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ORIGINAL ARTICLE

The "Creative Right Brain" Revisited: Individual Creativity and Associative Priming in the Right Hemisphere Relate to Hemispheric Asymmetries in Reward Brain Function

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Abstract

The idea that creativity resides in the right cerebral hemisphere is persistent in popular science, but has been widely frowned upon by the scientific community due to little empirical support. Yet, creativity is believed to rely on the ability to combine remote concepts into novel and useful ideas, an ability which would depend on associative processing in the right hemisphere. Moreover, associative processing is modulated by dopamine, and asymmetries in dopamine functionality between hemispheres may imbalance the expression of their implemented cognitive functions. Here, by uniting these largely disconnected concepts, we hypothesize that relatively less dopamine function in the right hemisphere boosts creativity by releasing constraining effects of dopamine on remote associations. Indeed, participants with reduced neural responses in the dopaminergic system of the right hemisphere (estimated by functional MRI in a reward task with positive and negative feedback), displayed higher creativity (estimated by convergent and divergent tasks), and increased associative processing in the right hemisphere (estimated by a lateralized lexical decision task). Our findings offer unprecedented empirical support for a crucial and specific contribution of the right hemisphere to creativity. More importantly our study provides a comprehensive view on potential determinants of human creativity, namely dopamine-related activity and associative processing.

Key words: asymmetry, creativity, dopamine, hemisphere, priming

Introduction

Creativity is commonly defined as the ability to generate novel and useful ideas (Mumford 2003). In recent years, creativity has become a most valued ability across many sectors of human activities, ranging from personal/psychological development to innovative entrepreneurship (Gardner 2011; Runco and Pritzker 2011; Lehrer 2012; Runco 2014). Several theories have been proposed to account for interindividual differences in creative thinking. One prominent theory supports that high creativity is associated with being able to connect distant concepts, hence promoting the combination of remotely-connected concepts into original ideas (Mednick 1962). Thus, individual differences in creativity may implicate differences in associative processing (Mohr et al. 2001; Gruszka and Necka 2002; Benedek and Neubauer 2013; Kenett et al. 2014).

On the one hand, it is classically believed that the right hemisphere (RH) plays an important role in the processing of remote associations (broad associative coding) while the left

hemisphere (LH) would favour close associations (narrow associative coding) (Beeman et al. 1994; Chiarello et al. 2003; Hutchison 2003; Jung-Beeman 2005). Thus, differences in associative processing between hemispheres may influence interindividual differences in creativity. On the other hand, associative processing may also relate to dopamine (DA) function. Animal data have shown that DA enhances cortical signal-to-noise ratios (Winterer and Weinberger 2004; Kroener et al. 2009) and computational accounts suggest that DA limits associative processing (Spitzer 1997). Thus, increased DA would prevent the coactivation of remotely related concepts (Kischka et al. 1996; Angwin et al. 2004; Roesch-Ely et al. 2006). Critically, the level of DA activity may differ between hemispheres (Molochnikov and Cohen 2014), and this difference may shift the balance between behaviours subserved by each hemisphere (Maril et al. 2013; Tomer et al. 2013; Porat et al. 2014; Tomer et al. 2014; Aberg et al. 2015, 2016). Importantly, interhemispheric difference in DA function, but not its absolute intrahemispheric level, predicts an individual's tendency to orient towards one specific side of space (Tomer et al. 2013), or display increased approach (vs. avoidance) behaviours (Tomer et al. 2014).

Yet, despite a growing need for understanding the underpinnings of creative thinking, the exact implication of DA function and associative processing in creativity is still unclear.

Based on these observations from different research fields, here we hypothesized that creativity is increased whenever broad associative processing is promoted, and that hemispheric asymmetries in DA function may determine the overall balance between broad and narrow associative coding. We specifically expected that decreased DA function in the RH (relative to the LH) would release the RH from the constraining effects of DA on associative processing and facilitate access to remote associations by the RH. We thus tested whether individuals displaying reduced DA function in the RH (i.e., LH DA dominance) would display both increased associative priming in the RH as well as increased creativity, as compared with individuals displaying relative increased DA function in the RH (i.e., RH DA dominance).

Our main measure of interest, that is, creativity, was estimated in 42 healthy participants using an alternative uses task (AUT) and a remote associates test (RAT), which implicate distinct aspects of creative cognition, that is, divergent- and convergent thinking, respectively (Guilford 1967). Functional MRI (fMRI) data were then acquired while the participants performed a reward task known to activate the mesolimbic DA reward system (Pessiglione et al. 2006; Jocham et al. 2011), and which allowed us to compute an index of hemispheric asymmetry in DA function (differential neural response in the left and right ventral striatum for positive and negative feedback; for further justification for estimating asymmetric DA function through reward-related ventral striatum activity, see Aberg et al. 2015). Associative processing in the different hemispheres was also investigated during fMRI scanning using a lexical decision task with laterally presented target words.

As predicted, individuals showing relatively less DA function in the RH (or LH DA dominant) displayed increased associative priming in the RH, as indicated both by faster response times (RTs) and decreased brain activity in the RH as a function of word pair relatedness. Critically, these participants also scored higher on both the divergent and convergent thinking tasks. While confirming the hypothesized role of associative processing in creativity, our study significantly extends previous research by showing, for the first time to our knowledge, that individual creative potential may be determined by hemispheric asymmetries in DA function through its modulation of associative priming in the RH.

Materials and Methods

Participants

A total of 42 healthy volunteers participated in the study after providing written consent according to the ethical regulations of the Geneva University Hospital. Inclusion criteria included no previous history of neurological or psychological disorders, right-handedness, and being a native French speaker. Four participants fell asleep in the scanner, 2 participants failed to follow task instructions, and 4 participants did not reach the performance criteria in the reward task (see later). Data from these participants were excluded in the analyses. Thus, data from 32 participants (15 males; average age 23.41 ± 0.78 years ± SEM) (standard error of the mean) were analyzed. The study was performed in accordance with the Declaration of Helsinki.

Overall Procedure

Prescanning Session

Participants were first informed about the experimental protocol, tasks, and the overarching goal of the study. After they provided written informed consent, participants practiced a probabilistic selection task (PST) and a lexical decision task to ensure good understanding of the tasks (the tasks are described later). Next, participants performed PST training blocks outside of the scanner until their performance reached specific learning criteria and then entered the MRI scanner.

Scanning Session

Inside the MRI scanner, participants performed the PST (i.e., 2 additional training blocks followed by a test phase, see later) and, after a short pause, the lexical decision task.

Postscanning Session

After the MRI session, participants first performed an AUT followed by a RAT, ranked the associations between words in the word pairs used for the lexical decision task, and were finally debriefed about the purpose of the study.

Below we first describe the reward task used to assess hemispheric differences in activity within ventral striatum, on the basis of which the participants were assigned to a left or right DA dominant group. We then describe the lateralized associative priming task, and the 2 tests used to assess individual levels of creativity. The reward and priming tasks were performed in an MRI scanner.

Probabilistic Selection Task

In the PST, participants learned to associate different symbols with different reward probabilities through a trial-and-error procedure (Frank et al. 2005). Here, the analysis of this task is limited to hemispheric asymmetries in reward processing. A full description of this task and analyses related to learning can be found elsewhere (Aberg et al. 2015).

First participants performed a training session outside the scanner. In each trial a central fixation cross was first presented for 1.25 s (randomly jittered between 0.5 and 2.0 s), followed by 1 of 3 possible pairs of symbols (AB, CD, or EF) presented for 1.0 s (Fig. 1A). After selecting one of the symbols, a positive or a negative smiley face was presented for 0.6 s. The type of feedback depended on the reward probability associated with each

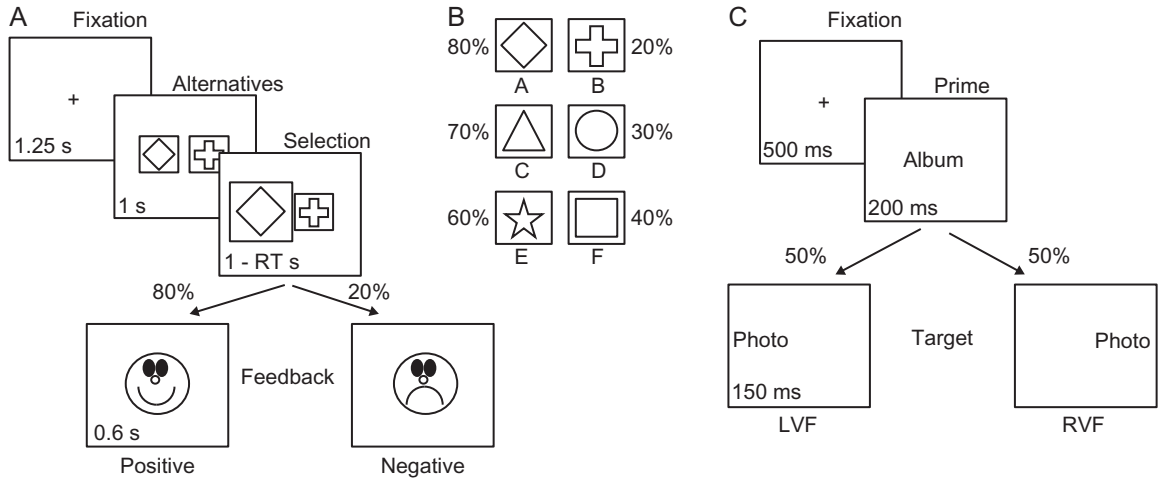

Figure 1. (A) One training trial in the probabilistic selection task. Participants had 1 s to select one of the symbols presented to the left or to the right. Based on the selected symbol's reward probability, positive or negative feedback was presented. RT = response time. (B) Reward probabilities associated with each symbol. The reward probabilities and symbols were randomized between participants. (C) One trial in the lexical decision task. After fixation a prime (word or nonword) was presented centrally for 200 ms directly followed by a 150 ms presentation of either a laterally presented target (word or nonword). Participants indicated whether the target was a real word or a nonword. LVF = Left visual field. RVF = Right visual field.

symbol (Fig. 1B). In the illustrated example, selecting the "A" symbol yields a happy smiley face with 80% probability while the corresponding probability is 20% for selecting the "B" symbol. Participants were instructed to collect as many happy smiley faces as possible while avoiding getting sad smiley faces. To ensure that participants had learned the task before entering the MRI scanner, training continued until the A and C symbols had been selected at least 60% and 55% respectively within one block, or until 45 minutes had passed. Data from participants failing to reach the criteria were excluded from further analyses ($n = 4$; for a similar procedure, see Frank et al. 2005). To investigate the neural correlates of reward processing, 2 training blocks were performed in the MRI scanner. However, to make the task design suitable for an event-related fMRI design, the central fixation cross was presented for 3.5 s (randomly jittered between 2.0 and 5.0 s). The assignment of symbols to different pairs was randomized between participants. In each block, each pair was presented 20 times, and a pair was not repeated until one of each other pair had been presented. Between participants, the symbols were randomly assigned to the different pairs and the reward probabilities were randomly assigned to different symbols. The fMRI data analyses are explained in the section MRI Data Analysis.

Lateralized Priming Task (Lexical Decision Task)

Associative priming was studied using a standard lexical decision task in which participants determined whether the second of 2 sequentially presented letter strings was a real word or a nonword (Pizzagalli et al. 2001; Mohr et al. 2006).

Stimuli

Associative priming was investigated by word pairs in which the 2 words differed in their degree of relatedness. Closely related word pairs were obtained from previous studies (Shelton and Martin 1992; Beeman et al. 1994), lists of closely associated words (Balota and Lorch 1986; Ferrand and Alario 1998; de la Haye 2003), or were created by us. Weakly related word pairs were obtained from previous studies (Balota and Lorch 1986; Richards and Chiarello 1995) or were created by us. Unrelated word pairs were created by us. Some of the words had to be translated from English to French. To ensure that participants perceived the word pairs with the intended degree of relatedness, 8 additional participants (who did not take part in the main experiment) indicated the relatedness for each word pair as either closely, weakly, or unrelated. Only word pairs with zero or one mismatch between these ratings and the predefined categories were included in the experiment. Finally, word pairs were selected such that word length and word frequency between the categories were balanced. Word frequency norms were acquired from the Lexique 3.80 database (New et al. 2001). Two separate 2-way analysis of variances (ANOVA) with factors Relatedness (closely, weakly, and unrelated) and Word type (Prime, Target) with word frequency and word length as dependent variables indicated main effects of Word type both for word frequency [$F(1,176) = 22.46$, $P < 0.001$] and word length [$F(1,175) = 6.91$, $P < 0.01$] because Prime words were on average longer and less frequent than Target words (Supplementary Table S1). Importantly there was no main effect of Relatedness nor interaction between Word type and Relatedness (all $P > 0.69$), indicating no differences in word length or word frequency between word categories. This was also confirmed by 2-sample Monte-Carlo permutation tests indicating no differences between word frequency and word length between categories within each Word type (all $P > 0.13$). In total, the 3 word pair categories contained 28 word pairs each with the average word frequency and word length listed in Supplementary Table S1. Nonwords were created either by replacing 2 consonants in target words of real word pairs not included in any of the 3 main word pair categories, or by randomly mixing the letters k, w, x, y, and z, which are the most infrequent letters in the French language (New et al. 2001). For example, from the words "melon" (melon) and "voiture" (car) the nonwords "telot" and "loicure" could be created. The length of the nonword pairs containing the consonant strings were matched to the word length of the real word pairs.

Task

Participants indicated whether the second of 2 sequentially presented letter strings was a real word or a nonword by pressing one of 2 buttons with their right hand. Each trial started

with a fixation cross (500 ms) directly followed by a prime (word or nonword) presented at the centre of fixation (200 ms) which was directly followed by a laterally presented target (word or nonword; 150 ms; Fig. 1C). The target was presented with a lateral offset of 2 degrees of visual angle from the centre. Half of the time the target was presented to the left visual field/RH (LVF/RH) and half of the time the target was presented to the right visual field/LH (RVF/LH). Participants needed to respond within 1.5 s, otherwise that trial was cancelled and the next trial was initiated. Each trial was separated by a random jitter between 2 and 5 s with an average jitter of 3.5 s.

For each category, the pairs of letter strings were presented in 4 blocks of 7 trials, together with interleaved nonword trials. Each block was presented twice, with targets being presented to the other hemifield the second time and the order of the pairs randomized between the 2 blocks. The number of lateral presentations of the target to the left or to the right was counterbalanced within a block and was limited to 3 presentations in a row on the same side. Finally, the order of blocks was counterbalanced such that no category was repeated until one block of each other category had been presented. To get familiarized with the task, participants trained the task before entering the MRI scanner. Additionally, a few training trials were performed inside the scanner before the main experiment. None of the letter strings used during the familiarization or the training was used during the proper experiment.

Importantly, to prevent eye movements (i.e., saccades to the target), the target presentation time (150 ms) was selected to be shorter than the typical saccade latency of 200 ms (Carpenter 1977). Moreover, it was practically impossible for participants to predict the presentation side of the targets because they were presented randomly to the left or to the right of fixation with the limitations of maximum 4 successive presentations to one side, equal number of presentations to each side within a block, and each target presented one time to each side. Participants were also instructed to fixate the centre of the screen at all times because the target would be presented too quickly to allow for eye movements, and that presentation sides were randomized and could not be predicted.

Individual Ratings of Relatedness

At the end of the experiment, each participant ranked the relatedness between the words in each real word pair on a scale from 1 (not related) to 7 (strongly related). These rankings were used to assign each word pair to 1 of 3 categories for each participant separately. Word pairs with a rank of 6–7, 3–5, and 1–2 were assigned to categories with closely related, weakly related, or unrelated word pairs, respectively. This is an important step as individuals differ in their ability to find associative relations (Gruszka and Necka 2002), something which may also underlie individual differences in creativity (Mednick 1962). Thus, creating categories on an individual bases ensures correct classification of the different word pairs. On average, word pair rankings for closely related word pairs were ranked as more strongly related than weakly related, while weakly related word pairs were ranked more strongly related than unrelated word pairs (Supplementary Table S2).

Data Analysis

RTs for correct lexical decisions were analyzed after RTs faster than 250 ms and RTs slower than 2 standard deviations above the mean RT (within each condition and side of presentation), had been removed from the analyses. The resulting RTs were averaged within each condition and side of presentation. An index of associative priming was created by calculating the regression slope for the RTs as a function of word pair category for each participant and side of presentation separately. Thus, a large difference in processing speed between different word categories is reflected in a large priming index, which in turn indicates increased modulation by associative strength. Analysis of the fMRI data is explained in the section MRI Data Analysis.

Creativity Tasks

Alternative Uses Task

Divergent thinking involves producing multiple solutions when generating creative ideas, and is commonly estimated by the AUT in which alternative uses to common day objects need to be listed (Guilford 1967).

Stimuli

Stimuli consisted of 6 pictures of everyday objects (a shoe, a newspaper, a brick, a car tire, a pencil, and a chair).

Task

In each trial, a picture of an everyday object was displayed on a computer screen together with a text box where alternative uses could by typed in. Participants were instructed to generate as many original and useful alternative uses for each object as possible. They were also informed that the task estimates creativity, that listing regular uses for the objects should thus be avoided, and that grammar or typography was not important. After 2 min the text box disappeared and the next trial was initiated. Before the experiment, participants were given the example of a coin, a regular use being to pay with it, while alternative uses could include flipping it, use it to draw a circle, or remove dirt from the shoe.

Data Analysis

The results were manually corrected by 2 independent raters based on the guidelines provided by Guilford (1967). First, regular uses (i.e., use a pencil to write or draw) and nonsensical uses (i.e., put a pencil in the fridge) were removed from the analysis. Next, participants were scored on 4 different components: Originality, Fluency, Flexibility, and Elaboration. For Fluency one point was awarded for each listed alternative. For Flexibility one point was awarded for each category provided, for example, only one point was awarded for the answers “to hit someone with” and “a weapon” because they belong to the same category (i.e., a weapon). For Elaboration one point was awarded for each listed detail, for example, 0 points were awarded for the answer “doorstop” while 1 point was awarded for the answer “a doorstop to prevent draft from closing the door.” For Originality one point was awarded for each alternative listed by <3 out of the 42 participants (i.e., <5% of participants in the present study), while 2 points were awarded for each alternative listed by only by one participant. Each component’s score was calculated as the average scores across the 6 objects and a final score was calculated as the average score of the 2 independent raters. Here, the analysis will focus on the Originality score because this measure is most representative of creativity and the ability to connect remotely related concepts (Mednick 1962).

Remote Associates Test

Convergent thinking is the type of thinking required to find the single best solution to a clearly defined problem (Cropley 2006), and is commonly estimated via the RAT. In the RAT, the connection between triplets of words needs to be discovered, that is, "egg" links the words in the triplet "chicken," "white," and "yellow." The RAT was originally developed to test the notion that high creativity is associated with the ability to combine remotely related concepts (Mednick and Mednick 1967).

Stimuli

Overall, 89 triplets of words which could be linked by a fourth word or concept were created by us or obtained from a French version of the popular board game "TriBond" (Wikipedia 2015, May 06). To ensure an adequate level of difficulty, 8 additional participants (who did not take part in the main experiment) tried to find the solution to each of these triplets. The triplets were then assigned to 1 of 4 categories based on how many participants managed to find the solution. In the Very easy, Moderately easy, Moderately difficult, and Very difficult categories, a solution was found by 7–8, 5–6, 3–4, and 1–2 of the 8 participants, respectively. Finally, 8 triplets from each category were selected for a total of 32 different triplets that were presented to each participant in the experiment.

Task

In each trial of the RAT, a triplet of words was presented on the screen together with a text box where participants could type in the solution. Participants were instructed to find a solution consisting of a fourth word or a brief sentence linking the words of the triplet. For example, the solution to the triplet "yellow," "white," and "chicken," is "egg." After 30 s the text box disappeared and the next trial was initiated. Before the experiment, participants were shown 9 different triplets (not part of the experiment proper) and their solutions in order to provide a range for the type of solutions expected.

Data Analysis

The answers were manually corrected by 2 independent raters. Alternative solutions were accepted for some of the triplets. For example, besides the correct solution "guitar," also the solution "music" was accepted for the triplet "classical," "Spanish," and "electric." The plausibility of alternative solutions was discussed between the raters and the researchers. Critically, both raters and the researchers were blind to the group assigned to each participant, as well as their performance on the other tasks. This was also the case for the AUT. Finally, the score was calculated as the total number of correct solutions and the final score was calculated as the average score of the 2 independent raters.

MRI Data

Image Acquisition

MRI images were acquired using a 3 T whole body MRI scanner (Trio TIM, Siemens, Germany) with a 12-channel head coil. Standard structural images were acquired with a T1 weighted 3D sequence (MPRAGE, flip angle = 9°, voxel dimensions = 1 mm isotropic, TR/TI/TE = 1900/900/2.27 ms, 256 × 256 × 192 voxels). Functional images were acquired with a susceptibility weighted EPI sequence (flip angle = 80°, voxel dimensions = 3.2 mm isotropic,TR/TE = 2100/30 ms, 64 × 64 × 36 voxels).

MRI Data Analysis

Neuroimaging data were preprocessed using the mean image to realign all functional volumes, which were then co-registered to the structural T1 image, slice time corrected, normalized to the MNI EPI-template, and finally an 8 mm FWHM Gaussian kernel was used for smoothing. Whole-brain, voxel-wise statistical analyses were performed using the general linear model (GLM) for event-related designs in SPM8 (Welcome Department of Imaging Neuroscience, London, UK; http://www.fil.ion.ucl.ac.uk/spm). For each participant, a standard synthetic hemodynamic response function (HRF) was used to model individual events with 6 rigid-body realignment parameters included as nuisance covariates. Contrasts between conditions (see later) were then calculated and the contrast images entered into second-level tests implemented in SPM.

Reward Processing in the PST

PST training blocks inside the MRI scanner was used to estimate hemispheric asymmetries in reward processing. The corresponding event-related design included 2 zero duration event-types time-locked to the onset of positive and negative feedback, respectively. Two parametric modulators reflecting reward prediction errors were also included in the analysis, but will not be discussed further here (Aberg et al. 2015).

Functional brain asymmetries are commonly estimated by either counting the number of active voxels, or looking at voxel intensity, within ROIs between hemispheres (Jansen et al. 2006; Wilke and Lidzba 2007; Seghier 2008; Abbott et al. 2010). Here, an asymmetry index was calculated based on the voxel intensity because the present study aimed to study hemispheric asymmetries in DA function and altered levels of DA function are known to impact the intensity of neural activation (Pessiglione et al. 2006; Knutson and Gibbs 2007; Jocham et al. 2011; van der Vegt et al. 2013). Moreover, recent reports indicate the estimates of functional brain asymmetries based on voxel intensities, as compared with the number of active voxels, provide more robust and reproducible results (Jansen et al. 2006). However, this requires the estimate to be based on the intensity of the most active voxels, and ROIs which are small and clearly defined through a combination of functional and anatomical landmarks (Jansen *et al.* 2006).

In accordance with these guidelines, using a functional localizer (i.e., the contrast between positive and negative feedback; Carlson et al. 2011; Jocham *et al.* 2011) constrained by previous anatomical reports (see section Region of Interest Analyses), we localized the ventral striatum (VStr), and estimated the intensity of the most activated voxels by extracting and averaging the beta values for all voxels within a sphere (radius = 3 mm) centred on the coordinates of the peak activity. The average beta values for the left and the right ventral striatum were then used to calculate a reward asymmetry index according to recent recommendations (Seghier 2008): Reward asymmetry index = $[(R - L) / (|R| + |L|)]$, where $R = [\text{PosFB-NegFB}]_{R\ VStr}$ and $L = [\text{PosFB-NegFB}]_{L\ VStr}$. A negative reward asymmetry index indicates increased reward processing in the left VStr while a positive value reflects increased reward processing in the right VStr.

Associative Priming in the Lexical Decision Task

Brain activity correlating with associative priming was investigated by using an event-related design which included 2 event-types of zero duration which were time-locked to the onset of the target presented to the LVF/RH or the RVF/LH for correct

lexical decisions. Individual ratings of the relatedness for each word pair (closely, weakly, or unrelated) were transformed to numbers and used as parametric modulators modelled at the time of target onset. This approach yields one value indicating the strength of associative priming for each voxel and side of presentation.

Region of Interest Analyses

For small volume corrections (SVCs), a priori region of interests (ROIs) were created as guided by previous literature. The ventral striatum ROI was created by combining 2 spheres (radius = 5mm) centred on coordinates provided by a previous study [Neto et al. 2008; left VStr: MNI $x = -9$, $y = 9$, $z = -8$; right VStr: MNI $x = 9$, $y = 8$, $z = -8$].

Associative priming is frequently reported in the inferior frontal gyrus (Inferior FG) and the middle frontal gyrus (Middle FG) (Bookheimer 2002; Kotz et al. 2002; Tivarus et al. 2006; Sachs et al. 2008; Sachs et al. 2011). Additionally, the right parietal lobe has been implicated in broad associative processing (Kiefer et al. 1998) and recent studies report the involvement of the bilateral inferior parietal lobe (Inferior PL) in creative performance (Fink et al. 2010; Fink et al. 2014), indicating a link between the parietal cortex, broad associative processes, and creativity. Therefore, to study the neural correlates of associative priming, ROIs for the bilateral Inferior FG, Middle FG, and Inferior PL were obtained using pre-existing ROIs from the WFU PickAtlas toolbox (Maldjian et al. 2003).

Statistical Analyses

Behavior

Group differences in associative priming and creativity were tested by comparing performance using ANOVA and Monte-Carlo permutation tests (Howell 2013). In particular, the directed prediction that associative priming is larger for word pairs presented to the LVF for participants displaying LH DA dominance was tested by comparing the RT priming index for the LVF between groups using a one-tailed permutation test. Increased LVF/RH priming is believed to reflect improved access to remote associates (Jung-Beeman 2005), something which may contribute to creativity by enhancing both convergent (Mednick 1962) and divergent thinking (Mednick and Mednick 1967). Because convergent and divergent thinking capabilities can be indexed by performance on the RAT and the AUT, respectively, the directed prediction that participants in the LH DA dominance group are more creative was tested by comparing AUT Originality and RAT scores between groups using one-tailed permutation tests.

Of note, Monte-Carlo methods are particularly useful in small sample sizes as these methods do not require any assumption concerning the distribution of data (Howell 2013). To ensure exchangeability between groups, Levene's test for Equality of Variance was used for each test [all $P > 0.13$], and 10 000 samples were used for each permutation test.

Functional MRI

Group differences in associative priming were tested by comparing conditions using two-sample *t*-tests implemented in SPM. In particular, the directed prediction that associative priming is larger (reflected in decreased neural responses) for real word pairs presented to the LVF for participants displaying LH DA dominance was tested by comparing the beta values for the parametric modulation by word-pair relatedness in the LVF between groups. The obtained results are reported using a height threshold of $P < 0.001$ and a minimum cluster size of 5 contiguous voxels. Small volume corrections (SVC) using a threshold of $P < 0.05$ Family-Wise Error Rate (FWER) for multiple comparisons were obtained using the a priori ROIs reported above.

Results

Probabilistic Selection Task

Hemispheric Reward Asymmetries

Figure 2A displays the average neural response to positive versus negative feedback. Activity in the bilateral ventral striatum (VStr) was higher for positive versus negative feedback [left VStr: peak voxel MNI $x = -12$, $y = 8$, $z = -11$, $t(1,30) = 4.136$, $p_{SVC} = 0.004$; right VStr peak voxel MNI $x = 9$, $y = 11$, $z = -11$, $t(1,30) = 6.292$, $p_{SVC} < 0.00001$]. Next, a hemispheric reward asymmetry index was calculated for each participant by extracting the neural response to positive and negative feedback from a 3 mm radius sphere centred on these coordinates. Figure 2B displays the distribution of participants as a function of their hemispheric reward asymmetry index. A total of 14 participants displayed a larger reward response in the left as compared with the right ventral striatum (the LH DA dominance group) while 18 participants displayed the reverse trend,

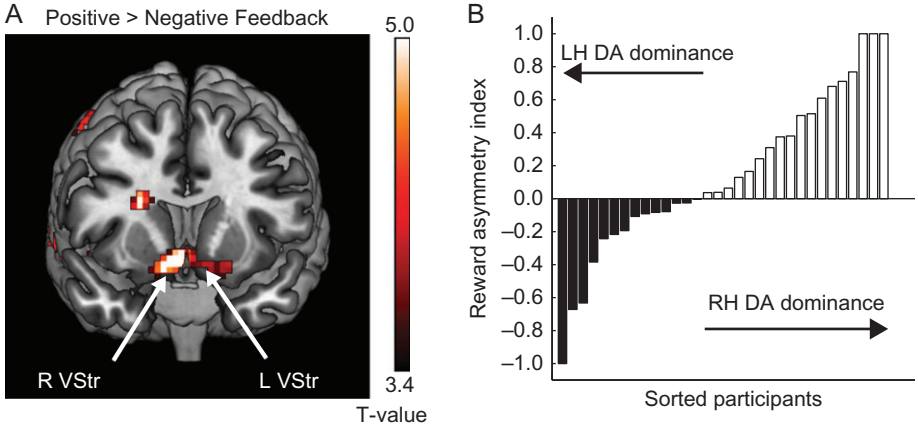

Figure 2. (A) Differential neural response to positive versus negative feedback. (B) Distribution of the hemispheric reward asymmetry index. L/R VStr = left/right ventral striatum.

for example, a larger response in the right as compared with the left ventral striatum (the RH DA dominance group). To test for the links between hemispheric asymmetries in DA function, on the one hand, and associative processing and creativity, on the other hand, we separated the participants into 2 groups based on their reward asymmetry index.

Creativity Tasks

To assess the relationship between asymmetric reward responses and creativity, we tested whether participants in the RH and LH DA dominance groups differed in creative performance on a divergent and a convergent thinking task.

The Alternative Uses Task

Participants tried to come up with alternative uses for 6 common objects. The generated ideas were rated on 4 dimensions estimating creative Fluency, Flexibility, Elaboration, and Originality. While participants in the LH DA dominance group came up with more original ideas [mean AUT Originality = 3.051 ± 0.320] as compared with participants in the RH DA dominance group [mean AUT Originality = 1.986 ± 0.355, $P = 0.021$ (one-tailed)], the groups did not differ in Fluency, Flexibility, or Elaboration (all $P > 0.1$; see Supplementary Table S3).

The Remote Associates Test

Participants had to propose a word or brief sentence that would link word-triplets. On average participants in the LH DA dominance group were significantly better at finding the correct solution [mean RAT score = 20.18 ± 0.673] as compared with participants in the RH DA dominance group [mean RAT score = 16.69 ± 1.174, $P = 0.012$ (one-tailed)]. These results confirm the prediction that hemispheric asymmetries in DA function relate to creative cognition.

Lexical Decision Task

To determine whether enhanced creative performance could be related to increased associative processing in the RH for participants in the LH DA dominance group, we tested whether participants in the 2 groups also differed in associative processing for real word pairs presented to different hemispheres.

Response Times

The average RTs for correct lexical decisions are displayed in Figure 3A. An index for the associative priming was calculated by the linear regression slope between RTs and word pair categories (Fig. 3B). As indicated by a mean priming index larger than zero, associative priming occurred in the RVF for both the LH DA dominance group (mean index = 22.092 ± 8.311, $P = 0.016$) and for the RH DA dominance group (mean index = 18.097 ± 5.086, $P = 0.003$), but did not differ between groups ($P = 0.669$). In the LVF, priming occurred for both the LH DA dominance group (mean index = 47.259 ± 13.378, $P = 0.001$) and the RH DA dominance group (mean index = 22.673 ± 6.510, $P = 0.002$). Critically, and in accordance with our prediction, a planned comparison revealed a larger priming index in the LVF for the LH DA dominance group as compared with the RH DA dominance group ($P = 0.042$, one-tailed). A more classical approach to study priming effects is to use the unrelated word pairs as baseline, such that priming in a condition is indicated by relatively faster RTs as compared with a condition with unrelated word pairs. Performing this supplementary analysis revealed that, while priming occurred for closely related word pairs in all conditions for both groups, priming for weakly related word pairs only occurred in the LVF and only for participants in the LH DA dominance group [Supplementary Table S4 for details]. Crucially, these results indicate that only participants in the LH DA dominance group displayed enhanced associative processing in the RH, as indicated by increased associative priming for weakly related word pairs presented to the LVF.

Functional MRI Data

LVF Presentation. RTs indicated significant group differences in associative priming for real word pairs presented in the LVF. Similar differences should therefore be reflected in brain regions sensitive to word pair relatedness. A direct comparison between the 2 groups using a two-sample *t*-test revealed differences in brain activity in the RH, but not in the LH, as a function of decreased relatedness for word pairs presented to the LVF (Fig. 4A). This included significant differences in the Inferior PL (peak voxel MNI $x = 48$, $y = -34$, $z = 49$; $t(1,30) = 3.783$, $p_{SVC} = 0.040$) and trends towards significance in the Inferior FG (peak voxel MNI $x = 54$, $y = 14$, $z = 25$; t

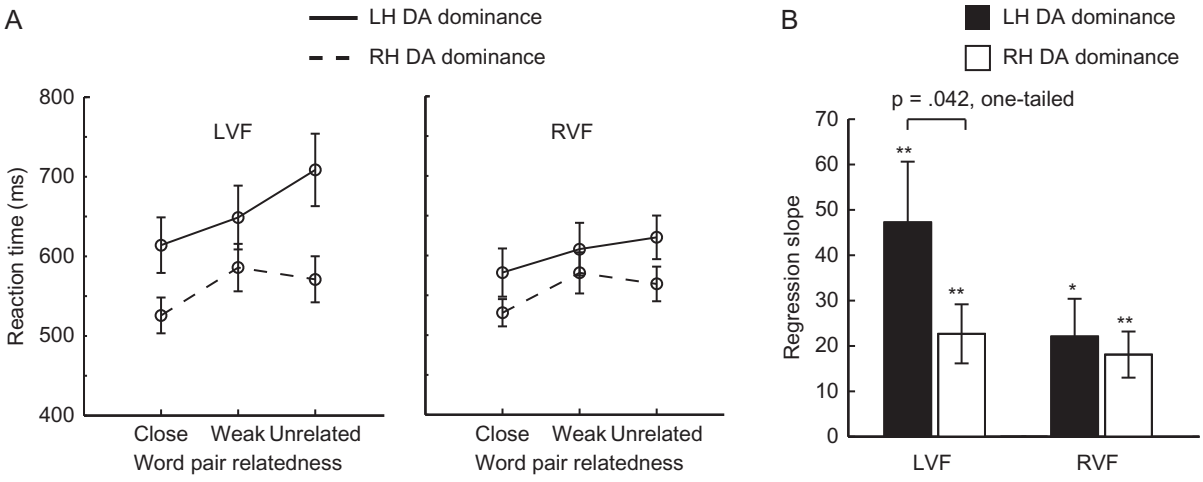

Figure 3. (A) Response time (RT) as a function of word pair relatedness and side of presentation for the 2 groups separately (B) Regressing RT as a function of word pair relatedness revealed that participants in the LH DA dominance group displayed increased associative priming for word pairs presented to the LVF as compared with the RH DA dominance group. Mean ± SEM. *$P < 0.05$, **$P < 0.01$.

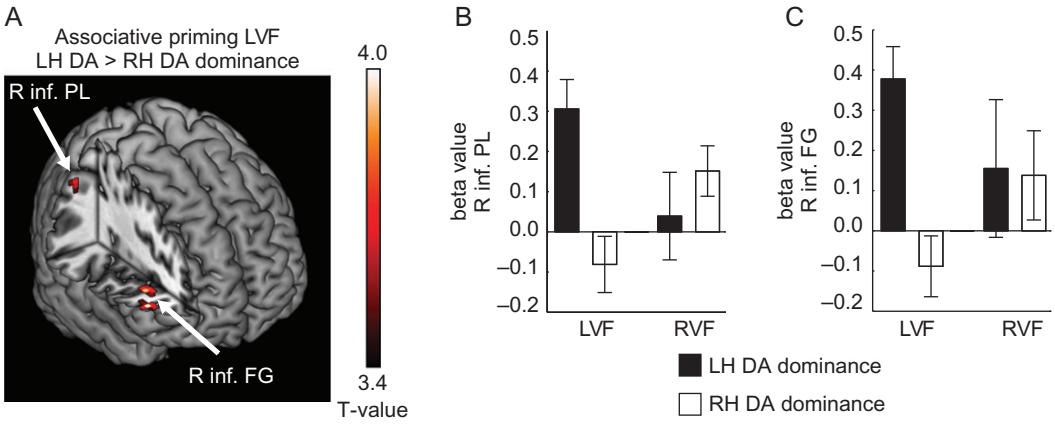

Figure 4. Brain regions displaying associative priming (i.e. increased activation as a function of decreased word pair relatedness) for word pairs presented to the LVF. (*A*) Participants in the LH DA dominance group displayed increased associative priming in the right hemisphere as compared with participants in the RH DA dominance group. (*B*) Extracted beta values for the parametric modulator with word pair relatedness values from the peak activated voxel in the right inferior parietal lobule (R Inferior PL). (*C*) Extracted beta values for the parametric modulator with word pair relatedness values from the peak activated voxel in the right inferior frontal gyrus (R Inferior FG). Mean ± SEM.

(1,30) = 4.182, p_{SVC} = 0.055). Importantly, beta values extracted from the peak voxel in the R Inferior PL (Fig. 4*B*; MNI *x* = 48, *y* = −34, *z* = 49) and the R Inferior FG (Fig. 4*C*; MNI *x* = 54, *y* = 14, *z* = 25) show that the group differences are not due to reduced priming effects for the RH DA dominance group, but rather increased priming for the LH DA dominance group. For separate LVF priming effects for the different groups, see Supplementary Table S5.

Thus, these results mirror the behavioural results and indicate increased associative processing in the RH for the LH DA dominance group. Crucially, these results also confirm the speculated links between hemispheric reward asymmetries, associative processing in the RH, and creative cognition. Of note, each event was modelled using a zero duration, something which is warranted given equal and brief stimulation times (<4000 ms) between trials (Henson 2003). However, to ensure that the results were not caused by different trial durations (i.e., as determined by different RTs) between conditions, another model was created where the duration of each event was set to the total trial time (presentation time for prime + target + RT). Mirroring the results obtained with the zero duration model, participants in the LH DA group displayed increased associative priming in both the Inferior PL and the Inferior FG (data not shown).

RVF Presentation. For the RVF, two-sample *t*-tests revealed no significant group differences in brain activity as a function of word pair relatedness, a result which mirrors the behavioural results. For separate RVF priming effects for the different groups, see Supplementary Table S6.

Discussion

The goal of this study was to clarify the potential links between individual creativity, hemispheric asymmetries in associative priming, and hemispheric asymmetries in DA function. We thus combined for the first time within the same experiment some measures that had previously been investigated within distinct research contexts. By looking at individual patterns of functional MRI and behavioural data, our study provides a comprehensive view on some major determinants of human creativity, namely DA-related activity and associative processing.

Hemispheric Reward Asymmetry and Lateralized Associative Priming

Computational accounts suggest that DA limits the spreading of activation within associative networks (Spitzer 1997), a notion which is supported by studies reporting reduced associative priming following pharmacologically increased DA levels (Kischka et al. 1996; Angwin et al. 2004; Roesch-Ely et al. 2006). Moreover, it was recently proposed that associative priming depends on the level of neuromodulation within each hemisphere (Lavigne and Darmon 2008). Accordingly, we hypothesized that decreased DA function in one hemisphere relates to increased associative priming in that hemisphere, that is, participants displaying relatively reduced DA function in the LH (LH vs. RH) should display relatively increased priming in the LH (vs. RH).

Using a lateralized lexical decision task we confirmed this hypothesis by showing that participants with weaker reward responses in the right (relative to left) ventral striatum (LH DA dominance group) displayed increased associative priming for word pairs presented to the LVF/RH. These results were mirrored by brain activity revealing significantly more priming-related activity in the RH for the LH DA dominance group compared with the RH DA dominance group. No significant group differences in priming-related behaviour or brain activity were found for word pairs presented to the RVF. While these results corroborate the proposal by Lavigne and Darmon (2008) that associative processing within each hemisphere is sensitive to differences in hemispheric neuromodulation, they do not support the prediction derived from Lavigne's model that asymmetric neuromodulation results in asymmetric associative priming because group differences were only found in the RH. Instead, our results suggest that the modulation of associative priming may depend on the type of associative processing favoured by each hemisphere. In particular, it has been suggested that narrow and broad associative processing occurs in the left and RH, respectively (Jung-Beeman 2005). The present findings may therefore indicate that broad associative processing occurring in the RH is more sensitive to

neuromodulation as compared with the narrow associative processing occurring in the LH.

For targets presented in the LVF, thus activating predominantly the RH, participants showing LH DA dominance displayed significantly stronger priming-related activity in the RH. Implicated brain regions include the inferior frontal gyrus (Inferior FG), a brain region previously implicated in associative priming (Kotz et al. 2002; Sachs et al. 2011), as well as in semantic retrieval and selection (Bookheimer 2002; Jung-Beeman 2005), and the right inferior parietal lobe (Inferior PL), a brain region suggested to be the locus of coarse associative processing (Kiefer et al. 1998). Interestingly, recent reports indicate that the bilateral Inferior PL is also engaged during creative thinking (Fink et al. 2010), and that activity in the right Inferior PL predicts individual divergent thinking scores (Fink et al. 2014). Thus, increased broad associative processing, evidenced here by both increased associative priming for words presented in the LVF and increased engagement of the right Inferior PL, may also subserve higher creativity for participants in the LH DA dominance group, consistent with our predictions and results (as we further detail later).

Hemispheric Reward Asymmetry and Creativity

Mednick's associative theory of creativity posits that high creativity results from the combination of remotely related concepts into highly original ideas (Mednick 1962). It has been suggested that the RH is particularly important for processing remote associations (Beeman et al. 1994; Richards and Chiarello 1995; Chiarello et al. 2003). Hence increased associative processing in the RH should be associated with increased creativity. Indeed, increased associative priming in the RH, as displayed by the LH DA dominance group, correlated with higher scores on both the AUT and the RAT. These results extend previous observations that highly creative participants are more likely to indicate that remotely associated words are related as compared with less creative participants (Gruszka and Necka 2002). Specifically, our study shows that this result may be due to highly creative participants engaging broad associative processes in the RH, something which not only increases the probability of finding a relationship between 2 remotely related words, but also allows the combination of more remote concepts believed to be key for high creativity (Mednick 1962). A relationship between creativity and hemispheric brain asymmetries has also been reported in 2 recent studies. Kowatari et al. (2009) asked design experts and novices to invent new designs for pens while undergoing fMRI scanning. Expert designers came up with more original designs as compared with novices, and more interestingly, the degree of originality in experts was associated with asymmetrically increased brain activity in the right prefrontal cortex during the invention task (see also Folley and Park 2005). Shamay-Tsoory et al. (2011) investigated divergent thinking in patients suffering from different types of brain lesions and found that patients with RH lesions came up with fewer original ideas as compared with patients with LH lesions and healthy controls, highlighting an important role for the RH in creativity. Particularly striking was the finding that more extensive lesions in the LH were associated with increased creativity while more extensive lesions in the RH decreased creativity. These results indicate that hemispheric imbalances in cortical function relate to individual creativity, a notion extended by the present study which highlights a crucial contribution of differences in associative processing between hemispheres.

Hemispheric Reward Asymmetry and Hemispheric Asymmetries in DA Function

Hemispheric asymmetries in ventral striatal function were used here to estimate hemispheric asymmetries in DA function. Justifications and limitations for using this approach are detailed below.

DA neurons originate in the midbrain (i.e., SN/VTA) and project to subcortical regions (including the ventral striatum), via the mesolimbic and nigrostriatal pathways, and to cortical brain regions via the mesocortical pathway (Alexander et al. 1986; Joel and Weiner 2000). Changes in DA function at the level of the midbrain may therefore have an impact on neural and cognitive processes relying on brain regions targeted by DA neurons. Supporting this notion, midbrain DA neuron loss in Parkinson's disease (PD) reduces neural responses to reward in the midbrain and in the ventral striatum (Schonberg et al. 2010; van der Vegt *et al.* 2013). Additionally, PD patients with larger loss of midbrain DA neurons in the right (vs. the left) hemisphere express more behavioural approach (vs. avoidance), while patients displaying larger DA neuron loss in the left (vs. the right) hemisphere show the reverse trend (i.e., increased avoidance vs. approach) (Maril *et al.* 2013; Porat *et al.* 2014). Similar biases in the expression of approach (vs. avoidance) behaviours have also been observed in healthy controls displaying asymmetric DA function in the striatum (Tomer *et al.* 2014), including reward responses (Aberg *et al.* 2015). It is therefore conceivable that striatal asymmetries in reward responses pertain to asymmetries in midbrain DA function, and can be used to study the impact of hemispheric asymmetries in DA function on cognitive processes, in particular those relying on mesocorticolimbic DA projection sites.

One limitation of the present study is that feedback-related neural responses, as measured by fMRI, do not represent a direct measure of DA release or DA neuron activity. Other neuromodulators and neurotransmitters may also contribute to the BOLD response in the striatum, such as acetylcholine, GABA, or glutamate (Knudsen 2011; Stormer et al. 2012; Yager et al. 2015). However, transient modulations of fMRI signal across the mesolimbic DA system during reward processing has previously been demonstrated to be highly consistent with neural recordings in animals (Schultz et al. 1997; Knutson et al. 2001a, 2001b; Tobler et al. 2005; D'Ardenne et al. 2008; Ferenczi et al. 2016). Additionally, in line with studies using more direct measures of DA function, such as PET (Tomer et al. 2013, 2014) and DA neuron loss in PD patients (Maril et al. 2013), we recently reported an association between hemispheric differences in striatal reward responses assessed by fMRI and biases in approach and avoidance learning (Aberg et al. 2015) and spatial orienting biases (Aberg et al. 2016). Thus, it is highly plausible that our measured reward asymmetry relates to hemispheric asymmetries in DA function.

Another issue which deserves attention is whether a hemispheric asymmetry in DA function, including the phasic response to reward, can be considered a stable individual characteristic. Supporting this claim, the magnitude of phasic responses to reward in the mesolimbic system, including the ventral striatum, was found to correlate with the expression of stable personality traits, such as approach motivation and reward sensitivity (Simon et al. 2010; Kennis et al. 2013). Moreover, we recently demonstrated that hemispheric asymmetries in phasic

reward responses related to the expression of spatial orienting biases (Aberg et al. 2016), and approach and avoidance behaviours (Aberg et al. 2015), which both are well-documented personality features (Carlson and Glick 1989; Elliot and Thrash 2002; Elliot 2008; Tomer 2008) associated with a hemispheric imbalance in DA function (Maril et al. 2013; Tomer et al. 2013, 2014; Porat et al. 2014). These observations converge to suggest that hemispheric asymmetries in DA function, including phasic reward responses, pertain to stable personality characteristics. Yet, the stability of hemispheric biases in reward-related striatal responses over a longer time period (i.e., equivalent to what is typically expected for personality traits) remains to be directly demonstrated experimentally.

Finally, we localized the ventral striatum by combining a functional localizer (i.e., the contrast between positive and negative feedback (Carlson et al. 2011)) and anatomical data (Neto et al. 2008). Because this approach was not constrained by individual anatomy, it cannot be excluded that for some individuals the reported ventral striatum activation may have been influenced by surrounding brain regions. However, we obtained the same results when defining groups based on the activity of the peak voxel only (i.e., increased LVF priming, and larger RAT and AUT scores in the corresponding LH DA group, data not shown). Moreover, as mentioned previously, we used the same approach to evident links between hemispheric asymmetries in reward responses and biases in spatial orienting (Aberg et al. 2016) and approach and avoidance learning (Aberg et al. 2015). Similar biases have been linked to hemispheric asymmetries in DA function (Maril et al. 2013; Tomer et al. 2013, 2014; Porat et al. 2014). Therefore, our approach seems sufficient to reliably capture hemispheric asymmetries in DA function.

Hemispheric Asymmetries in DA Function Relate to Genius, Madness, and Unleashed Creativity in PD

A striking example of unleashed creativity has been reported in PD patients undergoing DA treatment in order to restore impaired DA function caused by loss of DA midbrain neurons. This includes sudden interest in poetry (Schrag and Trimble 2001; Joutsa et al. 2012), writing and embroidery (Bindler et al. 2011), and painting (Chatterjee et al. 2006), as well as dramatic changes in artistic style in already established artists (Kulisevsky et al. 2009; Lopez-Pousa et al. 2012; Shimura et al. 2012). These patients also perform better than controls on tasks frequently used to estimate creative potential (Faust-Socher et al. 2014). Moreover, this creative boost is lost following withdrawal of DA treatment, thus suggesting a strong link between creativity and DA medication in these patients (Bindler et al. 2011; Lhommee et al. 2014). Paradoxically, it may be suggested that DA treatment should rather hinder creativity, because DA has been found to reduce broad associative processing (as previously reviewed) believed to underpin high creativity (Mednick 1962). What could explain this paradoxical effect of DA on creativity? The effect of DA medication on cognitive performance follows an inverted U-shape, with both too little and too much DA resulting in suboptimal cortical functioning (Goto et al. 2007; Cools and D'Esposito 2011). It has been suggested that DA treatment causes brain regions that are normally less affected by the loss of DA neurons to experience a "DA overdose" which then disrupts the cognitive functions they perform (Cools and D'Esposito 2011). Interestingly, DA treatment in PD patients with asymmetric loss of DA neurons between hemispheres resulted in separate cognitive deficits, suggesting distinct effects caused by DA overdosing of the left or the RH (Tomer et al. 2007). Additionally, deep-brain stimulation (DBS) of the left subthalamic nucleus, a procedure known to mimic enhanced DA function in the LH (Palminteri et al. 2013), negatively influenced creativity in one artist suffering from PD. Specifically, DBS caused a reduced appreciation of the quality of another artist's paintings and lower scores on a divergent thinking task (Drago et al. 2009b), as well as a significant reduction in the quality and creative style of the artist's own paintings (Drago et al. 2009a). In the light of these notions, our results may offer an explanation for the paradoxical effect of DA treatment on creativity. Specifically, similar to participants in the LH DA dominance group, creativity would be enhanced when DA treatment causes a relative imbalance in DA function between hemispheres which promotes broad associative processing.

Our results also provide pieces of information regarding the apparent link between madness and genius. Specifically, both madness (i.e., psychosis) and genius (i.e., high creativity) have been linked to a hyperactive RH, where facilitated formation of abnormal associations could stimulate both delusional and creative ideas (Bracha 1989; Leonhard and Brugger 1998; Pizzagalli et al. 2001; Taylor et al. 2002; Krummenacher et al. 2010). This notion is supported by studies showing that individuals expressing positive schizotypical traits, that is, schizophrenia-like thought patterns and perceptions including odd beliefs, paranormal thoughts, and unusual perceptual experiences, display increased associative processing (Gianotti et al. 2001; Mohr et al. 2001, 2006), specifically in the RH, as assessed through a lateral semantic priming task (Pizzagalli et al. 2001), and increased creativity (Leonhard and Brugger 1998; Weinstein and Graves 2002; Folley and Park 2005; Nettle and Clegg 2006; Acar and Sen 2013). Moreover, recent meta-analyses revealed a relationship between creativity, approach motivation (Baas et al. 2008) and vulnerability to approach-based psychopathologies (i.e., positive schizotypy and bipolar disorder; Acar and Sen 2013; Baas et al. 2016), and negative correlations between creativity, avoidance motivation and inclinations towards avoidance-based psychopathologies (i.e., negative schizotypy, anxiety, and depression Acar and Sen 2013; Baas et al. 2016). Strikingly, we recently showed that increased expressions of approach (vs. avoidance) behaviours were associated with relatively decreased ventral striatal reward responses in the RH (Aberg et al. 2015, see also Maril et al. 2013; Porat et al. 2014; Tomer et al. 2014). These converging pieces of evidence suggest that positive schizotypy should implicate a dampening of DA function in the RH. However, attempts to relate schizotypy to hemispheric asymmetries in DA function have been inconclusive. Specifically, using spatial orienting biases as an indirect estimate of hemispheric asymmetries in DA function, an approach justified by findings that animals and humans tend to orient away from the DA dominant hemisphere (Bracha 1989; Molochnikov and Cohen 2014), reveal that high positive schizotypy has been related to spatial biases towards the left (Taylor et al. 2002; Mohr et al. 2003, 2005), the right (Liouta et al. 2008), as well as towards no specific side of space (Gooding and Braun 2004; Schofield and Mohr 2014).

Notably, orienting biases implicate the nigrostriatal pathway, as indicated by research on animals (Bracha 1989; Molochnikov and Cohen 2014) and PD patients displaying asymmetric sides of motor deficiencies (Bracha et al. 1987). Because the nigrostriatal pathway is critically involved in motor production, hemispheric asymmetries in the activation of this pathway would determine the side of orienting biases

(Deumens et al. 2002). By contrast, the mesocorticolimbic DA system modulates motivated behaviour and higher cognitive functions residing in the prefrontal cortex (Adinoff 2004; Seamans and Yang 2004; Salamone and Correa 2012), and we showed here that creativity and the balance between broad and narrow associative processing relate to hemispheric asymmetries in the activation of this system. Our study thus suggests that the lack of consistency regarding the link between schizotypy and the side of the orienting bias may be explained by the fact that these behaviours rely on distinct DA pathways (but see also Liouta *et al.* 2008; Schofield and Mohr 2014). Thus, although schizotypy was not estimated in the present study, our results combined with the fact that positive schizotypy is associated with increased creativity and broad (vs. narrow) associative processing, suggest that positive schizotypy might relate to relatively decreased DA function in mesocorticolimbic system of the RH. This prediction is consistent with the notion that hyperactive language functions in the RH may contribute to both genius and madness (Leonhard and Brugger 1998), but contrasts with speculations that psychosis is related to a RH "hyperdopaminergia" (Bracha 1989).

Convergent and Divergent Thinking

Convergent and divergent thinking was estimated here using the RAT and the AUT, respectively. High scores on the AUT have been related to high composite scores of creative activities and accomplishments (Hocevar 1980), while RAT scores correlated positively with creativity ratings obtained by students in an architectural design course and by students displaying high research creativity (Mednick 1962). Moreover, musicians scored higher on both the RAT and the AUT, as compared with non-musicians (Gibson et al. 2009). Yet, it should be noted that the relationship between creativity in a broader sense and the concepts of convergent/divergent thinking is unclear and currently heavily debated (Davis 1989; Hocevar and Bachelor 1989; Cropley 2006; Fairweather 2011; Zeng et al. 2011).

Moreover, it has been reported that divergent and convergent thinking abilities are not related (Lee et al. 2014), that they differently rely on DA neuromodulation (Chermahini and Hommel 2010), and engage distinct brain regions (Razoumnikova 2000). Moreover, adults diagnosed with attention-deficit hyperactivity disorder score higher than controls on divergent thinking tasks, but lower on convergent thinking tasks (White and Shah 2006). Such dissociations between divergent and convergent thinking go well in hand with Guilford's suggestion that both types of abilities represent separate components of creativity (Guilford 1967). Intriguingly, in the present study, participants displaying LH DA dominance not only showed increased associative priming, but also scored higher on both the AUT and the RAT. These results indicate that divergent and convergent thinking partly relies on similar mechanisms, one of which could be related to associative processing. It has been suggested that the scope of associative processing determines the amount of knowledge related to a particular concept which can be retrieved from memory (Anderson 1983). Moreover, while it has been shown that convergent thinking relies heavily on knowledge (for a review see Cropley 2006), increased knowledge could also benefit divergent thinking. In particular, knowledge about the relationship between different concepts seems crucial for their successful combination into novel and useful ideas. Accordingly, both divergent and convergent thinking should benefit from improved associative processing, a notion corroborated by our results.

Conclusions

We conclude that individual hemispheric asymmetry in DA function, as estimated here by neural reward responses between the left and right ventral striatum, may be a major determinant of both creativity and associative processing. These findings combine 2 prominent yet largely disconnected ideas in the literature (but see Leonhard and Brugger 1998); namely that high creativity depends on processing remote associations (Mednick 1962), and that the RH is particularly important for remote associative processing (Jung-Beeman 2005). Additionally, these findings suggest that hemispheric asymmetries pertaining to DA function may selectively and differentially influence behaviors and cognitive functions performed by each hemisphere.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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Notes

Conflict of Interest: none declared.

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