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Linking personality and brain anatomy: a structural MRI approach to Reinforcement Sensitivity Theory

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Abstract

Reinforcement Sensitivity Theory (RST) proposes a widely used taxonomy of human personality linked to individual differences at both behavioral and neuropsychological levels that describe a predisposition to psychopathology. However, the body of RST research was based on animal findings, and little is known about their anatomical correspondence in humans. Here we set out to investigate MRI structural correlates (i.e. voxel-based morphometry) of the main personality dimensions proposed by the RST in a group of 400 healthy young adults who completed the Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ). Sensitivity to punishment scores correlated positively with the gray matter volume in the amygdala, whereas sensitivity to reward scores correlated negatively with the volume in the left lateral and medial prefrontal cortex. Moreover, a negative relationship was found between the striatal volume and the reward sensitivity trait, but only for male participants. The present results support the neuropsychological basis of the RST by linking punishment and reward sensitivity to anatomical differences in limbic and frontostriatal regions, respectively. These results are interpreted based on previous literature related to externalizing and internalizing disorders, and they highlight the possible role of SPSRQ as a measure of proneness to these disorders.

Key words: personality; voxel-based morphometry; limbic system; frontostriatal circuit; psychopathological predisposition

Introduction

The role of specific brain systems in personality development has long been hypothesized (i.e. Pavlov, 1941; Eysenck, 1960). One of the most influential models proposed in the past 50 years is Reinforcement Sensitivity Theory (RST; Gray, 1970; Gray, 1982; Gray and McNaughton, 2000; Pickering and Gray, 2001; Corr, 2008; McNaughton and Corr, 2008; Corr and McNaughton, 2012), which proposes a detailed neuropsychological description of the neural circuits underlying personality and psychopathological predisposition. The current version of the RST proposes three different systems responsible for taking control of behavior in the presence of emotional stimuli. The fight-flight-freeze system (FFFS) is neurally represented by an interconnected circuit comprising the amygdala (fear perception) and the medial hypothalamus and periaqueductal gray matter (behavioral response), and it mediates reactions to aversive stimuli, promoting defensive avoidance behavior. The behavioral inhibition system (BIS) has traditionally been related to the septo-hippocampal system, although in the last revision of the theory

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(Gray and McNaughton, 2000; McNaughton and Corr, 2004), the amygdala was also included, and it responds specifically to goal conflict (i.e. approach–approach, approach–avoidance or avoidance–avoidance) to initiate defensive approach behavior. Finally, the behavioral approach system (BAS) is dependent on the frontostriatal system, mainly the ventral [nucleus accumbens (NAcc)] and dorsal (caudate nucleus) striatum and its dopaminergic connections to the prefrontal lobe, and it mediates reactions to appetitive stimuli, promoting approach.

Although the description of the three neural systems should involve three different personality dimensions, the currently most accepted RST framework solution shows the existence of two general traits (Perkins *et al*., 2007). The first is punishment sensitivity, which depends on the combination of the FFFS and BIS systems in a global fear/anxiety dimension, and the second is reward sensitivity, which is associated with the BAS. These two dimensions could be assessed with specific measures such as the BIS/BAS scales, the SPSRQ or the combination of the extraversion and neuroticism dimensions of the EPQ (Torrubia *et al*., 2008). Overall, the different punishment sensitivity measures typically show stronger correlations with each other (and with anxiety and fear measures), whereas the reward sensitivity measures only have moderate relationships with each other (Caseras *et al*., 2003).

Predictions of RST are very precise in the field of learning and conditioning. The theory postulates that individual differences in the activity of the FFFS/BIS and the BAS would be associated with (i) a different capacity to detect aversive and appetitive stimuli, respectively and (ii) a different probability and intensity of emitting defensive and approach responses in the presence of these stimuli (see Ávila and Torrubia, 2008; Corr, 2008, for reviews). Different studies have confirmed that individuals with higher scores on measures of FFFS/BIS activity have better learning in the presence of aversive conditioned stimuli and a greater probability of behavioral inhibition and better learning of the contingencies in aversive contexts. Similarly, individuals with higher scores on BAS measures have better learning and make more intense and probable approach responses in appetitive contexts.

RST has acquired great relevance in relating individual differences in the functioning of the FFFS, BIS, and BAS to the vulnerability to different psychopathologies. The RST formulation has related high FFFS activity to panic and phobic disorders (Barlow, 1988) and high BIS activity to generalized anxiety disorders (Maack *et al*., 2012). At the other extreme, evidence exists relating low BIS activity to psychopathy in adults (Fowles, 1980; Newman *et al*., 2005) and to the presence of callous/unemotional traits in children (Quay, 1988; Blair, 2003). In addition, some proposals relate high BAS activity to disinhibitory disorders such as attention-deficit/hyperactivity disorder (ADHD; Newman and Wallace, 1993; Nigg, 2001; Mitchell and Nelson-Gray, 2006) or drug addiction (Sher and Trull, 1994; Franken *et al*., 2006). At the opposite extreme, some reports have related depressive disorders to lower BAS activity (Pinto-Meza *et al*., 2006; Kimbrel *et al*., 2007). Overall, all these data link punishment sensitivity to the presence of internalizing disorders and reward sensitivity to externalizing disorders (Bijttebier *et al*., 2009; Slobodskaya, 2016).

Although the detailed description of the brain circuits involved in these systems is one of the strongest points of the theory, this description is based on animal studies, and less research has been dedicated to verifying it in humans. The first attempt to test the neuropsychological basis of RST in the human brain was carried out by Barrós-Loscertales *et al*. (2006b), who reported a negative association between BAS activity and gray matter (GM) volume in the striatum and prefrontal cortex. Since then, only one study conducted in a large sample has provided new evidence relating BAS measures and brain anatomy (Holmes *et al*., 2016). In this study, a composite measure of novelty seeking was associated with reduced cortical thickness in brain areas related to cognitive control, such as the dorsal anterior cingulate cortex, the lateral prefrontal cortex and the supramarginal gyrus. Consistent with these anatomical studies, a DTI study that used the TCI of Cloninger showed that the two scales related to reward sensitivity were associated with different connectivity measures of the striatum (Lei *et al*., 2014). Specifically, the novelty-seeking scale was related to stronger connectivity between the striatum and the hippocampus/amygdala, whereas the reward dependence scale was related to stronger connectivity between the striatum and different medial and lateral areas of the prefrontal cortex. On the other hand, Barrós-Loscertales *et al*. (2006a) first linked BIS activity to higher GM volume in the amygdala and the hippocampus. However, these results have only been partially replicated. Previous studies only found associations with BIS measures in the amygdala (Iidaka *et al*., 2006) or the hippocampus (Cherbuin *et al*., 2008; Levita *et al*., 2014), whereas other studies found a relationship with both structures (Holmes *et al*., 2012). Thus, these previous studies have produced different results, and so further research is required to address this controversy.

Thus, the aim of the current study was to investigate the brain regions associated with the personality dimensions depicted in the RST. Specifically, our objective was to extend our previous reports (Barrós-Loscertales *et al*., 2006a; Barrós-Loscertales *et al*., 2006b) in a larger sample consisting of males and females. Additionally, we also conducted further analyses in order to investigate possible differences by sex. Based on previous studies, we hypothesized that an overactive BAS would be associated with lower GM volume in prefrontal and striatal areas, whereas an overactive FFFS/BIS would be linked to greater GM volume in the amygdala and hippocampus. Because personality traits in their extreme forms are considered vulnerability factors for personality and mood disorders (Gray and McNaughton, 2000; Bijttebier *et al*., 2009; Corr and McNaughton, 2015), greater knowledge about the underlying neural correlates of personality should also contribute to better understand these clinical conditions in unmedicated participants. Therefore, our reports would add new evidence to the RST model as a valid neuropsychological framework to study the proneness to psychopathological disorders in humans.

Materials and methods

Participants

Four hundred participants (233 males, 167 females; mean age 23.08, s.d. 5.32; range 18–44 years; years of education 14.46, s.d. 2.22) were studied after giving their prior informed consent. All the participants were recruited from a community sample through local advertisements and word of mouth. Most of them were undergraduate students (94.75%), given that our research group is integrated in a university campus. Participants had no history of neurological or psychiatric disorders, major medical illnesses or traumatic brain injury with loss of consciousness. Additionally, all participants were right-handed, according to the Edinburgh Handedness Inventory (Oldfield, 1971; Bryden, 1977).

The experiment was approved by the Ethical Committee of the University Jaume I (Spain).

Personality measurement

The Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ; Torrubia *et al*., 2001) was used to assess individual differences in personality. The SPSRQ provides two subscales; sensitivity to reward (SR) and sensitivity to punishment (SP), in order to evaluate the activity of the BAS and BIS/FFFS subsystems, respectively.

MRI acquisition and voxel-based morphometry

Images were all acquired with the same 1.5-T Siemens Avanto scanner (Erlangen, Germany). A high-resolution structural T1-weighted MPRAGE sequence was acquired (TE, 3.8 ms; TR, 2200 ms; flip angle, 15°; matrix, 256 × 256 × 160 mm; voxel size, 1 mm^3). Voxel-based morphometry (VBM) was performed with the VBM8 toolbox (version r445; http://dbm.neuro.uni-jena.de/vbm/) for the SPM8 package (version 6313; Wellcome Department of Imaging Neuroscience, London, UK). We performed the standard pre-processing procedure suggested in the VBM8 manual, which included (i) segmentation of the images into GM, white matter and cerebrospinal fluid, (ii) registration to a standard template provided by the International Consortium of Brain Mapping, (iii) DARTEL normalization of the GM segments to the MNI template and (iv) modulation by non-linear components derived from spatial normalization. After the pre-processing, a data quality check was carried out by analyzing the sample homogeneity using covariance. Ten participants showed a covariance of at least two standard deviations below the mean; however, only two participants were identified as outliers (poor data quality) and excluded from the final sample. Finally, images were spatially smoothed using an 8 mm FWHM Gaussian kernel.

Statistical analysis

Voxel-wise regression analyses were performed by taking GM volume as the dependent variable and scores on the SR and SP scales as covariates of interest within the framework of the general linear model in SPM8. We also added age, sex and years of education as nuisance covariates in order to control possible effects on brain volume. In addition, the absolute threshold masking was set at 0.20 to ensure that we only selected GM voxels. Finally, our results at the cluster level were also corrected for non-stationary smoothing.

The statistical significance threshold for the whole-brain analysis was determined following recent recommendations by Chen *et al*. (2019). Therefore, we established a voxel-level primary threshold of $P < 0.0005$ uncorrected, whereas we thresholded the obtained results at $P < 0.025$ FWE corrected at the cluster level. In addition, we also investigated focal VBM differences in small a priori regions of interest (ROIs). Based on the key regions involved in the BAS, BIS and FFFS subsystems, these ROIs were located in reward-related areas (NAcc and caudate) for the SR analyses and in punishment-related areas (amygdala and hippocampus) for the SP analyses. All the ROIs were defined for each hemisphere using the atlas provided by Neuromorphometrics, Inc. (http://Neuromorphometrics.com/) under academic subscription. Furthermore, as our previous study found differences in the anterior hippocampus (Barrós-Loscertales *et al*., 2006a), and this region has previously been related to anxiety-related behaviors (Bannerman *et al*., 2004; Fanselow and Dong, 2010), we decided to include this area as a ROI for the SP analysis. For this purpose, the left and right hippocampus were traced manually on contiguous coronal slices in an MNI template following the guidelines of Watson *et al*. (1992) and Hasboun *et al*. (1996). This segmentation was carried out by an expert tracer using the MRIcron software. Moreover, because the amygdala and the anterior segment of the hippocampus are adjacent structures, we applied an exclusive mask (the amygdala ROI) to the anterior hippocampal ROI in order to remove all the possible voxels contained in the anterior hippocampus that could be overlapping voxels in the amygdala. All the ROIs included in the SR and SP analyses are shown in Figure 1. The modulated GM volumes (without smoothing) were obtained for each ROI via a MATLAB script (http://www0.cs.ucl.ac.uk/staff/g.ridgway/vbm/get_totals.m), also applying an absolute threshold masking of 0.20. After that, partial correlations (one tailed based on a priori hypotheses) were performed using IBM SPSS Statistics 25 (Armonk, NY: IBM Corp.), including GM volumes and scores on the SR and SP scales as variables, controlling for age, sex and years of education. Because we used four ROIs for the SR (left and right NAcc and caudate) and SP (left and right amygdala and anterior hippocampus) analyses, the statistical threshold for multiple comparisons ($P < 0.05$ FWE) was set at $P < 0.0125$. Finally, because in our previous studies (Barrós-Loscertales *et al*., 2006a; Barrós-Loscertales *et al*., 2006b) the sample consisted only of male participants, we decided to conduct a new set of analyses in order to investigate possible sex differences. Thus, we carried out an omnibus model in SPM8 by calculating an interaction term with sex (including age and years of education as nuisance covariates). At the ROI level, as the analyses were performed in SPSS, sex differences were computed by analyzing the difference between the correlation coefficients using Fisher's z test.

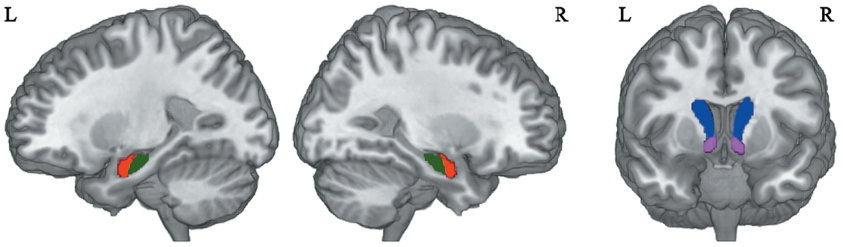

Fig. 1. ROIs included in the SR and SP analyses. The anterior hippocampus corresponds to a previous manual segmentation. Red: amygdala; green: anterior hippocampus; blue: caudate; violet: nucleus accumbens.

Table 1. Personality, demographic and volumetric data by sex

	Whole sample (N = 400)	Males (N = 233)	Females (N = 167)	t-value Males vs Females	P-value
Age	23.08 (5.32)	24.54 (6.07)	21.05 (3.04)	7.56	0.000**
	18–44	*18–44*	*18–42*		
Years of education	14.46 (2.22)	14.30 (2.41)	14.69 (1.91)	−1.85	0.066
	8–20	*8–20*	*8–19*		
SR	10.54 (4.68)	11.73 (4.80)	8.88 (3.98)	6.49	0.000**
	1–23	*3–23*	*1–20*		
SP	9.67 (5.24)	8.70 (5.01)	11.02 (5.27)	−4.46	0.000**
	0–23	*0–22*	*1–23*		
Left NAcc	0.51 (0.06)	0.50 (0.06)	0.53 (0.06)	−5.39	0.000**
	0.28–0.71	*0.28–0.67*	*0.39–0.71*		
Right NAcc	0.48 (0.06)	0.46 (0.05)	0.50 (0.05)	−7.07	0.000**
	0.26–0.64	*0.26–0.58*	*0.38–0.64*		
Left caudate	3.20 (0.39)	3.09 (0.37)	3.36 (0.36)	−7.51	0.000**
	1.86–4.27	*1.86–4.21*	*2.43–4.27*		
Right caudate	3.04 (0.40)	2.93 (0.38)	3.20 (0.36)	−7.33	0.000**
	1.50–4.13	*1.50–3.91*	*2.40–4.13*		
Left amygdala	1.04 (0.09)	1.03 (0.08)	1.05 (0.10)	−2.01	0.046*
	0.79–1.33	*0.79–1.25*	*0.81–1.33*		
Right amygdala	1.00 (0.09)	0.99 (0.08)	1.02 (0.09)	−3.56	0.000**
	0.78–1.27	*0.78–1.27*	*0.81–1.23*		
Left anterior hippocampus	1.13 (0.10)	1.12 (0.09)	1.14 (0.10)	−1.65	0.099
	0.83–1.45	*0.85–1.42*	*0.83–1.45*		
Right anterior hippocampus	1.29 (0.11)	1.28 (0.11)	1.31 (0.11)	−2.67	0.008**
	1.00–1.64	*1.00–1.64*	*1.06–1.59*		

** $P < 0.01$, * $P < 0.05$ (two-tailed *t*-tests). Volumetric data are reported in milliliters. The three first columns show mean, s.d. (in parentheses) and range (in italics) of each variable. NAcc: nucleus accumbens.

Results

Personality scores

Participants' mean score on the SR scale was 10.54 (s.d. 4.68), and the internal consistency was good (Cronbach's $\alpha = 0.81$). The mean score on the SP scale was 9.67 (s.d. 5.24), and its internal consistency was also high (Cronbach's $\alpha = 0.85$). Furthermore, SR and SP did not show any relationship with each other ($r = -0.05$; $P = 0.371$). Personality, demographic and raw volume data for males and females are summarized in Table 1.

Sensitivity to reward

The voxel-wise GM analysis for the whole sample showed a negative correlation between SR scores and GM volume in frontal and temporal areas (see Table 2 for details). The most relevant reductions were located in the medial prefrontal cortex (from dorsomedial to ventromedial regions and also including the dorsal anterior cingulate cortex) and the left lateral prefrontal cortex, with a cluster extending from the middle to the inferior frontal cortex (Figure 2A and Figure 3). No positive correlations were found between SR scores and GM volume. Moreover, the omnibus model did not reveal any significant differences by sex.

The partial correlations between SR scores and striatal ROI volumes appear on Table 3. Contrary to our hypothesis, the expected negative relationship between SR scores and striatum volume was only significant in males for the left NAcc and caudate volumes. Results of Fisher's z tests comparing the correlation coefficients between males and females reached significance only for the left NAcc ($z = -1.83$; $P = 0.034$; Figure 2B).

Sensitivity to punishment

The voxel-wise GM analyses for the whole sample did not show any significant negative or positive correlations with the SP scale. Similarly, the omnibus model did not reveal any significant differences by sex.

At the ROI level, we observed a significant positive correlation between the scores on the SP scale and the GM volume in the left amygdala ($r = 0.15$; $P = 0.002$, FWE corrected; Figure 2C). Moreover, when analyzing the correlation coefficients in males and females, only the left amygdala showed a significant, positive association in males (Table 4). However, Fisher's z test did not show any significant differences between males and females.

Discussion

In the present study, we aimed to reveal the neuroanatomical anatomical base underlying individual differences in the main personality dimensions depicted by the RST in a sample of 400 healthy participants studied with the same MRI scanner. Consistent with previous research, our results showed that scores on the SP scale were positively associated with the GM volume in the left amygdala. Regarding SR, we found a direct negative relationship between reward sensitivity and the volume of the left lateral and medial prefrontal cortex. Furthermore, we have replicated our previous results relating this dimension to the striatum volume (Barrós-Loscertales *et al.*, 2006b), although this result was not found in females. Thus, the main personality dimensions derived from the RST that measure vulnerability to the main psychopathological entities have been associated with differences in GM volume in target emotional brain areas. These

Table 2. Brain regions showing a negative correlation between SR scores and the voxel-wise GM volume

Region	Hemisphere	Coordinates MNI x, y, z	t-scores	k-voxels	P-value
Inferior frontal (pars opercularis)	L	−56, 8, 21	4.87	1731	0.0004
Middle frontal	L	−30, 45, 28	4.84		
Inferior frontal (pars triangularis)	L	−45, 44, 13	4.43		
Precentral	L	−54, −3, 30	4.23		
Inferior frontal (pars orbitalis)	L	−47, 20, −6	3.86		
Anterior cingulate	L	−2, 50, 1	4.37	1489	0.0008
Medial superior frontal	L	−6, 62, 15	4.17		
Medial superior frontal	R	3, 57, 15	3.95		
Middle temporal	L	−51, −30, 4	4.45	851	0.008
Superior temporal	L	−59, −15, 6	4.15		
Insula	L	−38, −16, −2	3.65		

R: right; L: left; $P < 0.05$ FWE cluster-level corrected (two-tailed tests).

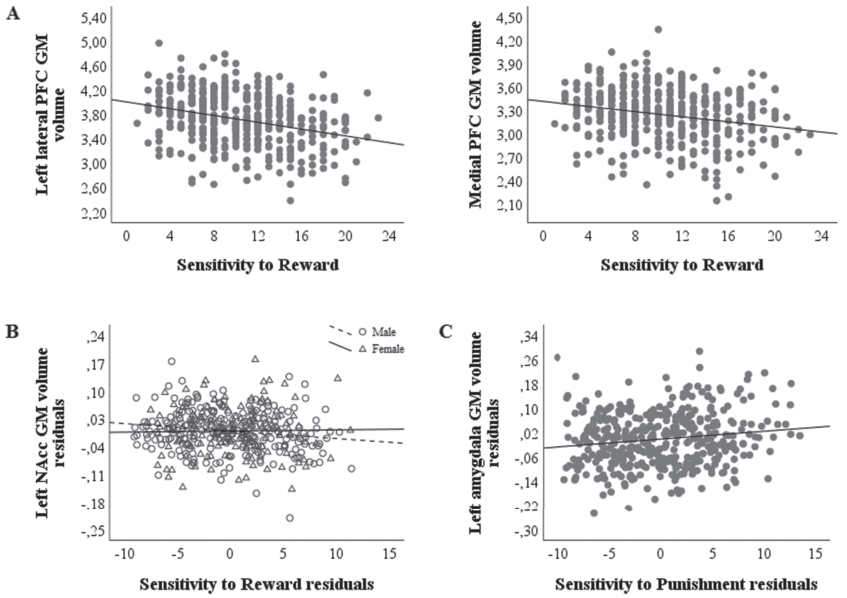

Fig. 2. A) Correlation between SR scores and GM volume in the left lateral and medial prefrontal clusters derived from the voxel-wise multiple regression analysis in the whole sample (controlling for age, sex and years of education). B) Partial correlations for males and females showing a GM reduction in the left NAcc in males with high SR in comparison with females (after regressing out age and years of education). C) Partial correlation of the left amygdala GM volume with SP scores in the whole sample (after regressing out age, sex and years of education). NAcc, nucleus accumbens; PFC, prefrontal cortex.

results reinforce the usefulness of the SPSRQ in measuring individual differences in the neuropsychological systems depicted by the RST.

Our results are consistent with the RST and previous reports relating a greater GM volume in the amygdala to the scores on the SP scale from the SPSRQ (Barrós-Loscertales *et al.*, 2006a), on the Harm Avoidance scale (Iidaka *et al.*, 2006) and on Neuroticism (Koelsch *et al.*, 2013). Furthermore, in a study conducted in a large sample (Holmes *et al.*, 2012), the authors reported a GM increase in the amygdala associated with scores on a customized scale based on behavioral inhibition and trait negative affect measures. Studies in healthy children have also demonstrated that inhibited or anxious personalities are linked to greater amygdala volume (Clauss *et al.*, 2014; Qin *et al.*, 2014). When studying pathological populations, enlargement of the amygdala has been reported in adults, children and adolescents with Generalized Anxiety Disorder (De Bellis *et al.*, 2000; Etkin *et al.*, 2009; Schienle *et al.*, 2011) and in adults with depression (Bremner *et al.*, 2000; Tebartz van Elst *et al.*, 2000; Lange and Irle, 2004; van Eijndhoven *et al.*, 2009; Vassilopoulou *et al.*, 2013), although results with depressive patients can vary depending on medication effects (Hamilton *et al.*, 2008). Moreover, the amygdala structure has also been associated with certain genetic alleles in panic disorder (Smoller *et al.*, 2014). At the opposite pole, the presence of psychopathic or callous/unemotional traits in children and adult populations has been consistently associated with lower amygdala volume (Yang *et al.*, 2009; Pardini *et al.*, 2014; Vieira *et al.*, 2015; Aghajani *et al.*, 2016; Coccaro *et al.*, 2016; Cohn *et al.*, 2016), which has also been associated with conduct problems in youths (Rogers and De Brito, 2016). Among the different factors that contribute to modulating the amygdala volume, previous studies have reported the influence of genetic factors (Smoller *et al.*, 2014) and early experiences with adverse situations

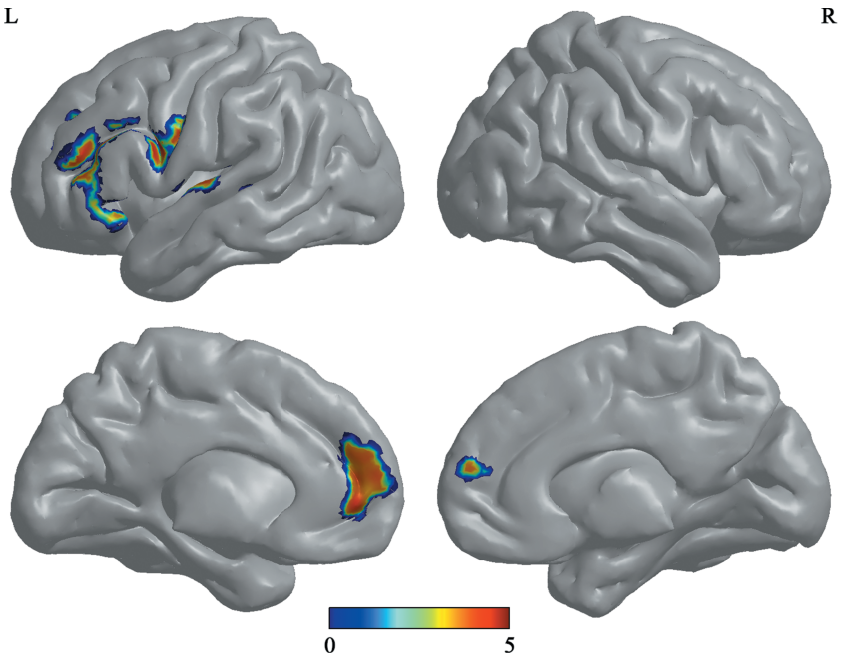

Fig. 3. Negative correlation between scores on the SR scale and GM volume in the left lateral and medial prefrontal cortex and superior temporal regions ($P < 0.05$ FWE corrected, two-tailed). Bar color represents *t*-values. L, left; R, right.

(Howell *et al*., 2014). Regarding the hippocampal volume, contrary to our expectations, the expected positive association between SP scores and GM volume in the anterior hippocampal ROI did not reach significance. Although previous studies have found a significant relationship between the GM volume in the hippocampus and scores on BIS measures (Barrós-Loscertales *et al*., 2006a; Cherbuin *et al*., 2008; Holmes *et al*., 2012; Levita *et al*., 2014), some methodological issues could account for these differences. One of them could be associated with the sample, as these previous studies were carried out with reduced sample sizes (Barrós-Loscertales *et al*., 2006a; Levita *et al*., 2014) or focused on a specific age range (middle-aged adults, who differ significantly from our sample; Cherbuin *et al*., 2008). Another methodological issue would be associated with the segmentation methods because, in contrast to our study, manual (Cherbuin *et al*., 2008) and automated (via FreeSurfer, Holmes *et al*., 2012; Levita *et al*., 2014) segmentations were applied to delimitate the amygdala and the hippocampus. Additionally, the study by Holmes *et al*. (2012) was carried out by taking a composite score of negative affect, which impedes the comparison with a direct single-scale score (i.e. SP). In addition, in the study by DeYoung *et al*. (2010), the authors did not find a positive association between the hippocampus and Neuroticism. In fact, they reported an inverse correlation between Neuroticism scores and hippocampal GM volume. Thus, further studies are needed to address the discrepancies about the involvement of the hippocampus and its anatomical correlates in behavioral inhibition. All in all, our results are in line with the last update of the RST and previous studies on the involvement of the amygdala in both fear and anxiety (McNaughton and Corr, 2004) and internalizing disorders.

The results have also shown a link between SR scores and reduced cortical volume in the lateral prefrontal cortex. The observed relationship was consistent with a recent study conducted in a large sample using impulsivity and sensation-seeking measures (Holmes *et al*., 2016) and with other studies that used the same self-reported measure of impulsivity (i.e. the Barratt Impulsivity Scale; Matsuo *et al*., 2009; Schilling *et al*., 2012; Cho *et al*., 2013). In addition, some studies have found that participants with lower GM volume in this region show a preference for immediate rewards on a delay-discounting measure (Bjork *et al*., 2009; Mohammadi *et al*., 2016; Wang *et al*., 2016; Wang *et al*., 2017). Therefore, less GM volume and cortical thickness in the lateral prefrontal area may predispose these people to worse cognitive control, which may determine a different probability of involvement in risky,

Table 3. Partial correlations (r) between a priori ROIs and scores on the SR scale (controlling for age, sex and years of education)

	Whole sample (*N* = 400)	Males (*N* = 233)	Females (*N* = 167)
Left NAcc	−0.09	−0.17*	0.02
Right NAcc	−0.03	−0.06	0.01
Left caudate	−0.09	−0.15*	−0.00
Right caudate	−0.09	−0.13	−0.04

One-tailed *t*-tests; *$P < 0.05$ FWE corrected.

Table 4. Partial correlations (r) between a priori ROIs and scores on the SP scale (controlling for age, sex and years of education)

	Whole sample (*N* = 400)	Males (*N* = 233)	Females (*N* = 167)
Left amygdala	0.15*	0.15*	0.13
Right amygdala	0.08	0.07	0.09
Left anterior hippocampus	0.09	0.11	0.05
Right anterior hippocampus	0.07	0.07	0.07

One-tailed *t*-tests; *$P < 0.05$ FWE corrected.

goal-directed activities such as substance use (Holmes *et al*., 2016). Consistent with previous studies on impulsivity (Cho *et al*., 2013; Korponay *et al*., 2017), SR also correlated negatively with the volume in the medial prefrontal cortex, a brain area crucial for evaluating rewarding stimuli (Hayes *et al*., 2014; Hiser and Koenigs, 2018), especially in subjective value-based decision-making (Bartra *et al*., 2013; Clithero and Rangel, 2014; Acikalin *et al*., 2017). Moreover, this region has traditionally been established as a key region for emotion regulation [via top-down regulatory control of limbic areas (Ridderinkhof *et al*., 2004; Etkin *et al*., 2011; Kim *et al*., 2011)]. Hence, the pattern of GM associated with the reward sensitivity dimension found in our study suggests that individuals with an overactive BAS have worse emotional control of reward experiences, facilitating goal-directed behavior in risky situations or even engagement in more violent behaviors (Coccaro *et al*., 2018). Furthermore, these reductions in prefrontal areas have also been related to externalizing disorders, principally substance use disorders (see Yang *et al*., 2016, for a meta-analysis on alcohol; Kaag *et al*., 2018) or even behavioral addictions, such as Internet gambling disorder (Yao *et al*., 2017).

Contrary to our expectations, the association between striatal volume and SR scores was modulated by sex. The negative correlation between the volume of the striatum and SR scores was observed in males but not in females. This result verified our previous results in males (Barrós-Loscertales *et al*., 2006b) and clarified that this relationship does not extend to females. Interestingly, this differential pattern in males *vs* females in striatal areas was discussed in a recent paper (Caravaggio *et al*., 2017) in which impulsivity scores, measured by the TCI of Cloninger, correlated negatively with the striatal volume in males but not in females. Furthermore, a recent prospective study reported a correlation between striatal volume and Facebook use but noting that effect sizes were clearly higher in males than females (Montag *et al*., 2017). Regarding its clinical impact, smaller striatal volumes have been reported in a number of externalizing disorders associated with an overactive BAS, with a higher prevalence in males. Some of these disorders included cocaine addiction (Barrós-Loscertales *et al*., 2011; Moreno-López *et al*., 2012), alcoholism (Makris *et al*., 2008; Yang *et al*., 2016), nicotine addiction (Das *et al*., 2012), pornography consumption (Kühn and Gallinat, 2014) and ADHD (see Hoogman *et al*., 2017, for a mega-analysis).

The explanation of this sex effect is less clear. Animal research has linked differences in the dopaminergic function to sex-specific transcriptome profiles within the NAcc (Hodes *et al*., 2015), with females being more susceptible to stress cues (i.e. less prone to reward-related behaviors, in comparison with males). However, these different transcriptome profiles could be associated with complex genetic and/or hormonal interactions (Becker and Chartoff, 2019). In humans, the sex effect on the striatal volume has also been associated with different functioning of the striatal dopaminergic system (i.e. dopamine receptor availability; Caravaggio et al., 2017). Moreover, the volume of the NAcc has been associated with changes in testosterone levels during adolescence in males (Wierenga *et al*., 2018), coinciding in time with the maximum activity during processing of reward stimuli (Braams *et al*., 2015). Thus, although more research is needed, genetic, hormonal and developmental factors may contribute to sex effects on the relationship between striatum volume and reward sensitivity. In addition, we should also take into account that these differences could be influenced by sex-specific behaviors in variables related to health and lifestyle; thus, future studies should also address the neuropsychological impact of these variables. In sum, we found an association between SR scores and the GM volume in frontostriatal areas, pointing to the link between individual differences in personality traits and brain structures found to be relevant in the development of externalizing disorders.

Since 1970, RST has developed into a sophisticated model of emotion, motivation, personality, psychopathology and neuroscience. Overall, our study adds new evidence to previous reports linking brain structure and personality traits, revealing that the amygdala, the striatum (especially in males) and the prefrontal cortex are key regions associated with personality development. These results strengthen the role of the SPSRQ in measuring the main dimensions of the RST and the usefulness of this model as a good, validated framework with which to investigate the predisposition to psychopathology.

Finally, our study has some limitations. Although we reported significant brain correlates of RST in a large sample, surface-based metrics could account for more specific effects than VBM. Indeed, VBM is a product of cortical thickness and surface area; however, the two measures have been shown to be genetically dissociated (Panizzon *et al*., 2009). Thus, future research should address this issue in order to better comprehend the biological underpinnings of personality traits. Another limitation would be related to the SPSRQ because this questionnaire provides a unique, combined measure (the SP scale) of the BIS and FFFS. Although both systems are strongly associated with the punishment sensitivity dimension and share neuroanatomical structures (i.e. the amygdala), they are described as separate neuropsychological systems. Nonetheless, no agreement exists about how the BIS and FFFS can be psychometrically isolated. Hence, future studies are required to address this question because the factorization of the SP scale would provide more accurate measures of the BIS and FFFS.

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