

Attentional modulation of the amygdala varies with personality

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Received 24 July 2005; revised 9 December 2005; accepted 14 December 2005

Available online 21 February 2006

The amygdala is implicated in emotional processing, and its rich subcortical connections 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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The amygdala has become a principal region of interest in investigations of emotion due to its rich connections to other brain regions, some of which have been argued to bypass cortical areas associated with attention and visual awareness (LeDoux, 2000; Morris et al., 1999). Such connections, in addition to informing neurobiological models of affective processing, have been interpreted to support hypotheses that stimulus emotionality is processed automatically, independent of attention or cognitive

control (e.g., Dolan and Vuilleumier, 2003; Öhman, 2002; Öhman and Mineka, 2001).

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 necessitate the absence of attention; accruing evidence suggests that effects of attention can be found without awareness (Kentridge 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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Available online on ScienceDirect (www.sciencedirect.com).

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 (see Eysenck and Calvo, 1992), participants additionally completed a self-rated attentional control scale, which has been shown to predict ability to disengage attention from emotionally evocative stimuli (Derryberry and Reed, 2002). Higher scores are associated with better 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

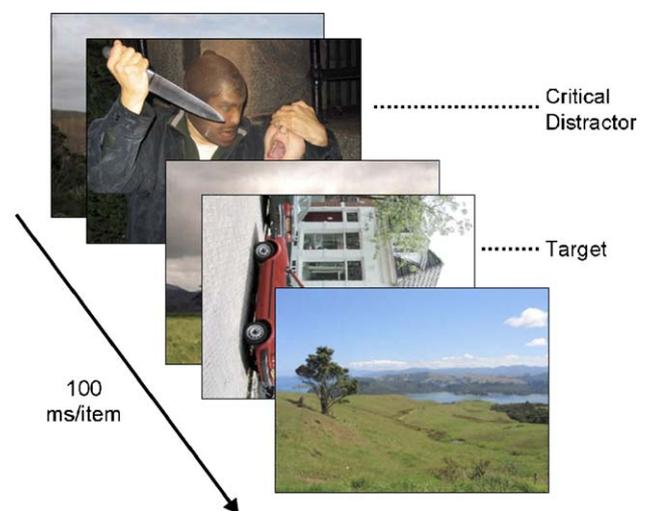


Fig. 1. Example of part of a target-present trial. Here, the critical distractor is a negative picture. In target-present trials, which were included for the collection of behavioral data, the critical distractor always preceded the target by two items. Target-absent trials, in which a critical distractor appeared without a subsequent target, were included for the collection of neuroimaging data.

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 INRIAAlign, 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 IIR 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 $x, y, z = 2, 44, 8$), 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 $x, y, z = \pm 34, 36, 24$), right and left VLPFC (MNI $x, y, z = \pm 36, 20, 0$).

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 neuro-imaging 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) \times 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 BUILDING or 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, $r = 0.24$, $P = 0.195$.¹ 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 VLPFC 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 gyri and cuneus through to the bilateral fusiform gyri, lingual gyri, 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 amygdalae 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, $r = 0.35$, $t(27) = 1.94$, $P =$

¹ An inverse correlation did emerge between the degree of attentional modulation of emotion-induced blindness and participants' scores on the attentional control scale: the higher one's attentional control score, the less that adopting a specific attentional set decreased emotion-induced blindness, defined as the relative performance decrement in the emotional versus the neutral condition, $r = -0.45$, $P = 0.014$. This relationship emerged in an ANCOVA as well, where attentional control entered into a 3-way interaction with Valence and Attentional Set, $F(1,27) = 7.84$, $P = 0.009$ (this analysis also yielded a significant interaction between Attentional Set and Valence, $F(1,27) = 7.92$, $P = 0.009$). Although initially counterintuitive, further analyses revealed that this relationship emerged because those high in attentional control were able to improve their accuracy in neutral trials when maintaining a specific attentional set relative to when maintaining a nonspecific attentional set, but they did not similarly improve performance on negative trials. In contrast, those scoring low in attentional control did not show a similar improvement on either neutral or negative trials in the specific attentional set condition.

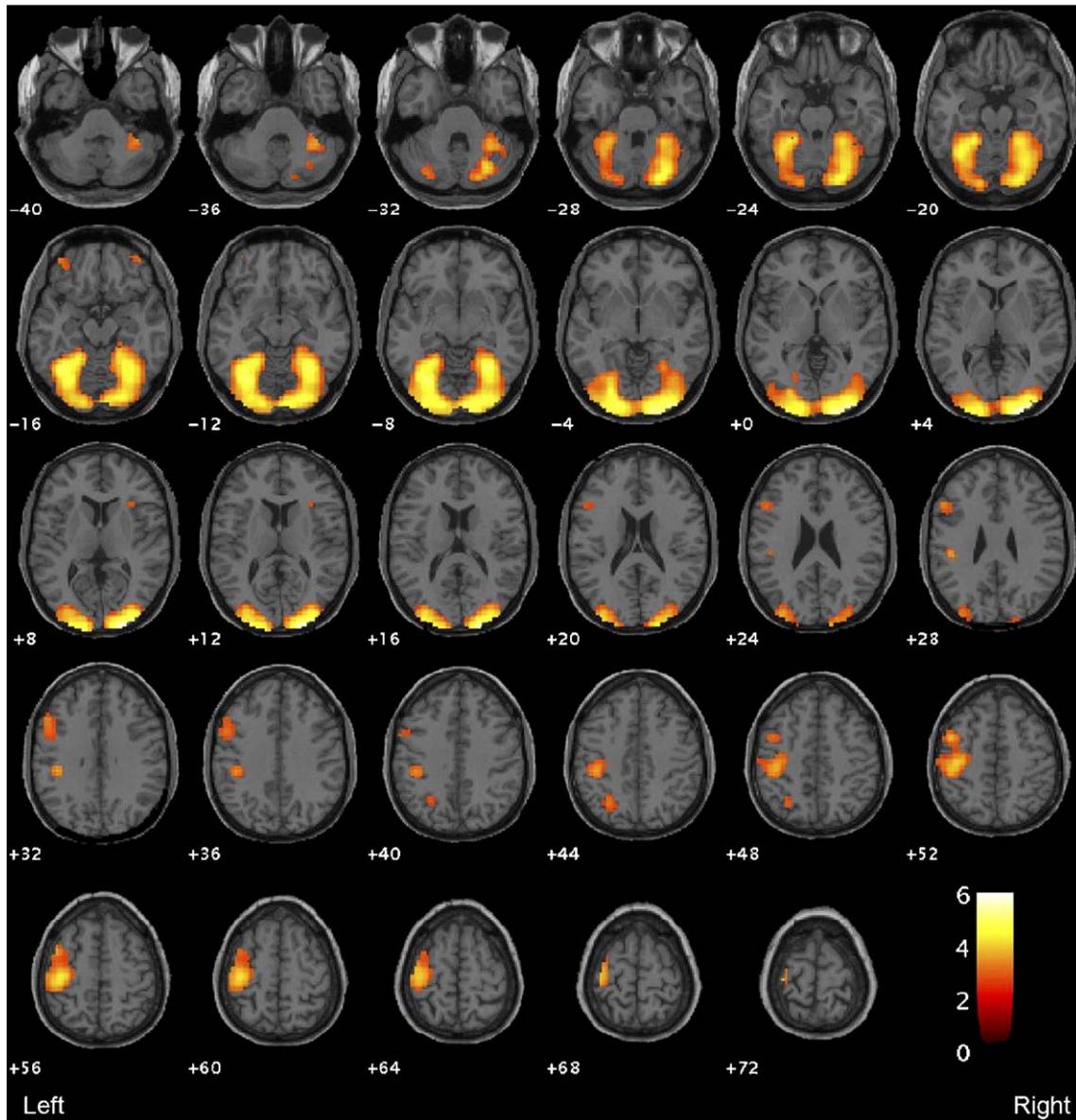


Fig. 2. Illustration of the areas in which the hemodynamic response was significantly greater in the specific attentional set condition than in the nonspecific attentional set condition ($P < 0.05$, one-tailed, FDR-corrected, with a minimum cluster of 5 voxels).

0.063 (see Fig. 3).² 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

² 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, $r = 0.35$, $t(25) = 1.87$, $P = 0.072$.

harm avoidance and the interaction was driven by the nonspecific 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, $P_s > 0.60$ (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)³ showed relatively little emotion-related activity, but participants high in harm avoidance showed much greater emotion-related activity (1) than when maintaining a specific attentional set, $t(12) = 2.42$, $P = 0.033$, and (2) than low harm-avoidant participants who maintained a nonspecific attentional set, $t(25) = 3.16$, $P = 0.004$. The pattern of activation

³ Two subjects whose harm avoidance score fell on the median were removed from this analysis.

Table 1

	x	y	z	t score	P (FDR-corr)
<i>Frontal lobes</i>					
1. L middle frontal gyrus	-45	6	54	4.12	0.005
2. L middle frontal gyrus	-51	21	30	3.54	0.013
3. L middle frontal gyrus	-36	45	-18	3.46	0.015
4. L inferior frontal gyrus	-51	9	36	3.28	0.021
5. R middle frontal gyrus	39	54	-15	3.22	0.024
6. R middle frontal gyrus	33	21	9	3.08	0.031
7. L precentral gyrus	-36	-21	57	4.43	0.004
<i>Parietal lobes</i>					
8. L inferior parietal lobule	-42	-30	30	4.28	0.004
9. L inferior parietal lobule	-30	-60	45	3.35	0.019
<i>Occipital–Temporal lobes</i>					
10. L middle occipital gyrus/cuneus	-15	-105	9	5.12	0.003
11. R. middle occipital gyrus/cuneus	24	-102	6	6.14	0.009
12. L fusiform gyrus/lingual gyrus	-33	-69	-12	5.24	0.003
13. R parahippocampal gyrus/fusiform gyrus/lingual gyrus	30	-54	-9	5.27	0.003
<i>Cerebellum</i>					
14. R cerebellum	24	-81	-27	5.02	0.004

Regional maxima with significantly greater activations in the specific attentional set condition (i.e., “look for the rotated building”) compared to the nonspecific attentional set condition (i.e., “look for the rotated landscape or building”), in a whole-brain analysis with a false discovery rate (FDR) correction at $P < 0.05$, one-tailed, and a minimum cluster of 5 voxels. Coordinates are in MNI space.

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 decreased, $r = -0.45$, $t(27) = 2.65$, $P = 0.012$ (see Fig. 3).⁴ 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, $t(27) = 2.39$, $P = 0.024$. 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

⁴ As with the amygdalae, in order to ensure that correlation between harm avoidance and the effect of attentional set on emotion-related rostral ACC activity was not driven by a few extreme participants, we screened for outliers. Although no points fell more than 3 standard deviations away from the regression line, two points fell more than 2 standard deviations away. When these points were removed from the analysis, the strength of this relationship increased to $r = -0.53$, $t(25) = 3.35$, $P = 0.002$.

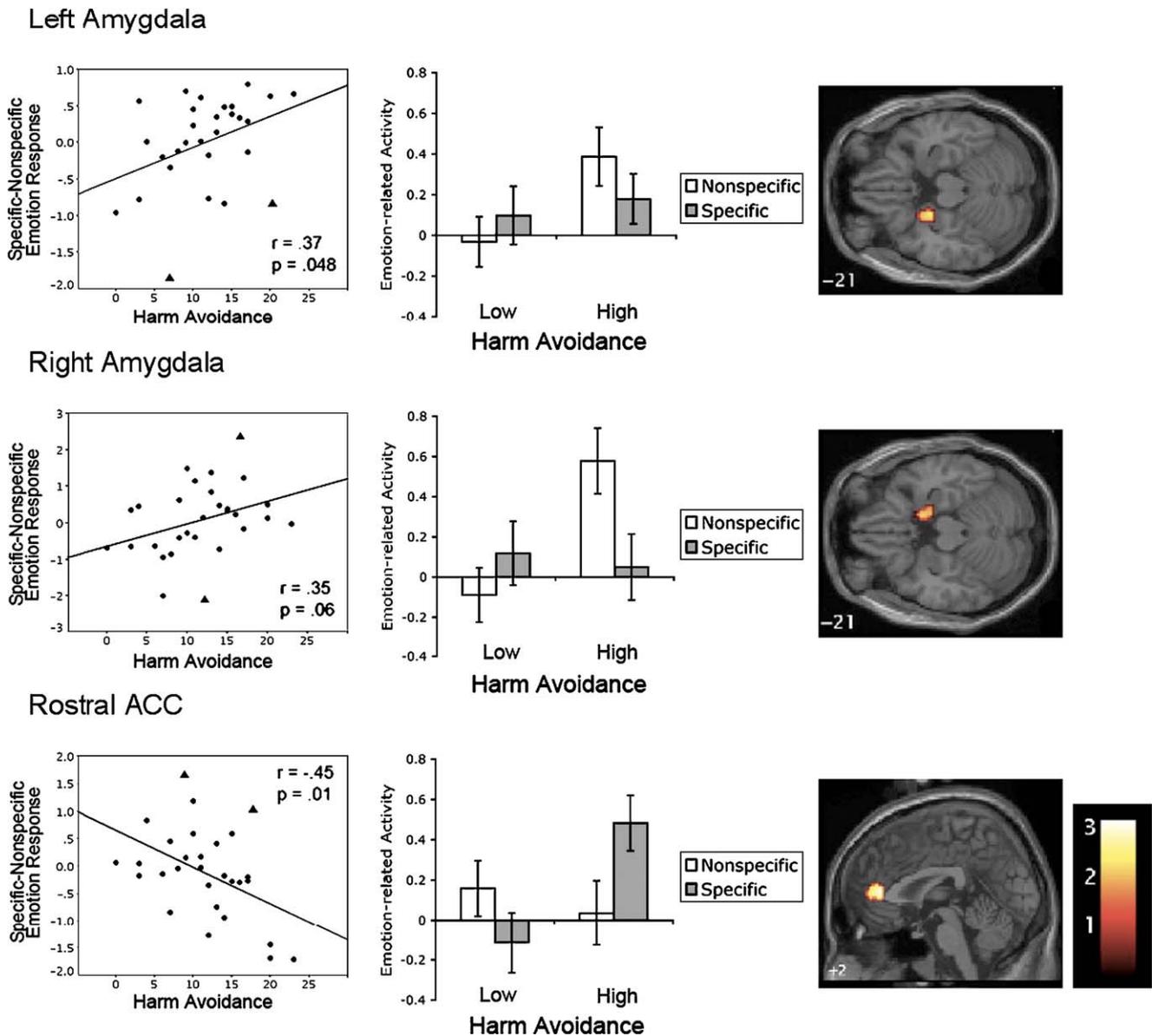


Fig. 3. In the left and right amygdalae, the degree to which attentional set modulated emotion-related activity (nonspecific-specific emotion-related activity) correlated with participants' harm avoidance score. This correlation was driven by the *nonspecific* attentional set condition, where high harm-avoidant 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.

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. When people maintained a specific attentional set, there was relatively little emotion-related amygdala activation regardless of harm avoidance score. Without specific target information, however, participants high in harm avoidance were less able to filter out the irrelevant

distractors and emotion-related amygdala activity increased (particularly in the left amygdala), whereas it did not increase among those low in harm avoidance. Thus, the degree to which people could ignore negative emotional distractors, as indexed through amygdala activation, was modulated by attentional set, but this modulation occurred primarily among those who seemed generally less efficient at ignoring them and thus for whom the benefits of maintaining a specific attentional set were more tangible. Consistent with this interpretation, participants scoring high in harm avoidance also tended to score low in self-rated attentional control, although this latter measure alone bore no statistical relation to attentional modulation of the

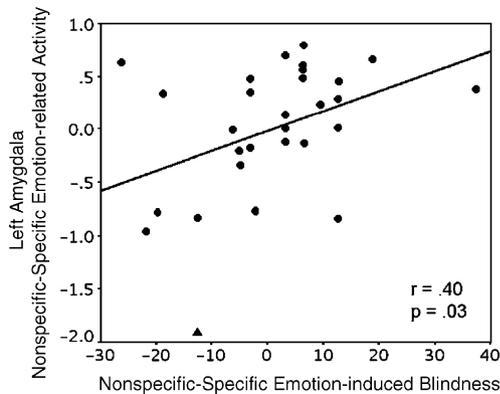


Fig. 4. The left amygdala and emotion-induced blindness. The degree to which adopting a specific, versus a nonspecific, attentional set decreased emotion-induced blindness correlated with the degree to which it decreased emotion-related activity in the left amygdala. Although no points fell more than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

amygdala.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.

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., building 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.

Elsewhere, it has been suggested that the rostral ACC activation signals the need for attentional control in the face of emotional distractors, and lower rostral ACC activity has been linked with weaker recruitment of prefrontal regions as well (Bishop et al., 2004a). But why should emotion-related rostral ACC activation be greater in the specific attentional set condition among high harm-avoidant people, particularly when emotion-related amygdala activation remained low in this condition regardless of harm avoidance score? A “processing efficiency theory” might provide insight here (Eysenck and Calvo, 1992). According to this theory and the data supporting it, cognitive efficiency decreases as anxiety increases; yet, the consequences of this are not always evident in terms of performance accuracy. Instead, high anxious individuals can compensate for decreased efficiency by devoting more effort to a task. In this study, the fact that high harm-avoidant people—by maintaining a specific attentional set—were able to attain the same low level of emotion-related amygdala activation as low harm-avoidant people might reflect the application of greater effort. That is, the extra target information given in the specific attentional set condition provided a fingerhold necessary for supporting attentional control among high harm-avoidant participants. Although high and low harm-avoidant people showed similarly low amounts of emotion-related amygdala activity, the greater rostral ACC activation among high harm-avoidant participants belied the additional effort. If this hypothesis is correct, then it is notable that patterns like that in the rostral ACC did not emerge in the prefrontal or dorsal ACC ROIs; the involvement of these regions in cognitive effort has been well established in prior literature (Bishop et al., 2004a; MacDonald et al., 2000). It may be that the rostral ACC is unique in the degree to which it reflects individual differences in cognitive control over emotion-related activity. Indeed, it has been suggested that this region, but not the dorsal ACC, is involved in the resolution of affective interference (Bush et al., 2000), and recent evidence has linked harm avoidance with decreased functional connectivity between the rostral ACC and amygdala (Pezawas et al., 2005). Activity in the prefrontal regions, like that in the dorsal ACC, may reflect cognitive effort generally but be less sensitive to affective regulation (but see Bishop et al., 2004a).

These 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 understanding 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 environment, 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

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 responsiveness to the irrelevant emotional distractors. In contrast, low harm-avoidant people demonstrated low amygdala responsiveness. 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 responsiveness.

Acknowledgments

We would like to thank the research staff at the Institute of Living/Hartford Hospital for their invaluable assistance in this

project. We are also grateful to David Zald, Vince Calhoun, Jeremy Gray, Kim Curby, and the Yale Visual Cognition group for helpful feedback and discussions. This study was funded by grant NIMH 1 R01 MH0705539-01 to Kent Kiehl, who was also supported by NIMH 1 R01 MH072681-01. Steve Most was supported by NIH NRSA MH66572. Marvin Chun was supported in part by NIH EY014193.

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.

Negative images			Neutral images		
1050	3071	3550	1450	2393	2749
2800	3100	6313	1640	2410	2840
3000	3101	6350	1670	2441	2850
3010	3102	6560	1942	2480	2870
3015	3110	7361	2005	2485	2890
3030	3120	9040	2020	2487	4100
3053	3130	9253	2190	2491	4233
3060	3140	9405	2191	2495	4533
3061	3168	9410	2200	2500	4536
3062	3170	9433	2208	2515	4571
3063	3261	9570	2210	2516	4605
3064	3266	9571	2214	2520	4631
3068	3301	9800	2215	2560	5410
3069	3350	9810	2221	2570	7503
			2230	2575	7550
			2250	2580	8040
			2270	2590	8160
			2370	2595	8311
			2372	2600	9070
			2383	2620	9210
			2385	2702	9331

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