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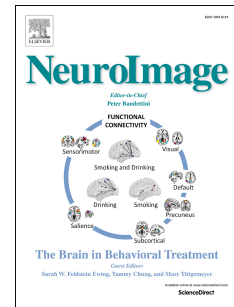
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Modulations in Resting State Networks of Subcortical Structures linked to Creativity

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ABSTRACT

Creativity is a sine qua non ability for almost all aspects of everyday life. Although very profound behavioural models were provided by 21th century psychologists, the neural correlates of these personality features associated with creativity are largely unknown. Recent models suggest strong relationships between dopamine release and various creative skills. Herein, we employed functional connectivity analyses of resting-state functional magnetic imaging data in order to shed light on these neural underpinnings of creative aspects. For improved sensitivity, we performed the study at ultra-high magnetic field (7 Tesla). Seed regions were defined based on subcortical (ventral tegmental area/substantia nigra, nucleus caudatus) activation foci of a remote associates task (RAT). In addition, bilateral PCC was used as seed region to examine the default-mode network. Network strength across subjects was regressed against a battery of psychological variables related to creativity. Dopaminergic network variations turned out to be indicative for individual differences in creative traits. In this regard, the caudate network showed stronger connectivity in individuals with higher extraversion measures, while connectivity with the midbrain network was found increased with higher ideational behaviour and emotional stability.

Keywords (max 6). 7-Tesla fMRI, connectivity, subcortical, creativity, personality, ideation

INTRODUCTION

Individual and societal progress is heavily reliant on our ability to generate novel and useful ideas. As such, creativity is a feature *sine qua non* for many aspects of everyday life. There are primarily two influential psychological approaches to the essential traits of the creative personality. First, Csikszentmihalyi (1996) described ten paradoxical personality traits of highly creative people such as being introverted and extraverted at the same time. Second, in their investment model of creativity, Lubart and Sternberg (1995) listed some essential characteristics to develop a person's creative potential. Among these are intellectual skills, such as problem definition and insightful thinking, a legislative thinking style driving the production of novel ideas, as well as intrinsic motivation. Furthermore, recent behavioural studies have proposed a variety of complementary personality traits linked to creative individuals, e.g., "norm doubting, ambition, impulsivity, willingness to take risks, autonomy, imagination, hostility, curiosity, self-confidence" (see Abler et al. (2006); Li et al. (2015)), self-efficacy (Prabhu et al., 2008) and versatility (Cassandro and Simonton, 2010).

This manifold of psychological theories shows the ample complexity of the concept "creativity". However, the idea that many creative traits arise from dopamine-coupled brain areas has been developing since creativity research first caught the interest of researchers (Heilman et al., 2003). Multilevel evidence on the dopaminergic relations to creativity is available reaching from the anecdotic point of view that genius and madness are closely related to each other (Andreasen, 1997), over evidence from altered creative performance in neuropsychiatric disorders as Parkinson's disease (Faust & Socher et al., 2014; Lhommée et al., 2014), Schizophrenia (Acar et al., 2018) or bipolar disorder (Power et al., 2015) to behavioural experiments with eye blink rates as a proxy for dopaminergic activity in divergent

thinking experiments (Chermahini and Hommel, 2010; Salvi et al., 2015) and studies linking dopamine-level driven sensation seeking to creativity (Bardo et al., 1996).

Topical literature draws attention to new biology-grounded theories of creative behaviour that base creative components on subcortical structures. Boot et al. (2017) suggest multiple creative traits, as flexible cognition and the convergence of remote associations, to be strongly based on fronto-striatal dopaminergic pathways. Beyond that, several studies have linked dopaminergic gene loci to creative behaviour (De Manzano et al., 2010; Maysless et al., 2013; Reuter et al., 2006; Runco et al., 2011; Zabelina et al., 2016), thus indicating a profound link between dopamine variation and creativity. In summary, while there are numerous indicators towards a relationship between creative traits and dopaminergic pathways available, evidence of the neural underpinnings of these traits is still sparse.

Neuroimaging methods have shown their potential for examining biological processes associated with creative traits, in particular to disentangle the neural dopaminergic core components that might underlie creativity aspects. In this respect Takeuchi et al. (2010) showed that grey matter varies in brain areas, which are part of the dopaminergic system, depending on creativity measures: Increased regional grey matter volumes in the midbrain and caudate nucleus were significantly correlated to divergent thinking performance. This finding is further supported on a functional level (Tik et al., 2018) by a study demonstrating recruitment of structures such as nucleus accumbens (NAcc), ventral tegmental area (VTA) and dorsolateral prefrontal cortex (DLPFC) areas, which belong to the dopaminergic system during insightful problem solving. In a very recent publication by Beaty et al. (2018) two brain states could be identified that were either predictive for high or low creativity. While the high-creativity network included frontal-parietal connections, the low creativity network was characterized by temporal-parietal connectivity. The low-creativity network included a variety of subcortical nodes, which is in contrast to the former results summarized above (Takeuchi

et al., 2010; Tik et al., 2018). In this respect, another recent study could identify a stronger top-down compared to a bottom-up effect in creativity, with more subcortical areas involved in networks that were negatively correlated to figurative creativity (Liu et al., 2018). However, in both studies subcortical nodes were also included in the highly creative state.

Insight by itself is the unifying entity that integrates creative processes. It is described as a moment of combining old information in an original manner in order to create an important idea, which is novel to the individual (Sternberg and Davidson, 1995). This insight goes along with strong positive affect and an improved memory formation for the novel idea that emerged from it, which links it phenomenologically to increased dopamine release (Kizilirmak et al., 2016; Milivojevic et al., 2015; Shen et al., 2016; Topolinski and Reber, 2010; Webb et al., 2017).

Taking these multilevel observations into account we aimed at linking a broad range of behavioural concepts associated with creativity to their neural anchoring, especially subcortical areas that are part of the dopamine system. We chose a variety of behavioural measures that have been linked to the core of the creative personality for a long time but – despite the flood of psychological studies concerned with creative personality traits – have never been empirically integrated into an overall concept. In this study, we employed: (1) the Ten Items Personality Inventory (Gosling et al., 2003), which includes the Big-Five factors extraversion, emotional stability, agreeableness, openness and conscientiousness, of which extraversion and openness have been associated with exploratory behaviour and increased dopamine release in the ventral tegmental area (Ashby et al., 1999; Depue and Collins, 1999b; Panksepp, 1999), being considered a good predictor of creativity (Batey and Hughes, 2017; Hughes et al., 2013; Peterson et al., 2002). Furthermore, Big-Five personality traits, especially openness and extraversion have been directly linked to creative behaviour, especially novelty seeking (Agnoli et al., 2016; Csikszentmihalyi, 1996; De Fruyt et al., 2000;

Fürst and Grin, 2018; Gołowska et al., 2018; Halder et al., 2017; Nakaya et al., 2006; Singh and Kaushik, 2015b; Strobel et al., 1999; Welsh, 1975). (2) The Mindset Questionnaire by Dweck et al. (1995b) in order to measure the individual's motivation on being creative, (3) the Runco Ideational Behaviour Scale (Runco et al., 2001), which is the most important scale for measuring day-to-day creativity.

Since we were interested in how these behavioural scales relate to insight-related activation in subcortical areas within the dopaminergic system, we calculated functional connectivity maps based on seed-regions in the midbrain derived from a 7T study on creative problem solving (Tik et al., 2018). In addition, the default-mode network (DMN) was examined as it has been linked to creativity in a number of previous studies (Beaty et al., 2014; Takeuchi et al., 2011). We tested for modulations in these networks depending on differences in creative personality traits. We thereby aimed at drawing a comprehensive picture on personality traits associated with brain structures of the dopaminergic system involved in insight and creativity.

PARTICIPANTS AND METHODS

Study population

This manuscript comprises resting-state data pooled over two separate 7T studies on creativity. In total, 43 healthy, right-handed volunteers (22 female, mean age: 26.34 ± 3.08 (SD) years) took part in this study. Participants were recruited via flyers and online platforms. Standard MRI exclusion criteria were applied, which included neurological or psychiatric abnormalities, claustrophobia, use or abuse of psychotropic substances, presence of metallic objects on or inside the body that could not be removed before the measurement, implants such as pacemakers, and pregnancy. The study protocol was approved by the local ethics committee of the Medical University of Vienna, Austria. All participants provided informed written consent and received financial reimbursement. The study was performed in accordance with the Declaration of Helsinki (1964), including current revisions, the Austrian Medical Devices Act, and the EC-GCP guidelines.

Resting-state fMRI Data Acquisition

Functional MRI scans were acquired on a MAGNETOM 7 Tesla whole-body MR scanner (Siemens Medical, Erlangen, Germany) at the MR Centre of Excellence, Medical University of Vienna. For resting-state data acquisition a 32-channel head coil (Nova Medical, USA) was used with the CMRR multiband (Moeller et al., 2010) EPI sequence (5 min, TR=1.4 s, TE=23 ms, 78 slices, voxel size: $1.5 \times 1.5 \times 1 \text{mm}^3$). Note that using such small voxel sizes increases fMRI sensitivity in ventral brain areas as signal losses from intra-voxel dephasing effects due to the presence of field inhomogeneity are strongly reduced (Robinson et al., 2004; Sladky et al., 2018; Windischberger et al., 2004). Participants were instructed to relax, think of nothing in particular and let their mind wander while visually fixating on a cross that was presented via a digital projector connected to a computer and a mirror.

Stimuli were shown via a video projector on a screen mounted at the rear scanner bore. A mirror was used to allow subjects to view the stimuli.

Remote Associates Task and Seed Voxel Extraction

In addition to resting-state data, the RAT paradigm was administered in 29 subjects. Sequence parameters for the RAT runs were identical to the resting-state acquisitions. The exact experimental procedure is described in Tik et al. (2018). In short, participants performed a German Version of the RAT, a common task known to trigger divergent and convergent thinking (Mednick, 1962; Mednick and Mednick, 1967) and finally the Aha!-moment. Subjects were instructed to find a target word associated with presented word triplets and pressed a button at the moment they felt confident about their solution. If they failed to find the answer within 20s, they were presented with a hint (i.e. first letter of the correct solution). If they were still unable to find the solution to the problem within 10s they were shown the correct solution. Finally, when solved they had to select the last letter of the correct solution choosing from three letters and one “other” option. After each trial they had to rate whether they experienced a moment of insight, as well as their level of impasse, on a six-point Likert-like scale. The task consisted of four runs with twelve trials per run. Subjects solved 58% (SD=49%) of the items. 71% of the subjects' solutions conformed to the predefined solutions.

For this study, we used the previous RAT results solely for defining seed regions. This was performed by mean splitting based on individual insight ratings for each run per subject and weighted for high-insights at the event of insight (button press). Figure 1 shows the according group-level activation map for high-insight events. Activation increases in the bilateral inferior frontal cortices, insular cortices, dorsomedial prefrontal cortices, precuneus, ventral tegmental area, hippocampus, striatum and thalamus can be seen.

These seeds, therefore, corresponded to subcortical regions of the dopaminergic system with heightened BOLD activity when participants subjectively experienced insight, while solving a task item. The statistical threshold used for delineating seed regions for this study was set to $p < 0.00001$, FWE-corrected. We chose such a strict threshold in order to extract clear-cut unilateral clusters from the areas of interest, namely left midbrain including ventral tegmental area and substantia nigra (VTA/SN) and nucleus caudatus (NC). To investigate for potential DMN contributions we additionally defined the bilateral posterior cingulate cortex (PCC) as seed region, based on an anatomy based bilateral seed-voxel (6mm spheres at 5 - 52 -30 and -5 -52 -30).

Behavioural Data

Outside the scanner, the following self-report questionnaires were administered: (i) Ten Item Personality Inventory (TIPI; Gosling et al. (2003)), (ii) Dweck's Mindset Questionnaire (Dweck et al., 1995b), and (iii) Runco's Ideational Behavior Scale (RIBS; Runco et al. (2001)). TIPI is a very brief measure of the Big-Five personality traits: conscientiousness, openness, extraversion, agreeableness and emotional stability (Gosling et al., 2003). Dweck's Mindset Questionnaire (Dweck et al., 1995a) is a scale to assess a person's mindset, growth vs. fixed, and therefore motivation, about the malleability of intelligence, morality and world outlook. Thus, an incremental mindset herein refers to the belief that individual traits and abilities are not fixed and in fact one could grow their skills through sheer hard work and determination. On the other hand, a fixed mindset refers to the belief that one's potential is set and cannot be changed.

fMRI RS Data Processing

As a first step, RS data were despiked using AFNI (<http://afni.nimh.nih.gov/afni>). It has been shown that slice-timing correction (temporal sinc-interpolation of the MR signal with respect to slice acquisition times) can successfully adjust time shift between the acquisitions of the

different slices and, therefore, increases the preciseness of the data analysis (Sladky et al., 2011). This step is implemented in our preprocessing pipeline using FSL 5 (FMRIB Software Library, Analysis Group, FMRIB, Oxford, <http://fsl.fmrib.ox.ac.uk>). Data was then bias-field corrected using ANTs (<http://stnava.github.io/ANTs>), realigned using FSL 5, and normalized to standard MNI space using ANTs in combination with a custom scanner-specific EPI-template, resulting in a 1.5 mm³ isotropic resolution and finally smoothed with a 6mm FWHM Gaussian kernel using FSL 5. Post-processing was carried out using in-house applications, which are mostly based on the GNU Scientific Library (<http://www.gnu.org/software/gsl>) and comprised the following steps: (1) regressing out the cerebrospinal fluid and white matter signal to reduce physiological artefacts using the first 5 components of a temporal PCA and their mean for both regions; (2) FFT-based band-pass filtering in the frequency range of 0.009-0.08 Hz; (3) motion-scrubbing according to Power et al. (2012). In order to model the subcortical underpinnings of creativity – in particular insight-related networks – we chose the two activation maxima in subcortical areas from the dopamine system from the RAT functional localizer task: VTA/SN and NC (MNI coordinates -5 -28 -9 and -12 20 0, respectively). We also employed one anatomical seed region in the PCC to examine the DMN. As such, seed voxel correlation was performed for left VTA/SN, left NC and bilateral posterior cingulate cortex (PCC) resulting in three functional connectivity maps for every subject. Finally, cross-correlation coefficients were converted to z-scores using Fisher's z-transformation. An overview of the data processing pipeline is shown in **Figure 2**.

Behavioural Data Analysis

To gain additional information about the psychological structure of our subjects we performed correlation analyses between the different behavioural variables per se. We tested for normal distribution using exact Kolmogorov-Smirnov tests and subsequently performed two-tailed Pearson correlation analyses.

Regression Analysis between RS Functional Connectivity and Behavioural Data

Functional connectivity maps for each seed region were regressed across subjects (second level) as implemented in SPM12 against the following questionnaire measures: incremental mindset (Dweck), ideational behaviour (RIBS), and the five TIPI variables extraversion, emotional stability, agreeableness, openness and conscientiousness.

RESULTS

Behavioural Data

Performing exact Kolmogorov-Smirnov Test revealed that all behavioral variables could be approximated by normal distributions. In order to get deeper insights into our sample, we performed additional correlation analyses between behavioral variables. The variable openness correlated significantly with ideational behaviour ($r_{43}=.49$, $p=.001$) and incremental mindset ($r_{43}=.501$, $p=.001$). The personality trait extraversion did significantly correlate with conscientiousness ($r_{43}=.337$, $p=.027$), emotional stability ($r_{43}=.307$, $p=.045$) and ideational behavior ($r_{43}=.396$, $p=.009$). Additionally, conscientiousness correlated with agreeableness ($r_{43}=.327$, $p=.032$).

Resting State Networks

Figure 3 shows the three resting-state networks examined within this study. The network calculated from the caudate nucleus seed included bilateral basal ganglia, thalamus, anterior and posterior cingulate cortex, bilateral insula and hippocampus, dorso-medial prefrontal cortex and middle temporal lobes. VTA/SN network comprised bilateral VTA/SN, caudate, putamen, globus pallidus, insula, hippocampus, thalamus, as well as left inferior parietal cortex. The default-mode network consisted of the bilateral inferior parietal cortex, precuneus, anterior and posterior cingulate cortex as well as bilateral caudate, hippocampus and temporal lobe.

Regression Analysis of Creativity Measures on Functional Networks

Regressing the three networks (NC, VTA/SN and DMN) against our behavioural data we found that extraversion modulated NC network connectivity, while RIBS and emotional stability modulated the VTA/SN network. The variables agreeableness, openness and conscientiousness, as well as the incremental mindset did not result in statistically significant

modulations of the target networks. Furthermore, the default mode network was not found to be modulated by any of our variables of interest.

Higher extraversion scores (TIPI) were associated with increased connectivity of the bilateral putamina to the NC network ($r=.601$, $p<.0001$, **Figure 4**, left putamen peak: -36 -13 -10, $p<.010$, $k=508$, right putamen peak: 24 -1 -8, $p<.018$, $k=443$). Participants with higher ideational behaviour (RIBS) showed increased connectivity within the VTA/SN-network ($r=.631$, $p<.0001$, **Figure 5**, VTA/SN peak: 3 -18 -4, $p=.001$, $k=813$). Finally, increased measures of emotional stability were correlated with increased VTA/SN connectivity to putamen and PFC ($r=.653$, $p<.0001$, **Figure 6**, right putamen peak: 18 12 -10, $p<.0001$, $k=1467$, left putamen peak: -15 8 -10, $p<.0001$, $k=1783$, right midbrain peak: 6 -10 -10, $p=.001$, $k=819$, right lateral PFC peak: 42 22 53, $p<.0001$, $k=2208$, right caudate head peak: 18 2 20, $p<.0001$, $k=1440$, left putamen peak: -12 -13 -6, $p=.045$, $k=391$, left dorsal PFC peak: -15 4 62, $p<.046$, $k=389$, right orbital PFC: 28 65 -1, $p=.040$, $k=403$).

DISCUSSION

In this study we used ultra-high field fMRI to test for variations in brain network structures with individual markers for creative behaviour, attitude and personality. In order to ensure functional specificity of the networks examined, two of these networks were defined based on the neural substrate recruited during a creative problem-solving task. In addition, the DMN effects were also assessed as this network is implicated in a number of creativity-related processes.

Herein, we show that insight-related resting-state networks originating from subcortical areas of the dopaminergic system are modulated by Big-Five personality traits and ideational behaviour. Extraversion was coupled with increased connectivity to the left caudate and emotional stability and ideational behavior were linked to connectivity from VTA/SN.

In more detail: (1) extraversion is linked to bilateral posterior putamen connectivity, (2) ideational behaviour to local VTA/SN connectivity and (3) emotional stability is associated with modulations in cortical (e.g. DLPFC) and subcortical (mainly basal ganglia) VTA/SN connectivity.

The personality traits agreeableness, openness and conscientiousness, as well as incremental mindset as a marker for motivation were not associated with the networks investigated (NC, VTA/SN, DMN).

The Big-Five personality traits extraversion and openness have traditionally been linked to creativity (Batey et al., 2010; Hughes et al., 2013; Singh and Kaushik, 2015b). However, neuroticism (negative pole of emotional stability) has also been linked to creativity since elevated neuroticism is considered a fruitful source of rumination and problem generation (Perkins et al., 2015). In order to assess the Big-Five personality traits, we employed the Ten Item Personality Inventory (TIPI) and linked it to putative brain networks associated with

creativity and/or the dopamine system. In this respect, we found extraversion to modulate the NC network and emotional stability to explain differences in VTA/SN network connectivity.

Higher extraversion scores were found to be correlated with increased connectivity between the NC network and bilateral putamina. The putamen has generally been associated with behavioural inhibition (Sweitzer et al., 2018; Thames et al., 2012). In a recent metaanalysis Shen et al. (2018) found the bilateral putamina to be associated with spontaneous insight solutions. The putamen was, furthermore, found to have a high density of D2 receptors (Willeit et al., 2016). The Big-Five personality trait extraversion for its part has previously been associated with stronger dopamine release in the VTA, a midbrain structure crucially involved in dopamine release and therefore associated with increased exploratory behaviour, positive affect and creativity (Ashby et al., 1999; De Fruyt et al., 2000; Depue and Collins, 1999b; Goldberg, 1992; Panksepp, 1999; Peterson et al., 2002; Politis and Houtz, 2015; Tellegen, 1985).

On a behavioural level our finding underlines the psychological model of the paradoxical traits by Csikszentmihalyi (1996) of creative individuals being among others introverted and extraverted at the same time. This is since our results show that the extraversion component is simultaneously associated with behavioural control, as reflected in the associated putamen connectivity. This idea is further supported by extraversion being correlated with conscientiousness in our study sample – a personality trait conventionally found negatively correlated to creative behaviour (Batey et al., 2010). Csikszentmihalyi (1996) suggests the need of an equilibrium between the extraversion and introversion poles: on the one hand a creative person has to be self-sufficient and withdraw themselves from the everyday life in order to keep the focus to produce something novel and useful, on the other hand they have to convince others from their idea in order to be successful.

On a neural level, extraversion is here linked to the caudate nucleus as part of the dopaminergic system. Boot et al. (2017) suggest moderate dopamine release in the striatum to be beneficial for flexibility in cognition, perspective switching and the broadening of the attentional focus. Furthermore, the putamina are involved in spontaneous insights (Shen et al., 2018). The putamen is moreover associated with behavioural inhibition (Sweitzer et al., 2018; Thames et al., 2012). Peterson et al. (2002) found an association between extraversion and decreased latent inhibition, a gating process that allows ignoring prior irrelevant information. The decreased inhibition group also showed increased scores on a creative personality scale in their study. Thus, the authors argue that individuals with decreased latent inhibition but good cognitive control are more likely to develop their creative potential.

We suggest based on the neuro-behavioural association between extraversion, the basal ganglia and insight, that dopaminergic modulation might underlie both, insight and extraversion.

Our second task-derived seed-voxel correlation at the left VTA/SN especially included the midbrain, putamen, globus pallidus, nucleus caudatus and thalamus. Subjects showed increased connectivity of this network to the putamen, midbrain and lateral PFC depending on higher emotional stability scores. To date there is only very little research on the influence of emotional stability on creativity. Perkins et al. (2015) suggest an association between creativity and neuroticism (emotional stability) based on observations of heightened neuroticism scores in creative individuals and the link between psychopathology and creativity. Furthermore, one “negative” component of emotional stability, namely volatility was found to be related to creative achievements (Clark and DeYoung, 2014). In our case, we found a correlation between the positive aspect of this variable, namely high emotional stability per se, with VTA/SN network variability. Possibly, emotional stability in creativity

serves as an indicator for endurance in dead-end situations, while Perkins et al. (2015) suggest high neuroticism levels as origin of creating many problems and ruminating a lot. Connectivity disruptions in the lateral PFC have, moreover, been associated with depressive symptoms, like anhedonia and distress (Young et al., 2016), supporting the assumption that better emotional stability supports the ability to work on a task unhindered by negative emotions (compare Perkins et al. (2015)).

Furthermore, the personality trait emotional stability has been linked to D2 receptors, which are prominently represented in the VTA, caudate nucleus and putamen (Suridjan et al., 2012; Willeit et al., 2016). A neuro-psychiatric disease traditionally associated with altered dopamine release is schizophrenia (Howes et al., 2017). Indeed, schizotypy in creative individuals was proposed by some authors (Peterson et al., 2002; Takeuchi et al., 2012). They also stress the role of cortical top down regulation of basal ganglia dopamine based informational inflow to produce more creative rather than pathologic results.

In summary, neuroticism might play a beneficial role in problem generation and increased attentional focus towards these problems, which is coupled with psychopathology (Perkins et al., 2015). On the other hand, a certain amount of cortical top down control is needed to maintain motivation and evaluate results as reflected in our emotional stability values being coupled with increased cortical-subcortical connectivity.

Besides the effects of emotional stability on the VTA/SN network, ideational behaviour performance increased local midbrain connectivity strength. The RIBS (Runco et al., 2001) is a self-report scale that assesses differences in individuals' recalled tendency to generate novel and original ideas. People who describe themselves as having these ideas more often show increased functional connectivity between the VTA/SN and mid-brain structures. Stronger VTA/SN connectivity of individuals having more ideational thoughts strongly

underlines the dopamine theory of creativity (Boot et al., 2017; Lhommée et al., 2014; Takeuchi et al., 2012). Even more so, since VTA dopaminergic neurons project to the ventral striatum (VS), an area, which is strongly associated with learning, reward processing and the Aha!-moment (Tik et al., 2018). We could link this interconnected striatal network to extraversion scores as seen above.

Although all of our neuro-behavioural results hint towards an association between the dopaminergic system and behavioural traits involved in creativity, direct dopamine receptor imaging methods are needed to investigate the specific association between the dopaminergic system and creativity (Boot et al., 2017).

Similarly to Batey et al. (2010), we found an association between extraversion and openness to experiences with ideational behaviour. Extraversion is a personality trait associated with positive emotionality and a tendency to experience such emotions and openness is marked by originality, curiosity and ingenuity (Gosling et al., 2003). Openness and extraversion were both shown to be involved in decreased latent inhibition, a gating process that allows ignoring prior irrelevant information, which is proposed as a good originator of developing creative ideas (Peterson et al., 2002).

Even though suggested to be involved in creativity in former studies (Beaty et al., 2014; Chen et al., 2016; Takeuchi et al., 2011; Takeuchi et al., 2012; Wei et al., 2014), the DMN was not modulated by the behavioural variables included in our study.

Traditionally, Big-Five's openness to experience is seen as a predictor for creativity (Batey et al., 2010; Jauk et al., 2013). On a behavioural level, we show a clear correlation between measures of openness and ideational behaviour and incremental mindset in this study. Li et al. (2015) were able to identify a connection between creativity, openness and posterior middle temporal gyrus activation. There is also clear evidence of openness playing a

modulatory role in the DMN, which is associated with creative idea generation (Beaty et al., 2016; Smallwood and Schooler, 2015). The absence of findings concerning openness and resting-state connectivity might be explained by our network pre-selection that focuses only on ROIs activated while performing insight-related tasks, although modulations within the default mode might have been expected based on former literature (Beaty et al., 2016). One alternative explanation of our negative finding could be that openness to experience does not directly influence creativity related neuronal fluctuations, but is a moderating factor for other creativity related personality traits.

On a behavioural level our network-modulating variables extraversion, emotional stability and ideational behaviour showed significant correlation with each other. All of these three variables are associated with creativity (Agnoli et al., 2016; De Fruyt et al., 2000; Hao et al., 2016; Perkins et al., 2015; Singh and Kaushik, 2015a). In particular, links to the dopaminergic system have been repeatedly described for extraversion (Cohen et al., 2005; Depue and Collins, 1999a; Golimbet et al., 2007; Lhommée et al., 2017; Rammsayer, 1998; Wacker et al., 2006) and neuroticism (emotional stability) (Barbato et al., 2012; Canli, 2008; Fischer et al., 1997; Tochigi et al., 2006). There is also some evidence for a relationship between fluency and dopamine (Murphy et al., 2013).

Our results indicate that all of the three variables have modulatory effects on brain networks linked to dopaminergic pathways. However, openness and an incremental mindset might be expected to be associated to the same latent constructs (McCrea, 2000; Myers et al., 2016), but our results did not show significant correlations to resting-state networks. This finding might be explained by assuming that these variables are bound to only subcomponents of dopamine-associated networks.

A limitation of this study is the modest sample size of 43 subjects. Limited sample sizes are always of concern in studies linking neurobiological features with behavioural data. In this study, we address sample size limitations regarding statistical power by performing fMRI scanning at ultra-high magnetic field (7 Tesla) where sensitivity is considerably increased compared to 3T imaging via higher signal-to-noise ratios in general and higher BOLD signal responses (effects sizes) in particular (Sladky et al., 2013; Uğurbil, 2014). Nevertheless, conclusions drawn from a limited sample may not always generalise to the whole population nor reflect creativity in all facets. Also, individual differences might not be captured in a smaller sample, and errors might emerge from the specific measure of creativity.

CONCLUSION

This is the first study to examine personality traits of creativity that might be associated with the dopaminergic system using 7 Tesla RS fMRI. Using a comprehensive battery of behavioural measures we identified brain networks based on the subcortical dopaminergic system as a neural substrate related to creativity-based traits, i.e. extraversion, emotional stability and ideational behaviour performances.

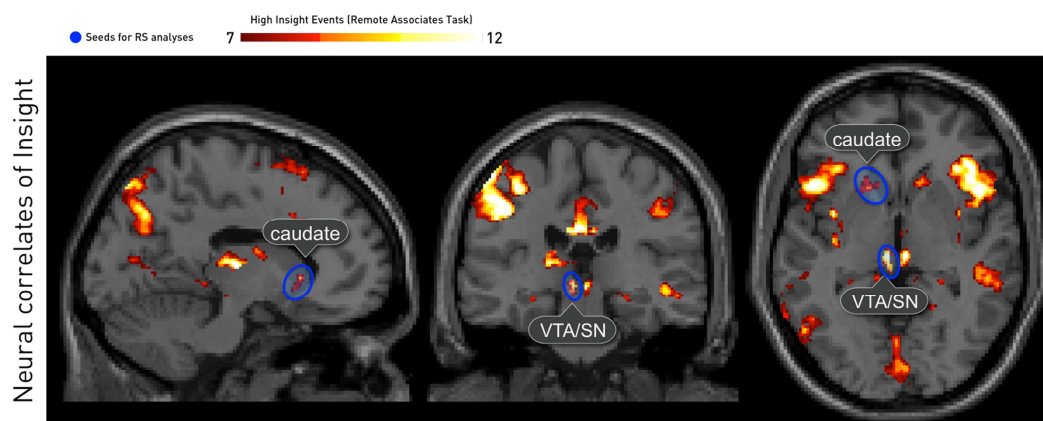


Figure 1. Neural Correlates of Insight. Insightful problem solving associated with a high-level of insight was coupled with increased activity in the VTA/SN and caudate head (Tik et al., 2018).

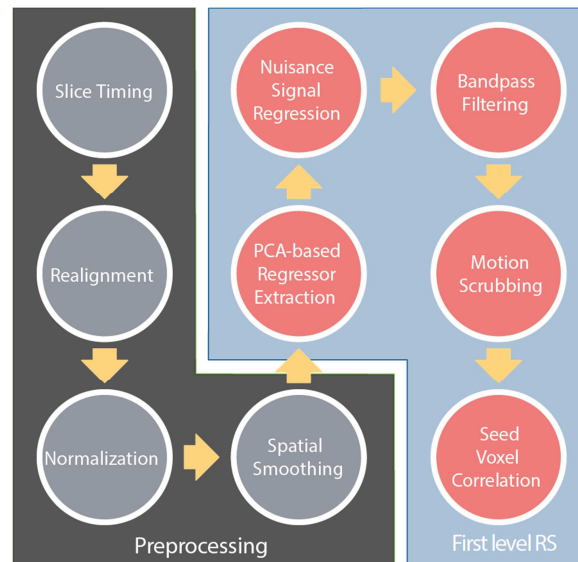


Figure 2. Preprocessing & First Level analysis of RS data. Resting-state data was de-spiked using AFNI, slice-timing corrected using FSL 5, bias-field corrected using ANTs, realigned using FSL 5, normalized to standard symmetric MNI space using ANTs in combination with a custom scanner-specific EPI-template, smoothed with a 6mm FWHM Gaussian kernel using FSL 5. Furthermore, the following steps were conducted using in-house applications: (a) CSF and WM signal was regressed out to reduce physiological artifacts, (b) FFT-based band-pass filtering in the frequency range of 0.009-0.08 Hz; (c) motion-scrubbing; and (d) seed voxel correlation using the mean time course of the seeds (based on task activation from (Tik et al., 2018)). Finally, the cross-correlation coefficients were converted to z-scores using Fisher's z-transformation.

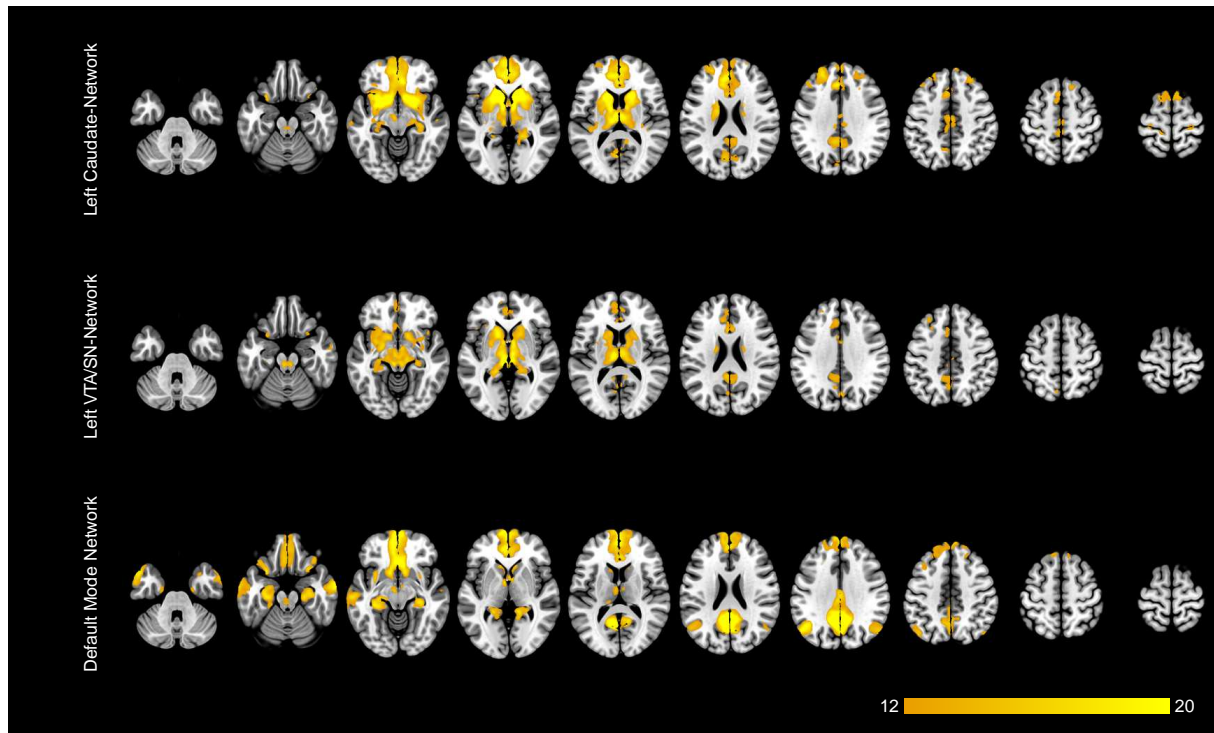


Figure 3. Networks of Interest. Seed-voxel correlation resulted in one caudate nucleus, one VTA/SN and the default mode network. In detail: (1) the left caudate network comprised the bilateral basal ganglia, thalamus, anterior and posterior cingulate cortex, bilateral insula and hippocampus, dorso-medial prefrontal cortex and middle temporal lobes. (2) The VTA/SN-network consisted of the bilateral basal ganglia, thalamus anterior and posterior cingulate cortex, bilateral insula and hippocampus as well as left inferior parietal lobule. (3) The default mode network consisted of the bilateral anterior and posterior cingulate cortex, caudate nucleus, hippocampus and inferior parietal lobule and precuneus.

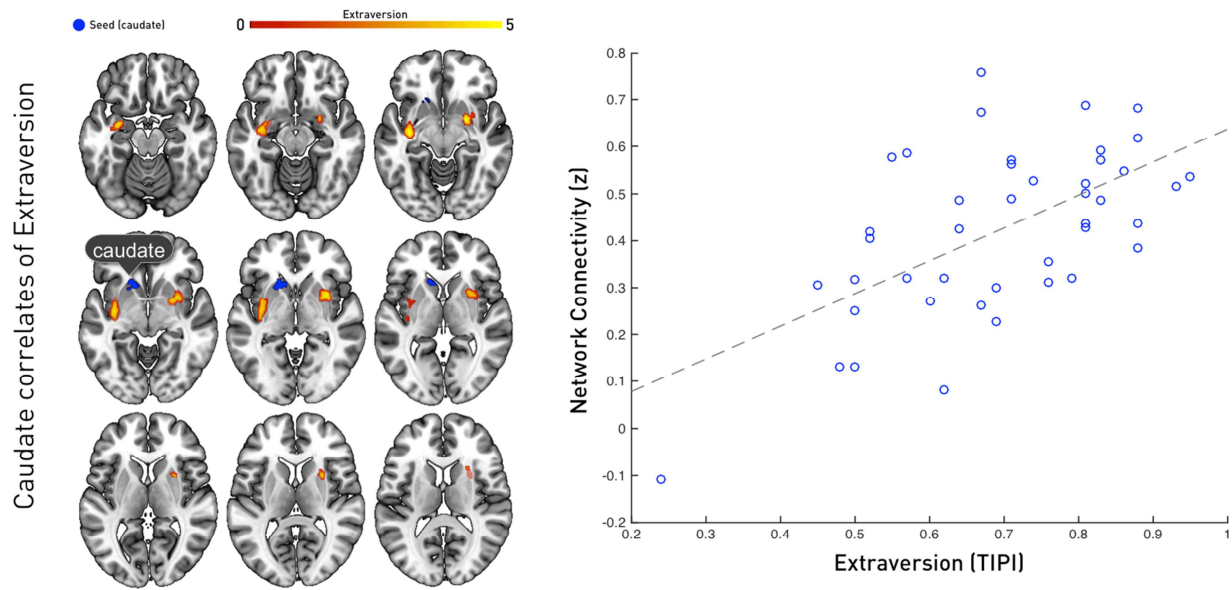


Figure 4. Altered Putamina Connectivity in the Caudate Network by Extraversion. For subjects with an increased extraversion level there is increased connectivity between the bilateral putamina (hot colours) and the NC seed-based (blue) network.

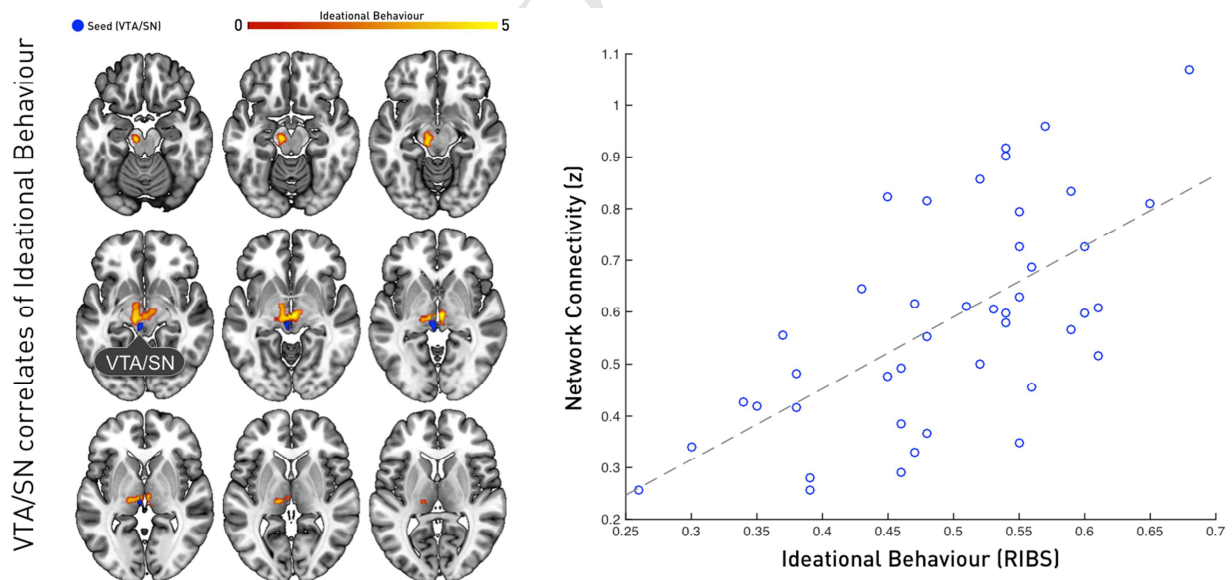


Figure 5. Midbrain Connectivity in the VTA/SN Network by Ideational Behaviour. For

subjects with an increased ideational behaviour there is increased connectivity between the midbrain (hot colours) and the VTA/SN seed-based (blue) network.

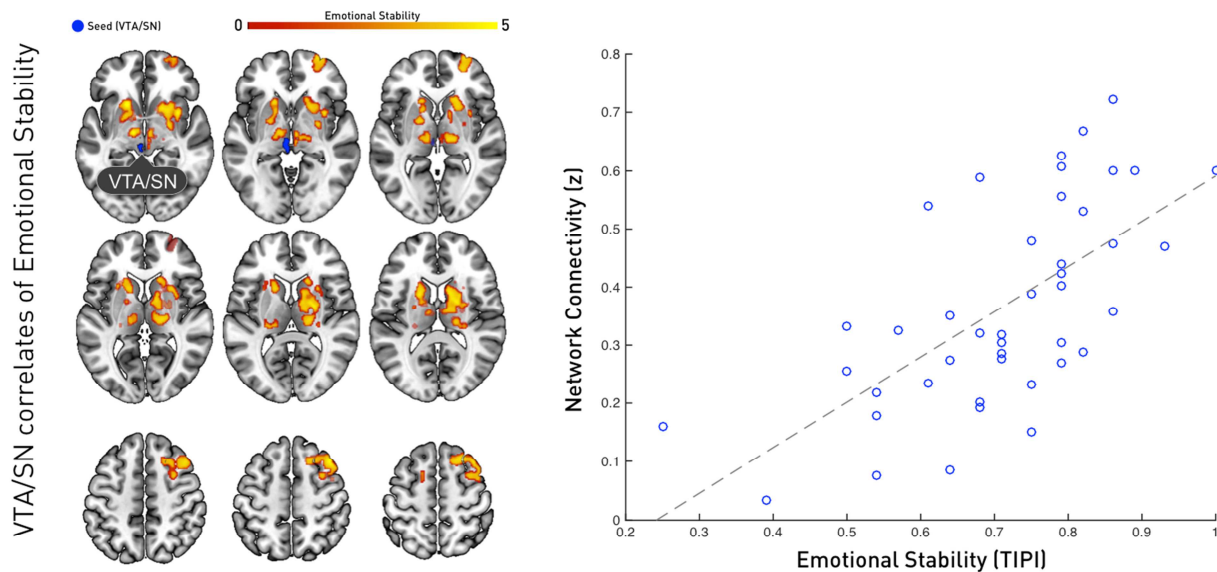


Figure 6. Altered Pallidal-Prefrontal Connectivity in the VTA/SN Network by Emotional Stability. For subjects with an increased emotional stability level there is increased connectivity between the pallidum (hot colours), lateral PFC and the VTA/SN seed-based (blue) network.

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Disclosure and Conflict of Interest

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