Attentional modulation of the amygdala varies with personality

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The amygdala has become a principal region of interest in investigations of emotion due to its rich subcortical connections which have led to suggestions that processing of emotional stimuli occurs independently of attention. Using a novel attentional manipulation in conjunction with fMRI, we showed that emotion-related amygdala activity was modulated by attention, but that the degree of such modulation correlated with the personality variable harm avoidance, associated with trait anxiety. Participants ignored emotional distractors while searching through a rapid stream of pictures for a target, about which they were provided either specific or nonspecific descriptive information (e.g., “look for a building” versus “look for a landscape or building”). Thus, they employed either a specific or a nonspecific attentional set in order to find the target and ignore distractors. In response to irrelevant emotional distractors, low harm-avoidant participants had relatively little emotion-related amygdala activity regardless of whether they maintained a specific or nonspecific attentional set. High harm-avoidant participants, however, showed strong emotion-related amygdala activity when maintaining a nonspecific attentional set and lower amygdala activity when maintaining a specific attentional set. This decrease was accompanied by increased activation of the rostral anterior cingulate cortex (ACC), which is often linked with the resolution of affective interference. In addition to demonstrating individual differences in attentional modulation of the amygdala, these results may indicate that the rostral ACC is sensitive to the increased effort that high harm-avoidant individuals must recruit in order to modulate amygdala responsivity.

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Indeed, evidence from some studies suggests that the amygdala responds to emotional stimuli even when people are unaware of them. For example, fearful faces elicited more amygdala activation than neutral faces even when the faces were masked and could not be reported (Whalen et al., 1998). However, recent efforts to replicate such results have found that, when awareness was more rigorously manipulated, emotion-related amygdala activity occurred only when people were aware of the emotional stimuli (Pessoa et al., 2006). Still, evidence for emotion-related amygdala activity without awareness comes from a range of studies, including one in which such activation was found in an individual with visuospatial neglect, when emotional stimuli were lost to visual extinction (Vuilleumier et al., 2002). Beyond debates about whether or not amygdala activation occurs without awareness, some studies have suggested that it depends both on the particular region of the amygdala explored and on individual differences between people. For example, in one experiment, masked emotional faces elicited a response in the right amygdala, whereas unmasked emotional faces elicited a response in the left amygdala (Morris et al., 1998). In another experiment, consciously processed fearful faces elicited a response in the dorsal amygdala, whereas unconsciously processed ones elicited a response in the basolateral amygdala; furthermore, this basolateral response was correlated with participants’ trait anxiety (Etkin et al., 2004).

Absence of awareness for a stimulus, however, does not necessarily the absence of attention; accruing evidence suggests that effects of attention can be found without awareness (Kennedy et al., 1999; McCormick, 1997; Most et al., 2005b; Woodman and Luck, 2003). Some fMRI studies have begun to test whether—awareness aside—manipulations of attention influence emotion-related activity in the amygdala. For example, in one study, participants judged whether two simultaneously presented stimuli were identical on each trial while ignoring two other simultaneously presented stimuli (Vuilleumier et al., 2001). Two of the items were always houses, and two were faces, which could be either neutral or fearful. The results revealed stronger amygdala activity to fearful than neutral faces regardless of whether the

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faces or the houses were the targets, suggesting that amygdala activations to emotional stimuli occurred independently of spatial attention (also see Anderson et al., 2003, for similar results with object-based, rather than spatial, attention). However, a later study suggested that the apparently inconsequential role for spatial attention could be attributed to the relatively easy nature of the task: that is, because the attention task had been undemanding, attentional resources could “spill over” to the nontarget items (Pessoa et al., 2002; see also Rees et al., 1997; Yi et al., 2004). This hypothesis was further tested in an experiment where emotional faces were always irrelevant (Pessoa et al., 2005). Participants ignored faces and judged whether two bars had the same orientation. The more difficult the judgment, the less the amygdala responded to the ignored emotional faces. (It is interesting to note, as well, that amygdala activity decreased overall—regardless of stimulus emotionality—when greater cognitive effort was required for the task.) Thus, the suggestion that amygdala activity to emotional stimuli is subject to attentional control seems credible.

Consistent with this possibility, more recent studies have shown relatively less amygdala activation to emotional stimuli when people attended to nonemotional, rather than the emotional, aspects of a stimulus (Mathews et al., 2004) and when people were given a chance to reinterpret stimuli in a less emotional way (Ochsner et al., 2002). In addition, evidence suggests that attentional modulation of the amygdala might vary systematically with state anxiety. For example, one study using houses and faces replicated the Vuilleumier et al. (2001) findings among high state-anxious individuals: when attending to houses while ignoring emotional faces, amygdala activity was no less than when attending to the faces. However, among low state-anxious people, amygdala activity was reduced when attending to houses compared to emotional faces (Bishop et al., 2004b).

Can people ignore emotional stimuli even when they try to? Some evidence suggests that the very function of the amygdala is to orient attention to emotionally evocative information (Anderson and Phelps, 2001), suggesting that it will respond even to emotional stimuli that are initially ignored. With few exceptions (see Pessoa et al., 2005), most investigations of attentional modulation of the amygdala compare conditions where people try to attend to emotional stimuli to conditions where they ignore them, but can attentional strategies influence amygdala activation to emotional stimuli that are always task-irrelevant? Most studies have also employed manipulations of spatial attention (but see Anderson et al., 2003). However, people can direct attention on the basis of properties other than spatial location; they can, for example, attend to objects or features (e.g., Scholl, 2001). When given enough information about a target, people can also adopt a narrow—or specific—attentional set, which minimizes the range of distractors that receive consideration in the search for the target (Bacon and Egeth, 1994; Most et al., 2005a). Here, we manipulated the specificity of participants’ attentional sets in order to directly investigate (1) whether people can ignore emotional information when they explicitly try to do so, as indexed by hemodynamic activity in the amygdala, and (2) whether manipulations of attentional set influence the effectiveness of ignoring always irrelevant emotional stimuli.

We employed a modified version of a task described in a previous behavioral experiment (Most et al., 2005a). In that earlier experiment, participants viewed a rapid (100 ms/item) stream of mostly upright landscape scenes and searched for the one scene that was rotated 90° either to the right or to the left; when the target was immediately preceded by an irrelevant emotionally evocative picture, participants were substantially worse at detecting it than when it was preceded by an irrelevant neutral picture. The emotional distractor apparently captured attention, producing a deficit for the subsequent target event, an effect known as the attentional blink (Chun and Potter, 1995; Folk et al., 2002; Raymond et al., 1992). Importantly, this deficit was modulated by the specificity with which participants searched for the target. For example, when they were given relatively specific information about what their target might look like (e.g., “look for a rotated BUILDING”), they were better able to ignore the emotional distractors than when given less specific information (e.g., “look for a rotated BUILDING or LANDSCAPE”), and target detection improved despite the fact that all analyzed trials only contained buildings as targets. The decreased ability to report the target after an emotional distractor, relative to a neutral distractor, was referred to as emotion-induced blindness or attentional rubbernecking. Instances where participants were given more specific target information represented cases where they established a specific attentional set; when they were given less specific target information, participants established a nonspecific attentional set. Notably, the effect of this attentional manipulation on accuracy was associated with individual differences in “harm avoidance”, a personality measure linked to trait anxiety: although everyone was relatively more distracted by emotional than by neutral distractors when maintaining a nonspecific attentional set, when they adopted a specific attentional set, it was participants low in harm avoidance who were then able to avoid such distraction.

In adapting this paradigm for use in the MR scanner, we examined a priori regions of interest (ROIs). In addition to the right and left amygdalae, these included the rostral anterior cingulate cortex (ACC), which is thought to be involved in affective processing, particularly with the resolution of affective interference (Bishop et al., 2004a; Bush et al., 2000; Kiehl et al., 2000). We also examined five regions associated with cognitive control: the right and left dorsolateral prefrontal cortices (DLPFC), the right and left ventrolateral prefrontal cortices (VLPFC), and the dorsal ACC (see Bishop et al., 2004a). We predicted greater activation in these “control” areas when participants maintained a specific, rather than a nonspecific, attentional set.

Finally, we explored an additional hypothesis based on “cognitive processing efficiency theory” (Eysenck and Calvo, 1992). According to this theory, anxiety is associated with less efficient cognitive control, but this is not always observable through performance measures such as accuracy; instead, less cognitively efficient individuals can achieve the same levels of accuracy as more efficient individuals through the application of greater mental effort (Eysenck and Calvo, 1992). Nevertheless, the consequences of this greater effort might be observable through measures of response time (Eysenck and Calvo, 1992; see also Lieberman and Rosenthal, 2001) or neural functioning (Gray and Braver, 2002; Gray et al., 2005). Thus, we explored the additional possibility that, should individual differences in attentional modulation of behavior or amygdala activity not emerge as a function of harm avoidance, high harm-avoidant participants— who might have greater interference to overcome—would show greater activation in the rostral ACC or the other control-related ROIs than low harm-avoidant participants. Relevant individual differences in rostral ACC activation have been found before: for example, in one study, participants scoring high on a measure
related to trait anxiety showed enhanced rostral ACC activity when attending to nonemotional, rather than emotional, aspects of emotional stimuli (see Mathews et al., 2004, Fig. 6).

Methods

Participants

Thirty-two right-handed participants were recruited for paid participation. Three were removed prior to analyses due to excess movement during scanning (>1 voxel), leaving a final sample of 29 participants (20 female; mean age = 22.5 years). All participants gave informed consent in a protocol approved by the Institutional Review Board at The Olin Neuropsychiatry Research Center at The Institute of Living/Hartford Hospital (IOL), Hartford, CT.

Personality measures

All participants completed the harm avoidance scale from the Tridimensional Personality Inventory (Cloninger et al., 1991), developed to assess potentially heritable, stable personality traits related to the intensity of responses to aversive stimuli. Low harm avoidance scores tend to be associated with confident temperaments, risk-taking behavior, and quick recovery from stress, whereas high scores tend to be associated with anxious and tense temperaments, risk-avoiding behavior, and slow recovery from stress. Rather than focusing on individuals’ reports about subjective, chronic moods, the harm avoidance scale taps into more objectively observable tendencies in dealing with aversive or threatening stimuli and situations. Scores can range from 0 to 34. To probe the possibility that higher harm avoidance scores are associated with lower attentional control, and scores can range from 20 to 80.

fMRI data acquisition

MR images were collected with a Siemens 3 T Allegra, a head-dedicated scanner optimized for functional brain imaging. Functional scans were acquired using an EPI gradient-echo pulse sequence, covering the entire brain and aligned to the anterior commissure–posterior commissure (AC–PC) line (TR/TE 1500/27 ms, flip angle 60°, FOV 22 × 22 cm, 3.4 × 3.4 in plane resolution, 4 mm slice thickness with a 1 mm gap, 29 slices).

Stimuli were projected onto a high-resolution screen located behind the participants’ heads and were viewed via a mirror attached to the head coil, which provided an unobstructed view subtending a visual angle of 60°. Stimuli were delivered using custom software (VAPP) developed by the last author (http://www.nilab.psychiatry.ubc.ca/vapp) and were synchronized with pulses generated by the scanner at the beginning of each scan sequence.

Task

Participants completed 8 self-contained runs of 48 trials each (about 5.5 min per run; one participant completed 6 runs). Each trial consisted of 17 pictures flashed for 100 ms per picture, with no gap between presentations. Most of the pictures were upright landscape scenes, with two exceptions: first, in place of one of the upright landscapes, 32 trials in each run contained a critical distractor that was either an emotionally negative or a neutral picture. Most of these were taken from the International Affective Picture System (IAPS; Lang et al., 2001; see Appendix), and these were supplemented by similar pictures from publicly available sources (see Most et al., 2005a). Negative pictures were of people or animals and included graphic images of violence, distress, and medical trauma; neutral pictures were balanced with the negative pictures for numbers of pictures of people and animals. Second, also in place of an upright landscape, half of the emotionally negative trials and half of the emotionally neutral trials contained a target that was always a 90° rotated picture of a building. The target was always the second item after the critical distractor (see Fig. 1). Each critical distractor appeared twice: once in a target-present trial and once in a target-absent trial. In addition, each run contained 16 “filler” trials, which contained no critical distractor but did contain a rotated target, the identity of which depended on the attentional set manipulation; depending on the instructions (see below), this target was a 90° rotated picture of either a building or a landscape. These “filler” trials were never included in subsequent analyses and were included for the sole purpose of manipulating attentional set.

On each trial, participants searched for the rotated target and then, using a button box, indicated whether it was rotated to the left or the right. Instructions emphasized that targets would never contain people or animals, and that all such pictures should be ignored. Participants were also instructed to guess an answer for trials in which they did not detect a target. Thus, a response was recorded for all trials, regardless of whether a target was present or not (trials with no button presses were eliminated from the behavioral analyses). Participants were instructed to search for their target based on one of two sets of instructions: one set of instructions read “Look for the rotated BUILDING” (the specific attentional set condition), and the other set read “Look for the..."
rotated LANDSCAPE or BUILDING” (the nonspecific attentional set condition). At the start of each run, participants received one of these instructions, and halfway through the run, they received the alternate set of instructions. Runs alternated in terms of which set of instructions came first, and participants alternated in terms of whether the first run began with the specific or the nonspecific instructions. Although all analyzed trials contained buildings as targets, the attentional manipulation was accomplished through the inclusion of the “filler” trials, which were not included in any analyses; under the specific attentional set instructions, the filler trials always contained buildings as targets (thus, all trials in this condition were homogeneous in terms of the type of target), and under the nonspecific attentional set instructions, they always contained landscapes as targets (thus, trials in this condition were heterogeneous in terms of type of target). For each run, the types of trials were evenly split between the specific and the nonspecific target conditions, and within these conditions, trials were presented as part of an event-related, pseudo-random design.

Because our main interest was neural response to the critical distractors, hemodynamic activity was analyzed only for trials in which no targets appeared; thus, we avoided confounds that might arise from differential rates of target detection between the two attentional set and the two emotional valence conditions. Trials in which the targets actually appeared were used to gather behavioral data in order to determine the effect of emotional distractors and attentional manipulation on target detection.

fMRI data analysis

Analyses were conducted using SPM2 software (Wellcome Department of Imaging Neuroscience, London, UK). Functional images were realigned using INRIAlign, a motion correction algorithm unbiased by local signal changes (Freire and Mangin, 2001; Freire et al., 2002), and brains were spatially normalized using a tailored algorithm with both linear and nonlinear components (Friston et al., 1995). Normalized data were smoothed with a 12-mm FWHM kernel and a fifth-order FIR Butterworth low-pass filter of 0.25 Hz was applied to remove any high-frequency noise associated with alternations in the applied radio frequency field. A high-pass filter (cutoff period 128 s) was incorporated to remove noise associated with low-frequency confounds (e.g., scanner drift or respiratory artifact). Contrasts were specified that evaluated the effects of (1) emotional valence (negative–neutral); (2) attentional set (specific–nonspecific); and (3) the interaction of valence and attentional set [(negative/nonspecific–neutral/nonspecific)–(negative/specific–neutral/specific)]. Additional contrasts also evaluated the effects of (4) valence within each attentional set condition and (5) attentional set within each valence condition. In order to reduce the influence of spatially varying hemodynamic delays and delays due to slice timing, the true amplitude of the hemodynamic response (a function of both the nonderivative and derivative terms) was calculated and used in the subsequent analyses (Calhoun et al., 2004). Images containing these amplitudes were then entered into the second level analyses (i.e., random effects analyses) for each comparison of interest.

Regions of Interest (ROIs) were defined a priori, using the MarsBaR ROI toolbox for SPM2 (http://www.marsbar.sourceforge.net/). The left and right amygdala ROIs were defined by locating the approximate center of each amygdala on the Montreal Neurological Institute (MNI)–International Consortium for Brain Mapping template (MNI x, y, z = −21, 0, −21 and 21, 0, −21, respectively), and constructing an 8-mm radius sphere around it. ROIs for the rostral and dorsal ACC were also located structurally and were constructed by building 8-mm radius spheres around central coordinates: rostral ACC (MNI x, y, z = 2, 4, 8), dorsal ACC (MNI x, y, z = 4, 14, 36). ROIs for the dorsolateral and ventrolateral PFC were constructed by building 8-mm radius spheres around coordinates previously established in the literature (Bishop et al., 2004a): right and left DLPFC (MNI x, y, z = ±34, 36, 24), right and left VLPFC (MNI x, y, z = ±36, 20, 0).

Results

We examined the main effects of valence (i.e., negative versus neutral distractor) and of attentional set (i.e., specific versus nonspecific). Most central to our investigation, we then examined (1) the interaction between valence and attentional set, with the hypothesis that the effect of valence would be smaller when people adopted a specific, rather than a nonspecific, attentional set, and (2) the degree to which this interaction varied with personality. We investigated these effects separately for behavioral and neuroimaging data.

Personality variables

Harm avoidance scores ranged from 0 to 23 (mean = 11.6, SD = 5.6), and attentional control scores ranged from 38 to 74 (mean = 56.2, SD = 8.7). Consistent with predictions based on prior literature (Derryberry and Reed, 2002), participants’ scores on the harm avoidance measure and on the attentional control scale correlated inversely with each other: participants who scored higher on harm avoidance tended to score lower on attentional control, r = −0.58, P < 0.001. These scores did not vary systematically with sex.

Behavioral data

A 2 (valence: negative versus neutral distractor) × 2 (attentional set: specific versus nonspecific) ANOVA revealed that, consistent with our predictions and with previous research (Most et al., 2005a), participants’ accuracy in reporting the targets’ orientation was worse when targets followed an emotionally negative distractor (mean accuracy = 84.2%, SD = 7.6%) than when they followed a neutral distractor (mean accuracy = 90.6%, SD = 6.0%), F(1,28) = 27.19, P < 0.001, an effect referred to as emotion-induced blindness. Also consistent with our predictions, accuracy was better when participants maintained a specific attentional set (e.g., “look for the rotated BUILDING”; mean accuracy = 89.0%, SD = 5.18%) than when maintaining a nonspecific attentional set (e.g., “look for the rotated LANDSCAPE”; mean accuracy = 85.8%, SD = 8.2%), F(1,28) = 7.26, P = 0.012. Importantly, this effect of attentional manipulation emerged despite the fact that all analyzed trials contained buildings as targets, regardless of attentional set, and so could not be attributed to targets in one condition simply being easier to see. A lack of an interaction between valence and attentional set revealed that attentional set did not, group-wise, modulate the performance difference between neutral and negative trials, F(1,28) = 0.07, P = 0.783. This is consistent with previous behavioral results, which had found that—rather than attentional modulation emerging from a group-wise analysis—such modulation correlated with harm avoidance (Most et al., 2005a). However, in the present study, we found no such
correlation behaviorally, \( r = 0.24, P = 0.195 \). Indeed, when the analysis was repeated as an ANCOVA incorporating harm avoidance as a covariate, there was no 3-way interaction between Valence, Attentional Set, and Harm Avoidance, \( F(1,27) = 1.77, P = 0.195 \). Nor did Harm Avoidance interact with Valence, \( F(1,27) = 1.17, P = 0.288 \), or with Attentional Set, \( F(1,27) = 0.002, P = 0.966 \). It did, however, account for enough variance to eliminate the main effect of Attentional Set, \( F(1,27) = 1.18, P = 0.286 \), but not of Valence, \( F(1,27) = 9.01, P = 0.006 \). Despite the fact that attentional modulation of emotion-induced blindness did not correlate with harm avoidance, it did bear a statistical relationship with attentional modulation of the left amygdala, as described below.

**Neuroimaging data**

When considering the effect of the emotional distractor on neural activity or its modulation by attentional set, we defined a priori the left and right amygdalae and the rostral ACC as our primary ROIs. When considering the effects of attentional set alone, we defined a priori the dorsal ACC and the left and right DLPFC and VPFC as our primary ROIs. Although SPM returns \( P \) values for one-tailed \( t \) tests, all \( t \) tests reported here are two-tailed except where noted.

**Main effects**

Consistent with our predictions for a main effect of emotion, amygdala activation was greater in response to negative than to neutral distractors. This was especially apparent when both amygdalae were combined as a single ROI, \( t(28) = 2.47, P = 0.019 \). Examined separately, such activation was evident in both the left amygdala, \( t(28) = 2.03, P = 0.052 \), in the right amygdala, \( t(28) = 2.35, P = 0.026 \), and marginally in the rostral ACC, \( t(28) = 1.84, P = 0.076 \). We will refer to the greater activation in negative than in neutral trials as “emotion-related activity”. Separate SPM contrasts incorporating harm avoidance and attentional control scores as regressors revealed no systematic relationship between the main effect of emotion and either personality variable.

Also consistent with our predictions for a main effect of attentional set, prefrontal areas were more active when participants maintained a more specific attentional set than when maintaining a less specific attentional set (i.e., searching for a rotated building versus a target that could be either a building or a landscape). This effect was prominent in the ventrolateral PFC but not the dorsolateral PFC: the contrasts for the right and (marginally) the left ventrolateral regions of interest achieved significance (\( t(28) = 2.38, P = 0.024 \), and \( t(28) = 1.98, P = 0.058 \), respectively), whereas neither the right nor left dorsal regions did, \( P > 0.20 \). This effect of attentional set was not significant in the dorsal ACC, \( t(28) = 1.63, P = 0.114 \). The degree to which activity was greater in the specific than in the nonspecific attentional set condition did vary as a function of attentional control score (incorporated as a regressor) in the left DLPFC, where this difference was greater among those scoring high in self-rated attentional control, \( t(27) = 2.23, P = 0.034 \). A similar relationship emerged with harm avoidance, where lower harm avoidance scores were marginally associated with relatively greater activation in the specific attentional set condition in the left DLPFC, \( t(27) = 1.86, P = 0.074 \).

The comparison between attentional set conditions was the only contrast yielding significant activations in a subsequent whole-brain analysis, with a false discovery rate (FDR) correction at \( P < 0.05 \) and a minimum cluster of 5 voxels (see Fig. 2 and Table 1). Such differences survived the whole-brain analysis even though stimuli were the same in both conditions (balanced for number of neutral and negative trials) and even though no targets actually appeared in these trials (and thus could not be attributed to greater target detection). In this analysis, regions more active in the specific than in the nonspecific attentional set condition included areas implicated in the control of attention, such as the right and left middle frontal gyri, the left inferior frontal gyrus, and the left inferior parietal lobule (Hopfinger et al., 2000). In addition, areas previously found to be modulated by attention were also more active when participants maintained a specific attentional set, including striate and extrastriate visual areas (Kastner and Ungerleider, 2001; Tallon-Baudry et al., 2005). These regions extended bilaterally from the middle occipital gyrus and cuneus through to the bilateral fusiform gyrus, lingual gyrus, and the right parahippocampal gyrus. Greater activation also emerged in the left precentral gyrus, possibly reflecting attentional priming of an area underlying target responses (Hopfinger et al., 2000), and in the cerebellum, which either might reflect attentional priming of motor-related areas or, consistent with its hypothesized role in temporal processing (Casini and Ivry, 1999), differential engagement in the temporal attention task.

**Interaction**

The most critical comparisons of interest involved the effect of attentional set on emotion-related amygdala activation. We predicted that emotion-related activity would be greater in the nonspecific attentional set condition than in the specific attentional set condition, and that the degree to which attentional set modulated this difference would vary systematically with participants’ score on the personality measure harm avoidance. A contrast modeling this 2 (type of distractor: negative versus neutral) \times 2 (attentional set: specific versus nonspecific) interaction revealed no group-wise modulation of the amygdala (or any of the ROIs) by attentional set, \( P > 0.30 \). However, when harm avoidance was incorporated as a regressor, the contrast revealed a substantial relationship between the effect of attentional set and harm avoidance. Higher harm avoidance scores were associated with greater effects of attentional set on emotion-related activity in the amygdala when they were combined in a single ROI, \( r = 0.39, t(27) = 2.16, P = 0.040 \), as well as separately in the left amygdala, \( r = 0.37, t(27) = 2.07, P = 0.048 \), and marginally in the right amygdala, \( r = 0.35, t(27) = 1.94, P = \).
0.063 (see Fig. 3). The only other ROI in which such a relationship emerged was in the rostral ACC, which is discussed below (all other ROIs, \( P > 0.25 \)).

Further contrasts comparing emotion-related activity separately for the two attentional set conditions, and incorporating harm avoidance as a regressor, revealed that the relationship between harm avoidance and the interaction was driven by the nonspecific attentional set condition for both the left amygdala, \( t(27) = 2.20, P = 0.036 \), and the right amygdala, \( t(27) = 2.49, P = 0.020 \), not by the specific attentional set condition, \( Ps > 0.60 \) (see Fig. 3). The activations in the right amygdala tell a compelling story: when participants maintained a specific attentional set, the degree of emotion-related activity was relatively small regardless of harm avoidance score. However, in the nonspecific attentional set condition, those scoring low in harm avoidance (via a median split) showed relatively little emotion-related activity, but participants high in harm avoidance showed much greater emotion-related activity than low harm-avoidant participants who maintained a nonspecific attentional set, \( t(25) = 3.16, P = 0.004 \). The pattern of activation strength was such that the relationship between harm avoidance and the interaction was driven by the nonspecific attentional set condition for both the left amygdala, \( t(27) = 2.20, P = 0.036 \), and the right amygdala, \( t(27) = 2.49, P = 0.020 \), not by the specific attentional set condition, \( Ps > 0.60 \) (see Fig. 3). The activations in the right amygdala tell a compelling story: when participants maintained a specific attentional set, the degree of emotion-related activity was relatively small regardless of harm avoidance score. However, in the nonspecific attentional set condition, those scoring low in harm avoidance (via a median split) showed relatively little emotion-related activity, but participants high in harm avoidance showed much greater emotion-related activity than low harm-avoidant participants who maintained a nonspecific attentional set, \( t(25) = 3.16, P = 0.004 \).

Fig. 2. Illustration of the areas in which the hemodynamic response was significantly greater in the specific attentional set condition than in the nonspecific attentional set condition (\( P < 0.05 \), one-tailed, FDR-corrected, with a minimum cluster of 5 voxels).

In order to ensure that correlation between harm avoidance and the effect of attentional set on emotion-related amygdala activity was not driven by a few extreme participants, we screened for outliers. No data points fell more than 3 standard deviations away from the regression line for either the left or the right amygdala (see Fig. 3). For both the left and right amygdalae, two data points did fall more than 2 standard deviations away from the regression line (these points are indicated with a triangle in the scatterplots in Fig. 3). When these liberally defined “outliers” were removed from the analyses, the relationship between harm avoidance and the effect of attentional set actually became stronger in the left amygdala, \( r = 0.49, t(25) = 2.82, P = 0.009 \), although it became less weaker in the right amygdala, \( r = 0.35, t(25) = 1.87, P = 0.072 \).

Two subjects whose harm avoidance score fell on the median were removed from this analysis.
in the left amygdala was similar: the variance between participants scoring high and low in harm avoidance was attributable to activation in the nonspecific attentional set condition, where high scorers had greater emotion-related activity than low scorers did, \( t(25) = 2.22, P = 0.036 \) (see Fig. 3). Activations in the specific attentional set condition in the left amygdala, like those in the right amygdala, did not differ between high and low harm-avoidant participants, \( P > 0.60 \).

Interestingly, the third emotion-related ROI, the rostral ACC, appeared to have the opposite relationship with harm avoidance. As harm avoidance scores increased, the degree to which emotion-related activity was greater in the nonspecific than specific attentional set condition, where high scorers had greater emotion-related activity than low scorers did, \( r(25) = 0.36, t(27) = 2.65, P = 0.019 \). In contrast to the amygdalae, this relationship appeared driven by the specific attentional set condition, where emotion-related activity increased as harm avoidance score increased, \( r(27) = 0.24, P = 0.024 \). When participants maintained a nonspecific attentional set, emotion-related activity showed no relationship with harm avoidance, \( P > 0.20 \).

**Brain–behavior correlation**

Notably, there was a significant relationship between individual differences in attentional modulation of the left amygdala and individual differences in attentional modulation of emotion-induced blindness (see Fig. 4). That is, the degree to which maintaining a specific attentional set decreased emotion-induced blindness, relative to when maintaining a nonspecific attentional set, was correlated with the degree to which maintaining a specific attentional set led to decreased emotion-related activity in the left amygdala, \( r = 0.40, t(27) = 2.26, P = 0.032 \). This relationship was not significant in the right amygdala, \( P > 0.10 \), nor in the rostral ACC, \( P > 0.20 \).

In order to ensure that this brain–behavior relationship in the left amygdala was not driven by extreme scores, we screened for outliers. No points fell more than 3 standard deviations away from the regression line, although one point did fall more than 2 standard deviations away. Removing this point from the analysis decreased the strength of the relationship slightly to \( r = 0.36, t(26) = 1.98, P = 0.058 \) (two tailed). Thus, the relationship was marginally significant even with one liberally defined outlier removed.

**Discussion**

Even when people explicitly tried to ignore negative emotional distractors that they knew to be irrelevant to the task, they were unable to do so. Behaviorally, this was evident from participants’ decreased ability to report a target when it followed soon after an emotional distractor than after a neutral one, an effect termed “emotion-induced blindness” (or “attentional rubbernecking”; Most et al., 2005a). Neurally, this was evident from greater bilateral amygdala and rostral ACC activation in negative emotional trials than in neutral trials, even though the critical distractors had been presented for only 100 ms per trial. Furthermore, although manipulations of attentional set were accompanied by different levels of activation in predicted “control-related” regions such as the bilateral VLPFC, as well as a network of attentional control-related areas revealed through a whole-brain analysis, at a group level such manipulations did not result in a decrease in emotion-related neural activation. At first glance then, it appears that emotional information captures...
attention automatically, and that such distraction is impervious to manipulations of attentional set.

When looking beyond the group level, however, it becomes evident that attentional modulation of the amygdala varied systematically as a function of the personality measure ‘harm avoidance’, which is associated with trait anxiety (Cloninger et al., 1991). In the amygdalae, this variation was driven by the nonspecific attentional set condition, where high harm-avoidant participants had increased emotion-related activation (bar graphs). In the rostral ACC, the degree to which attentional set modulated emotion-related activity was inversely correlated with harm avoidance. (The activation maps here represent the positive correlation in the amygdalae and the inverse correlation in the rostral ACC.) This inverse correlation was driven by the specific attentional set condition, where high harm-avoidant participants had increased emotion-related activation. In the bar graphs, the division between high and low harm-avoidant participants was based on a median split; two participants whose scores fell on the median are not included in the bar graphs. Note that in the scatterplots, no points fell more than 3 standard deviations away from the regression lines; however, two points in each plot fell more than 2 standard deviations away. These points are indicated with triangles.
an ANCOVA, with harm avoidance as a covariate. Again, there was a
was treated as a continuous variable, we additionally submitted the data to
0.190. On the chance that an interaction might emerge if harm avoidance
regardless of task instructions. Thanks to an anonymous reviewer for this
interaction between filler trial type and harm avoidance,
increased rostral ACC activity in more anxious individuals.

[Image 79x580 to 262x724]

Fig. 4. The left amygdala and emotion-induced blindness. The degree to
which adopting a specific, versus a nonspecific, attentional set decreased
emotion-induced blindness correlated with the degree to which it decreased
emotion-related activity in the left amygdala. Although no points fell more
than 3 standard deviations away from the regression line, one point did fall
more than 2 standard deviations away and is indicated with a triangle.

5 Notably, the degree to which attentional set
modulated emotion-related activity in the left amygdala
was also correlated with the degree to which attentional set
modulated emotion-induced blindness.

In light of the fact that amygdala activation in the nonspecific
attentional set condition was greater among those high, rather than
low, in harm avoidance, it is particularly interesting to note that
rostral ACC activation showed a different pattern. In contrast with
the amygdalae, systematic variation in the rostral ACC was driven
by the specific attentional set condition; in this case, participants
high in harm avoidance showed greater emotion-related activation
when maintaining a specific attentional set than those low in harm
avoidance did. Note that this is roughly reminiscent of findings that
people high in anxiety showed greater rostral ACC activity when
trying to ignore, rather than attend to, emotional aspects of a
stimulus (see Mathews et al., 2004, Fig. 6). In both cases, the
condition designed to aid ignoring of emotional quality led to
increased rostral ACC activity in more anxious individuals.

This clear individual differences in cognitive control over
emotional distraction at the neural level were not always apparent
in the behavioral results, underscoring the importance of under-
standing such individual differences at multiple different levels.
For example, the behavioral measure of emotion-induced blindness
did not interact with attentional set; this is somewhat different than
results of an earlier study, where adopting a specific attentional set
decreased emotion-induced blindness among low harm-avoidant
participants but not among high harm-avoidant participants (Most
et al., 2005a). However, in the current study, we modified the task
for the scanner in important ways. For example, half the trials in
the current protocol contained no target (all trials contained a target
in the earlier version), and when a target was present, it was always
the second item after the critical distractor (in the earlier version,
the temporal relationship between the target and critical distractor
was less predictable). The relatively unfamiliar scanner environ-
ment, itself, may also have contributed to an elevated baseline level
of arousal compared to that in the purely behavioral study; consistent with this, behavioral performance across all participants in
the current study resembled that of the high harm-avoidant
participants in the previous, behavioral version.

At first glance, the direction of the relationship between harm
avoidance and the influence of attentional set seems different in

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5 An alternative explanation for the weaker attentional set \times valence
interaction among low harm avoidant people is that these participants
adhered to the instructions less, maintaining a specific attentional set
regardless of the condition. We were able to assess this possibility by
comparing behavioral accuracy on filler trials in the nonspecific attentional
set condition to filler trial accuracy in the specific attentional set condition
(these had been coded separately for 24 of our participants) and seeing
whether this differed between those high and low in harm avoidance (using
a median split; two participants fell at the median and were not included in
this analysis). The results revealed a main effect of filler trial type (i.e.,
based versus landscape target), \( F(1,20) = 151.71, P < 0.001 \), with
accuracy being greater for buildings than landscapes. However, there was
no main effect of harm avoidance, \( F(1,20) = 1.09, P = 0.308 \), nor an
interaction between filler trial type and harm avoidance, \( F(1,20) = 1.84, P =
0.190 \). On the chance that an interaction might emerge if harm avoidance
was treated as a continuous variable, we additionally submitted the data to
an ANCOVA, with harm avoidance as a covariate. Again, there was a
significant main effect of filler trial type \( (P < 0.001) \), but neither a main
effect of harm avoidance \( (P = 0.867) \) nor an interaction between filler trial
type and harm avoidance \( (P = 0.483) \). Thus, it does not appear that our
results are due to low anxious participants using a narrow attentional set
regardless of task instructions. Thanks to an anonymous reviewer for this
suggestion.
the current study than in the previous behavioral version of this task. In the behavioral version, adopting a specific attentional set, relative to a nonspecific attentional set, led to improved ignoring of distractors among those low, but not high, in harm avoidance (Most et al., 2005a). Thus, it would have been reasonable to expect that the influence of attentional manipulations on amygdala activity would be greater among low harm-avoidant people as well (this type of pattern, after all, was found by Bishop et al., 2004b). In contrast, in the current study, adopting a specific attentional set affected amygdala activity in those high, but not low, in harm avoidance. Although seemingly contradictory, both patterns of data may suggest weaker levels of attentional control among high harm-avoidant individuals. In the behavioral version, both high and low harm-avoidant participants suffered emotional interference when maintaining the nonspecific attentional set; only low harm-avoidant people were able to eliminate this interference when adopting a more specific attentional set. Thus, low harm-avoidant individuals were better able to impose attentional control. In the current version, both high and low harm-avoidant individuals were able to ignore the emotional distractors (as indexed through low amygdala activation) when maintaining a specific attentional set; when adopting a nonspecific attentional set, low harm-avoidant people were still able to ignore the emotional distractors, but high harm-avoidant people were not. This pattern again suggests that high harm-avoidant people were less able to filter out the emotional distractors. In other words, both patterns of data suggest similar conclusions, though their manifestations are different. Differences in task instructions, the experimental environment, or simply in the participants themselves may be the reason that such differences in attentional control were manifested differently in the previous behavioral and current neuroimaging experiments.

In conclusion, when people searched for a target and ignored emotional distractors, the effectiveness of such ignoring—indexed through diminished emotion-related amygdala activity—depended on a combination of attentional “tuning” and peoples’ own personalities. When people were unsure about what their target would look like—that is, when they could not establish a specific attentional set—high harm-avoidant participants showed substantial amygdala responsivity to the irrelevant emotional distractors. In contrast, low harm-avoidant people demonstrated low amygdala responsivity. When people had more specific information about what their target would look like, high harm-avoidant participants improved their ability to ignore the emotional distractors, and their levels of amygdala activation came to resemble that of the low harm-avoidant participants. Additionally, in a result underscoring the complexity of individual differences in control over emotional distraction, when high harm-avoidant participants lowered emotion-related activity in the amygdala in this way, activation in the rostral ACC increased. Thus, in situations where personality does not predict emotion-related amygdala activity, such differences may still be found in areas like the rostral ACC, which possibly constitute part of the engine regulating emotional responsivity.

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Appendix A

Reference numbers to images taken from the International Affective Picture System (IAPS; Lang et al., 2001). Stimuli included 42 negative IAPS images (valence = 1.84, SD = 0.40; arousal = 6.34, SD = 0.63) and 63 neutral IAPS images (valence = 5.37, SD = 0.84; arousal = 3.72, SD = 0.82), which were supplemented by similar images drawn from publicly available sources.

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