Personality and Individual Differences 74 (2015) 214–219

Contents lists available at ScienceDirect

Personality and Individual Differences

journal homepage: www.elsevier.com/locate/paid

Evidence for an antagonistic interaction between reward and punishment sensitivity on striatal activity: A verification of the Joint Subsystems Hypothesis

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ARTICLE INFO

Article history:
Received 19 May 2014
Received in revised form 10 October 2014
Accepted 14 October 2014
Available online 12 November 2014

Keywords:
fMRI
Joint Subsystems Hypothesis
Reward sensitivity
Striatum
Dopamine
Reinforcement Sensitivity Theory

ABSTRACT

The Reinforcement Sensitivity Theory proposes that the Behavioral Approach System (BAS) comprises dopaminergic brain regions and underpins reward sensitivity causing impulsivity. It has been shown in a supraliminal priming task that highly reward sensitive subjects have a larger reaction time (RT) priming effect and make more commission errors to prime-incongruent targets. We adapted a similar task to event-related fMRI and hypothesized that (1) high reward sensitivity is associated with increased activation in dopaminergic brain regions, the ventral striatum in particular, (2) that BAS related personality traits predict impulsivity and (3) that the BAS effects are larger after adjusting for the interactive influence of trait avoidance, as predicted by the Joint Subsystems Hypothesis. Fourteen healthy females participated in the fMRI experiment and were scored on sensitivity to reward (SR) and trait avoidance, i.e., sensitivity to punishment (SP) and neuroticism (N). SR scores were adjusted by SP and N scores. As hypothesized, adjusted SR scores predicted, more than SR scores alone, activity in the ventral striatum (left caudate nucleus and nucleus accumbens). SR+/ SP− scores predicted increased impulsiveness, i.e., a right side RT priming effect. These results support the Joint Subsystems Hypothesis.

1. Introduction

The Reinforcement Sensitivity Theory describes three brain-behavior systems: The Behavioral Approach System (BAS), the Behavioral Inhibition System (BIS) and the Fight–Flight–Freeze System (FFFS). It proposes that the reactivity of each of these systems underpins the major personality dimensions (Corr, 2008; Gray & McNaughton, 2000). BAS facilitates reward-orientation and approach behavior, and is driven by midbrain dopaminergic projections, in particular to the ventral striatum (Pickering & Gray, 2001). Here, the dopaminergic release is strongest to unexpected rewards or reward cues (Schultz, 1998). Hyper-reactive BAS is proposed to lead to reward sensitivity and impulsiveness (Pickering, Corr, & Gray, 1999). In contrast, FFFS and BIS mediate avoidant behavior; FFFS with a fight–flight–freeze response to aversive stimuli and BIS with inhibition, anxiety and problem solving in response to conflicts. Whereas the periaqueductal gray matter, medial hypothalamus and amygdala are considered core structures for FFFS, the septo-hippocampal system is understood as a central substrate for BIS (Gray & McNaughton, 2000).

Testing predictions of the Reinforcement Sensitivity Theory with psychophysiological and behavioral tasks has yielded conflicting results (Corr, 2004). One reason may be the assumption that personality dimensions have state-independent outputs, and that the behavioral effects of one personality dimension can be studied isolated from other dimensions. However, BAS, BIS and FFFS have mutual antagonistic properties: approach, inhibition and avoidance. The Joint Subsystems Hypothesis proposes that an individual's activations in dopamine innervated striatal and prefrontal structures depend, not only on reward sensitivity (BAS) but also on antagonistic influences of BIS and FFFS (Corr, 2001). Thus, BAS related brain activation should be highest in individuals with high BAS reactivity (BAS+) and low FFFS/BIS reactivity (FFFS−/BIS−).

The aim of the current study was to disclose associations between BAS related brain activity, personality traits and behavior, and to examine the proposed antagonistic influence of FFFS/BIS reactivity. To this end we adapted a supraliminal priming task to event-related fMRI. In a similar task, highly reward sensitive indi-

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http://dx.doi.org/10.1016/j.paid.2014.10.023
0191-8869/

viduals exhibited increased impulsive behavior measured by the reaction time (RT) priming effect and commission errors to prime-incongruent targets (Avila & Parcet, 2002). We hypothesized that (1) high BAS related trait scores are associated with increased activation in brain areas richly innervated by ascending dopaminergic projections, in particular the ventral striatum, and that this activity is trigged by unexpected reward cues. We further hypothesized that (2) personality trait measures of BAS predict impulsive behavior, i.e., a stronger RT priming effect and more commission errors to prime-incongruent targets. Finally, we hypothesized that (3) the association between BAS reactivity and striatal activity is stronger when taking FFFS/BIS trait scores into account in line with the Joint Subsystems Hypothesis.

2. Materials and methods

2.1. Subjects

The study was approved by the regional ethical committee, and adhered to the Helsinki Convention. Fifteen healthy female volunteers without MRI contraindications and no history of neurological or psychiatric disease provided written informed consent. One participant was excluded due to technical errors. All remaining subjects were right-handed; laterality index of 80.2 ± 12.5 (Oldfield, 1971).

2.2. BAS/BIS/FFFS related trait-measures

Each participant completed the Sensitivity to Punishment and Sensitivity to Reward Questionnaire (SPSRQ) which is based on the Reinforcement Sensitivity Theory (Torrubia, Avila, Molto, & Caseras, 2001). SPSRQ measures sensitivity to reward (SR), i.e., BAS reactivity, and sensitivity to punishment (SP), a combined measure of FFFS and BIS reactivity. The Joint Subsystems Hypothesis was not formulated specifically to expect differential impacts of BIS and FFFS on BAS (Corr, 2001, 2004). Since FFFS and BIS serve different adaptive purposes, it is important to investigate the unique contributions from each system. However, there was no validated Reinforcement Sensitivity Theory derived measure separating BIS and FFFS, and we thus decided to apply neuroticism (N) from the Eysenck Personality Questionnaire (Eysenck & Eysenck, 1975) as a supplement to SP. *A priori*, SP should lie closer to FFFS and N closer to BIS because SP places a stronger emphasis on fear related avoidance compared to N which emphasizes anxious rumination. Adjusted BAS reactivity measures, SR+/SP− (BAS-SP scores) and SR+/N− (BAS-N scores) were calculated and subsequently used to test if the Joint Subsystems Hypothesis is a more sensitive measure of activation of dopaminergic innervated brain structures than the original Reinforcement Sensitivity Theory.

2.3. fMRI task

A priming task based on a Posner task (Avila & Parcet, 2002) was adapted for event-related fMRI and compiled in E-Prime (Psychology Software Tools, Pittsburgh, USA). The task stimuli consisted of cue-primes, i.e., two small hatches pointing left or right (<< or >>), neutral primes, i.e., two small hatches pointing to the center (><), and target stimuli, i.e., one larger hatch pointing left or right (< or >). A trial was defined as valid if the target was preceded by a cue-prime pointing in the same direction as the target, invalid if preceded by a cue-prime pointing in the opposite direction, and neutral if preceded by a neutral prime. Each prime was displayed for 50 ms followed by a blank screen for 450 ms before the target presentation. This constituted a stimulus onset asynchrony of 500 ms, which is adequate for exploring reward sensitivity (Avila & Parcet, 2002). The target was displayed for 500 ms, followed by a 2600 ms rest period plus null-events of different lengths (1800, 3600, 5400 and 7400 ms). 180 valid, 56 invalid and 44 neutral trials (a total of 280) were randomly presented over four runs. The predominance of valid trials ensured expectation of prime-target correspondence.

The paradigm was presented on an LCD screen (Philips Medical Systems, The Netherlands) located in the rear of the magnet bore, visible to the participants via a mirror mounted on the head coil. Responses were obtained with response grips (Nordic NeuroLab AS, Bergen, Norway) and logged in E-Prime. Paradigm presentation and fMRI scanning were synchronized with a sync-box (Nordic NeuroLab AS, Bergen, Norway). Participants were instructed to respond as quickly and accurately as possible by pressing a button with their right thumb in response to a target pointing right, and their left thumb to a target pointing left. They practiced the task outside the scanner until complete task compliance.

2.4. Behavioral analysis

Mean RTs for valid, invalid and neutral trials were calculated after excluding all trials with commission errors and RT <100 ms. The excluded trials encompassed 3.1% of all trials and were evenly distributed across participants. Due to the expectation of prime-target correspondence, cue-primes should decrease the RT in valid relative to neutral trials and increase commission errors in invalid trials. The RT priming effect was estimated by subtracting RT in valid trials from RT in neutral trials. The percentage commission errors was log-transformed to fit parametric analyses. Right-handed participants respond faster to targets pointing right and make more commission errors with targets pointing left (Avila & Parcet, 2002). Hence, repeated measures ANOVA analyses were used to investigate the effects of both trial type and hand on RT and commission errors, separately, followed by paired *t*-tests. In linear regression analyses, SR, SR+/SP− and SR+/N− were predictors for RT priming effect and commission errors in invalid trials for each hand separately and for both hands combined.

2.5. MRI data acquisition

MR images were acquired on a Philips Intera 3 Tesla scanner (Philips Medical Systems, Best, The Netherlands) with Quasar Dual gradients using a six-channel SENSE head-coil (InVivo, Gainesville, USA). The participants' heads were immobilized using foam padding. During the task, T2*-weighted gradient-echo single-shot echo-planar-imaging whole brain measurements were obtained with 42 contiguous axial slices, slice thickness = 4.0 mm, TR = 1800 ms, TE = 35 ms, flip angle = 90°, SENSE reduction factor = 2.2, field-of-view = 256, and in plane voxel resolution 2 × 2 mm. Four functional runs, each consisting of 182 volumes, were acquired in each participant. Every run was preceded by four dummy scans which were discarded before analysis. A B0 field map was acquired for fMRI scan distortion correction (unwarping) and a 3D MP-RAGE sequence for anatomical reference.

2.6. MRI processing

Image analyses were carried out in FSL 4.1.5 (Smith et al., 2004). B0 unwarping, brain extraction, motion correction, spatial smoothing (Gaussian kernel FWHM: 5 mm), high-pass temporal filtering (cut-off: 60 s), slice timing correction were performed. The functional images were registered to the 3D MP-RAGE volume and warped to the Montreal Neurological Institute (MNI)-152 standard template using FLIRT (Jenkinson, Bannister, Brady, & Smith, 2002).

Statistical analyses were based on FILM, which performs prewhitening, and fits a general linear model voxel-wise. Brain activity was modeled with five predictors, (1) cue-primes, (2) neutral

primes, (3) neutral trial targets, (4) valid trial targets and (5) invalid trial targets. The prime-predictors included both the display of the prime (50 ms) plus waiting time (450 ms) before target display. The target-predictors started at the target on-set time and ended when the subject responded. The expected signal time courses were convolved with a two-gamma hemodynamic response function (Glover, 1999) and its temporal derivative. Within-subjects parameter estimates were obtained separately for each run, and then pooled across runs with a fixed effects model of variance. SR, SR+/SP− and SR+/N− were entered as separate regressors in a mixed effects GLM analysis (FLAME; FMRIB's Local Analysis of Mixed Effects) for the prime and target contrasts. In addition, a post hoc analysis was performed with the left and right RT priming effect as covariates in order to investigate the influence of a hand effect on brain activity. *Z* statistic images were thresholded using an uncorrected voxel *p*-value of .005 ($Z = 2.576$) and a cluster size threshold of $\geqslant$20 voxels (Lieberman & Cunningham, 2009).

In the priming task, the reward can be seen as successful task compliance, defined by the researcher's instructions as fast and accurate responses. Reward cues are primes and targets associated with successful task compliance. In order to isolate brain areas activated to unexpected reward cues, three statistical contrasts were examined; (1) prime (cue-primes > neutral primes) isolates activity related to unexpected reward-cues vs. unexpected non-reward cues; (2) neutral > valid (neutral trial targets > valid trial targets) isolates activity related to unexpected reward-cues vs. expected reward-cues; (3) neutral > invalid (neutral trial targets > invalid trial targets) isolates activity related to unexpected reward-cues vs. unexpected non-reward-cues.

2.7. Region-of-interest analyses

To quantify the predictive value of SR, SP and N, the BAS related brain activity obtained in the voxel-by-voxel analysis was investigated in region-of-interests (ROI) analyses. The ROIs investigated were restricted to the left ventral striatum because activity here correlated with SR, SR+/SP− and SR+/N− in all three contrasts, and because the ventral striatum, was the location where BAS was expected to exert its largest influence. ROIs were based on activations in the three contrasts: ROI-1: prime, ROI-2: neutral > valid, ROI-3: neutral > invalid and defined separately by the SR+/SP− and SR+/N− related activation patterns, thus forming 6 ROIs. The ROIs included every activated voxel exceeding the statistical threshold in the covariate analyses. For each participant the max *Z*-values from these ROIs were entered as dependent variables in multiple linear regression analyses, with SR, SP and N scores as independent variables.

3. Results

The participants were between 19 and 41 years (median 27 years) with a median education of 12 years. Mean SP score was 6.3 ± 3.9 (range 1–12 of max 24), mean SR score was 8.9 ± 3.4 (range 4–15 of max 24) and mean N score was 7.1 ± 4.7 (range 1–15 of max 23).

3.1. fMRI task performance

The repeated measures ANOVA showed main effects of trial type ($F(2,26) = 43.14$, $p < 0.001$) and hand ($F(1,13) = 22.99$, $p < 0.001$) on RTs. The combined mean RT in valid trials was significantly shorter than in neutral ($p < .001$) and invalid trials ($p < .001$) (Table 1). No RT difference was found between invalid and neutral trials ($p = .301$). Right hand responses were faster than left hand responses across all trials ($p < .001$). There was no interaction between trial type and hand responses on RT ($p < .596$). The RT priming effect was 43 ± 21 ms for both hands combined. For commission errors significant main effects of trial type ($F(2,26) = 9.25$, $p < 0.001$) and hand ($F(1,13) = 11.83$, $p = 0.004$) were present. Commission errors for both hands combined was significantly larger in invalid trials compared to valid ($p = .020$) and neutral trials ($p = .010$) (Table 1). No difference was found in commission errors between valid and neutral trials ($p = 1.000$). There was no interaction between trial type and hand responses on commission errors ($p = .052$). There were more commission errors in left than in right hand trials ($p = .004$).

3.2. Linear regression analyses of BAS related behavior and trait-measures

The right side RT priming effect (ms) increased with higher SR+/SP− scores, which explained 29.4% of the variance ($F(1,12) = 4.992$, $p = .045$). The analyses of left hand ($p = .394$) and each hand combined ($p = .065$) were not significant. Non-significant were also the analyses of SR and SR+/N− as predictors for the RT priming effect and all the analyses for SR+/SP−, SR+/N− and SP as predictors for commission errors in invalid trials.

3.3. Relationship between BAS reactivity and brain activity – voxel-by-voxel analyses

Results with SR scores as covariate are shown in Table 2. In both target contrasts, i.e., neutral > valid and neutral > invalid, higher SR scores were associated with increased activation of left caudate nucleus extending into nucleus accumbens. In the prime contrast, this activation was limited to left caudate nucleus (Fig. 1). In the prime contrast and target contrast neutral > invalid, activation in right caudate nucleus increased with higher SR scores (Fig. 1). Across all three contrasts, high SR scores were associated with increased activity in left posterior hippocampus, spreading into adjacent parahippocampal gyrus. In the prime and target neutral > valid contrast, increased activity in right medial orbitofrontal cortex/frontal pole was associated with higher SR scores, as was increased activity in left thalamus in the neutral > valid contrast.

Results with SR+/SP− and SR+/N− scores as covariates are shown in Tables 3 and 4 and the ventral striatal activity in the prime contrast in Fig. 1. In all contrasts, high SR+/SP− and SR+/N− scores were associated with brain activity peaking in the left ventral striatum. The peak activity for SR+/SP was localized more anterolaterally in the caudate head spreading into nucleus accumbens and putamen, while the SR+/N− related peak activity was situated more posteromedially spreading into nucleus accumbens only. Both SR+/SP− and SR+/N− scores were associated with activity in the bilateral medial orbitofrontal cortex and left thalamus. In addition SR+/SP− was associated with activity in the left posterior hippocampus spreading into adjacent parahippocampal gyrus and fusiform cortex, right lateral occipital cortex and left opercular cortex while SR+/N− scores was associated with activity in the bilateral inferior temporal gyrus, left middle temporal gyrus, right

Table 1
Task performance.

	Valid trials	Neutral trials	Invalid trials
Reaction time (ms) (Mean ± SD)	421 ± 26[a,b]	455 ± 29	460 ± 25
Commission errors (%) (Median (range))	1.7 (0–4.5)	0 (0–9.3)	3.6 (0–17.9)[c,d]

[a] Valid < neutral ($p < .001$).
[b] Valid < invalid ($p < .001$).
[c] Invalid > valid ($p = .020$).
[d] Invalid > neutral ($p = .010$).

Table 2
Peak activity for the prime and target contrasts with SR as covariate.

Anatomical region (left/right)	Cluster size	*Z*-max MNI coordinates *x*, *y*, *z*	*Z*-max value
Hippocampus/parahippocampal gyrus posterior (L)	129	−38, −32, −10	3.38[a]
	118	−42, −38, −12	3.38[b]
	101	−42, −38, −10	3.2[c]
Caudate nucleus (L/R)	32	12, 6, 8	3.31[a]
	34	12, 6, 8	3.22[c]
	28	−14, 14, 0	3.29[a]
Caudate nucleus/nucleus accumbens (L)	46	−14, 14, 0	3.06[b]
	56	−8, 12, −8	3.2[c]
Medial orbitofrontal cortex/frontal pole (R)	20	14, 54, −12	3.04[a]
	20	16, 52, −14	2.78[b]
Thalamus (L)	22	−4, 0, 2	2.86[b]

Significant BOLD signal estimates with a statistical threshold of uncorrected $p < .005$, cluster size ⩾20 voxels, mixed effects.
[a] Prime.
[b] Neutral > valid.
[c] Neutral > invalid.

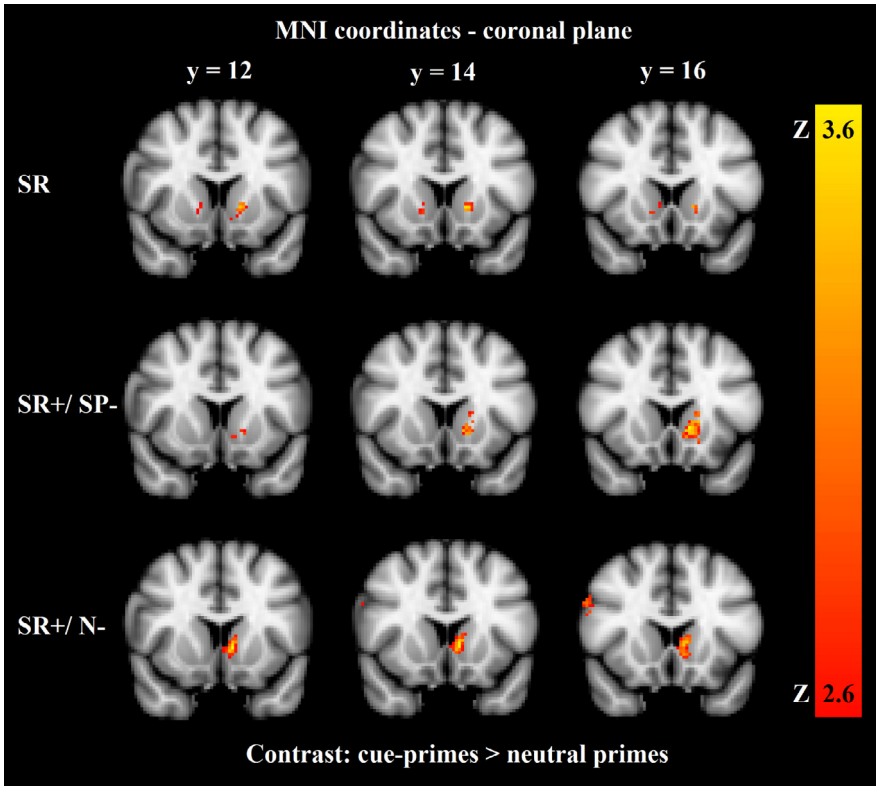

Fig. 1. Ventral striatal activity in the prime contrast co-varying with sensitivity to reward (SR) and SR adjusted with sensitivity to punishment (SP) scores, i.e., the variable SR+/SP−, and neuroticism scores (N), i.e., the variable SR+/N−. The activation maps were superimposed on the MNI standard brain. The analyses was performed with an uncorrected cluster significance threshold of $p = .005$ (*Z*-value = 2.576), cluster size ⩾20 voxels. Right side of the brain is displayed on the left side of the image in accordance with radiological convention.

inferior and middle frontal gyrus and the bilateral lateral orbitofrontal cortex.

The right RT priming effect was associated with bilateral striatal activity (cluster size: 409, *x*–*y*–*z* = 14–4–6, max *Z*-value = 3.8) where the left striatal activity was localized more ventrally compared to the right striatal activity. Striatal activation was not observed with the left RT priming effect as covariate.

3.4. Relationship between BAS reactivity and brain activity – ROI analyses

Multiple linear regression analyses with max *Z*-values from the 6 ROIs in the left ventral striatum associated with SR+/SP− and SR+/N−, showed that SR scores significantly increased brain activity while SP and N significantly decreased brain activity and that a substantial portion of the variance was explained by SR, SP and N (Table 5).

4. Discussion

The results support the Joint Subsystems Hypothesis, as adjusted SR scores, more than SR, predicted increased activity in the left ventral striatum. In addition, SR+/SP− scores predicted an increased right, but not left, RT priming effect. The right RT priming effect was also associated with ventral striatal activity. This indicates that stronger reward associations were formed for right than

Table 3
Peak activity for the prime and targets contrasts with SR+/SP− as covariate.

Anatomical region (left/right)	Cluster size	*Z*-max MNI coordinates *x*, *y*, *z*	*Z*-max value
Caudate nucleus/putamen/nucleus accumbens (L)	89	−12, 16, 0	3.35[a]
	172	−14, 16, −4	3.29[b]
	147	−14, 16, −4	3.38[c]
Hippocampus/parahippocampal gyrus/temporal fusiform cortex, posterior (L)	58	−42, −36, −12	3.34[a]
	91	−42, −36, −12	3.56[b]
	91	−42, −36, −12	3.59[c]
Lateral occipital cortex (R)	35	46, −60, 10	3.28[a]
	85	46, −60, 10	3.37[b]
	45	40, −60, 10	3.28[c]
Opercular cortex/precentral gyrus (L)	31	−44, −16, 24	3.12[a]
	52	−42, −18, 24	3.44[b]
	56	−42, −18, 26	3.4[c]
Medial orbitofrontal cortex (L/R)	25	−18, 34, −8	3.07[a]
	29	16, 36, −10	3.2[b]
	51	16, 36, −10	3.33[c]
Thalamus (L)	20	−14, −6, 12	2.8[b]

Significant BOLD signal estimates with a statistical threshold of uncorrected $p < .005$, cluster size $\geqslant 20$ voxels, mixed effects.
[a] Prime.
[b] Neutral > valid.
[c] Neutral > invalid.

Table 4
Peak activity for the prime and targets contrasts with SR+/N− as covariate.

Anatomical region (left/right)	Cluster size	*Z*-max MNI coordinates *x*, *y*, *z*	*Z*-max value
Caudate nucleus/nucleus accumbens (L)	345	−8, 12, 0	3.64[a]
	57	−8, 12, −2	3.38[b]
	21	−16, 20, −6	2.89[b]
	24	−8, 10, −2	3.11[c]
Inferior temporal gyrus posterior (L/R)	117	54, −60, −20	3.32[a]
	103	−52, −62, −16	3.13[a]
	35	62, −50, −12	3.16[a]
	39	54, −62, −20	3.0[b]
	24	54, −62, −20	2.97[c]
Middle temporal gyrus posterior (L)	81	−56, −58, 2	3.19[a]
Inferior frontal gyrus (R)	74	56, 18, 30	3.25[a]
	21	58, 20, 30	2.84[b]
	22	56, 18, 30	2.92[c]
Middle frontal gyrus (R)	66	50, 28, 32	3.18[a]
Lateral orbitofrontal cortex (L/R)	33	42, 24, −10	2.91[a]
	31	−40, 24, −16	3.13[a]
Medial orbitofrontal cortex (L/R)	28	16, 34, −12	3.22[b]
	25	−18, 32, −8	3.14[b]
	24	16, 34, −14	3.23[c]
	23	−18, 32, −8	3.09[c]
Thalamus (L)	33	−4, −4, 4	2.93[b]

Significant BOLD signal estimates with a statistical threshold of uncorrected $p < .005$, cluster size $\geqslant 20$ voxels, mixed effects.
[a] Prime.
[b] Neutral > valid.
[c] Neutral > invalid.

for left primes and targets, most likely related to right-handedness. We observed that RTs were faster for right hand responses while there were more commission errors in left trials similar to previous reports (Avila & Parcet, 2002). Handedness reduces the precision and speed of the non-preferred hand (Flowers, 1975). Thus, successful trial completion seemed to yield reward associations and drive BAS related impulsivity in the present task.

As hypothesized, high SR scores were associated with increased brain activity in the dopamine innervated ventral striatum, a central BAS structure (Pickering & Gray, 2001). The ventral striatal activity was elicited by unexpected reward cues, i.e., cue-primes and neutral trials targets which were both unforeseen and associated with successful trial completions. In comparison, neutral primes were not reward associated as indicated by their stimulus neutrality. Invalid trial targets were not reward associated as indicated by increased commission errors, while targets in valid trials were expected rewards as indicated by the RT priming effect. Thus, the current results support that ventral striatal activity is a reward prediction error signal, and more than a mere reinforcement signal (Schultz, 1998). Moreover, BAS related activation was present in the medial orbitofrontal cortex, which is connected to reward anticipation in reward sensitive subjects (Hahn et al., 2009). When an unexpected reward cue is identified by the ventral striatum, the individual forms an anticipation of a rewarding event in the medial

Table 5
Multiple linear regression of SR, SP and N as predictors of left ventral striatal activity.

ROIs	Personality measure	*t*-Value	R^2	*p*-Value
SR+/SP−				
Prime	SR	4.163	.502	.002
	SP	−2.819	.209	.017
	Model		.711	.001
Neutral > valid	SR	4.815	.501	.001
	SP	−3.850	.286	.003
	Model		.788	.000
Neutral > invalid	SR	4.539	.457	.001
	SP	−4.101	.328	.002
	Model		.785	.000
SR+/N−				
Prime	SR	3.860	.330	.003
	N	−3.187	.322	.009
	Model		.652	.003
Neutral > valid	SR	3.797	.275	.003
	N	−3.675	.400	.004
	Model		.675	.002
Neutral > invalid	SR	3.360	.224	.006
	N	−3.584	.418	.004
	Model		.642	.004

orbitofrontal cortex (Bechara, Damasio, & Damasio, 2000; Kringelbach & Rolls, 2004).

Also as hypothesized, we found an antagonistic influence of BIS/FFFS on BAS related brain activation and behavior, supporting the Joint Subsystems Hypothesis (Corr, 2001). According to the view of separable subsystems, either an avoidance- or an approach related brain-behavior system is in exclusive control of the behavioral execution at any moment, with each activation level independent of the other (Pickering, 1997). Most studies inspired by the Reinforcement Sensitivity Theory have adopted this view, which, if incorrect, might explain the conflicting results in the literature (Corr, 2004). Corr suggested that the effects of joint subsystems will be more pronounced in situations with weak appetitive or conflicting stimuli (Corr, 2002) which was supported by this fMRI study.

The distinct effects from N and SP on SR related brain activity and behavior in the present study shed light on the unique contributions of BIS and FFFS. According to the Reinforcement Sensitivity Theory FFFS cancels approach behavior due to aversive stimuli while BIS limits, but supports approach behavior under conflicts (Gray & McNaughton, 2000). One could thus expect that the strongest antagonistic effect on BAS stem from FFFS which we believed would be more closely related to SP than N. In fact, low SP promoted approach behavior demonstrated by the predictive strength of SR+/SP− scores on the right RT priming effect. Notable, this impulsivity measure is a more sensitive BAS measure than commission errors (Avila & Parcet, 2002), perhaps because commission errors reduce reward associations by dopaminergic depression (Schultz, 1998). Furthermore, SR+/SP− was related to activation in the hippocampus on which dopaminergic action facilitates declarative memory for both unexpected reward cues and subsequent stimuli (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Wittmann et al., 2005). Finally, while SR+/SP− was related to activation in the anterolateral part of the ventral striatum spreading into putamen, the SR+/N− related peak activity was localized more posteromedially. The former area is associated with reward related learning independent of negative feedback while the latter responds to both aversive and appetitive stimuli (Jensen et al., 2003; Mattfeld, Gluck, & Stark, 2011). In sum, low SP (or low FFFS) rendered subjects less sensitive for negative feedback and promoted both BAS related learning and approach while low N (or low BIS) did not. However, low N (or low BIS) may still be related to impulsivity, but then under other conditions than focused on in the present study, i.e., conflicted circumstances.

In conclusion, researchers studying reward sensitivity should be aware of possible confounding effects of subsystems underpinning trait avoidance, and perhaps fear related avoidance in particular.

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