −16
Anterior hippocampus	R	35	3.51[*]	24, −12, −14
Superior parietal gyrus	L	7	6.73	−16, −40, 64
Precuneus	R	5	6.1	6, −40, 58
Superior temporal sulcus (anterior)	R	22	5.82	48, −10, −10
Superior temporal sulcus (anterior)	L	21	5.68	−40, −18, −6
Temporal pole	L	38	4.55	−54, 4, −18
Substantia nigra			4.39	6, −10, −10
Middle cingulate	R	23	4.29	16, −16, 36
Middle occipital gyrus	R	19	4.24	40, −70, 14

[*] $p = .002$, uncorrected for multiple comparisons.
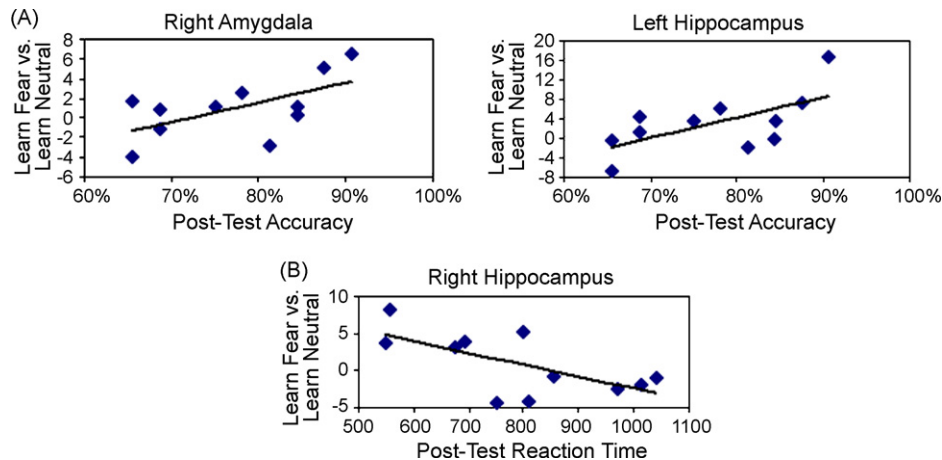
Fig. 4. (A) Neural activity in the right amygdala and left hippocampus during Learn Fear vs. Learn Neutral is positively correlated with accuracy of recognizing the learned objects (both Fear Objects and Neutral Objects) on the post-test. (B) Neural activity in the right hippocampus during Learn Fear vs. Learn Neutral is negatively correlated with reaction time for correctly recognizing the learned objects (both Fear Objects and Neutral Objects) on the post-test.

3.2.5. Correlation of personality variables and neural activity during observational reward learning

3.2.5.1. Learn Happy versus Learn Neutral. To investigate whether neural activity in the amygdala and hippocampus varied according to individual differences in extraversion, we correlated neural activity for the contrast Learn Happy versus Learn Neutral with scores on BFI extraversion. There was a negative correlation such that low scores on BFI extraversion (i.e. high introversion) were related to more activity in the left amygdala during Learn Happy versus Learn Neutral. See Fig. 6 and Table 8.

3.2.5.2. Happy Object versus Neutral Object. Neural activity in the amygdala for Happy Object versus Neutral Object was negatively correlated with BFI extraversion, such that lower extraversion was related to greater activity in the amygdala in response to the happy associated object (see Fig. 6). BFI extraversion was significantly pos-

itively correlated with neural activity in the right and left posterior parahippocampal gyrus during recognition of the Happy Object versus Neutral Object. See Table 8.

All significant correlations between neural activity during reward learning and the other big five personality traits are shown in Table 9.
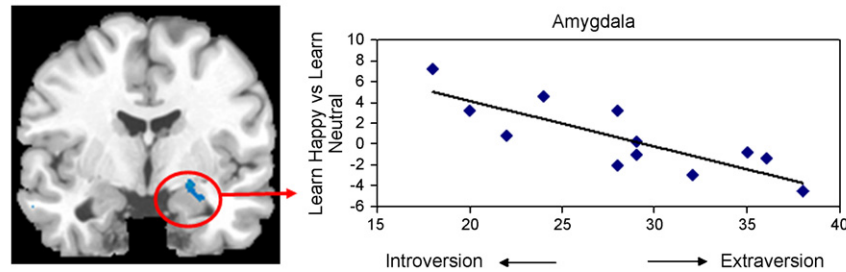
3.2.6. Correlation of neural activity during observational reward learning and post-test performance

3.2.6.1. Learn Happy versus Learn Neutral and post-test learned objects. We extracted neural activity for each participant from the significant clusters in the hippocampus and ventromedial prefrontal cortex that were identified at the group level analysis for reward learning (Learn Happy vs. Learn Neutral) and correlated it with post-test accuracy for learned objects in the reward learning experiment (i.e. Happy Objects and Neutral Objects from the reward
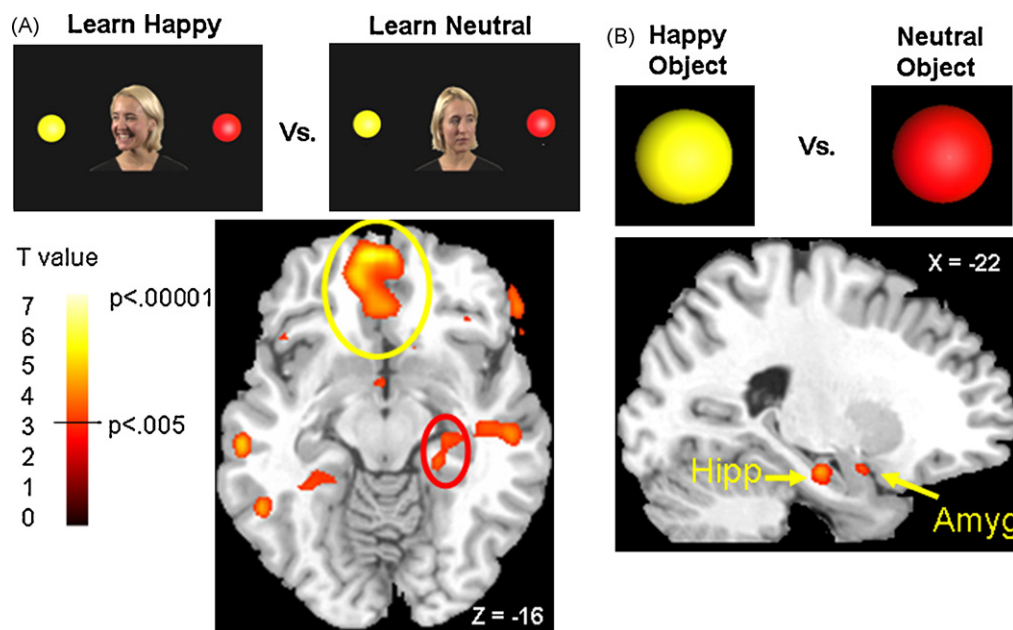

Fig. 5. Neural activity for observational reward learning. (A) During the learning task, there was greater ventromedial prefrontal cortex (yellow circle) and right hippocampus (red circle) activity when learning object-reward associations from a happy face relative to object-neutral associations from a neutral face (Learn Happy vs. Learn Neutral). (B) During recognition trials after learning, there was greater amygdala and hippocampal activity to the happy associated object as compared to the neutral associated object (Happy Object vs. Neutral Object) when these objects were presented alone. Data shown at the threshold $t(11) = 3.11$, $p < .005$.
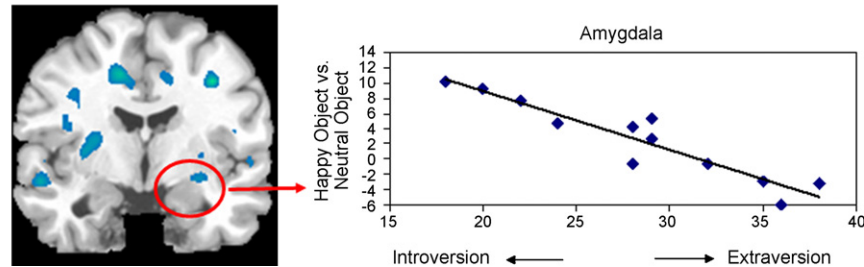
Fig. 6. Whole brain correlation of neural activity during learning and recognition with individual sum score on BFI extraversion scale with negative correlations shown in blue. (A) *Learning.* Those with low extraversion scores had more amygdala activity for Learn Happy versus Learn Neutral. (B) *Recognition.* Those with low extraversion scores had more amygdala activity to the Happy Object versus Neutral Object. Data shown on coronal slice $y = -4$ and displayed on template brain at threshold $p < .005$.

learning runs). There was no significant association between neural activity in the left hippocampus during reward learning and post-test accuracy ($r = -.06$, ns) or reaction time ($r = -.46$, ns). There was no significant association between neural activity in the ventromedial prefrontal cortex during reward learning and post-test accuracy ($r = .23$, ns) or reaction time ($r = .14$, ns).

3.2.6.2. Happy Object versus Neutral Object and post-test learned objects. There was no significant correlation between individual level of neural activity in hippocampus or amygdala for recognition of the reward object versus the neutral object and post-test performance. The correlation coefficients are as follows: hippocampus and post-test accuracy ($r = -.04$, ns) and reaction time ($r = .03$, ns); amygdala and post-test accuracy ($r = -.27$, ns) and reaction time ($r = -.34$, ns).

3.2.6.3. Correlation between neural activity during the task and task performance. Additionally, we investigated the relationship between neural activity in the VMPFC and hippocampus during learning and behavioral performance during the learning task, there was one significant relationship: neural activity in the hippocampus for Learn Happy versus Learn Neutral was negatively correlated with accuracy for the neutral object ($r = -.63$, $p < .05$). In other words, more activity for the neutral object relative to the happy object in the hippocampus predicted better accuracy for the neutral object. There were no other significant correlations between hippocampal activity and task performance during learning.

There was no significant relationship between amygdala or hippocampal activity during recognition of Happy Object versus Neutral Object and behavioral performance during recognition of the Happy Object or Neutral Object.

4. Discussion

The goal of this study was to identify the behavioral and neural mechanisms of observational fear and reward learning and investigate how these mechanisms are modulated by indi-

vidual differences in neuroticism and extraversion. In regard to basic mechanisms of observational learning, we found the following: (1) the amygdala–hippocampal complex was involved in both observational fear and reward learning. Specifically, the amygdala–hippocampal complex was active when learning the object-fear association from someone else's fearful expression; the hippocampus but not the amygdala was active when learning the object-happy association. After learning, the amygdala was active to the fear (vs. neutral) associated object and the happy (vs. neutral) associated object when these object were presented alone; (2) greater amygdala–hippocampal activity during fear learning predicted better long-term memory for objects with a learned association (i.e. both fear objects and neutral objects from the fear learning experiment); (3) reaction time was faster for behavioral prediction of the emotional expression and recognition of emotional objects. Personality influenced observational learning in the following ways: (1) higher levels of neuroticism predicted greater neural activity in the amygdala–hippocampal complex during fear (vs. neutral) learning; (2) low levels of extraversion (i.e. high introversion) were related to enhanced behavioral performance for both fear and reward learning; (3) low extraversion was related to greater amygdala activity during happy (vs. neutral) learning and happy (vs. neutral) object recognition.

4.1. Behavioral and neural mechanisms of observational learning

The results of our experiment suggest that observational learning uses the same behavioral and neural mechanisms as learning from direct experience. More specifically, the data suggest that during observational learning, amygdala activity in response to arousal associated with the emotional facial expression neurally ascribes the associated object (i.e. the CS+) with emotional value, thereby enhancing encoding and consolidation of the emotional association. In addition, arousal from the emotional expression most likely facilitates behavioral performance for predicting emotion associations and recognizing emotion associated objects.

Table 8
Brain regions in which neural activity for happy association learning as compared to neutral association learning (Learn Happy vs. Learn Neutral) significantly correlated with extraversion in the positive and negative direction

Brain region	R/L	BA	T-Value	MNI x, y, z coordinates
Learn Happy > Learn Neutral positive correlation with extraversion				
Cerebellum	R		5.21	46, −44, −32
Happy Object > Neutral Object positive correlation with extraversion				
Posterior parahippocampal gyrus	L	30	4.49	−14, −30, −12
Posterior hippocampus	R	20	6.42	18, −28, −6
Cerebellum	R		5.81	36, −40, −38
Posterior cingulate	R/L	23	4.83	2, −42, 34
Learn Happy > Learn Neutral negative correlation with extraversion				
Amygdala	R	34	4.46	26, 0, −20
Dorsal amygdala	R	34	4.19	22, −6, −10
Superior frontal gyrus	R	8	4.43	14, 28, 62
Postcentral gyrus	R	4	4.7	56, −6, 42
Middle temporal gyrus	R	21	5.54	60, −34, −4
Inferior temporal gyrus	R	37	5.28	60, −46, −2
Temporal pole	R	36	5.03	28, 16, −36
Caudate	L		4.72	−14, 14, 8
Cuneus	L	19	4.46	−20, −82, 22
Lingual gyrus	L	17	4.68	−14, −92, −4
Middle occipital gyrus	R	19	4.26	26, −86, 20
Happy Object > Neutral Object negative correlation with extraversion				
Dorsal amygdala	R	34	5.67	28, 0, −10
Inferior frontal gyrus	L	48	9.33	−40, 8, 14
Inferior frontal gyrus	L	48	8.99	−56, 4, 4
Orbital frontal cortex	R	11, 48	7.13	28, 12, −14
Orbital frontal cortex	L	11	4.59	−20, 28, −14
Middle frontal gyrus	L	46	4.34	−32, 40, 22
Anterior cingulate gyrus	R	23, 24	5.51	14, −16, 48
Anterior cingulate gyrus	L	23, 24	6.27	−14, −2, 46
Central gyrus	R	6	6.97	34, −6, 42
Posterior insula	R	48	4.85	36, −20, 4
Posterior insula	L	48	6.58	−30, −26, 18
Supramarginal gyrus	L	48	4.89	−52, −28, 24
Superior temporal sulcus (anterior)	L	21	4.55	−46, −14, −10
Superior temporal gyrus	L		5.41	−60, −34, 20
Fusiform gyrus	R	37	6.04	44, −66, −4
Fusiform gyrus	L	37	5.17	−44, −66, −8
Superior parietal lobe	L	7	4.61	−28, −44, 62
Calcarine	R	17	5.59	16, −66, 10
Middle occipital gyrus	L	19	4.23	−20, −76, 26

4.1.1. Observational fear learning

This observational learning mechanism is most evident in the observational fear learning experiment. Like classical conditioning, the amygdala–hippocampal complex was more active when learning an association between a neutral object and a fearful expression than a neutral object and a neutral expression. Importantly, after learning, the amygdala was more active to the fear associated object than the neutral associated object (CS+ vs. CS−) when these objects were presented alone. These findings suggest that amygdala activity during the observation of another person's fearful reaction to an object neurally 'tagged' that object with emotional value. Amygdala activity to the fear associated object presented alone after learning reflects the neural representation of this emotional value and suggests that the CS+ has acquired a conditioned response (CR).

Our behavioral data was also consistent with classical conditioning (Critchley, Mathias, & Dolan, 2002; Gottfried et al., 2002). Reaction time was faster when predicting a fear response versus a neutral response and when recognizing the fear object versus the neutral object. Speed of prediction for the fear expression improved over successive acquisition trials, suggesting that acquisition continued throughout the learning block. On the subsequent memory post-test, participants were more accurate at recogniz-

ing the fear associated objects than the neutral associated objects. Overall, these data show a consistent behavioral advantage for the fear association over the neutral association.

Importantly, amygdala–hippocampal activity during fear (vs. neutral) learning was significantly correlated with better behavioral performance, including accuracy and reaction time, for both the fear and neutral associated objects on the post-test. These findings are consistent with data showing that amygdala activity during encoding of emotional stimuli predicts later memory for those stimuli (Cahill et al., 1996; Hamann, Ely, Grafton, & Kilts, 1999) and suggests that amygdala response to emotional arousal modulates hippocampal dependent encoding and consolidation processes (Phelps, 2004, 2006; Phelps & LeDoux, 2005; Richardson, Strange, & Dolan, 2004).

However, in most prior studies, emotional and neutral stimuli are presented separately, making it difficult to distinguish the effects of emotion and arousal on memory. In our paradigm, the fear object and the neutral object are on the screen at the same time during learning trials, and it is the woman's direction of attention when she expresses emotion that designates the association. The fearful expression which indicates one object as a threat (i.e. fear object) simultaneously indicates that the other object is safe (i.e. neutral object). Even though the reverse is true – i.e. a neutral expression to the safe object indicates that the other object is a threat – it is only the elevated neural response during fear learning which predicts subsequent memory for both objects.

The reason that neural response during fear learning correlates with subsequent memory for both objects is most likely due to the fact that arousal instigated by the observation of fear enhances the encoding and consolidation of both the fear object and the neutral object. Recent investigations are consistent with this interpretation. For example, amygdala and hippocampal activity during encoding of neutral words in an emotional context is related to subsequent memory of those neutral words (Maratos, Dolan, Morris,

Table 9
Brain regions in which neural activity for the main contrasts of the observational reward learning experiment (Learn Happy vs. Learn Neutral and Happy Object vs. Neutral Object) showed a significant positive correlation with the BFI personality traits neuroticism, openness, agreeableness, and conscientiousness

Brain region	R/L	BA	T-Value	MNI x, y, z coordinates
Learn Happy > Learn Neutral positive correlation with neuroticism				
Precuneus	R	5	6.77	12, −48, 66
Middle frontal gyrus	L	8	8.62	−26, 30, 56
Postcentral gyrus	R	3	7.87	32, −36, 60
Intraparietal sulcus	L	7	5.63	−26, −72, 52
Fusiform gyrus	L	19	4.69	−22, −72, −14
Calcarine	L	17	4.46	−12, −52, 4
Happy Object > Neutral Object positive correlation with neuroticism				
Thalamus	L		5.29	−12, −2, 2
Superior frontal gyrus	R	6	4.21	18, −4, 64
Learn Happy > Learn Neutral positive correlation with conscientiousness				
Cerebellum	L		6.67	−34, −40, −34
Happy Object > Neutral Object positive correlation with conscientiousness				
Middle temporal gyrus (posterior)	L	37	8.32	−46, −64, 24
Precuneus	R/L	23, 7	7.14	−6, −46, 38
Happy Object > Neutral Object positive correlation with openness				
Middle frontal gyrus	R	8	4.67	28, 16, 48
Precuneus	R	7	5.35	10, −58, 46
Middle temporal gyrus	L	39	5.23	−40, −72, 16
Inferior temporal gyrus	L	20	5.17	−56, −56, 0
Fusiform gyrus	L	37	4.92	−48, −38, −20
Parahippocampal gyrus	L	20	4.45	−30, −22, −20
Cerebellum	L		5.58	−48, −48, −40

Only those contrasts with significant correlations are listed.

Henson, & Rugg, 2001; Smith, Henson, Dolan, & Rugg, 2004). In addition, highly arousing (but not non-arousing) emotional pictures presented immediately after a neutral stimulus results in retrograde enhancement of long-term memory for that neutral stimulus (Anderson, Wais, & Gabrieli, 2006). Similarly, memory for neutral information is enhanced by an injection of adrenaline immediately after learning (McGaugh et al., 1993).

4.1.2. Observational reward learning

Results from observational reward learning show that participants learned the reward value of the object based on the woman's happy expression, and there is evidence that this occurred through a classical conditioning process, but the pattern of results were not as consistent as observational fear learning. The hippocampus (though not the amygdala) was active when learning the association between the object and happy response as compared to the object and neutral response. The ventromedial prefrontal cortex, a region highly responsive to rewarding stimuli (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001), was also active when learning from the happy (vs. neutral) face, suggesting that the happy expressions were rewarding (O'Doherty et al., 2003). After learning, both the amygdala and the hippocampus were active in response to the happy associated object as compared to the neutral object when these objects were presented alone, suggesting that the acquired reward value of the object is stored in the amygdala.

Behavioral performance during observational reward learning was generally consistent with classical conditioning (Critchley et al., 2002; Gottfried et al., 2002). Participants responded faster when predicting the happy expression than the neutral expression, and when recognizing the happy object than the neutral object. However, there was no difference in reaction time between early and late trials suggesting that learning may not have continued throughout each learning block. On the surprise post-test, there was no difference in behavioral performance for the happy associated object versus the neutral object, and there was no relationship between neural activity in the hippocampus during learning and behavior on the post-test.

These results are generally consistent with observational learning (Carver & Vaccaro, 2007; Mumme, Fernald, & Herrera, 1996) and classical conditioning studies, showing that reward learning does not produce as strong or as reliable effects as fear learning. This may be because reward stimuli used in experiments are not as arousing as commonly used aversive stimuli, and therefore do not engage the amygdala in learning. Classical fear learning using highly aversive stimuli, such as shock, reliably activate the amygdala, whereas reward learning from appetitive stimuli, such as money or pleasant sounds or smells, do not reliably activate the amygdala (Zald, 2003). Similarly, amygdala response to happy facial expressions is less reliable than to fearful expressions (Yang et al., 2002; Zald, 2003). Our findings suggest that across the group of participants, the happy facial expression was not arousing enough to activate the amygdala during learning. However, the personality data indicates that the amygdala was involved in reward learning for highly introverted people who may have higher baseline arousal levels.

In summary, our data adds to growing evidence that observational learning occurs through a classical conditioning process.

In particular, our findings show that emotional facial expressions act as an unconditioned stimulus which facilitates learning by activating the amygdala–hippocampal complex. This is consistent with behavioral evidence showing that when a CS+ is unconsciously perceived, participants acquired a conditioned response after learning from direct experience and observation but not

verbal instruction (Olsson & Phelps, 2004), suggesting that an observed fearful expression can activate the amygdala through a non-conscious, subcortical optho-thalamic pathway (LeDoux, 1992; Vuilleumier et al., 2002; Williams, Morris, McGlone, Abbott, & Mattingley, 2004), thereby facilitating learning and creating a conditioned response.

4.2. Influence of personality on observational learning

4.2.1. Personality and observational fear learning

In line with our prediction, neuroticism was positively correlated with amygdala–hippocampal activity during fear learning versus neutral learning. However, neuroticism was not related to amygdala–hippocampal activity during reward learning, and it was not strongly related to behavioral performance during the task or on the post-test. These results suggest that neuroticism is specifically related to increased amygdala–hippocampal sensitivity to punishment. Further, we show that, in the context of fear learning, greater amygdala–hippocampal activity is related to better long-term memory of learned associations. Therefore, this limbic system sensitivity for people high in neuroticism may mediate the development of maladaptive fear after a fear experience.

Genetically determined dysregulation of the serotonin system may be the cause of increased amygdala–hippocampal sensitivity. Neuroticism is genetically transmitted (Bouchard, Lykken, McGue, Segal, & Tellegen, 1990; Lake, Eaves, Maes, Heath, & Martin, 2000). People with high levels of neuroticism are more likely than those with low neuroticism to have the short allele of the serotonin transporter (5-HTT) polymorphism (Lesch et al., 1996) which is associated with serotonin dysregulation and an increased risk for mood and anxiety disorders (Canli & Lesch, 2007; Lesch, 2007). Furthermore, those with the short allele of the 5-HTT polymorphism have more amygdala activity to fearful faces than those without the allele (Hariri et al., 2005; Hariri, Drabant, & Weinberger, 2006). This effect is most likely the result of depleted serotonin, since temporary, dietary depletion of serotonin results in greater amygdala activity to fearful faces (Cools et al., 2005) and enhances the ability to predict punishment in an observational reversal learning task (Cools, Robinson, & Sahakian, 2007). Together, this suggests that neuroticism involves a genetic vulnerability for anxiety that is expressed in amygdala–hippocampal sensitivity during fear learning, leading to more in-depth and persistent learned associations.

Low extraversion/high introversion was related to enhanced behavioral performance for almost every behavioral learning variable during observational fear learning: low extraversion/high introversion was related to faster reaction times when predicting the fear expression and neutral expression during learning as well as recognizing the fear object (at the trend level) and the neutral object during recognition trials. This relationship between low extraversion/high introversion and enhanced conditionability during fear learning is consistent with multiple models of personality (Eysenck, 1967; Gray, 1982), and suggests that individuals with combination of high neuroticism and low extraversion would be particularly vulnerable for developing anxiety disorders after observational fear learning. This idea is consistent with a recent study which found that the genetic liability of high neuroticism and low extraversion explained 100% percent of the variance for the risk for social phobia and agoraphobia (Bienvenu et al., 2007).

4.2.2. Personality and observational reward learning

Our findings shed light on three competing models of the influence of extraversion on observational reward learning. The evidence supports Eysenck's model of personality which emphasizes that a high baseline arousal level for people with low extraver-

sion/high introversion will facilitate reward learning. There was a strong, consistent relationship between low extraversion/high introversion and facilitated performance as well as enhanced amygdala–hippocampal activity on almost every behavioral and neural measure of reward learning. People with low extraversion/high introversion had greater amygdala activity when learning happy associations versus neutral associations. People with low extraversion/high introversion had more amygdala activity when recognizing the happy object versus neutral object. Furthermore, low extraversion/high introversion was related to faster reaction times to predict the happy expression as well as the neutral expression during learning trials and was marginally related to faster reaction time to recognize the happy object during recognition trials.

These findings are consistent with the idea that low extraversion/high introversion is related to high baseline arousal which is an optimal arousal level for emotional learning under mildly-to-moderately challenging conditions, such as an easy task, predictable reinforcement schedule, and a relatively 'weak' (i.e. non-arousing) unconditioned stimulus (Eysenck, 1967; Matthews & Gilliland, 1999; Zinbarg & Revelle, 1989). Under these conditions introverts are, theoretically, performing at the peak of the Yerkes-Dodson inverted U-shaped curve; the optimal level of arousal for learning (Eysenck, 1967). All of these conditions were operative in our task: accuracy levels were close to 100%, the reward was predictable and did not vary according to performance, and the rewarding stimuli (the happy face) was relatively 'weak'.

Interestingly, we did not find a relationship between low extraversion/high introversion and amygdala–hippocampal activity during observational fear learning but we did see a relationship between low extraversion/high introversion and amygdala–hippocampal activity during observational reward learning. An independent group of participants rated the fearful face stimulus as more intense and arousing than the happy face. According to Eysenck's theory, highly arousing stimuli cause neural inhibition for introverts, presumably because arousal has exceeded optimal levels (Eysenck, 1967). Thus it is possible that over-arousal caused neural inhibition during fear learning with the fearful face, but the relatively non-arousing happy face presented an optimal learning situation. This fits with the results showing that there was no amygdala activity across the group of participants when learning from the happy face, suggesting that there was not a significant level of emotion related arousal. Instead, neural activity to the happy face varied according to individual differences in extroversion, with low extraversion predicting higher amygdala activity which can be interpreted to suggest that the happy face stimulus was arousing for the low extraversion participants. These low extraversion/high introversion participants likely responded with moderate arousal levels to the happy stimuli which then enhanced performance.

We did not find evidence for the idea that extraversion is related to general reward sensitivity (Depue & Collins, 1999). However, results from our task do not demonstrate evidence against the notion that a core component of extraversion is sensitivity to social reward, social attention, or novelty (Ashton et al., 2002; Lucas et al., 2000; Zuckerman, 2004). We purposefully kept face identity and facial emotion constant in order to reduce neural activity in response to sociability and novelty and thus isolate learning from emotional expression. Prior research showing that people high in extraversion had more amygdala activity to happy faces may be reflecting enhanced amygdala response to the socially rewarding or novelty components of extraversion (Canli et al., 2002). Furthermore, in cognitive tasks, people with high extraversion may respond more to reward incentives used to motivate behavior (Depue & Collins, 1999) especially in challenging circumstances (Lieberman & Rosenthal, 2001; Wacker, Chavanon, & Stemmler,

2006). Thus it might be the case that high extraversion facilitates performance on operant conditioning paradigms, in which rewards are contingent on behavior, whereas low extraversion facilitates performance on classical conditioning paradigms, in which rewards are not contingent on behavior.

4.3. Limitations and directions for future research

Although our results suggest that observational learning uses the same behavioral and neural mechanisms as learning from direct experience, we did not compare observational learning versus direct experience, nor did we create conditions, such as conscious awareness, that would disallow learning from other means. Therefore, observational learning and classical conditioning may be partially, rather than fully, overlapping systems. It is also possible that another learning process may be contributing to the acquisition of aversive or appetitive value in our experiment, such as evaluative learning in which the association of a neutral stimulus with an emotional stimulus subsequently changes the evaluation of the neutral stimulus (Davey, 1994; De Houwer, Thomas, & Baeyens, 2001). Additionally, participants may have relied on episodic memory retrieval of the learning context, such that amygdala activity to the emotion associated object alone may reflect a memory of emotional context rather than a reflection of acquired emotional value (Maratos et al., 2001). These issues can be addressed in future work by comparing observational learning and classical conditioning directly, and by manipulating conditions that restrict the use of other learning strategies.

Future experiments will also benefit from separating the cue and outcome portion of the learning trial. Separating these two components will provide the opportunity to investigate neural activity associated with behavioral predictions as well as neural activity associated with outcomes that are expected versus unexpected (Schultz, 1998; Schultz & Dickinson, 2000). For example, if quick reaction time for fear predictions is associated with arousal in anticipation of a fear response, one would expect a negative correlation between prediction reaction time and amygdala activity at the cue. Furthermore, recent learning theory suggests that unexpected reward is associated with more reward related activity than expected reward (Schultz, 1998; Schultz & Dickinson, 2000).

Finally, although our findings suggest that high baseline arousal levels for people with low extraversion facilitated learning, we did not measure arousal. Measuring arousal level of participants when they perform the task would provide more exact information about the interaction of personality, arousal, and emotional learning.

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