Spontaneous cognition and its relationship to human creativity: A functional connectivity study involving a chain free association task

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ARTICLE INFO

Keywords:
Creative cognition
Spontaneous cognition
Free association
Default mode network
Resting state functional connectivity
fMRI

ABSTRACT

Resting-state functional connectivity (RSFC) between various brain regions is thought to be associated with creative abilities. Extensive research correlating RSFC with performance on creativity tasks has revealed some of the RSFC patterns characterizing ‘the creative brain’. Yet, our understanding of the neurocognitive processes underlying creative thinking still remains limited. This limitation results, in part, from the fact that standard creativity tasks used in these studies do not distinguish between the different modes of cognitive processing that are critical in creative cognition (e.g., spontaneous cognition vs. controlled cognition). In the present fMRI research we address this limitation by using a chain free association task – a task that we have recently refined and validated for the purpose of isolating measures of spontaneous cognition that are relevant for creative thinking (referred to as associative fluency and associative flexibility). In our study, 27 female participants completed standardized creativity tasks, a chain free association task, and a fMRI scan in which RSFC was measured. Our results indicate that higher scores on associative fluency are associated with stronger positive RSFC within the default mode network (DMN; i.e., between DMN regions). Critically, we provide evidence that the previously-identified relationship between performance on creativity tasks and connectivity within the DMN is partially mediated by associative fluency. Thus, our observations suggest that the heightened DMN connectivity observed in ‘the creative brain’ can be explained, at least to some extent, by spontaneous cognition. Overall, our study identifies unique RSFC patterns that are related specifically to spontaneous cognitive processes involved in creative ideation, thus shedding new light on mechanisms of creative processing.

1. Introduction

Creative ideas—broadly defined as ideas that are both novel and useful (e.g., Fink et al., 2009)—are the foundation of innovation in all areas of life, including technology, culture, and science. Accordingly, one of the main goals of research on creativity is to understand the cognitive and neural processes that give rise to creative ideas (Beaty et al., 2015; Beaty et al., 2017b; Benedek et al., 2014b; Benedek et al., 2018; Faust, 2012; Green et al., 2015; Maseless et al., 2015; Shah et al., 2013)). A potentially fruitful approach to achieving such an understanding is to identify what distinguishes the minds of more-creative individuals from those of less-creative ones, in terms of thought processes (Beaty et al., 2014c; Benedek et al., 2014c; Kenett et al., 2014) and brain characteristics (Bashwiner et al., 2016; Beaty et al., 2014a; Beaty et al., 2018; De Pisapia, Bacci, Parrott and Melcher, 2016; Takeuchi et al., 2012; Wei et al., 2014). In particular, substantial research has been devoted to identifying the specific brain activity patterns that characterize highly-creative individuals—where brain activity refers not only to activation of specific regions, but also to the functional connectivity between them, i.e., the extent to which specific disparate brain regions and networks cooperate (Friston et al., 1993).

Studies in this vein typically evaluate correlations between measurements of brain functional connectivity (obtained through functional magnetic resonance imaging; fMRI) and measurements of performance on creativity tasks administered behaviorally (see Beaty et al., 2019 for a review). Several prominent works have relied on the measurement of functional connectivity patterns of participants who were actively engaged in a creative task, such as production of creative ideas (Beaty

https://doi.org/10.1016/j.neuroimage.2020.117064

Received 31 July 2019; Received in revised form 24 May 2020; Accepted 13 June 2020
Available online 20 June 2020

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et al., 2015, 2018; De Pisapia et al., 2016; Shi et al., 2018). Other studies measured functional connectivity patterns when the brain was at rest (resting-state functional connectivity; RSFC) (Beaty et al., 2014a; Liu et al., 2018; Lotze et al., 2014; Shi et al., 2018; Takeuchi et al., 2012, 2017; Wei et al., 2014; Zhu et al., 2017), as these patterns are thought to reflect trait brain activity, or brain activity fingerprints (Finn et al., 2015; Mars et al., 2018). Notably, reliance on RSFC measurements enables researchers to avoid potential biases associated with calculating functional connectivity based on task performance (Cole et al., 2019). In addition, functional connectivity measured during a task might be influenced by aspects of task performance that go beyond creative processing (Buckner et al., 2013).

Though these studies have all provided valuable insights regarding the functional connectivity patterns characterizing the creative brain, it remains challenging to determine how these patterns translate into cognitive processes underlying creative thinking. A key factor in this limitation is the fact that most of these studies correlated functional connectivity measurements to performance on standard creativity tasks—which do not isolate the specific cognitive processes that are critical in creative thinking. In particular, they do not distinguish between two key modes of cognitive processing, or cognition: spontaneous cognition vs. controlled cognition (see Marron and Faust, 2019). Spontaneous cognition can broadly be described as thought that arises spontaneously (e.g., not-deliberately) or that unfolds spontaneously, i.e., free from constraint, flowing flexibly in a dynamic manner (see (Christoff et al., 2016) for a precise conceptualization of spontaneous thought). Controlled cognition, in turn, refers to thought that arises deliberately or thought that is deliberately guided in a goal-directed manner by top-down executive processes (Christoff et al., 2016).

We suggest that a distinction between spontaneous and controlled modes of processing is crucial to the development of a comprehensive understanding of the cognitive and neural mechanisms of creativity. The current study aims to address this limitation by establishing clear connections between individuals’ RSFC patterns (measured through fMRI), their creative ability, and the extent to which their creative cognition is characterized by spontaneous processing. To measure the latter, we use a behavioral task that we have recently refined and validated for isolating two measures of spontaneous cognition that are relevant to creativity. This task is based on chain free association (chain FA), discussed in the following section, and the measures that it produces are referred to as associative fluency and associative flexibility, and collectively as associative abilities.

2. Background and hypothesis development

2.1. RSFC and other brain activity patterns as a function of individual creativity

Research measuring individual RSFC has identified several brain activity patterns that characterize highly-creative individuals (as opposed to less-creative individuals). In particular, highly-creative individuals show higher strength of (positive) RSFC: (i) within the default mode network (DMN) (Liu et al., 2018; Ogawa et al., 2018; Takeuchi et al., 2012, 2017; Wei et al., 2014; but see Li et al., 2016; Zhu et al., 2017)—a network functionally associated with self-generated thought and spontaneous thinking (Andreas-Hanna et al., 2010a; Axelrod et al., 2017a; Axelrod et al., 2015b; Christoff et al., 2016; Fox et al., 2015; Marron et al., 2018; Molnar-Szakacs and Uddin, 2013; (ii) within the executive network (Beaty et al., 2014a; Li et al., 2016; Liu et al., 2018; Zhu et al., 2017), which is functionally related to executive control processes (Chrysikou, 2019; Friedman and Miyake, 2017); and (iii) between nodes of the DMN and nodes of the executive network (Beaty et al., 2014a; Liu et al., 2018; Shi et al., 2018; Takeuchi et al., 2017; Zhu et al., 2017), notably, Takeuchi et al. (2017) found this relationship only in women. Similar observations of enhanced connectivity within the DMN, within the executive network, and/or between the two networks were also obtained in studies that tested functional connectivity during creative idea production (Beaty et al., 2015, 2018; De Pisapia et al., 2016; Mayseless et al., 2015; Shi et al., 2018). These functional connectivity patterns, including the unique coupling of the DMN and executive network, have led to the prominent notion that creative thought might be related to an interplay between two categories of seemingly opposing modes of processing: spontaneous cognition and controlled cognition (Andrews-Hanna et al., 2018; Beaty et al., 2015; Beaty et al., 2016; Beaty et al., 2014c; Benedek and Fink, 2019; Benedek and Jauk, 2018; Christoff et al., 2016; Chrysikou, 2019; Ellam et al., 2012; Marron and Faust, 2018; Volle, 2018). Spontaneous and controlled cognition, defined broadly above, are higher-order constructs, each of which comprises multiple finer-grained processes. In what follows, we will use the term ‘spontaneous processes’ to refer to the collective set of cognitive processes pertaining to spontaneous cognition, and the term ‘controlled processes’ to refer to the cognitive processes pertaining to controlled cognition.

Spontaneous processes, also referred to as ‘type 1’ processes (see Sowden et al., 2015 for a review), have been linked to DMN activity (Andrews-Hanna et al., 2010a; Christoff et al., 2016; Fox et al., 2015). These processes are usually characterized as associative in nature and involve rapid information retrieval that is mostly unconscious (Sowden et al., 2015). Spontaneous processes, including spontaneous retrieval from episodic memory (i.e., personal experiences) (Benedek et al., 2018; Madore et al., 2015) and semantic memory (i.e., conceptual knowledge stores) (Gilhooly et al., 2007), are assumed to be essential for the generative aspect of producing creative ideas. It is important to note that, though many spontaneous processes are associative, not all associative cognitive processes are completely spontaneous in nature. For example, an individual tasked with coming up with a list of animals (i.e., a semantic fluency task) may be engaged in associative thinking. Because the ideas are not generated non-deliberately and also cannot unfold without constraint (i.e., each idea must be the name of an animal), these associative processes are also controlled (Birn et al., 2016; Vonk et al., 2018) and not completely spontaneous (Marron et al., 2018). Controlled processes (also referred to as ‘type 2’ processes), in turn, have been linked to executive network activity. In the context of creative ideation, these processes are assumed to be related to evaluation of the ideas produced and selection of appropriate and useful ones (Benedek and Fink, 2019; Benedek et al., 2014c; Chrysikou, 2019).

As noted in the introduction, tasks that are typically used to measure creativity consider creative cognition as a single unified construct, without distinguishing between spontaneous and controlled processes (see Beaty et al., 2019; Marron and Faust, 2019 for reviews). For example, the alternative uses task (AUT), in which the participant is asked to come up with creative uses for common objects, measures divergent thinking (producing multiple unique ideas from diverse domains) (Rungo and Acar, 2012), which includes both spontaneous processes such as retrieval from episodic memory (Benedek et al., 2012b; Benedek et al., 2018; Madore et al., 2019), and controlled processes, such as the inhibition of salient but irrelevant responses (Beaty et al., 2014a; Benedek et al., 2012a; Benedek and Jauk, 2018; Benedek et al., 2014c; Vartanian et al., 2014). Accordingly, tests that correlate functional connectivity measurements with performance on such tasks cannot attribute specific brain activity patterns to specific modes of cognition. Recent studies have attempted to overcome this limitation by identifying tasks that elicit specific cognitive processes related to creativity, and testing functional connectivity during these tasks (e.g., response inhibition during constrained idea production; Beaty et al., 2017a; self-generated thought; Benedek et al., 2016). Additional studies further correlated RSFC patterns with scores on such tasks (e.g., episodic memory (Madore et al., 2019)). The current study contributes to this stream of research by identifying unique RSFC patterns that are specifically related to spontaneous processes involved in creative ideation, and using these findings to explain previously shown brain activity patterns that characterize highly-creative individuals. Notably, whereas other studies have shown which brain activity patterns characterize creative individuals (Beaty
have been shown to explain a significant amount of variance in performance on common creativity tasks such as AUT (Benedek et al., 2012b; Marron et al., 2018). For convenience, in what follows, associative abilities and brain activity patterns observed during the chain FA task—(i) associative fluency—the number of associations produced, a measure that reflects rapid generation of associations through self-guided memory search; (ii) associative flexibility—the capacity to spontaneously shift between diverse fields when producing associations; and (iii) semantic remoteness between associations (see section 3.3.1 for additional details). In particular, both associative fluency and associative flexibility have been shown to explain a significant amount of variance in performance on common creativity tasks such as AUT (Benedek et al., 2012b; Marron et al., 2018). For convenience, in what follows, associative fluency and associative flexibility (defined similarly to the measures referred to as FA fluency and FA flexibility in Marron and Faust (2018)) are referred to as associative abilities and, in accordance with the results of Marron and Faust (2018), are considered to serve as measures of spontaneous cognition.

2.2. The chain FA task and its relation to creativity

To isolate brain network dynamics corresponding to spontaneous processes, we leverage a behavioral task that has recently been established by neurobehavioral methods as an appropriate tool for eliciting and measuring spontaneous cognitive processes—and specifically, associative spontaneous cognitive processes—that are relevant for creative thinking (Marron et al., 2018): the chain FA task. This task involves verbalizing one’s train of thought in single words in response to a cue word, each word associating to the previous word in the form of a chain, for a limited amount of time (Benedek et al., 2012b; Marron et al., 2018). From an individual’s association chains it is possible to calculate scores of (i) associative fluency—the number of associations produced, a measure that reflects rapid generation of associations through self-guided memory search; (ii) associative flexibility—the capacity to spontaneously shift between diverse fields when producing associations; and (iii) semantic remoteness between associations (see section 3.3.1 for additional details). In particular, both associative fluency and associative flexibility have been shown to explain a significant amount of variance in performance on common creativity tasks such as AUT (Benedek et al., 2012b; Marron et al., 2018). For convenience, in what follows, associative fluency and associative flexibility (defined similarly to the measures referred to as FA fluency and FA flexibility in Marron and Faust (2018)) are referred to as associative abilities and, in accordance with the results of Marron and Faust (2018), are considered to serve as measures of spontaneous cognition.

2.3. Brain activity during chain FA

Our recent research (Marron et al., 2018) has shown that individuals who are actively engaged in chain FA, as compared with associative tasks of a more controlled nature (e.g., a semantic fluency task; see subsection 2.1), show more brain activity in major hubs of the DMN (specifically, the left temporal parietal junction (TPJ), the left and right middle temporal gyrus (MTG), the dorsal medial prefrontal cortex (dMPFC), and the parietal cingulate cortex (PCC)), which are known to be highly relevant for internally-directed cognition and spontaneous thinking; along with the left inferior frontal gyrus (IFG) (a major node in the executive network known for its role in executive control and inhibition) and left motor areas. Notably, each of the measures of associative ability has been shown to correlate with slightly different patterns of brain activity during chain FA production. Specifically, high scores on associative fluency are related to enhanced activity of the dMPFC (DMN) and motor cortex, and high scores on associative flexibility measures are related to lower activation in the left IFG (Marron et al., 2018). These observations, coupled with the relations observed between associative abilities and performance on creativity tasks, suggest that associative fluency might be related to associative-generative abilities that include the scope and speed of internally-directed un-cued (spontaneous) retrieval of associations related to memory, whereas associative flexibility might be related to the capacity to naturally shift between contexts and concepts in memory, and as such might also be related to disinhibition of control processes, allowing access to networks that are more distinct and remote (Marron et al., 2018).

Whereas our previous work identified correlations between associative abilities and brain activity patterns observed during the chain FA task, in the current study our goal was to identify the associations between associative abilities and brain activity patterns at rest (RSFC, obtained via fMRI), as a means of avoiding potential confounding factors associated with task performance (mentioned above; Cole et al., 2019), and, more broadly, as a means of characterizing the brains of individuals with high measures of associative ability—reflecting high propensity for spontaneous cognition. In other words, we show how the ‘highly-associative brain’ (i.e., brains of individuals with high scores on associative abilities) relates to the ‘highly-creative brain’. The relationships revealed herein have the potential to provide a crucial step forward towards deciphering the mechanisms of creativity.

2.4. Hypotheses

Drawing from the research discussed above, we put forward the following hypotheses:

H1. On the basis of prior observations regarding RSFC patterns of creative individuals, behavioral scores in common creativity tasks are expected to be positively associated with connectivity within the DMN (i.e., connectivity between DMN regions), and to be positively correlated with connectivity between the left IFG (a major hub in the executive network) and areas of the DMN.

H2. Increased RSFC between areas inside the DMN, and specifically with the dMPFC (Marron et al., 2018), may be related to higher associative fluency in the chain FA task.

H3. RSFC values between the DMN and the left IFG will be negatively associated with associative flexibility scores (Marron et al., 2018).

H4. Higher associative ability scores (obtained through behavioral tasks) will be related to higher creativity scores.

H5. Associative fluency will mediate the relationship between RSFC within the DMN and creativity scores.

We note that although associative flexibility has been found to be related to creativity (Benedek et al., 2012b; Marron et al., 2018) we do not put forward a hypothesis about this measure in terms of mediation of creativity scores and RSFC. The reason for this is that we expect higher associative flexibility to be related to lower RSFC between the left IFG and DMN (H3), whereas we expect higher creativity scores to be related to higher RSFC between the left IFG and DMN (H1).

We emphasize that though we expect associative fluency to mediate the relationship between within-DMN RSFC and performance on creativity tasks (“creativity scores”), we do not necessarily expect creativity scores to mediate the relationship between within-DMN RSFC and associative flexibility. These expectations arise from the common assumption in neurocognitive creativity research that creative thinking is a higher-order construct that entails a combination of different modes of thought (namely, spontaneous and controlled cognition, discussed above; Andrews-Hanna et al., 2018; Beaty et al., 2015, 2016; Beaty et al., 2014c; Benedek and Fink, 2019; Benedek and Jauk, 2018; Christoff et al., 2016; Chrysikou, 2019; Ellamil et al., 2012; Marron and Faust, 2018; Volle, 2018). In other words, and in line with previous research that tested similar models (Beaty et al., 2014c; Benedek et al., 2012b; Lee and Therriault, 2013) and research that tested models with an experimental manipulation (e.g., Madore et al., 2019), we expect creative abilities to build upon lower-order processes, such as associative abilities representing spontaneous cognition, and not vice versa.

We further note that in our hypotheses and analyses, RSFC measures serve as predictors and not as outcome variables. Given that our analyses are based on correlations from a cross-sectional mediation design (Maxwell and Cole, 2007; Maxwell et al., 2011), the choice to use RSFC measures as predictors—though in line with previous research (e.g., Beaty et al., 2018)—is effectively arbitrary and does not imply directionality and causality. Indeed, the question of whether brain activity gives rise to cognition, cognition gives rise to brain activity, or both are two different aspects of a single entity (Solms and Friston, 2018) is an important issue that has been explored extensively through philosophical debate and empirical research, yet has not yet been resolved. To evaluate the specificity of our results, we also examine alternative mediation paths (see subsection 4.4).
3. Methods

3.1. Participants

The original sample consisted of 36 healthy, Hebrew (mother-tongue) speaking students (30 females) from Bar-Ilan University, from a wide range of majors. All participants were right-handed, as assessed by a standard self-report questionnaire (Oldfield, 1971), with normal or corrected-to-normal vision. Participants received either cash payment or a combination of course credit and cash payment for their involvement in the study. This dataset was part of a larger study (see Marron et al., 2018) that included two fMRI scanning sessions (i.e., visits) and several meetings with a psychological intervention (Marron et al., in preparation). In the present paper we report only the results of the behavioral testing on the first day and the results of the first fMRI scanning session. Three participants (two female and one male) were excluded from the imaging analysis due to excessive head movement during the scan (3 participants > 3 mm). One additional female participant was excluded from behavioral analysis due to a malfunction in the sound recording of the chain FA task. Thus, our final sample comprised 32 participants (27 females and 5 males; mean age: 22.72, age range: 19–26). Unfortunately, the small number of male participants with valid data (5 participants) prevented us from generalizing any results to the male population. Given previously-observed differences between females and males in brain connectivity patterns (Gong et al., 2011; Takeuchi et al., 2017; Yang et al., 2015; Zhang et al., 2016), we wished to avoid erroneously presenting our results as valid for the general population, and therefore decided to focus our main analysis only on the data of female participants (N = 27; mean age: 22.6, age range: 19–26) (see section 5.4. for further discussion of this potential limitation). For robustness, we reran all our analyses on the complete sample, comprising both females and males. The results of the expanded analysis, presented in the Supplementary Material (Supplementary Tables S1–S7 and Supplementary Figures S1–S3, S9–S12), were qualitatively similar to those obtained with only female participants. The procedure was approved by the Ethics Committee of the Tel Aviv Sourasky Medical Center (TASMC) as well as by Bar-Ilan University’s Ethics Committee, and all participants provided written informed consent prior to participation.

3.2. General procedure

After initial screening, participants completed a battery of questionnaires: a socio-demographic questionnaire and creativity tasks, including the alternative uses task (AUT; Milgram and Milgram, 1976) and the comprehension of metaphors task (CoM; Faust, 2012). About two days after behavioral tests, each participant took part in a brain imaging session that included two scans: a resting-state fMRI scan (reported here; see below) and a task-based fMRI experiment (reported previously: Marron et al., 2018). The task-based fMRI experiment included a behavioral chain FA task that is also reported here. Thus, overall, in the present paper we report results of the resting-state fMRI scan and three behavioral tasks (AUT and CoM were conducted at the lab and the chain FA task was conducted in the fMRI scanner).

3.3. Behavioral assessment

3.3.1. Chain FA task

Procedure. The chain FA task and the fMRI paradigm we used are described in detail in our previous publication (Marron et al., 2018). Briefly, the chain FA task is a computerized task in which participants are instructed to generate single words that arise in their minds following a given stimulus word, in an association chain manner (i.e., only the first association should relate to the presented stimulus, whereas each subsequent association should relate to the previous associative response). The participants are instructed to produce associations freely—whatever comes to their mind—with as little inhibition as possible (see Fig. 1). All stimulus words are taken from a network analysis of the Hebrew lexicon (Rubinstein et al., 2005). The stimulus words are nouns controlled for concreteness, familiarity, orthographic neighbors and naming time.

Participants performed 6 trials (task blocks) of chain FA (with a different stimulus word on each trial), in a pseudo-randomized order. Task blocks of 18 s were separated by visual fixation of 6–9 s. In each block, an instruction and a stimulus word appeared for the first 2 s of the block, and then a black screen appeared for the remaining 16 s (during the participants’ overt response). Stimuli for the chain FA task were chosen on the basis of a behavioral pretest (N = 30) to ensure similar levels of difficulty (i.e., similar numbers of answers produced; Shapira-Lichter et al., 2013). Participants received a short training session...

![Fig. 1. Chain free association task.](image-url)

*Fig. 1. Chain free association task. Top row is a schematic flow of a trial: The task was performed six times (with six different stimulus words) as part of a fMRI task-based paradigm. Task blocks of 18 s were separated by visual fixation of 6–9 s. In each block, an instruction and a stimulus word appeared for the first 2 s of the block, and then a black screen appeared for the remaining 16 s during which the participants produced overt responses. Bottom row is an example of a trial. The words written in italic have been generated by the participant.*
before the main session. Visual stimuli were presented using the software Presentation (Neurobehavioral Systems, Albany, CA; version 18.0). Participants’ overt verbal responses were recorded and analyzed offline using Audacity software (version 2.1).

**Derivation of measures of associative fluency and associative flexibility.** Measures of associative fluency and associative flexibility were derived in procedures described in Marron et al. (2018). Specifically, all FA chains produced by participants were recorded and transcribed to a spreadsheet. Each FA chain was assigned an associative fluency score reflecting the number of associations. Additionally, each chain was scored by four independent expert judges for associative flexibility (similarly to Benedek et al., 2012b)). To derive this score, each judge calculated the number of discriminable ‘concepts’ (conceptual categories) included in the chain. To identify the number of discriminable concepts in a given FA chain, each judge compared each FA response produced in the chain, according to the sequence of the chain, to an ‘anchor’ word, where the first anchor was the original stimulus word used to generate the FA chain. Then, each judge decided if the FA response was related conceptually to the anchor (by answering the question: “Are these words related?”). When an FA response was judged as being unrelated conceptually to the anchor (i.e., did not belong to the same conceptual category), the judge added one to the FA chain’s number of discriminable concepts, and that FA response became the new anchor word. For example, in the sample trial shown in Fig. 1, ‘table’ is considered to be conceptually related to ‘chair’. The next FA response, ‘food’, is not directly related to ‘chair’, and therefore a point is added to the chain’s count of discriminable concepts, and ‘food’ becomes the new anchor. The next term, ‘pancakes’, is related to ‘food’, and so on. Judge evaluations were subjective, but interrater reliability across the four judges was high [Intraclass correlation coefficient (ICC) = 0.91 (Koo and Li, 2016)]. After the four judges scored the chain (i.e., determined the number of discriminable concepts), we divided the average score for the chain by the FA chain’s fluency score to produce an associative flexibility score. This step is motivated by the observation that the number of discriminable concepts in a chain is highly correlated with the number of words produced (see Benedek et al., 2012b; Frick et al., 1959; Marron et al., 2018). To obtain each participant’s final associative fluency and associative flexibility scores, we averaged the individual associative fluency and flexibility scores (respectively) of the 6 FA chains she/had produced.

3.3.2. Creativity tasks

To measure participants’ creative thinking, we used data from two creativity tasks that we have found to be related to associative abilities (Benedek et al., 2012b; Marron et al., 2018): the AUT (Part of the Tel-Aviv Creativity Test; Milgram and Milgram, 1976) and the CoM task (Faust, 2012). We note that participants performed additional tasks for the purposes of the larger study; however, these data were not included in the current study because they were not found to be related to associative abilities.

In the AUT, participants listed creative uses for four common objects (e.g., car tire). Each participant’s performance was scored along three dimensions: AUT creativity, AUT flexibility, and AUT fluency. AUT fluency was measured as the number of ideas produced by the participant (Takeuchi et al., 2012; Vartanian et al., 2009). AUT flexibility scores, which were measured as the number of categories or themes that the participant’s responses referred to, were highly correlated with AUT fluency (r = 0.96, p < 0.001); therefore, this measure was not analyzed. Participants’ AUT creativity scores were generated by two independent judges, who used a 5-point Likert scale to rate the degree to which each idea a given participant had produced was creative (1 = uncreative, 5 = very creative) (Silvia et al., 2013). Judges were instructed to score an idea’s creativity on the basis of its originality, uniqueness and appropriateness (e.g., Benedek et al., 2013; Runco and Acar, 2012). Interrater reliability was high (ICC = 0.85). Then, for each participant, we selected the three ideas that the judges had jointly scored as most creative (see Benedek et al., 2013), and we averaged the scores of these ideas into a single AUT creativity score.

The CoM (Faust, 2012) is an online task in which participants are presented with word-pairs in Hebrew, with different semantic relations between the two words in the pair. Specifically, the semantic relation between the two words can either be literal (L; broken vase), conventional metaphoric (CM; bright student), novel metaphoric taken from poetry (NM; locked cry), or nonexistent (“unrelated”, UR; childish straw). Participants are asked to decide whether the two words constitute a semantically meaningful expression or not by press of a button (meaningful/not meaningful) (Faust, 2012).

We derived two creativity scores from this task: the percentage of NM word pairs that the participant correctly recognized as being plausible (CoM accuracy)—reflecting flexibility of access to remote semantic categories—and response time of correct recognition of NM (CoM response time) (reviewed in Faust, 2012; Faust and Mashal, 2007; Gold et al., 2012; Zeev-Wolf et al., 2015; Zeev-Wolf et al., 2014). For convenience we reverse-coded CoM response time such that higher scores corresponded to faster recognition and higher creativity, for further details see Marron et al. (2018).

3.3.3. Task administration

In this study, we administered two versions of all six behavior tests, such that half the participants completed one version (version 1), whereas the other half completed the other version (version 2). The two versions comprised the same types of tasks but differed in the stimuli presented to participants. The use of two versions was necessary for a counterbalance procedure implemented in the larger study that the current research is a part of (see Marron et al., 2018 for details).

Thus, in the current research, 15 of the participants completed version 1, and 12 participants completed version 2. No differences in performance were found between versions on the AUT fluency scores (t = −0.23, n.s.), AUT creativity scores (t = −0.24, n.s.), CoM response time scores (t = −0.1, n.s.), CoM accuracy scores (t = −0.08, n.s.), and associative fluency scores in the chain FA task (t = −0.72, n.s.). A significant difference was found between versions on the associative flexibility score (t = −3.69, p = .001). Therefore, in all analyses using this variable, we controlled for the version variable as a covariate (partial correlations in the Pearson correlations and covariant in the mediation model; see more details in subsection 3.5).

3.4. fMRI data acquisition

Whole brain imaging was performed on a 3.0 T S MRI scanner, (MAGNETOM Prisma, Germany) using a 64-channel head coil, at TASMIC. Functional T2*-weighted images were obtained using field of view = 220 mm, matrix size = 96 × 96, repetition time = 3000 ms, echo time = 35 ms, flip angle = 90°, 44 axial slices of 3-mm thickness, and gap = 0. We obtained a high-resolution, Axial T1-weighted MPRAE structural scan (a 3D spoiled gradient echo sequence, voxel size = 0.9 × 0.9 × 0.9 mm, gap = 0). Resting state data were acquired for 6 min while participants fixated on a plus sign on a screen (e.g., Weissenbacher et al., 2009).

3.5. Data analysis

3.5.1. fMRI data analysis

SPM12 (Wellcome Trust Center for Neuroimaging, London, UK; http://www.fil.ion.ucl.ac.uk) was used for data analysis. The general preprocessing was conducted according to a pipeline described in previous publications (Axelrod et al., 2015a; Axelrod and Yovel, 2012) and included the following steps: realignment, slice-time correction, motion correction, normalization (2 × 2 × 3 mm voxel size) and spatial smoothing (FWHM = 6 mm kernel). Afterwards, the preprocessing needed for functional connectivity analysis included a “scrubbing” procedure to identify problematic frames (Power et al., 2012). This analysis
was conducted using the Artifact Detection toolbox for MATLAB (ART). In accordance with previous literature (Stoodley et al., 2012; Stosic et al., 2014), the following ART threshold parameters were used: global signal: 3 standard deviations; global motion: 2 mm; scan-to-scan subject motion: 0.5 mm; scan-to-scan subject rotation: 0.02 radians. Frames marked as outliers were subsequently regressed out as covariates in the connectivity analysis (Chai et al., 2014) (see below).

Connectivity analysis was conducted using the CONN MATLAB toolbox (Whitfield-Gabrieli and Nieto-Castanon, 2012). The CONN toolbox implements an aCompCor strategy to remove confounding effects from the BOLD signal (Behzadi et al., 2007). aCompCor uses an anatomical mask in non-grey matter voxels, performs Principal Component Analysis, and then top components are selected as noise regressors (Liu et al., 2017). Thus, no global signal regression is applied. aCompCor has been shown to effectively remove artifacts, including motion (Liu et al., 2017; Yeo et al., 2015). Preprocessing included band-pass filter (0.008–0.09 Hz), detrending and despiking using default toolbox values. Six motion parameters from the preprocessing stage and ART outliers were used as covariates. Analysis was conducted for the dMPFC, left IFG, PCC, left TPJ and right TPJ seed regions (see next paragraph). Connectivity values between the six regions for each participant were extracted and correlated with behavioral measures (see below).

Previous studies that explored associative abilities and brain activity during performance of the chain FA task (see subsection 2.3 and Marron et al., 2018) revealed two brain regions specifically related to associative abilities: activity in the dMPFC was found to be positively correlated with associative fluency scores (but not with associative flexibility scores), and activity in the left IFG was found to be negatively correlated with associative flexibility scores (but not with associative fluency scores). Thus, both these regions were included as seed regions in our analysis (the coordinates of the dMPFC were taken from the study of Andrews-Hanna et al. (2010b) and the coordinates of the left IFG were taken from the study of Beaty et al. (2014a)). We examined connectivity between these areas (dMPFC and left IFG) and three additional main nodes of the DMN: PCC, left TPJ and right TPJ; coordinates were taken from Andrews-Hanna et al. (2010b). All ROIs were 8-mm sphere masks that were created using the WFU Pickatlas toolbox (Maldjian et al., 2003) (Table 1). We note that the ROIs in the studies of Andrews-Hanna and colleagues (Andrews-Hanna et al., 2010b) and Beaty and colleagues (Beaty et al., 2014a) (i.e., the ROIs we used here) were defined on the basis of functional data. The WFU Pickatlas toolbox in our study was used only for creating binary masks based on these coordinates.

### 3.5.2. Correlation analyses, regression analysis, and mediation model

To test H1–H4 (see subsection 2.4) we first conducted a series of Pearson correlation analyses between RSFC values and behavioral task scores. This approach has been widely used in the past to establish relationships between neuronal loci and behavioral measures (Clare Kelly, Uddin, Biswal, Castellanos and Milham, 2008; Dai et al., 2014; Erdman et al., 2020; Liu et al., 2018; Tian et al., 2012). The analysis was conducted using the statistical software SPSS 22.0 (IBM Corp.) and custom MATLAB code (Axelrod, 2014). MATLAB 2017A was used for data analysis. In line with the rationale outlined in sections 2 and 3.5.1 above, we wished to focus on RSFC (i) within the DMN and (ii) between the DMN and the left IFG, where the latter region is part of the executive network. Accordingly, drawing from previous research (see also sections 2 and 3.5.1 above), we used the left IFG and the dMPFC as seed regions for the executive network and the DMN, respectively. For the DMN we focused on the following key regions: the dMPFC, PCC, left and right TPJ. As behavioral measures we used associative fluency, associative flexibility, AUT fluency, AUT creativity, CoM response time, and CoM accuracy. Significance of correlation was established using the bootstrap resampling method with 10,000 bootstrap sets (Axlrod et al., 2017b; Wilcox, 2012). The advantage of the bootstrapping method is that it does not make any assumptions regarding the underlying distribution of the data. For each of the analyses we applied a family-wise Bonferroni multiple comparison correction for the number of correlations examined. Correlations of associative flexibility with other measures were calculated as partial correlations, by taking into account the version of the test (recall that we used two versions; version 1 and version 2; see subsection 3.3.3) as a confound variable. Accordingly, the scatter plots with associative flexibility reflect residuals of regression analysis of each of two measures (e.g., associative flexibility and CoM accuracy) with the type of test.

For robustness we conducted three sets of linear stepwise multiple regressions using the statistical software SPSS 22.0 (IBM Corp.). The first two sets of regressions examined the relationships between RSFC values and behavioral measures: creativity task scores and associative ability scores respectively. In each of these regressions, a behavioral measure (i.e., creativity task score or associative ability score) served as the dependent variable, and seven RSFC values (i.e., from the seven pairs of ROIs) served as independent variables. A third set of regressions examined the relationships between creativity task scores and associative ability scores. In each of these regressions an associative ability score served as the dependent variable, and the four creativity task scores as the independent variables. In regressions with associative flexibility as the dependent variable, the version of the test was entered as a covariate (see subsection 3.3.3). To establish significance and reliability of the model, we used the bootstrapping resampling method with 5000 iterations, which was found reliable for small-sized samples. For each set of regressions, we applied a family-wise Bonferroni multiple comparison correction for the number of regressions in the set.

To further validate the reliability of the results, following this regression procedure, we conducted a prediction analysis (leave-one-out and a non-parametric permutation scheme) (Cohen et al., 2011; Nemmi et al., 2016; Qin et al., 2014; Supakar et al., 2013; Wang et al., 2018). Specifically, for each of the regression analyses described above, we estimated a regression model based on N-1 participants. Based on this model, and using the independent variables corresponding to participant N, we predicted the dependent value corresponding to participant N. Then, we calculated the absolute difference between the actual and predicted dependent values of participant N. The procedure was repeated N times, enabling us to obtain an average difference between actual and predicted dependent values. To evaluate statistical significance, we randomly reshuffled the data by altering correspondence between dependent and independent variables. Then, the prediction procedure described above was conducted for the permuted data. This procedure was conducted 10,000 times, enabling us to obtain an empirical null distribution. Significance was assessed by calculating the percentage of values in the null distribution that were larger than those in the non-permuted data.

To test whether associative fluency mediates the relation between within-DMN RSFC values and creativity scores (H5), as well as to examine additional mediation relationships, we used the PROCESS macro in SPSS 22.0 (IBM Corp.; Hayes, 2017). This method relies on bootstrapping, which enables the researcher to simulate repeated subsamples from an original database, allowing the assessment of the stability of parameter estimates and reporting their values with a greater

| Region | Full region name | MNI coordinates |
|--------|------------------|-----------------|
| dMPFC | dorsal medial Prefrontal Cortex | X=0 Y=52 Z=26 |
| left TPJ | Temporal Parietal Junction | X=-54 Y=-54 Z=28 |
| right TPJ | Temporal Parietal Junction | X=54 Y=54 Z=28 |
| PCC | Posterior Cingulate Cortex | X=-8 Y=-56 Z=26 |
| left IFG | Inferior Frontal Gyrus | X=-34 Y=24 Z=-11 |
degree of accuracy (Preacher and Hayes, 2008). We used bootstrapping based on 5000 iterations to assess the estimators, and 95% confidence intervals for direct and indirect effects. In each estimation involving associative flexibility, we controlled for test version (see section 3.3.3).

4. Results

4.1. Relationships between RSFC values and performance on creativity tasks (H1)

4.1.1. Pearson correlation analysis

In line with our hypothesis (H1), we found significant positive correlations between RSFC values within the DMN (i.e., dMPFC and right TPJ) and scores on both AUT fluency and CoM response time (higher score = faster response) (Table 2 and Fig. 2 top row). Also in line with H1, our analysis revealed a positive significant correlation between RSFC between the left IFG (executive network) and the DMN (i.e., right TPJ) and CoM response speed. In addition to significant correlations, we observed several additional relatively high correlations that did not reach significance after multiple comparison correction. Specifically, we observed that RSFC between the left IFG and the DMN (i.e., dMPFC) was correlated both with AUT fluency and with CoM response time (Table 2 and Fig. 2 middle row). Interestingly, contrary to H1, we also found negative correlations between AUT creativity scores and connectivity between the left IFG and areas of the DMN (i.e., PCC, right TPJ, left TPJ) (see Table 2 and Fig. 2 bottom row).

4.1.2. Robustness check: linear stepwise regression analysis and prediction analysis

Table 3 shows the results of our linear stepwise regression analysis. The results that we obtained were qualitatively very similar to those obtained in the correlation analysis (section 4.1.1). Specifically, in line with H1 and our correlation analysis, RSFC values within the DMN (i.e., dMPFC and right TPJ) were positively and significantly associated with AUT fluency ($B = 3.289, CI [0.237, 6.402]$), and RSFC between the left IFG (executive network) and the DMN (i.e., right TPJ) was significantly associated with CoM response time ($B = 1188.469, CI [153.247, 2245.167]$). Moreover, we see that the magnitude of the (negative) relationship between AUT creativity and RSFC between the left IFG and PCC was relatively strong ($B = -1.162, CI [-2.553, 0.353]$), though it attained only marginal significance ($p < .08$). In this analysis, the RSFC between the dMPFC and the right TPJ was not significantly associated with CoM response time.

Prediction analysis (leave-one-out and non-parametric permutation scheme; see Methods section 3.5.2) provided further support to the reliability of these results. Specifically, in each of the three regression models used in this analysis (corresponding to the dependent variables AUT fluency, AUT creativity, and CoM response time, respectively), we were able to successfully predict the dependent variable (i.e., creativity score) on the basis of RSFC (AUT fluency: $p = .017$; AUT creativity: $p = .022$; CoM response time: $p = .0046$).

4.2. Relationships between RSFC values and associative abilities (H2 and H3)

4.2.1. Pearson correlation analysis

In examining the hypothesis that associative flexibility is positively associated with connectivity within the DMN (H2), we focused on connectivity between the dMPFC and other DMN regions, based on the prior finding that associative flexibility scores positively correlated with activity in the dMPFC among participants who were actively engaged in the chain FA task (Marron et al., 2018). In line with H2, higher scores on associative flexibility were positively significantly correlated with the strength of RSFC between the dMPFC and the right TPJ (see Table 4 and Fig. 3).

We then tested the hypothesis (H3) that associative flexibility is negatively associated with connectivity between the DMN and the left IFG, based on our prior findings in participants engaged in the chain FA task (Marron et al., 2018). In line with our hypothesis, we observed a negative significant correlation between associative flexibility scores and the RSFC between the left IFG and the DMN (i.e., PCC, left TPJ) (see Table 4 and Fig. 3).

4.2.2. Robustness check: linear stepwise regression analysis and prediction analysis

Table 5 shows the results of our linear stepwise regression analysis. Again, the results were qualitatively similar to those obtained in correlation analysis (see above). In line with H2 and the results of our correlation analysis, we found that RSFC values within the DMN (i.e., between the dMPFC and right TPJ) were significantly associated with associative fluency ($B = 2.854, CI [0.755, 5.081]$). Likewise, in line with H3 and our correlation analysis, RSFC between the left IFG (executive network) and the DMN (i.e., PCC) were significantly negatively associated with associative flexibility ($B = -0.134, CI [-0.208, -0.001]$). In this analysis, the relationship between the RSFC between the left IFG and left TPJ and associative flexibility was not significant.

Prediction analysis provided further support to these results: In each of the two regression models used in this analysis (corresponding to the dependent variables associative fluency and associative flexibility, respectively), we were able to successfully predict the dependent variable (i.e., associative ability score) on the basis of RSFC (associative fluency: $p = .013$; associative flexibility: $p < .001$).

Table 2

| AUT Fluency | AUT Creativity | CoM Response time | CoM Accuracy |
|-------------|----------------|-------------------|--------------|
| dMPFC       | Left IFG       | dMPFC             | Left IFG     |
| 1           | $R = .36$      | 1                 | $R = .13$    |
|             | $p = .018$     |                   | $p = .377$   |
|             | [.14,.69]      |                   | [.5,.31]     |
| Left TPJ    | $R = .3$       | $R = .21$         | $R = .37$    |
|             | $p = .048$     |                   | $p = .678$   |
|             | [.07,.71]      |                   | [.46,.63]    |
| Right TPJ   | $R = .38^*$    | $R = .34$         | $R = .45^*$  |
|             | $p = .004$     |                   | $p = .003$   |
|             | [.01,.7]       |                   | [.04,.81]    |
| PCC         | $R = .39$      | $R = .48$         | $R = .13$    |
|             | $p = .601$     |                   | $p = .113$   |
|             | [.39,.48]      |                   | [.37,.73]    |
|             | $R = .26$      |                   | $R = .12$    |
|             | $p = .855$     |                   | $p = .44$    |
|             | [.76,.20]      |                   | [.48,.43]    |
|             | $R = .26$      |                   | $R = .12$    |
|             | $p = .855$     |                   | $p = .44$    |
|             | [.76,.32]      |                   | [.66,.3]    |
4.3. Relationships between associative abilities and scores on creativity tasks (H4)

4.3.1. Pearson correlation analysis

In line with H4 and previous literature (e.g., Beaty et al., 2014c; Benedek et al., 2012a,b; Kenett et al., 2018a; Marron and Faust, 2018; Marron et al., 2018), associative ability scores were positively and significantly correlated with scores on creativity tasks. Specifically, associative fluency correlated positively with AUT fluency and CoM response time scores, and associative flexibility positively correlated with AUT creativity and CoM accuracy (see Table 6 and Fig. 4).

4.3.2. Robustness check: linear stepwise regression analysis and prediction analysis

Once again, the results of this robustness check were qualitatively similar to those of our correlation analyses (see Table 7). In line with H4 and our correlation analysis, we found that associative fluency was significantly associated with AUT fluency ($B = 0.375, CI [0.119, 0.710]$)
Pearson Correlations between associative abilities (fluency and flexibility) and resting state functional connectivity values. N = 27. Abbreviations: dMPFC = dorsal Medial Prefrontal Cortex, TPJ = Temporal Parietal Junction, PCC= Posterior Cingulate Cortex, IFG= Inferior Frontal Gyrus. \( \alpha = 0.05/4 = 0.0125 \). R reflect results of Pearson correlation, p-values were obtained using bootstrapping (see subsection 3.5.2). Confidence intervals in brackets. Correlations of associative flexibility with other measures were calculated as partial correlations, by taking into account the version of the test as a confound variable (see section 3.3.3). For results of the corresponding analyses conducted with 32 participants (both females and males), see Supplementary Table S5.

| Associative Fluency | Associative Flexibility |
|---------------------|-------------------------|
| dMPFC Left IFG       | dMPFC Left IFG           |
| R = .1               | R = -.12                |
| p = .495             | p = .387                |
| [-.26,.46]           | [-.47,.22]              |
| Left TPJ R = -.11    | R = -.04                |
| p = -.577            | p = .011                |
| [-.30, .58]          | [.36, .64]              |
| Right TPJ R = -.47*  | R = -.02                |
| p = .002             | p = .168                |
| [.08, .78]           | [.54, .54]              |
| PCC R = -.26         | R = -.05                |
| p = .127             | p = .012                |
| [-.20,.63]           | [.62, .8]               |
| &lt; .01             | .005                    |
| CoM Accuracy R = 4   | R = 49*                 |
| p = .041             | p = .001                |
| [.02, .77]           | [.08, .8]               |

and CoM response time scores \( B = 0.001, CI [0.000, .002] \). We also found that associative flexibility was significantly associated with AUT creativity \( B = 0.052, CI [0.007, 0.088] \). The relationship between associative flexibility and CoM accuracy was not significant in this analysis.

Prediction analysis provided further support to these results, such that in the two regression models used in this analysis (corresponding to the dependent variables associative fluency and associative flexibility, respectively), we were able to successfully predict the dependent variable (i.e., associative ability score) on the basis of creativity scores (associative fluency: \( p < .001 \); associative flexibility: \( p < .001 \)).

**Fig. 3.** Scatter plots of correlations for all significant correlations between resting state functional connectivity (RSFC) values and associative abilities. Abbreviations: dMPFC = dorsal medial Prefrontal Cortex, TPJ = Temporal Parietal Junction, PCC= Posterior Cingulate Cortex, IFG= Inferior Frontal Gyrus. In all plots, the tendency lines reflect an ordinary least squares (OLS). Correlation of associative flexibility with other measures were calculated as partial correlations, by taking into account the version of the test as a confound variable (see section 3.3.3). Accordingly, the scatter plots with associative flexibility reflect residuals of regression analysis of each of two measures (e.g., associative flexibility and left IFG & PCC) with type of the test. RR \( = \) denotes that values are residuals of regression of the variable with version type. Note the positive correlation of associative flexibility with within-DMN RSFC, and the negative correlation of associative flexibility with RSFC in the DMN and the left IFG. For the corresponding scatter plots for analyses conducted with 32 participants (both females and males), see Supplementary Figure S2.

**Table 4**

| Associative Fluency | dMPFC Left IFG |
|---------------------|----------------|
| R = .1              | R = -.12       |
| p = .495            | p = .387       |
| [-.26,.46]          | [-.47,.22]     |

**Table 5**

Linear stepwise regressions with resting-state functional connectivity values as independent variables and each associative ability score (fluency and flexibility) as a dependent variable. N = 27. Abbreviations: dMPFC = dorsal medial Prefrontal Cortex, TPJ = Temporal Parietal Junction, PCC= Posterior Cingulate Cortex, IFG= Inferior Frontal Gyrus. \( \alpha = 0.05/2 = 0.025 \). Stepwise regression with associative flexibility as the dependent variable was calculated by taking into account the version of the test as a confound variable (see section 3.3.3). p-values and confidence intervals were obtained using bootstrapping (see subsection 3.5.2). For results of the corresponding analyses conducted with 32 participants (both females and males), see Supplementary Table S4.

| Associative Ability | Retained Predictor | B   | Standard Error | Beta | p    | 97.5% Confidence Interval |
|---------------------|--------------------|-----|----------------|------|------|--------------------------|
|                     |                    |     |                |      |      | Lower | Upper |
| Associative Fluency | dMPFC - right TPJ  | 2.854 | .959          | .475 | .008*| .755 | 5.081 |
| Associative Flexibility | left IFG - PCC | -.134 | .046             | -.442 | .014*| -.208 | -.001 |

**Table 6**

Pearson Correlations between associative abilities (fluency and flexibility) and creativity task scores. N = 27. Abbreviations: AUT = Alternative uses task. Com = Comprehension of metaphors task. \( \alpha = 0.05/4 = 0.0125 \). R reflect results of Pearson correlation, p-values were obtained using bootstrapping (see subsection 3.5.2). Confidence intervals in brackets. \# denotes that the scale was reversed so that higher scores = faster response. Correlation of associative flexibility with other measures were calculated as partial correlation, by taking into account two versions of the test as a confound variable (see section 3.3.3). For results of the corresponding analyses conducted with 32 participants (both females and males), see Supplementary Table S5.
To examine whether associative fluency mediates the links between RSFC values and measures of creativity (H5), we conducted a mediation model analysis. Prior to running the model, we prepared the variables by conducting the following steps. First, because each measure is ranged on a different scale, we standardized the scores into z scores ranging between regions within the DMN (and specifically, between the DMN region dMPFC and each of the other ROIs in the DMN, i.e., the left TPJ, right TPJ and PCC; in what follows we refer to these RSFC scores as ‘within-DMN RSFC’) (3 values per participant; correlations between pairs of values ranged between 0.17 and 0.57), and (2) RSFC between the left IFG (executive network) and each of the DMN areas we examined (dMPFC, left TPJ, right TPJ, PCC; 4 values per participant; correlations between pairs of values ranged between 0.15 and 0.58). Note that separate aggregation of (1) RSFC values between areas within the DMN (2) and RSFC values between the left IFG (executive network hub) and areas in the DMN is compatible with our theoretical focus on connectivity both within the DMN and between the DMN and the executive network. Moreover, this approach is in line with previous research (Beaty et al., 2014a; Li et al., 2016; Z. Liu et al., 2018; Ogawa et al., 2018; Shi et al., 2018; Takeuchi et al., 2012, 2017; Wei et al., 2014; Zhu et al., 2017; see subsection 2.1). In addition, we averaged the creativity indices (4 values per participant) into a single ‘creativity score’ for each participant (correlations between pairs of values ranged between 0.14 and 0.47). This aggregation provided us with a straightforward means of distinguishing ‘more creative’ individuals from ‘less creative’ individuals (though it cannot provide insights regarding connectivity patterns of individuals who score well on certain facets of creativity and less well on others). The choice to...
aggregate creativity indices in this manner was also in line with previous research that created one creativity score based on a composite of ideational fluency and originality (i.e., creativity) (Beaty et al., 2018; Benedek et al., 2012b), as well as with prior research that combined CoM performance scores and AUT scores to assess creativity, in light of observations that performance on the CoM task (in terms of response time and accuracy, the two measures we derived) relates to high scores on fluency and creativity on the AUT (Kenett et al., 2014; Kenett et al., 2018b; Kenett et al., 2018b).

We evaluated four possible mediation models (see section 3.5.2), derived from the combinations of RSFC values in each of the two factors (within-DMN and between left IFG and DMN), both associative abilities (associative flexibility and associative fluency), and a single main outcome (aggregated creativity index). In order to avoid inflation of the error term, we assessed the significance of indirect effects using Bonferroni correction. Table 8 shows the bootstrapping indirect effects of all four possible models.

The only path that yielded a significant indirect effect is the path in which associative fluency mediates the association between within-DMN RSFC and creativity score (see Fig. 5). Specifically, it was found that RSFC within the DMN was positively correlated with associative fluency, \( B = 0.76, S.E. \ B = 0.38, CI [0.01, 1.55], p = .03 \), which it turn, was positively correlated with creativity, \( B = 0.32, S.E. \ B = 0.06, CI [0.18, 0.45], p < .001 \). The results for the nonsignificant paths are shown in Supplementary Material (Fig. S4–S6).

Examining the reverse mediation model, in which creativity is associated with associative fluency, which in turn is associated with within-DMN RSFC, yielded a non-significant indirect effect, \( B = 0.31, S.E. \ B = 0.23, CI [-0.11, 0.81] \) (see Supplementary Figure S7). In addition, examining a mediation model in which within-DMN RSFC is related to creativity, which in turn is associated with associative fluency, yielded a non-significant indirect effect, \( B = 0.36, S.E. \ B = 0.23, CI [-0.09, 0.81] \) (see Supplementary Figure S8). Thus, our results support the hypothesized mediation model (H5; see subsection 2.4).

5. Discussion

In this study we investigated the links between individuals’ RSFC patterns, their performance on creativity tasks, and propensity for spontaneous cognition—measured through so-called ‘associative ability’, using a specially designed and validated chain FA task. Our findings enable us to provide insights regarding the role of spontaneous cognition in the neurocognitive patterns that characterize the highly creative brain, and thus to shed light on the mechanisms underlying creative thinking. They further enable us to identify the RSFC patterns characterizing the ‘highly-associative brain’ (as opposed to the less-associative brain), which, as our analyses reveal, are related, but not equivalent, to the patterns characterizing the highly-creative brain. Our main results were as follows: First, a highly-associative brain is characterized by high within-DMN RSFC, and low RSFC between the left IFG (major node of the executive network) and the DMN. Second, we found that associative fluency partially mediates the relationship of within-DMN RSFC values and creativity scores, supporting the notion that the brain connectivity characteristics characterizing highly creative individuals are attributable, in part, to spontaneous cognition. In what follows we discuss some of the main implications of our results for brain research on creativity.

5.1. Relationships between brain functional connectivity patterns and creativity

Our observations regarding the brain connectivity patterns associated with performance on creativity tasks strengthen and provide potential interpretations for previous findings. An extensive corpus of knowledge suggests that creative thinking involves higher activity of both the DMN and the executive network, as well as higher connectivity within the DMN and between the executive network and the DMN (Andrews-Hanna et al., 2018; Beaty et al., 2015, 2016; Beaty et al., 2014c; Benedek and Jauk, 2018; Christoff et al., 2016; Chrysikou, 2019; Ellamil et al., 2012; Marron and Faust, 2018; Voile, 2018). In line with these studies, we found that higher fluency scores on a common creativity task (i.e., AUT) positively correlated with increased RSFC within the DMN (between the dMPFC and the right TPJ). Moreover, in line with previous findings, we found that higher CoM task response time scores positively correlated with increased RSFC between the left IFG (part of the executive network) and the right TPJ (part of the DMN). Our Pearson correlation analyses also suggested a significant correlation between speed of recognizing novel metaphors (CoM response time) and increased RSFC within the DMN (between the dMPFC and the right TPJ); however this association was not significant in our robustness analysis, perhaps due to collinearity between the different independent variables. The MPFC (Benedek et al., 2016; Takeuchi et al., 2012; Wei et al., 2014) and left IFG (Beaty et al., 2015; Beaty et al., 2014a) have been shown to be major hubs in functional connectivity related to the highly creative brain.

It is noteworthy that previous findings related to the relationship between activity and functional connectivity of the right TPJ and performance on creativity tasks are mixed. On the one hand, Beaty (2015) found the right TPJ to be functionally connected with the right dorsal lateral PFC during completion of the AUT, and in a different study the right TPJ was functionally connected to the left IFG during rest in highly creative individuals (Beaty et al., 2014a). On the other hand, studies have also found that deactivation, but not activation of the right TPJ is related to idea generation (Benedek et al., 2014a; Benedek et al., 2014b) and to expertise in musical improvisation (Beaty, 2015; Berkowitz and Ansari, 2010). This reason for these mixed findings might be that the right TPJ actually has several sub-regions (Mars et al., 2012), and while the anterior part of the TPJ is highly connected to the ventral attention network, the posterior area of the right TPJ (to which our ROI coordinates correspond) is more connected to the areas of the DMN (e.g., MPFC, PCC). Even more so, the specific connectivity between the dMPFC and the right TPJ have been found to be related to internal thinking, specifically about one’s own or another’s mental state or present situation (Andrews-Hanna et al., 2010a; Klapwijk et al., 2013). The latter form of thinking may rely on associative processes that are critical for creative ideation (Takeuchi et al., 2012; see subsection 5.2). In the future, taking into account detailed functional parcellation of the TPJ (Bzdok et al., 2013) might contribute towards elucidating the extent to which creative thinking is supported by activation of the DMN relative to activation of other networks.

Interestingly, in contrast to what we expected based on prior research (Beaty et al., 2014a; Liu et al., 2018; Shi et al., 2018; Takeuchi et al., 2017; Zhu et al., 2017), we observed a relatively high negative correlation (though it did not reach significance after multiple comparison correction) between creativity scores on the AUT and the connectivity between the left IFG and the DMN (PCC, left TPJ, right TPJ). Indeed, several studies have produced similar findings of an inhibiting effect of the left lateral prefrontal cortex (e.g., Saggard et al., 2017) and specifically

| Independent | Mediator | Outcome | B   | Confidence Interval |
|-------------|----------|---------|-----|---------------------|
| Within-DMN RSFC | Associative Fluency | Creativity score | 0.24 | 0.06, 0.64 |
| Within-DMN RSFC | Associative Flexibility | Creativity score | -0.01 | -0.20, 0.19 |
| RSFC between left IFG and DMN | Associative Fluency | Creativity score | -0.03 | -1.30, 1.31 |
| RSFC between left IFG and DMN | Associative Flexibility | Creativity score | 1.13 | -2.09, 0.08 |
of the left IFG on creativity scores (Chrysikou, Hamilton, Coslett, & Thompson-schill, 2011; Chrysikou et al., 2014; Chrysikou and Thompson-Schill, 2011; Ivancovsky et al., 2019; Kleinnitz et al., 2018; Mayseless and Shamay-Tsoory, 2015; Pobric et al., 2008). Further research is needed to shed light on this phenomenon.

5.2. Resting-state characterization of the highly-associative brain

As noted above, an important novel aspect of our study is that we identified RSFC patterns that significantly correlate with so-called associative abilities, i.e., measures of spontaneous cognition that are relevant for creative ideation (associative fluency and associative flexibility). We found that individuals with higher scores on associative fluency (produced more spontaneous associations in a given time) showed enhanced RSFC within the DMN (specifically between the dMPFC and the right TPJ). Notably, our prior work has identified a similar association between increased activity of the dMPFC and associative fluency scores during chain FA task performance (Marron et al., 2018). Prior studies have suggested that high activity within the DMN is associated with an enhanced capacity for self-generated thought and rapid retrieval of information from memory (Andrews-Hanna et al., 2018; Christoff et al., 2016; Fox et al., 2015; Marron and Faust, 2018; Marron et al., 2018; Zabelina and Andrews-Hanna, 2016). Interestingly, both the dMPFC and the right TPJ are major nodes in a sub-network of the DMN - the dorsal medial subsystem. The dorsal medial subsystem has been specifically related to tasks that involve internally reflecting on one’s (and others) mental state as well as elaboration of spontaneous thoughts (Andrews-Hanna et al., 2018; Andrews-hanna et al., 2010a,b; Fox et al., 2015; Klapwijk et al., 2013; Raichle, 2015). Accordingly, it is possible that the brain activity we observed that was related to associative fluency was an indication of individuals’ ability to engage in the metacognitive processes of reflecting and elaborating one’s thoughts, processes that are likely to be elicited during the chain FA task, given the instructions provided (see subsection 3.3.1), and are relevant for creative ideation (Takeuchi et al., 2012).

We further observed that individuals with higher associative flexibility (more diverse associative chains) showed lower RSFC between an executive control hub (left IFG) and the DMN (PCC). We also observed a negative correlation between associative flexibility and RSFC between the left IFG and the left TPJ (DMN); however, this relationship was not significant in our multivariate robustness test. The relationships we observed may suggest that, as indicated by previous research (Marron et al., 2018), low involvement of executive control (as reflected in low activation of the left IFG) coupled with activation of the DMN could be related to higher ability to spontaneously access and shift between remote semantic fields and episodic memory (semantic fields and episodic memory are likely related to the PCC and the left TPJ, among other areas; Addis et al., 2009; Aminoff et al., 2007; Benedek et al., 2014a; Binder et al., 2009; Burianova and Grady, 2007; De Souza et al., 2010; Krieger-Redwood et al., 2016; Mayseless and Shamay-Tsoory, 2015b; Shapira-Lichter et al., 2013). Put differently, this observation supports the notion that the left IFG area that we tested might be related to inhibition of spontaneous access to remote semantic fields and episodic memories. In our study we used RSFC – a correlational method that, by definition, cannot provide information about causal links. In the future, it would be of interest to examine this question using causal measurements of connectivity (Bielczyk et al., 2019).

5.3. The role of spontaneous cognition (associative ability) in the RSFC patterns characterizing more creative individuals

Finally and importantly, we found that associative fluency partially mediated the relationship between within-DMN RSFC and creativity scores. This finding provides important support to what has been hypothesized about the creative brain but not yet examined (Beaty et al., 2016; Beaty et al., 2014a; Liu et al., 2018; Takeuchi et al., 2012, 2017; Wei et al., 2014; Zhu et al., 2017): The observation of high within-DMN connectivity among highly-creative individuals may be related to the fact that these individuals have heightened capacity to engage in spontaneous generative processes, such as those captured in the associative fluency score of the chain FA task.

Our other mediation models were not significant. We note that though we did not hypothesize that associative flexibility would mediate the relationship between RSFC between the left IFG and DMN and performance on creativity tasks, the reason for this lack of a mediation path diverged from our expectations. Specifically, we assumed that RSFC patterns linked to high associative flexibility would be in the opposite direction of the RSFC patterns linked to enhanced creativity scores (Beaty et al., 2014a; Liu et al., 2018; Shi et al., 2018; Takeuchi et al., 2017, Zhu et al., 2017), thereby making a mediation path unlikely. Yet, our results showed that, in contrast to our hypothesis, scores on both creativity (e.g., AUT creativity scores) and associative flexibility correlated negatively with RSFC scores between the left IFG and the DMN. Regardless of similar directionality, associative flexibility did not mediate the relation of RSFC between the left IFG and the DMN and creativity scores.

The lack of a mediation effect might have been due to our small sample size, the initial weak relationship between creativity scores and RSFC values, or the covariate that we entered into this model (see subsection 3.3.3). Accordingly, it is necessary to reexamine this relationship in future research. However, there is also a possibility that lower connectivity of the DMN with the left IFG affects several cognitive processes that differentially influence creativity scores and associative flexibility scores. It might be that, on the one hand, the specific left IFG area that we examined relates to inhibiting spontaneous shifting between semantic fields, thereby reducing associative flexibility (Marron et al., 2018), and on the other hand it might enhance creativity scores by reducing the tendency to evaluate ideas strictly, and to regard more deviant responses as acceptable (Kleinnitz et al., 2018). In other words, the RSFC patterns linked to associative flexibility may point to more complex relationships than we expected and to specific cognitive processes that underlie each.

Fig. 5. Results of mediation model with resting state functional connectivity (RSFC) within the default mode network (DMN) as the predictor, associative fluency as the mediator, and measures of creativity as the outcome. N = 27. ** p-value < 0.01. * p-value < 0.05. This model indicates that associative fluency partially mediates the relationship between within-DMN RSFC and creativity score. For the corresponding significant mediation model for analysis conducted with 32 participants (both females and males), see Supplementary Figure S9. The results for the nonsignificant paths for analyses conducted with 32 participants are shown in Supplementary Figures S10-S12.
task. Recent review articles have attempted to reconcile various discrepancies between observations of brain activity and creative performance by delving deeper into the different cognitive control processes (and their suggested underlying brain areas) relevant for creative cognition and important differences between them (Chrysikou, 2019; Dajani and Uddin, 2015). Research should test these different control processes in the same sample to perhaps identify the exact areas of the left IFG relevant for each process (see further discussion below).

5.4. Limitations and future directions

The present research used a recently validated task (chain FA) to examine relationships between creativity, RSFC and spontaneous cognition (associative ability). Our results extend recent studies by clarifying the contribution of spontaneous processing to RSFC patterns related to creative cognition. Importantly, our work provides support to the proposition, which research has only recently begun to test (e.g., Madore et al., 2019), that spontaneous cognitive processes, and specifically, associative spontaneous processes, can explain part of the relation between creativity scores and RSFC within the DMN but not between the DMN and the executive network (specifically the left IFG).

However, the present study has several limitations. Perhaps the most serious limitation is that our study used 27 participants, which is a modest sample size in the context of studies that examine individual differences. In the future, it would be very important to replicate our findings using larger sample sizes (at least 85 participants (King, 2019) or even more ideally 150 participants (Mar et al., 2013)). Another limitation of the sample used in our main analyses is that it consisted only of female participants (N = 27). Our original recruited sample did include several male participants (N = 6), and when we repeated our analyses on data from the complete sample of males and females (see Supplementary Material), we obtained results very similar to those presented in the main analysis. However, the number of male participants recruited was simply too small to produce reliable conclusions regarding the male population. Given that numerous fields of research—including medicine (e.g., Legato et al., 2016; Ostane et al., 2016), psychology (e.g., Bleidorn et al., 2016; Street and Dardis, 2018), and specifically neuro-cognitive research of creativity (e.g., Abraham et al., 2014)—are increasingly emphasizing the importance of interpreting and understanding gender differences, coupled with the fact that previous studies have indeed identified differences in functional connectivity between males and females (Gong et al., 2011; Takeuchi et al., 2017; Yang et al., 2015; Zhang et al., 2016), we preferred to focus our main results on our female participants rather than on the pooled sample. It is important for future studies to examine whether our results generalize to the whole population, and whether there are differences between males and females on the measures we examined.

An additional limitation, mentioned in previous subsections, is that our mediation model used a cross-sectional design, and thus did not take into account the unfolding of the variables over time. Although our final model is supported theoretically (see subsection 2.4) and statistically (see subsection 4.4), using this type of design can cause bias, and interpretation should be cautious (Maxwell and Cole, 2007; Maxwell et al., 2011). In an attempt to gain some insight into directionality and causality in brain research, specifically when using fMRI (in which the capacity to differentiate rapid fine-grained processes is limited due to the scan time), recent studies have been using temporal connectivity analysis (time windows) (e.g., Beaty et al., 2015), Dynamic Causal Modeling (DCM; e.g., Vartanian et al., 2018), and designs using experimental manipulation (e.g., Madore et al., 2019). Additional designs should be tested in the future to support our results.

It should also be noted that, although we generated a clearer picture of the contribution of one mode of cognitive processing (namely, spontaneous cognition, as reflected in associative ability) to the RSFC of the creative brain, future research should add into this model additional measures that are potentially relevant to creativity, e.g., measures of controlled cognition, such as evaluation (Kleinmintz et al., 2014), inhibition (Benedek et al., 2012a), and deliberate switching (Gilhooley et al., 2007). A more comprehensive model will provide a more fine-grained understanding of the relationships between network connectivity and performance on creativity tasks.

Finally, we would like to note that the duration of the resting-state session that we used was 6 min. This approximate duration is used in many resting-state studies in general (e.g., Guo et al., 2016; Muschelli et al., 2014; Yao et al., 2009) and in creativity research in particular (e.g., Beaty et al., 2014a; Takeuchi et al., 2017). Nevertheless, a longer scan duration might produce more reliable results (Birn et al., 2013). Thus, in the future, it would be important to show similar effects using a longer scan (e.g., 10 min).

5.5. Concluding remarks

The present research is one of the first to relate functional connectivity patterns to specific associative abilities. In doing so, it contributes to fields that study spontaneous cognitive processes, including spontaneous thoughts that are relatively free from external and internal constraints such as those generated during mind wandering, night dreaming, and incubation processes (Axelrod et al., 2015, 2017; Axelrod et al., 2018; Baird et al., 2012; Christoff et al., 2016; Fox et al., 2015; Gable et al., 2019; Marron and Faust, 2019; Nir and Tononi, 2010), in addition to creative ideation. These processes are increasingly attracting scientific attention, as they are thought to constitute a significant proportion of human cognition (see Andrews-Hanna et al., 2018 for a review). Importantly, this research contributes to advancing one of the primary tenets of creativity research—namely, discovering what underlies human creativity, which is central to innovation in all areas of life. Specifically, by measuring associative abilities—measures that represent spontaneous cognition related to creativity—and by identifying the extent to which brain activity patterns characterizing creative individuals can be attributed to such measures, this research contributes towards the development of a comprehensive model of the multiple cognitive sub-processes involved in creative ideation. Such a model is crucial for identifying factors that might promote creative thinking (e.g., relaxation of inhibitions) or hinder it (e.g., intellectual, emotional or cultural blocks), and, by extension, for the development and refinement of protocols for enhancing creativity (e.g., Bott et al., 2014; Green et al., 2016; Saggar et al., 2017), as well as for measuring it.

Declaration of competing interest

None.

Acknowledgements

The authors are grateful to Professor Talma Hendler for her devoted help and knowledge and for her thoughtful feedback and assistance throughout this research, and to Karen Marron for her skillful editing and creative input. This research was supported by the I-CORE Program of the Planning and Budgeting Committee and The Israel Science Foundation (grant No.51/11). The funding source had no involvement in the study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.117064.

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