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

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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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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