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Aspects of neuroticism and the amygdala: Chronic tuning from motivational styles

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ABSTRACT

Recent research and theory has highlighted the dynamic nature of amygdala activation. Rather than simply being sensitive to a few limited stimulus categories, amygdala activation appears to be dependent on the goals of the perceiver. In this study, we extend this line of work by demonstrating that the means by which a person seeks to accomplish a goal also modulates the amygdala response. Specifically, we examine the modulatory effects of the aspects of neuroticism (volatility/withdrawal), a personality variable that has been linked to both generalized anxiety and differences in amygdala sensitivity. Whereas Neuroticism-Volatility is proposed to be associated with the fight-flight-freeze system (FFFS) and a sensitivity for any cues of negativity, Neuroticism-Withdrawal is proposed to be associated with the behavioral inhibition system (BIS) and a generalized tendency toward passive avoidance. During fMRI scanning, participants were presented with positive, negative, and neutral images and were required to approach (move perceptually closer) or avoid (move perceptually farther away) stimuli in different blocks of trials. Consistent with hypotheses proposing a dissociation between these two aspects of neuroticism, participants higher in Neuroticism-Volatility had increased amygdala activation to negative stimuli (regardless of whether they were approached or avoided), whereas participants higher in Neuroticism-Withdrawal had increased amygdala activation to all approached stimuli (regardless of stimulus valence). These data provide further support for the motivational salience hypothesis of amygdala function, and demonstrate that both the ends and means of goal pursuit are important for shaping a response.

1. Introduction

Traditionally, the amygdala has been understood as a threat detector (LeDoux, 2003; Öhman & Mineka, 2001; Whalen, 1998). Recently, however, this narrow understanding of the amygdala's affective function has been expanded/revised and become more nuanced. For example, studies have found amygdala activation to positive stimuli (Garavan, Pendergrass, Ross, Stein, & Risinger, 2001; Hamann, Ely, Hoffman, & Kilts, 2002; Said, Baron, & Todorov, 2009; Todorov, Baron, & Oosterhof, 2008; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007), novel stimuli (Schwartz et al., 2003; Wilson & Rolls, 1993), ambiguous stimuli (Whalen, 1998), intense stimuli (Anderson et al., 2003; Cunningham, Raye, & Johnson, 2004), and goal relevant stimuli (Cunningham, Raye, & Johnson, 2005; Van Bavel, Packer & Cunningham, 2008). To account for these findings, we have recently proposed the motivational salience hypothesis, which states that the amygdala is sensitive to motivational relevance (Cunningham, Van Bavel, & Johnsen, 2008; Cunningham, Jahn, & Johnsen, in press), perhaps recruiting additional resources to facilitate appropriate interactions with stimuli (Anderson & Phelps, 2001; Sander, Grafman, & Zalla, 2003). According to this view, a primary function of amygdala processing is to signal what is important in any particular situation, and then modulate the appropriate perceptual, attentional, autonomic, and cognitive/conceptual processes to deal with the challenges or opportunities that are present.

By expanding the class of stimuli that the amygdala responds to from only threatening cues to motivationally relevant stimuli, we can account for the various amygdala effects observed in the literature. For example, although learned affective cues are certainly cues to the potential relevance of a stimulus, they alone are only a subset of information than can be gleaned from the environment. For example, motion cues alone are sufficient to result in amygdala activation (Bonda, Petrides, Ostry, & Evans, 1996); an approaching object or one that spontaneously appears in the periphery will nearly always be deemed relevant until one determines whether the change in the perceptual status quo is something that needs

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to be dealt with. More abstractly, changes in goal priorities can change the affective meaning of a stimulus. For example, when one is hungry, food (an appetitive stimulus) will be more relevant, whereas when one is walking home at night, potential criminals (an aversive stimulus) will be more relevant. Consistent with this idea, Cunningham et al. (2008) presented participants with famous names and asked them to focus on either the positive or negative aspects of the person. Activity in bilateral amygdala was found to vary as a function of evaluative fit. That is, when focusing on negativity, greater amygdala activity was associated with participants' negativity ratings of the names, but not positivity ratings. The opposite pattern was found for the positive focus condition, such that greater activity was observed in these same regions to ratings of positivity than negativity.

Through experience with the environment and/or genetic differences at birth, people develop different expectations about the state of the world and the most adaptive ways to interact with it (Caspi & Moffitt, 2006). These chronic motivational or affective styles are thought to operate like situational goals, but rather than adapting situation by situation, they operate by tuning the affective system to be more sensitive toward one class of stimuli than another. For example, individual differences in promotion focus (a motivational system tuned towards rewards) predicted greater amygdala activation to positive stimuli, whereas individual differences in prevention focus (a motivational system tuned towards punishments) predicted greater activation to negative stimuli (Cunningham et al., 2005). Further, individual differences in neuroticism, a trait characterized by experiences of negative emotion, anxiety, and emotional lability, have been shown to predict greater amygdala activation to negative stimuli (Harenski, Kim, & Hamann, 2009), greater amygdala and hippocampus activity during fear learning (Hooker, Verosky, Miyakawa, Knight, & D'Esposito, 2008), and greater amygdala-dorsolateral prefrontal cortex connectivity while viewing angry and fearful facial expressions (Cremers et al., 2010).

Although the work exploring the neural correlates of personality has yielded a number of important insights, for the most part it has explored only one level of personality dynamics. That is, personality exists at multiple psychological levels, and the Big-5 only represents a midlevel of analysis. Specifically, research using factor analysis has shown that two meta-traits (Stability and Plasticity) exist at a level of analysis more abstract than the Big-5 (DeYoung, 2006; Digman, 1997; Olson, 2005). Moreover, each of the Big-5 personality traits can be further decomposed into particular aspects. As we consider personality at a more concrete, specific level, we move from more core general aspects of personality to more specific manifestations. In other words, a core motive can be achieved in multiple ways, and more specific facets or aspects may reflect these various motivational styles.

In the case of neuroticism, DeYoung, Quilty, and Peterson (2007) suggest that there are two critical aspects of Neuroticism-Volatility and withdrawal. Neuroticism-Volatility is proposed to be associated with a predisposition toward agitation and anger, a tendency toward attending to negative information in the environment, and generating negative attributions. Neuroticism-Withdrawal, on the other hand, is less sensitive to specific information per se, but rather reflects a behavioral tendency toward passive avoidance. Thus, in contrast to people high in Neuroticism-Volatility, in which approach or avoidance behavior may be deemed appropriate following the perception of a negative cue, people high in Neuroticism-Withdrawal deal with potential threats by developing a default strategy of non-engagement and a discomfort with approach behaviors. Thus, the aspects of Neuroticism-Volatility and Neuroticism-Withdrawal both influence how individuals deal with anxiety, but through different means. Neuroticism-Volatility causes a hyper-vigilance to negative stimuli followed by a behavioral decision to act, whereas Neuroticism-Withdrawal creates a disposition toward passive avoidance so that one never enters a situation where something negative can occur.[1]

Making more explicit links between individual differences, processes, and neural activation, DeYoung (in press) has suggested that these two aspects of neuroticism may be linked to the motivational systems proposed by Gray (1981, 1982); see also McNaughton and Gray (2000) that underlie responses to threat. Specifically, DeYoung et al. (2007) and DeYoung (in press) proposed that the fight-flight-freeze system (FFFS) is sensitive to negatively valenced or potentially threatening information. When something negative in the environment has been detected, one can defensively fight (approach; e.g., Harmon-Jones, 2003) or flee from (actively avoid) it. Whereas the FFFS is sensitive to specific aspects of information, the behavioral inhibition system (BIS) is characterized primarily by inhibition of approach behaviors, disengagement, and passive avoidance. Both FFFS and BIS serve a protective function against potential threats but do so in different ways. Thus, individual differences in Neuroticism-Volatility may reflect differences in FFFS, and individual differences in Neuroticism-Withdrawal may reflect differences in BIS.

Combining our motivational salience perspective (Cunningham et al., 2008) and the functional differences in the aspects of neuroticism, we propose that although both Neuroticism-Withdrawal and Neuroticism-Volatility should be associated with activation in the amygdala, these aspects should be associated with different stimulus features and thus different patterns of activation within this region. Specifically, whereas Neuroticism-Volatility should be associated with increased activation to negative as compared to positive stimuli, Neuroticism-Withdrawal should be associated with approach and avoidance situations with greater amygdala activation during approach than avoidance. However, because Neuroticism-Withdrawal is associated with a generalized behavioral tendency, we predict that it will not be associated with any particular stimulus category. To examine this role of the amygdala, we presented participants with pictures differing in valence and arousal ratings from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005). To further manipulate approach and avoidance behavior, participants approached (making the stimulus move closer) or avoided (making the stimulus move away from them) the images in separate blocks of trials.

2. Methods

2.1. Participants

Participants were 21 right-handed individuals with no history of neurological problems and normal or corrected-to-normal vision. Two participants were dropped from analyses for excessive motion during scanning (consecutive image movement > 1.72 mm or drift > 3.44 mm within a run), and one was dropped for corrupted data, leaving 18 participants (10 female; mean age = 20.5 years). All participants provided informed consent.

2.2. Procedure

During 6 runs of fMRI scanning, participants were presented with pictures randomly selected from a subset of IAPS (Lang et al., 2005) photographs selected to vary on valence, extremity, and arousal. This subset of IAPS photos contained 87 positive and negative stimuli that were selected and matched on normed ratings of arousal ($M_{Positive} = 4.88$, $SD_{Positive} = 0.96$; $M_{Negative} = 5.16$, $SD_{Negative} = 0.86$) and valence extremity ($M_{Positive} = 2.07$, $SD_{Positive} = 0.32$; $M_{Negative} = -1.85$, $SD_{Negative} = 0.34$). An additional 77 neutral stimuli were included to allow for an investigation of stimulus extremity as compared to stimulus valence ($M_{Arousal} = 3.36$, $SD_{Arousal} = 0.82$;

[1] Individual differences in BIS/BAS scores have been shown to be associated with differences in brain activity when processing valenced stimuli. For example, Reuter et al. (2004) found that BIS scores were correlated with activity in anterior cingulate, amygdala, and thalamus when looking at emotion-evoking pictures. Interestingly, no consistent pattern emerged as being associated with individual differences in BAS scores.

$M_{Valence} = -0.21$, $SD_{Valence} = 0.37$). Pictures were presented one at a time, and participants were instructed to press one button to "approach" the stimulus and another to "avoid" the stimulus.[2] All pictures were initially presented to fill 75% of the monitor display. If participants pressed the button to "approach" the stimulus, the picture would expand until it filled 100% of the monitor screen to give the appearance of it moving towards the participant. If participants pressed the button to "avoid" the stimulus, the picture contracted until it only filled 50% of the monitor screen to give the appearance of it moving away from the participant. Participants were also instructed to imagine that they were approaching or avoiding the stimulus or scene in the picture as it grew or shrank. The image moved at 5% increments to create fluid motion and took 3 s to reach 100% or 50%, respectively. The image did not move until participants made a response.

To create a motivational frame and to ensure that participants equally approached and avoided positive and negative stimuli, participants were instructed to make only one button press in each block of trials. Participants would approach or avoid 7 stimuli, and then the motivational frame would reset randomly to one of the two conditions. Participants completed 6 blocks of trials per run, for a total of 36 blocks, thus responding to stimuli a total of 216 times. Instruction screens appeared for 4 s between each block to indicate whether participants were to approach or avoid forthcoming stimuli. A fixation cross appeared for 4 s after the instruction screens, and a variable fixation of 2 s, 4 s, or 6 s appeared between each IAPS photo to allow for the estimation of the hemodynamic response. After scanning, participants completed the big five aspects scale (BFAS; DeYoung et al., 2007) and the BIS/BAS scales (Carver & White, 1994), as well as demographic measures.

2.3. fMRI scanning parameters and analysis

Scanning was conducted using a Philips 3T Achieva Scanner at the Wright Center for Innovation at The Ohio State University. Functional scanning was prescribed at an angle of 20° relative to the AC/PC line, and nearly isotropic functional images were acquired from inferior to superior using a single-shot gradient echo planar pulse sequence (40 slices; 3.93 mm thick; $TE = 22$ ms; $TR = 2000$ ms; in-plane resolution = 3.44 × 3.44 mm; matrix size = 64 × 64; $FOV = 220$ mm). The first five volumes were discarded to allow for T1 equilibration effects. Following functional imaging, a high resolution T1 anatomical image (160 sagittal slices; $TE = 3.75$ ms, $TR = 25$ ms; resolution = 1.00 × 0.43 × 0.43 mm) was collected for normalization.

Data were prepared for analysis using SPM8 (Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm). Data were motion-corrected using SPM's Realign and Unwarp procedure, which helps to correct for movement artifacts at the preprocessing stage. For each participant, functional EPI scans were then co-registered to their corresponding high-resolution T1 anatomical image. The unsegmented T1 anatomical images were then spatially normalized to the SPM8 MNI template using the default settings. The transformations from the co-registration and normalization steps were applied to the EPI functional scans and new images were created that were interpolated to have voxel dimensions of 3 mm × 3 mm × 3 mm. To enhance signal-to-noise ratios, these images were smoothed using an 8 mm FWHM (full-width-half-maximum) kernel. The BOLD signal was modeled as a function of a canonical hemodynamic response function and its temporal derivative with a 128 s high-pass filter.

3. Results

Data were analyzed using the general linear model as implemented by SPM8. Participant level (1st level) effects were modeled by convolving an event related hemodynamic response function and its temporal derivative against the preprocessed data for each of the six experimental conditions (approach-positive; approach-neutral; approach-negative; avoid-positive; avoid-neutral; avoid-negative). An additional regressor was constructed to remove variance associated with the presentation of the directions for each block. Because of the focused nature of this investigation, we generated an explicit mask of amygdala voxels using MRIcron with the AAL atlas (Rorden, Karnath, & Bonilha, 2007) and used this mask to limit the number of statistical comparisons to the bilateral amygdala. This mask contained 102 voxels (51 in each amygdala; total volume: 1377 mm^3). When only examining this restricted set of voxels, Monte Carlo simulations using AlphaSim (Ward, 2000) indicated that a cluster size of at least 10 contiguous voxels was required for multiple comparison correction at an alpha threshold of $p < .05$ (uncorrected). In this paper, we report effects that survive this criterion as well as an SPM8 small volume FWE correction.

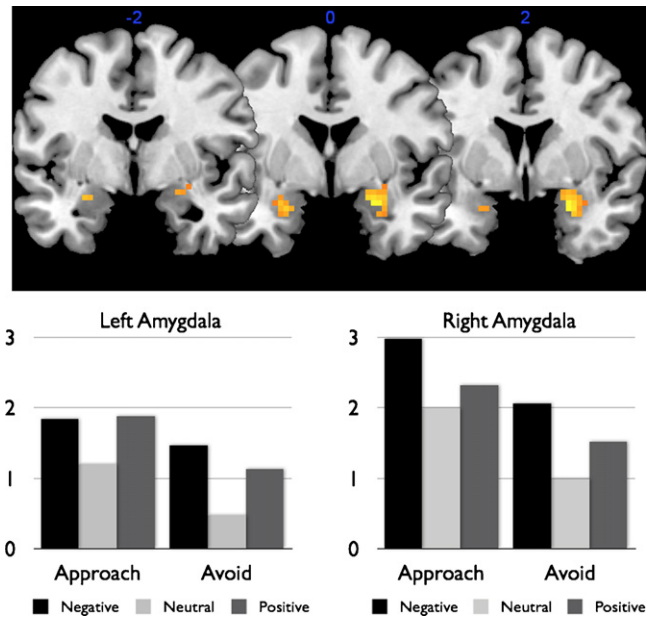

Fig. 1. Main effects and interactions with condition. (a) Significant voxels from the omnibus *F*-test comparing the 6 conditions are overlaid on the MNI template image ($p < .05$, small volume corrected). (b and c) Mean signal from these significant voxels are plotted separately for the left and right amygdala for each condition. The *y*-axis reflects the signal intensity regression parameter from SPM8.

Previous work on the amygdala has suggested that activation is closely linked to motivationally relevant or important stimuli or stimulus features. In the context of this study, two dimensions fit this category– valenced stimuli (either positive or negative) and approached stimuli. Thus, prior to examining individual differences in neuroticism, we examined the main effects of valence, motivational direction (approach/avoid), and the interaction of valence and direction with the goal of replicating (valence) and extending (motivational direction) the link between amygdala activation and motivational relevance. Specifically, first level contrast maps were subjected to a 2 (Approach–Avoid) × 3 (valence) repeated measures analysis of variance (ANOVA). Replicating previous work, we found a main effect of valence in right amygdala ($F_{2,85} = 9.15$, $p < .001$, $p_{FWE} = .01$; MNI: 24, −1, −20; cluster size = 32). As shown in Fig. 1, the pattern of results suggests a standard U-shaped function, where both negative and positive images elicit more amygdala activation than neutral images. Further, also shown in Fig. 1, there is a significant main effect for motivational direction, in that there is a larger amygdala response to approached than avoided images ($F_{2,85} = 10.81$, $p < .001$, $p_{FWE} = .044$; MNI 24, −1, −20; cluster size = 43). There were no significant interactions of valence and motivational direction.

Our central hypothesis was that the relationship between amygdala activation and the two aspects of neuroticism would be differentially related to two independent aspects of our stimulus presentation. Specifically, we predicted that Neuroticism-Volatility would be associated with valence processing (specifically, greater activation to negative than positive images), and that Neuroticism-Withdrawal would be associated with motivational direction (specifically, to approached stimuli). To test these hypotheses, we constructed individual-level contrasts for comparing negative and positive images collapsing across motivational direction, and comparing approached and avoided images collapsing across valence. Group-level regression analyses were run predicting individual

[2] Button box keys were counterbalanced across participants for approach and avoidance.

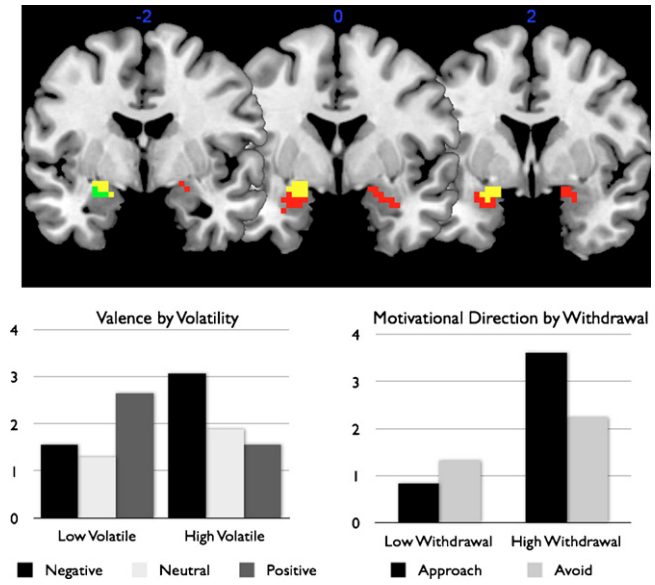

Fig. 2. Relationships between aspects of neuroticism and experimental condition. (a) Voxels showing a significant correlation between Neuroticism-Volatility and negative–positive are displayed in red. Voxels showing a significant correlation between Neuroticism-Withdrawal and approach–avoidance are displayed in green. Voxels that are significant for both analyses are presented in yellow. (b) Predicted scores are plotted for participants one standard deviation above and below the mean on Neuroticism-Volatility for each of the six conditions. (c) Predicted scores are plotted for participants one standard deviation above and below the mean on Neuroticism-Withdrawal for each of the six conditions. The *y*-axis reflects the signal intensity regression parameter from SPM8. (For interpretation of the references in color in this figure legend, the reader is referred to the web version of this article.)

differences in these contrast estimates from the neuroticism personality aspects of Volatility and Withdrawal.

As predicted, Neuroticism-Volatility was significantly associated with increased amygdala activation to negative compared with positive images in both the left ($t_{16} = 3.58$, $p < .001$, $p_{FWE} = .037$; MNI −18, −1, −11; cluster size = 42) and the right amygdala ($t_{16} = 3.51$, $p < .001$, $p_{FWE} = .042$; MNI 18, −1, −14; cluster size = 48). To plot these effects for each of the valence conditions (positive, neutral, and negative), predicted scores for participants one standard deviation above and below the mean on Neuroticism-Volatility were estimated for each of the three levels of valence (see Fig. 2). Because effects were similar for right and left amygdala, data are collapsed for laterality. Participants higher in Neuroticism-Volatility had the greatest activation to negative images, whereas participants low in Neuroticism-Volatility had the greatest activation to positive images.

In contrast to Neuroticism-Volatility, which we predicted to be sensitive to stimulus valence, we predicted that Neuroticism-Withdrawal would be associated with behavioral tendencies rather than with any particular valence. Specifically, we hypothesized that participants higher in Neuroticism-Withdrawal would have a greater amygdala response to approached than avoided stimuli. Consistent with this hypothesis, we found that individual differences in Neuroticism-Withdrawal were significantly associated with increased amygdala activation to approached stimuli than to avoided stimuli ($t_{16} = 3.55$, $p < .001$, $p_{FWE} = .045$; MNI −24, 2, −14; cluster size = 30). Again, to plot these effects, predicted scores for participants one standard deviation above and below the mean on Neuroticism-Withdrawal were estimated for the approached and avoided stimuli (see Fig. 2).

To provide additional support for our hypotheses, we constructed a series of analyses in which differences in amygdala activation were extracted for the negative–positive and the approach–avoid contrasts using an independent functional mask.

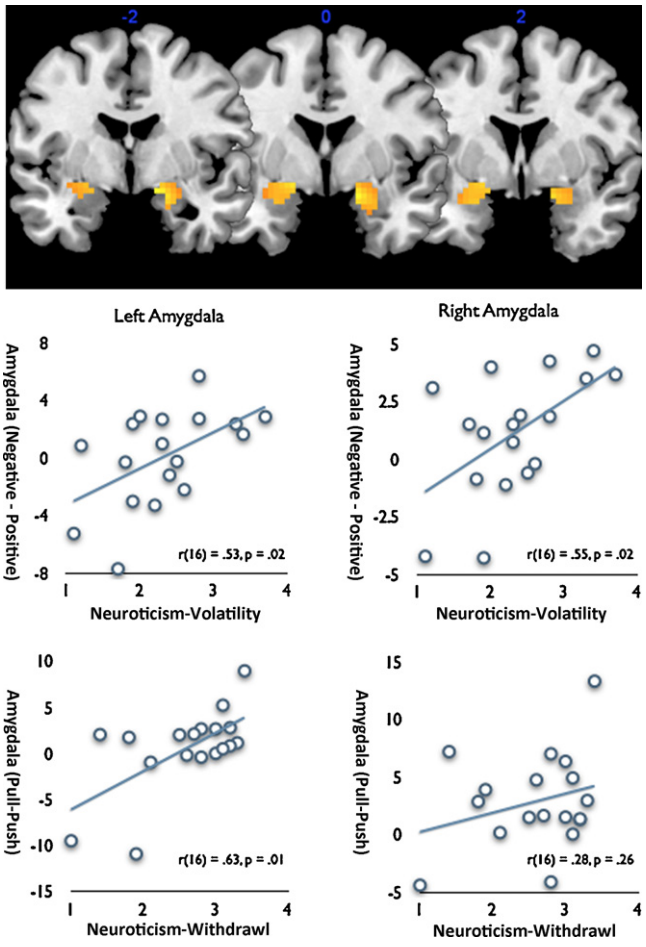

Fig. 3. Correlations between aspects of neuroticism and negative–positive and approach–avoidance contrasts. (a) Voxels from Cunningham et al. (2008) used for data extraction. (b–e) Scatterplots display the relationship between individual differences in aspects of neuroticism and the negative–positive and approach–avoidance contrasts

Specifically, differences in amygdala activation were extracted from the regions identified in Cunningham et al. (2008) to be sensitive to motivational influences. Estimates of amygdala activation differences were computed by taking the average of all voxels in the mask for right and left amygdala separately. Because this is an a priori region of interest, a threshold of $p < .05$ was used for all analyses. Consistent with the results reported above, Neuroticism-Volatility was correlated with negative–positive amygdala activation in both the left ($r_{16} = .554$, $p = .02$) and right amygdala ($r_{16} = .554$, $p = .02$), and there was no interaction between volatility and laterality ($F_{1,16} = 0.23$, $p = .64$; See Fig. 3). When examining the bivariate correlations, Neuroticism-Withdrawal was correlated only with activity in left amygdala ($r_{16} = .633$, $p = .01$), though it should be noted that the relationship was in the predicted direction for right amygdala as well ($r_{16} = .227$, $p = 26$). This difference in the magnitude of the Withdrawal/Avoidance relationship was trending towards significance ($F_{1,16} = 3.61$, $p = .08$).

To examine the distinct effects of Volatility and Withdrawal on the valence and approach–avoidance effects, we conducted a series of multiple regression analyses to decompose the effects. Because there were no laterality effects found for the volatility/valence relationship, right and left amygdala were collapsed into a single variable. For the Withdrawal/Avoidance relationship, only left amygdala was further analyzed. When predicting a greater amygdala response to negative than positive images, Volatility ($\beta = .51$, $t_{16} = 2.36$, $p = .03$) but not Withdrawal ($\beta = -.006$, $t_{16} = -0.023$,

$p = .82$) predicted unique variance. Providing additional support for the dissociation between Volatility and Withdrawal, Withdrawal ($\beta = .50$, $t_{16} = 2.33$, $p = .03$) but not Volatility ($\beta = .005$, $t_{16} = 0.022$, $p = .83$) predicted unique variance for the approach–avoid amygdala contrast. Thus, although the two aspects of neuroticism are robustly correlated ($r_{16} = .63$, $p = .005$), they predict sensitivity to different aspects of the environment that may reflect different strategies toward dealing with a potentially threatening world.

As noted previously, Neuroticism-Withdrawal is proposed to be associated with the behavioral inhibition system, and Neuroticism-Volatility is proposed to be associated with the fight-flight-freeze system (DeYoung et al., 2007). Consistent with this idea, we found that individual differences in the Neuroticism-Withdrawal aspect were robustly correlated with BIS scores ($r_{16} = .79$, $p < .001$). Using the BIS and BAS scales (Carver & White, 1994) as predictors, we replicated the effects predicting approach–avoidance responses in the amygdala. Specifically, we found that BIS ($\beta = .53$, $t_{16} = 2.47$, $p = .03$), but not BAS ($\beta = .015$, $t_{16} = -0.062$, $p = .55$), predicted the approach–avoidance amygdala difference. Although neither BIS nor Neuroticism-Withdrawal were significant predictors of the approach–avoidance amygdala difference when predicting simultaneously because of a high degree of multicollinearity between the predictors, it should be noted that Withdrawal ($\beta = .35$, $t_{16} = 1.49$, $p = .15$) was a better predictor than BIS ($\beta = .14$, $t_{16} = 0.56$, $p = .58$). Indeed, a stepwise regression gave full credit in assignment of variance to the Withdrawal scores ($F_{1,16} = 10.75$, $p = .005$). Providing further divergent validity for the neuroticism concept beyond BIS/BAS, neither BIS ($\beta = .21$, $t_{16} = 0.86$, $p = .40$) nor BAS ($\beta = .05$, $t_{16} = -0.21$, $p = .83$) predicted negative–positive amygdala differences.

4. Discussion

The myriad ways that people differ can be understood in part by understanding what people find important and meaningful and the means by which they attempt to accomplish the goals that they set for themselves. In this study, we found that amygdala activation was predicted by both the valence of stimuli (both positive and negative stimuli elicit more amygdala activation than neutral stimuli) and also the behavioral responses with respect to these stimuli (approached stimuli are more important and also elicit more amygdala activation). More importantly, we found that amygdala activity varies as a function of the ways that people chronically seek to deal with threatening information. Specifically, for people high in Neuroticism-Volatility, more activation was found for negative than positive stimuli regardless of whether the stimulus was approached or avoided. For people high in Neuroticism-Withdrawal, more activation was found for approached than avoided stimuli regardless of valence. Thus, the amygdala response to specific aspects of the environment such as the valence of a perceived object or the action taken with respect to the object is moderated by the chronic motivational styles that people use to deal with affective information.

Although previous work has linked amygdala activation to neuroticism, this study extends these previous findings by demonstrating two means by which people can satisfy their neurotic tendencies. That is, neuroticism is clearly associated with anxiety and emotional instability, but the strategies that one chooses to express this predisposition can dramatically vary. One can be hyper-vigilant for negative environmental cues and then act with hostility (approaching in anger) or retreat (avoiding in fear) depending on the construal of the situation. For such a person, neuroticism is not associated with any particular behavioral tendency, as approach or avoidance will be largely determined by the particulars of the situation. What is critical, however, is identifying potential threats so that an "appropriate" course of action can be determined. According to DeYoung et al. (2007) and DeYoung (in press), these people manifest the aspect of Volatility, the personality dimension most associated with Gray's (1981) concept of the fight-flight-freeze system (FFFS). Consistent with this idea, we found that individual differences in Neuroticism-Volatility were associated with increased amygdala activation to negative stimuli. Further, because approach and avoidance are equally plausible behavioral strategies for someone high in Volatility, we found no relationship between the Volatility aspect and amygdala activation to approached versus avoided stimuli when controlling for Withdrawal.

In addition to being responsive to particular stimuli, another strategy for dealing with a world that is perceived to be threatening is to develop behavioral strategies to simply stay out of situations where danger might be present. That is, by generally avoiding uncertain or ambiguous situations, one is not caught by surprise by an unexpected negative event. This aspect of neuroticism, labeled Withdrawal, is thought to be most associated with the behavioral inhibition system (DeYoung et al., 2007). As predicted, individual differences in Withdrawal were associated not with valence, but with the behavioral action of the participant. Specifically, for participants higher in Withdrawal, there was a greater amygdala response to approached than avoided stimuli. Further, there was a significant main effect such that participants with higher withdrawal scores had greater amygdala responses to all presented stimuli. This finding is consistent with the functional description of Withdrawal in that participants had no control over which stimuli were being presented on any given trial.

In parallel with the work on personality and amygdala function, research has also linked amygdala structure and function to genetic factors that are thought to be associated with the development of neurotic traits. Specifically, differences in the expression of the serotonin transporter (5-HTT) that modulates the reuptake of serotonin from the synapse has been linked both to amygdala activity and individual differences in neuroticism (Hamann & Canli, 2004). Individuals with copies of the short allele of the serotonin transporter have been found to exhibit greater amygdala activity to fearful stimuli. The direction of causality between these genetic variations and amygdala activity has been researched extensively, with some evidence suggesting that the expression of the transporter modulates amygdala reactivity to threat (Hariri et al., 2002). Subjects possessing the short allele of the transporter may be more susceptible to the expression of neurotic personality traits, which in turn leads to increased sensitivity for threatening stimuli, as well as affective disorders such as major depression (Munafó, Clark, Roberts, & Johnstone, 2006; Pezawas et al., 2005). This work has led to important advances in our understanding of gene-environment interactions, and how our biological makeup can alter of affective states. Yet, this research has focused on only one level of personality analysis. It will be important for future research to determine whether these effects lead to general neuroticism and emotional instability, or whether the aspect level is influenced.

Together, these findings suggest that personality neuroscience can be informed by taking a motivational perspective. In many ways, the study of personality dynamics and motivation are inherently coupled. What is important to us guides our perceptual, affective, and cognitive functioning at a moment-to-moment level. These become implicit theories that we use to guide our behavior, or heuristics that we use to inform decisions. In this study, we show how a fundamental personality trait, neuroticism, can be further understood by elucidating the strategies that different people can use to deal with the affective instability that characterizes it. By focusing attention to either stimulus features or a default behavioral strategy, one can deal with threat. These responses likely

shape an initial response in the amygdala, which then serves to guide subsequent processing.

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