Behavioral activation system modulation on brain activation during appetitive and aversive stimulus processing

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The reinforcement sensitivity theory (RST) proposed the behavioral activation system (BAS) as a neurobehavioral system that is dependent on dopamine-irrigated structures and that mediates the individual differences in sensitivity and reactivity to appetitive stimuli associated with BAS-related personality traits. Theoretical developments propose that high BAS sensitivity is associated with both enhanced appetitive stimuli processing and the diminished processing of aversive stimuli. The objective of this study was to analyze how individual differences in BAS functioning were associated with brain activation during erotic and aversive picture processing while subjects were involved in a simple goal-directed task. Forty-five male participants took part in this study. The task activation results confirm the activation of the reward and punishment brain-related structures while viewing erotic and aversive pictures, respectively. The SR scores show a positive correlation with activation of the left lateral prefrontal cortex, the mesial prefrontal cortex and the right occipital cortex while viewing erotic pictures, and a negative correlation with the right lateral prefrontal cortex and the left occipital cortex while viewing aversive pictures. In summary, the SR scores modulate the activity of the cortical areas in the prefrontal and the occipital cortices that are proposed to modulate the BAS and the BIS-FFFS.

Keywords: personality; behavioral activation system; individual differences

The Reinforcement Sensitivity Theory (RST; Gray, 1982, 1987; Gray and McNaughton, 2000) predicts that reinforcing stimulus detection and reactivity may vary among individuals depending on the sensitivity of their proposed neurobehavioral systems. One such system is the Behavioral Activation/Approach System (BAS) that was characterized by its sensitivity to reward stimuli to promote the behavioral approach. In this context, sensitivity may be defined as the global reactivity of the neurobiology associated with this motivational system in the presence of rewarding stimuli (Depue and Collins, 1999). The neurobiology of the BAS is related to the commonly identified dopaminergic reward circuitry. It involves the projections from the substantia nigra and the ventral tegmental area (VTA) to the dorsal and ventral striatum, and also their corresponding cortical projections to the prefrontal cortex (Depue and Collins, 1999; Pickering and Gray, 2001; Knutson and Cooper, 2005). Within the prefrontal cortex, the mesial prefrontal cortex (MPFC) and the orbitofrontal cortex (OFC) are proposed to be relevant areas during reward processing (McClure et al., 2004; Knutson and Cooper, 2005; Knutson and Wimmer, 2007). The MPFC seems to play a role in reward outcome evaluation (Knutson et al., 2003; Ramnani et al., 2004), choosing immediate rewards (McClure et al., 2004) and processing secondary emotional stimuli (Kawabata and Zeki, 2004). On the other hand, the OFC has been proposed to be an area for storing the reward value of sensory stimuli (McClure et al., 2004), while its function has been related to the processing of secondary emotional stimuli (Kawabata and Zeki, 2004; Meseguer et al., 2004), processing secondary emotional stimuli (Kawabata and Zeki, 2004; Meseguer et al., 2004), reward prediction (Critchley et al., 2001; Tanaka et al., 2004) and the reward value of stimuli (Montague and Berns, 2002). All these results propose that both the MPFC and OFC are a potential neural basis of individual differences in reward sensitivity.

RST predictions on BAS functioning are straightforward: appetitive motivational stimuli are expected to activate the BAS, and this activation should be greater in those individuals with higher scores in BAS-related trait measures. The first prediction received clear support from neuroimaging studies that have served to clarify the role of the ventral striatum, the dorsal striatum, the OFC and the MPFC in reward processing (see McClure et al., 2004; Knutson and Cooper, 2005, for reviews). However, there is less evidence to support the second prediction. Current studies have
associated BAS-related traits with a reduced striatum volume (Barrós-Loscertales et al., 2006) and with an increased perfusion in these areas (O’Gorman et al., 2006). An fMRI study has shown that individual differences in the BAS-related trait correlated with the brain activation of the mesocorticolimbic structures during the passive viewing of appetizing foods (Beaver et al., 2006). Although this result is consistent with the RST, it would be interesting to replicate it in a larger sample and to use other kinds of appetitive stimuli.

The RST also states that sensitivity to aversive stimuli is mediated by two biobehavioral systems. First, the Fight-Flight-Freeze System (FFFS; Gray and McNaughton, 2000) is activated by all aversive stimuli. Secondly, the Behavioral Inhibition System (BIS; Gray and McNaughton, 2000) does not mediate direct reactions to aversive stimuli, but to those stimuli giving way to a conflict of goals. These two systems are proposed to work as a double system that activates aversive stimuli (Corr, 2004). At the neurobiological level, the reactions to these stimuli are mediated by the hippocampal formation (BIS), the core of Gray’s (1982) neuropsychology of anxiety and by the amygdala that plays a role in both systems (FFFS and BIS; McNaughton and Corr, 2004). The theoretical differentiation of two sensitive systems to aversive (FFFS/BIS) and appetitive (BAS) stimuli leads to a unipolar view that does not involve the BAS during aversive stimulus processing. However, several experimental studies have shown that, under specific circumstances involving goal-directed responses frequently followed by reward, highly sensitive BAS subjects show a diminished processing of aversive secondary cues when compared with individuals with low BAS sensitivity (Newman et al., 1985; Patterson et al., 1987; Ávila and Parcet, 2000, 2001; Ávila, 2001; Ávila and Torrubia, 2004). This view is consistent with the RST since Gray proposed the existence of inhibitory influences between the BAS and the BIS/FFFS as this inhibition is greater when activation of the BAS is stronger (Gray, 1970; Gray and McNaughton, 2000). Other theoretical approaches to Gray’s theory have highlighted that the relevant input to the systems in the RST is not the actual stimuli, but the motivational context or expectancy (Patterson and Newman, 1993; Zinbarg and Mohlman, 1998; Ávila and Torrubia, 2008; Ávila et al., 2008). From this perspective of the RST, it is possible to expect that a BAS-related trait manifestation in appetitive motivational contexts involving goal-directed behavior would not only be directly related to the enhanced activation of BAS-related structures while processing background appetitive stimuli, but also to the diminishing activation of BIS/FFFS-related structures while processing background aversive stimuli.

In order to test both hypotheses, we used a paradigm that our group had previously applied (Meseguer et al., 2007) that showed the activation of BAS and BIS-FFFS during erotic and aversive stimulus processing, respectively. Therefore, in the current study, we investigated individual differences in BAS-sensitivity for brain functional activation during the processing of appetitive and aversive stimuli while subjects were involved in a simple goal-directed task. The task consisted of a continuous letter discrimination task while subjects viewed background pictures of the IAPS in a block-design fashion. Consistent with previous research (see Wager et al., 2003), we found (Meseguer et al., 2007) that appetitive images produced the activation of the left lateral prefrontal and the orbitofrontal cortices, the amygdala and the ventral striatum, as well as the bilateral dorsal striatum and the occipital cortex. On the other hand, background aversive pictures produced the activation of the bilateral middle, dorsolateral and inferior frontal cortices, the bilateral amygdala and the occipital cortex, among other areas (see Meseguer et al., 2007). Thus, appetitive and aversive pictures showed the activation of the dopamine-irrigated BAS structures and FFFS/BIS limbic structures, respectively, and of the prefrontal and occipital areas that are known to modulate the action of both the BAS and the FFFS/BIS structures (Ochsner et al., 2002, 2004; Phan et al., 2005).

Our study was designed to analyze brain-related activation with BAS-sensitivity during emotional/motivational stimulus processing as others have done (Beaver et al., 2006; Hahn et al., 2009), and following our previous research interest [see Ávila et al. (2008) for a review]. In order to measure BAS sensitivity, we used the Sensitivity to Reward (SR) scale, a reliable and valid measure (Zuckerman et al., 1999; Torrubia et al., 2001; Smillie et al., 2008) included in the Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ; Torrubia et al., 2001). The SR scale in the SPSRQ was originally designed to measure Gray’s impulsivity concept by linking the SR to BAS sensitivity. This measure has been suggested to be more closely related to the tendency to approach appetitive situations (Smillie and Jackson, 2006). However, the SR scale shows a similar range of positive correlations with other subscales that measure different hedonic or motivational aspects within the BAS (Caseras et al., 2003). The SR scores were previously shown to be positively related to psychopathy (Newman et al., 2005), alcohol and drug consumption (Genovese and Wallace, 2007; Pardo et al., 2007; Simons and Arens, 2007), ADHD (Mitchell et al., 2006) and also to the presence of a binge eating disorder and Taq1A (Davis et al., 2008). They negatively relate to depression (Pinto-Meza et al., 2006) and age of alcohol use (Pardo et al., 2007). Furthermore, the SR scores have been related to behavioral disinhibition (Ávila, 2001; Ávila and Parcet 2001), better set-shifting (Ávila et al., 2003) and to lower striatum volumes (Barrós-Loscertales et al., 2006).

Within this framework, we proposed different hypotheses in terms of the stimulus’ valence. Consistently with the behavioral results, individuals with higher BAS scores are predicted to show a lower processing of secondary aversive pictures when focusing on a goal-directed task (Patterson and Newman, 1993; Ávila and Torrubia, 2008). In contrast, BAS overactivity is associated with a stronger processing of...
appetitive pictures as found in previous research (Beaver et al., 2006). Our specific hypotheses for the present study are (i) appetitive conditions would activate BAS-related structures (i.e. the striatum, the OFC and the MPFC), and the cortical areas that are known to modulate the action of the BAS (i.e. the lateral prefrontal and occipital cortices), and these activations would correlate positively with the SR scores and (ii) aversive pictures would activate the BIS-FFFS structures (i.e. hippocampal formation and the amygdala), as well as those cortical areas that are known to modulate the action of the BIS-FFFS (i.e. the lateral prefrontal and occipital cortices), and these activations would correlate negatively with the SR scores.

METHODS

Participants

Our participants were 45 healthy male heterosexual university students (mean age = 21.82; age group of 18–27 years). The participants were thoroughly questioned about sexual orientation, and psychiatric, neurological or medical diseases, as well as their use of psychoactive substances. No subject included in the study had a history of Axis I or Axis II disorders, or of neurological or severe medical illnesses. Afterward, they completed the Sensitivity to Reward scale (mean = 11, ranging from 1 to 20) of the Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ; Torrubia et al., 2001). All the participants signed a written informed consent prior to participation.

FMRI paradigm

Stimuli. One hundred and fifty pictures were drawn from the International Affective Picture System (IAPS; Lang et al., 1997). Three categories of 50 stimuli each were used for the experimental trials and were classified into block conditions in terms of their valence for the male population: neutral, appetitive and aversive. The contents of the neutral condition included those images with a valence rate of 5 or scores from the norming data closest to 5. Aversive stimuli were selected from those with a lower valence rate and that were related to mutilations, murdered people, human threat, guns, etc. Finally, all the appetitive stimuli were related to erotic pictures with couples sexually erotic or romantic scenes. These images were selected according to the norming studies conducted in large Spanish samples (Molto et al., 1999; Vila et al., 2001) that yielded comparable results to the norming studies conducted in the USA (Lang et al., 1997). The mean valence ratings from the selected pictures were 2.66 (s.d. = 0.77) for aversive pictures, 7.56 (s.d. = 0.37) for erotic stimuli and 5.20 (s.d. = 0.46) for neutral stimuli. The valence differences between the stimuli selected by conditions were significant between all the conditions \[F(2, 147) = 231, P < 0.001\]. The mean arousal scores were 6.33 (s.d. = 0.99), 6.52 (s.d. = 0.90) and 3.33 (0.74) for aversie, erotic and neutral pictures, respectively. The arousal differences between the stimuli selected by conditions were significant between the neutral and both the erotic and aversive conditions \[F(2, 147) = 1087, P < 0.001\], but not between the two last conditions.

Task. The task was programmed using the Presentation software (Neurobehavioral systems, Inc.). Pictures were displayed inside the scanner using Visuastim goggles (Resonance Technologies, Inc.). The participants were told that they were about to do a letter discrimination task, and that the pictures were used as a background and were not relevant for the task. Each picture was presented for 2.5 s with an ITI of 500 ms. To ensure picture processing, white letters inside a small black square were presented in the middle of the screen that were also superimposed on the picture that had already appeared 500 ms before. The subjects’ task was to slightly raise their dominant hand when a vowel letter appeared (30% of trials, three per block). The pictures were presented in blocks of 30 s in the following order: N, A, E, N, E, A, N, A, E, N, E, A, N, A, E (N = neutral; A = aversive; E = erotic; with a total task duration of 7.5 min).

The experiment was run as a single session. Prior to the scanning session, the participants viewed a reduced version (2 min) of the task with neutral pictures, while they were carefully instructed to perform the letter-discrimination task. After the scanning session, each subject evaluated each image’s valence and arousal on a rating scale of 1–9. The images during the valence and arousal ratings were randomly presented. Three or more continuous pictures of the same emotional condition to be scored were also avoided.

FMRI acquisition

Scanning was performed on a 1.5 T Siemens Avanto (Germany). A gradient-echo T2weighted echo-planar MR sequence was used for fMRI (TE = 50 ms, TR = 3000, DFOV = 150.8 × 150.8, matrix = 64 × 64, voxel size = 3.94 × 3.94 mm, with 5-mm thickness and a 1-mm gap). We acquired 29 interleaved axial slices parallel to the anterior-posterior commissure (AC-PC) plane covering the entire brain. Prior to the functional MR sequence, an anatomical 3D volume was acquired by using a T1-weighted gradient echo pulse sequence (TE = 4.9 ms; TR = 11 ms; FOV = 24 cm; matrix = 256 × 224 × 166; voxel size = 1 × 1 × 1).

Image analyses

Image processing and statistical analyses were carried out using SPM2 (Statistical Parametric Mapping, Wellcome Institute of Cognitive Neurology, London, UK). Anatomical and functional volumes were coregistered and realigned, respectively, to the first functional volume. Next, anatomical images were normalized to the standard stereostatic space (Montreal Neurological Institute template), and their derived normalization parameters were applied to the subjects’ corresponding functional volumes (voxel size was rescaled to 2 mm\(^3\)). Finally, the functional volumes were
smoothed using an 8-mm FWHM Gaussian kernel. In addition, the time series of hemodynamic responses were high-pass filtered (192 s) to eliminate low-frequency components.

Image analyses were performed using a general linear model approach. Time series were modeled at each condition using the hemodynamic response function and its temporal derivative since slice timing was not preprocessed and, besides, it reduces error variance due to a temporal delay variation in different spatial locations. Moreover, movement parameters from the motion correction were included for each subject as regressors of non-interest at this first-level analysis. For the fMRI analyses, all the images of all the subjects were analyzed in a design matrix to generate a random effects’ model in order to allow inferences about the general population.

**Statistical analyses**

First, a categorical analysis was done across subjects for each emotional condition contrast (Erotic > Neutral; Aversive > Neutral). Secondly, whole volume voxel-based multiple regression analyses were performed to study whether the areas of activation for the Erotic > Neutral and Aversive > Neutral condition contrasts showed the hypothesized correlations with the SR scores. The subjects’ ages were included in the equation as a nuisance variable to control age effects. Analyses at the random effects level were presented at a statistical threshold of $P < 0.001$ and an extended threshold of 20 voxels. The local maxima for each analysis were reported in the MNI coordinates.

**RESULTS**

**Behavioral results**

The subjects’ image ratings clearly presented effects of content. The following results were obtained for the valence evaluation ratings for each condition: neutral (mean ± s.d.; 5.20 ± 0.30), aversive (2.42 ± 0.71) and erotic (7.03 ± 0.74), and also for arousal: neutral (4.20 ± 0.097), aversive (6.52 ± 1.02) and erotic (6.04 ± 1.03). When differences among the conditions based on valence and arousal were tested, differences regarding image selection were found. Thus, significant differences were seen among the valence ratings for the images corresponding to each condition: $F(2,147) = 647.2; P < 0.001$. Moreover, significant differences were found between neutral images and both the emotional conditions for the arousal ratings $F(2,147) = 126.27; P < 0.001$, while negative images were rated slightly but were significantly more arousing than pleasant images ($P < 0.001$). On the other hand, performance during the primary discrimination task showed an expected sparse number of errors (mean < 1%) with no differences between the conditions ($P > 0.1$). Subjective valence or arousal ratings were not significantly correlated to the SR scores ($P > 0.1$).

**FMRI results**

**Overall tasks activation.** As expected, erotic picture viewing produced brain activations in the neurobiological substrates of the BAS (see Table 1, Figure 1), which involved structures in the striatum and the limbic cortex, such as the dorsal (caudate) and ventral (nucleus accumbens) striatum, the amygdala and the anterior cingulate. Additional activations were located in the medial, bilateral lateral and medial prefrontal cortices, the precentral gyrus and the supplementary motor area (see Table 1).

Aversive picture viewing produced activation in the brain areas of the limbic system and the frontal lobe, among others (see Table 2, Figure 2). Thus, there was an activation of limbic and paralimbic structures like the posterior cingulate, the hippocampus and the bilateral amygdala. Prefrontal activations were located bilaterally in the lateral and inferior parts, and in the superior medial prefrontal cortex.

**Relationship between sensitivity to reward and emotional brain activation.** As expected, the SR scores showed a positive correlation (see Table 3, Figure 3) with the MPFC during erotic stimulus processing. However, they did not show a positive correlation with the activation of either the striatum or the OFC, contrary to our hypotheses. The left lateral inferior frontal gyrus and the precuneus also positively correlated with SR during the same condition. Although not already hypothesized a priori, a negative correlation between the SR scores and activation in the sub-gyral portion of the left superior frontal gyrus was observed during erotic stimulus processing.

On the other hand, our second hypothesis was not fully confirmed as no negative correlation was found between the SR scores and the BIS- and FFFS-related structures during aversive picture viewing. However, negative correlations were obtained between the SR scores and activation in the areas that modulate the action of BIS-FFFS structures, like the left occipital cortex and the right lateral prefrontal cortex (see Table 3, Figure 4). SR-correlated activation during aversive stimulus viewing was not hypothesized and a whole-brain voxel-wise correlation only reported a significant related activation in the right claustrum. Our overall results are shown in Table 3.

**DISCUSSION**

Behavioral correlates of the SR scale have consistently shown that individuals with higher scores on this scale had better appetitive learning and were more prone to risky behavior (Zuckerman, 1999; Corr, 2004; Ávila and Torrubia, 2008). Specifically, BAS sensitivity has been associated with stronger sexual arousability and excitability (Aluja and Torrubia, 2004; Carpenter et al., 2008). Different studies have also shown that BAS sensitivity is associated with a diminished processing of secondary aversive stimuli (see Ávila and Torrubia, 2008; Patterson and Newman, 1993, for reviews). This study has been designed to investigate the neural basis...
of these processes using a simple cognitive task in which emotional stimuli were presented as a background.

We studied the processing of appetitive (erotic) and aversive stimuli presented as being secondary to a simple goal-directed task, which could affect the reported activations (Lane et al., 1997; Hariri et al., 2000; Lange et al., 2003; Phan et al., 2003; Taylor et al., 2003; Northoff et al., 2004). Following previous proposals (Patterson and Newman, 1993; Avila, 2001), our interest was to investigate BAS-related differences in the processing of emotional stimuli when individuals were involved in goal-directed behavior. At the same time, however, our paradigm was designed to ensure emotional stimulus perception. That is, the objective of the experiment was to present emotional pictures as a background to a main cognitive task, and to also ensure that the emotional processing was really done. This aim was achieved since the brain structures of the BAS and the BIS-FFFS were activated for the whole sample the first time we applied this paradigm in a reduced sample (Meseguer et al., 2003, 2004; Mouras et al., 2003; Meseguer et al., 2002, 2004; Phan et al., 2002, 2004; Avila, 2001).

As expected, brain activations during the erotic picture condition in all the participants activated several structures related to the BAS, such as the substantia nigra, the caudate, the putamen, the nucleus accumbens, the MPFC and the OFC. Meanwhile, the aversive picture condition led to the activation of areas within the limbic system, such as the amygdala, the hippocampus and the posterior and anterior cingulates. Furthermore, other areas in the frontal lobes were activated during the erotic and aversive picture conditions, and are summarized in Tables 1 and 2. These results agree with previous studies using erotic and aversive pictures (see Phan et al., 2002, 2004; Mouras et al., 2003; Meseguer et al., 2007; Sabatinelli et al., 2007).

Our first hypothesis, which relates the SR scores with activation in the BAS structures, has been partially supported by the results as the SR scores positively correlated with activation in the MPFC, but not in the striatum and the OFC. Recent research has specifically related the pleasantness rating, while the passive viewing of erotic pictures of the IAPS with the activation in the nucleus accumbens and the MPFC (Sabatinelli et al., 2007). Knutson and Cooper (2005) related the MPFC to the reward evaluation processes which, in the case of erotic pictures, may relate to image post-processing and could impel action toward reward. Even though the erotic pictures activated the striatum for the overall study sample, this activation did not correlate with the SR scores. These data contrasted with a recently published study involving 12 participants that analyzed brain activation while passively viewing pictures of appetizing and bland foods (Beaver et al., 2006). Appetizing foods, unlike bland ones, activated the ventral striatum, the orbitofrontal cortex, the amygdala and the ventral tegmental areas, and these activations correlated positively with the BAS scores. However, there was a clear difference between both studies as all the subjects rated the erotic pictures presented in our study as highly pleasant (mean pleasantness was

<table>
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<th>MNI coordinates</th>
<th>Z score</th>
<th>k-voxels</th>
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<td>Cerebellum</td>
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<td>40, -60, -22 -36, -76, -22</td>
<td>7.21 6.38</td>
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Table 1 Brain activation in the proposed neural basis of the BAS and the other active structures during erotic stimulus processing (P < 0.001, uncorrected)

R: right; L: left; B-cluster extended bilaterally within the same structure, but local maxima located at the reported coordinate.
7.03 over 9), which did not come over as clearly for all foods (mean pleasantness was 4.75 over 7). If we consider the means and standard deviations of the ratings of pictures provided in Beaver’s study, we could state that pizzas, or indeed chocolate, may be perceived as appetizing food for most participants, but may represent neutral stimuli for some participants. Thus, the differential activations found in Beaver’s study may reflect differences in sensitivity to stimuli in terms of how they were perceived, whereas the results in our study reflect the brain differences in responsiveness to stimuli perceived as pleasant by all the participants. Otherwise, the relationship between the BAS scores and activation in the striatum may reflect different sensitivity to appetitive stimuli, whereas the correlation between the BAS scores and MPFC activation could relate more to the post-processing of these stimuli. In fact, Hahn et al. (2009) showed the positive association between the SR scores and activation in the OFC and the ventral striatum during reward anticipation. The analysis based on regions-of-interest (ROIs) of this study (Hahn et al., 2009) did not consider the MPFC, probably because it has shown a differential involvement of this area in reward outcome evaluation compared to anticipation (Knutson et al., 2003). Importantly, BAS-sensitivity, as measured by the SR scale included in the SPSRQ (Torrubia et al., 2001), has been related to the activation of the subcortical BAS-related structures and the OFC in the frontal lobe during reward anticipation. Otherwise, the fact that erotic pictures may restrict the effects of studying BAS traits correlation with the activation of BAS-related structures should also be considered. Further research should be done to confirm these possibilities.

The results of this study do not fully confirm our second hypothesis. During the passive viewing of aversive pictures, the SR scores were not associated with the differences activation in the BIS- or FFFS-related structures. Although the processing of these pictures activated the FFFS/BIS structures (see Table 2), the SR scores did not modulate their activity. Our theoretical model emphasizes the fact that BAS activity was related to the diminished processing of secondary aversive stimuli (Patterson and Newman, 1993; Ávila et al., 2008). Our task presented emotional stimuli as a...
background. However, it is likely that the strong activation obtained for all the participants indicates that these stimuli were not secondary. The fact that emotional stimuli were equally detected by all the subjects may transfer the effect of individual differences to the appraisal processes, which are typically involved in emotions and are probably more dependent on individual differences. Then, personality differences may affect appraisal more than the detection of emotions. This means that the diminished processing of secondary aversive stimuli would depend more on other cortical areas than those associated with both the FFFS and BIS. However, this interpretation may be speculative and has not been directly extracted from the theory. Thus, further research is needed whose starting point may be based on studies already done on clinical samples (Johnstone et al., 2007).

Consistent with this interpretation, the present study has found relevant correlations with other neocortical emotional areas, i.e. the occipital cortex and the lateral prefrontal cortex. Increased activations in the occipital cortex are common when contrasting emotional and neutral stimuli, and have been interpreted as a reflection of the backward connections from the amygdala and the striatum to the visual cortex in order to reactivate the processing of emotionally relevant stimuli (Pickering and Gray, 2001; Bradley et al., 2003; Sabatinelli et al., 2004). Our results show that SR correlated positively with activation in the right occipital cortex while viewing erotic slides, and that it correlated negatively with activation in the left occipital cortex while viewing aversive slides. Following Bradley et al. (2003), these activations were related to motivated attention, which facilitates the perceptual processing of relevant stimuli. In this sense, the processing of appetitive stimuli and the diminishing attention toward aversive stimuli would be enhanced in individuals with greater BAS activity.

This effect was also found for the results in the lateral prefrontal cortex. The SR scores positively correlated with activation in the left lateral prefrontal cortex while viewing erotic pictures, and negatively correlated with activation of the right lateral prefrontal cortex while viewing aversive pictures. The prefrontal cortex is thought to play a crucial role in the top–down regulation of the basal structures in the appraisal and reappraisal for emotion regulation when emotional stimuli are encountered. The regulation of positive stimuli has been shown to be left-lateralized (Kim and Hamann, 2007), and right-lateralized for that of negative stimuli in normal subjects (Ochsner et al., 2004; Kim and Hamann, 2007). These results agree with previous proposals of brain-related emotion asymmetry, especially in the lateral prefrontal cortex, which has been specialized for different types of emotion where the left hemisphere and the right hemisphere are predominant for positive emotions and negative emotions, respectively (Davidson, 1992, 1995).

Neuroimaging research has partially confirmed this model

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### Table 2

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<thead>
<tr>
<th>Area</th>
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<th>MNI coordinates</th>
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<tr>
<td>Amygdala</td>
<td>L</td>
<td>-28, 2, -18</td>
<td>4.12</td>
<td>32</td>
</tr>
<tr>
<td>R</td>
<td>28, -8, -14</td>
<td>3.94</td>
<td>51</td>
<td></td>
</tr>
<tr>
<td>Hippocampus</td>
<td>R</td>
<td>30, -8, -16</td>
<td>4.21</td>
<td>34</td>
</tr>
<tr>
<td>L</td>
<td>-24, -18, -12</td>
<td>3.55</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Thalamus</td>
<td>B</td>
<td>-2, -14, 0</td>
<td>4.18</td>
<td>67</td>
</tr>
<tr>
<td>R</td>
<td>18, -10, 18</td>
<td>4.69</td>
<td>49</td>
<td></td>
</tr>
<tr>
<td>Prefrontal lobe</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle/inferior frontal cortex</td>
<td>R</td>
<td>42, 16, 24</td>
<td>6.75</td>
<td>1428</td>
</tr>
<tr>
<td>(frontal operculum)</td>
<td>L</td>
<td>-34, -4, 50</td>
<td>6.96</td>
<td>861</td>
</tr>
<tr>
<td>Medial/superior frontal cortex</td>
<td>B</td>
<td>-2, 64, 24</td>
<td>6.21</td>
<td>887</td>
</tr>
<tr>
<td>Superior medial prefrontal cortex</td>
<td>B</td>
<td>-2, 64, 24</td>
<td>6.21</td>
<td>877</td>
</tr>
<tr>
<td>Supplementary motor area/medial</td>
<td>R</td>
<td>18, -10, 52</td>
<td>4.79</td>
<td>164</td>
</tr>
<tr>
<td>frontal cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inferior frontal gyrus</td>
<td>L</td>
<td>-30, 28, 6</td>
<td>4.44</td>
<td>100</td>
</tr>
<tr>
<td>Central prefrontal cortex</td>
<td>B</td>
<td>4, 8, 64</td>
<td>3.89</td>
<td>69</td>
</tr>
<tr>
<td>Inferior/superior Parietal lobe</td>
<td>L</td>
<td>-30, -56, 54</td>
<td>5.07</td>
<td>184</td>
</tr>
<tr>
<td>Occipital cortex</td>
<td>L</td>
<td>-2, -88, 4</td>
<td>Inf (T = 13.53)</td>
<td>6953</td>
</tr>
<tr>
<td>R</td>
<td>2, -86, 2</td>
<td>Inf (T = 14.55)</td>
<td>7186</td>
<td></td>
</tr>
<tr>
<td>Cerebellum</td>
<td>L</td>
<td>-38, -58, -22</td>
<td>6.63</td>
<td>2294</td>
</tr>
<tr>
<td>R</td>
<td>36, -52, -24</td>
<td>7.20</td>
<td>2753</td>
<td></td>
</tr>
</tbody>
</table>

R: right; L: left; B-cluster extended bilaterally within the same structure, but local maxima located at reported coordinate. Inf: undefined Z-value tends to infinite, but t-score reported.

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especially if arousal is controlled (Canli et al., 1998). The present study shows the possible hypothesized role of personality differences in the modulation of these processes, which other authors have termed ‘affective style’ (Davidson, 1992, 1998, Davidson and Irwin, 1999).

In short, individual differences in BAS activity were associated with different patterns of brain activation during...
erotic and aversive stimulus processing. Since the task was
designed to ensure emotional picture processing, these BAS
differences were more related to appraisal of emotion than to
areas related to the detection of emotion. In other words, the
brain differences associated with BAS scores relate more to
the brain areas that modulate the action of the BAS and the
FFFS-BIS, that is, the occipital cortex and the lateral pre-
frontal cortex. Future research will determine whether per-
sonality differences modulate the action of the BAS and
FFFS-BIS structures when emotional stimuli are presented
c covertly or when the goal-directed task is more complex.

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