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ORIGINAL PAPER

Creativity Is Enhanced by Long-Term Mindfulness Training and Is Negatively Correlated with Trait Default-Mode-Related Low-Gamma Inter-Hemispheric Connectivity

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Abstract It is becoming increasingly accepted that creative performance, especially divergent thinking, may depend on reduced activity within the default mode network (DMN), related to mind-wandering and autobiographic self-referential processing. However, the relationship between trait (resting-state) DMN activity and divergent thinking is controversial. Here, we test the relationship between resting-state DMN activity and divergent thinking in a group of mindfulness meditation practitioners. We build on our two previous reports, which have shown DMN activity to be related to resting-state log gamma (25–45 Hz) power and inter-hemispheric functional connectivity. Using the same cohort of participants (three mindfulness groups with increasing expertise, and controls, $n = 12$ each), we tested (1) divergent thinking scores (Flexibility and Fluency) using the Alternative Uses task and (2) correlation between Alternative Uses scores and DMN activity as measured by resting-state gamma power and inter-hemispheric functional connectivity. We found that both Fluency and Flexibility (1) were higher in the two long-term mindfulness groups (>1000 h) compared to short-term mindfulness practitioners and control participants and (2) negatively correlated with gamma inter-hemispheric functional connectivity (frontal-midline and posterior-midline connections). In addition, (3) Fluency was significantly correlated with mindfulness expertise. Together, these results show that long-term mindfulness meditators exhibit higher divergent thinking scores in correlation with their expertise and demonstrate a negative divergent thinking—resting-state DMN activity relationship, thus largely support a negative DMN-creativity connection.

Keywords Creativity · Divergent thinking · Electroencephalography (EEG) · Gamma band · Functional connectivity · Default mode network (DMN) · Mindfulness

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Introduction

Creativity is the capacity to produce work that is both novel (i.e., original) and appropriate (i.e., useful) (Sternberg and Lubart 1993). Behaviorally, the first component—generation of new ideas—can be measured by divergent thinking tests, whereas the second component concerning task constraints can be measured by convergent thinking tests (Jung et al. 2013). Despite a five-decade long effort to localize creative processes within the human brain (for review, see Dietrich and Kanso 2010), the notion that certain aspects of creativity can be precisely localized has not born yet a consistent pattern of brain activity that is associated with creative information processing (Mok 2014). As it is increasingly accepted that brain function relies on coordinated "networks" (Bressler and

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Menon 2010), a novel approach to creativity seems warranted, targeting creative processes in the brain based on the notion of networks (recently reviewed by Beaty et al. 2015; Gonen-Yaacovi et al. 2013).

In line with the networks approach to creativity, idea generation tasks are suggested to be related to default mode network (DMN) activation, while idea evaluation condition is related to a dynamic DMN—frontoparietal (FPN) cooperation (Beaty et al. 2016). The DMN is a set of regions intensively studied by blood oxygenated level dependent (BOLD) functional magnetic resonance imaging (fMRI) that includes the medial prefrontal cortex, inferior parietal lobule (IPL), posterior cingulate/precuneus, and the medial temporal lobe (Buckner et al. 2008; Raichle et al. 2001). Cognitively, elevated BOLD-DMN activity has been related to heightened intrinsically oriented functions, including mind-wandering, autobiographic self-related processing, memorizing the past and planning the future (Buckner et al. 2008). The DMN, also called the "intrinsic network," was demonstrated using fMRI to typically anticorrelate with the "extrinsic," external-task-related network (Fox et al. 2005; Golland et al. 2007). Interposed between them is suggested to be the frontoparietal network (FPN), which includes the anterior prefrontal cortex (PFC), dorsolateral (DL)-PFC, dorsomedial superior frontal, anterior cingulate cortex (ACC), anterior IPL, and anterior insular cortex (Vincent et al. 2008). The FPN can be broken down into two subnetworks (Seeley et al. 2007), the "executive control network" (DLPFC and IPL) and the "salience system" (anterior insula and ACC), with the former being related to working memory, directed attention, and relational integration, while the latter being specifically attributed the role of switching between the intrinsic and extrinsic systems (Menon and Uddin 2010). The FPN cooperates with either one of these typically antagonistic systems, possibly integrating information from, and adjudicating between, these two potentially competing brain systems (Smallwood et al. 2012; Spreng et al. 2010; Vincent et al. 2008). More specifically, accumulating fMRI evidence shows that divergent thinking is related to increased functional connectivity between the DMN and FPN, both as a state (during the task) and as a trait (measured during resting state) (Beaty et al. 2014a, b, 2015, 2016).

However, the evidence concerning the involvement of the DMN in divergent thinking is still controversial, both as a state (during the creative task), but more so as a trait. Jung et al. (2013) recently reviewed evidence showing that both increased and decreased brain measures (both structural and functional) within the default mode network (DMN) are associated with creativity. On the one hand, Jung and colleagues (2013) state that "the production of something 'novel and useful' appears to depend, at least in part, on disinhibitory neuronal processes within this core network" (p. 9), that is, increased DMN activity could intuitively be associated with increased divergent thinking. This is in line with previous notions associating "disinhibition" of cognitive control mechanisms with divergent thinking (Dietrich 2004; Martindale 1971), where multiple ideas can be generated in a non-judgmental environment, without selection pressures, as is the case for DMN activity. However, at the same time, Jung et al. (2013) provide evidence that this hypothesis is not well fitted by some data showing a negative relation between creativity and DMN structure integrity. Thus, the relationship between DMN activity, as a trait (i.e., during resting state and not during a task), and creativity remains puzzling.

An independent but highly relevant line of research has related mindfulness meditation practice to reduced DMN activity and functional connectivity, as measured by fMRI (e.g., Berkovich-Ohana et al. 2016; Brewer et al. 2011; Farb et al. 2007; Hasenkamp and Barsalou 2012). Mindfulness meditation, as often studied in research paradigms, is a technique of remaining aware and noticing the salient features of present experience while refraining from judgmental processes, conceptual elaboration, and mind wandering (Kabat-Zinn 2003). While the DMN is commonly studied by means of fMRI, in two previous studies, we were able to show that the DMN can also be reflected in electroencephalography (EEG), as activity in the low-gamma (25–45 Hz) band. Specifically, Berkovich-Ohana et al. (2012) employed mindfulness practitioners, including three levels of expertise and a suitable control group, reporting two major findings. The first was the manifestation of DMN deactivation as reduced low gamma power within frontal-midline regions during a time-production (extrinsic-network related) task compared with a resting state (intrinsic, DMN activity). The second was that mindfulness practitioners generally exhibited reduced resting-state frontal low gamma power as compared to controls, suggesting a trait (long-lasting) effect of reduced mind-wandering and self-related processing in mindfulness practitioners. Berkovich-Ohana et al. (2013) then expanded the analysis to include functional connectivity, identifying DMN deactivation as a reduction in overall long-range gamma inter-hemispheric functional connectivity, showing a mindfulness-induced decrease in resting-state gamma functional connectivity in the long-term mindfulness group.

Yet another line of research has investigated the effect of meditation on creativity. Although there are many meditative techniques, for simplicity, we adopt here the conceptualization of Lutz et al. (2008), grossly dividing meditation into two forms: Focused Attention—learned control over the focus of one's attention by using a stable object with the goal of quieting the mind (for example, a mantra), and Open Monitoring—maximizing the breadth and clarity of maintained attention in order to bring higher momentary awareness to internal processes (the latter includes, for example, mindfulness and Zen). While it has been argued that meditation practice supports creativity, the evidence is inconsistent (Horan 2009; Lippelt et al. 2014), possibly due to the wide variety of meditation techniques and creativity measures employed. Early studies focused on Focused Attention meditation (including Transcendental Meditation and Ananda Marga) and found no support (e.g., Domino 1977; O'Haire and Marcia 1980), while others provided supporting evidence (Orme-Johnson et al. 1977; Orme-Johnson and Granieri 1977). In contrast, later studies focused on Open Monitoring meditations, and supporting evidence started to accumulate, specifically for an Open Monitoring meditation-divergent thinking connection. For example, in an early study of Zen practitioners, meditators out-performed a relaxation group in divergent thinking using the Torrance Test of Creative Thinking (TTCT) (Cowger and Torrance 1982). A later study showed that trait—and state—variations in mindfulness in undergraduate volunteers predict greater creative elaboration, measured by a variant of the TTCT (Zabelina et al. 2011). Another study examining cognitive rigidity, using a variation of the Einstellung water jar task, found that experienced mindfulness practitioners had significantly lower rigidity scores than non-meditators (Greenberg et al. 2012). In yet another recent study, a week of integrative body–mind training (IBMT, a form of Open Monitoring) was shown to improve divergent thinking, measured by the TTCT (Ding et al. 2014). Based on the accumulating evidence, Colzato et al. (2012) suggested that Focused Attention and Open Monitoring induce two almost opposite cognitive-control states that support convergent and divergent thinking, respectively. To test this hypothesis, they compared the impact of Focused Attention and Open Monitoring meditation practice on both convergent and divergent thinking, using the Remote Associates task and the Alternative Uses task, respectively. They found that while convergent thinking tended to improve after Focused Attention, divergent thinking was significantly enhanced after Open Monitoring, as hypothesized.

As the evidence in the literature is inconclusive for the creativity—trait (resting-state) DMN activity connection, and as mindfulness meditation has been shown to generally reduce trait DMN activity, as well as to increase creativity measures, here, we converge the above three lines of research in an attempt to add to the current state of the art in these fields. To this end, we build on our previous reports, and use the same cohort of participants, to test the following questions: (1) What is the effect of mindfulness expertise on divergent thinking? and (2) How do measures of divergent thinking correlate with DMN activity, as measured by resting-state low gamma power and inter-hemispheric functional connectivity? We specifically hypothesized that mindfulness expertise will increase divergent thinking and that divergent thinking will negatively correlate with DMN activity.

Method

Participants

A total of 48 healthy, right-handed individuals are reported in the study: 36 mindfulness meditation practitioners recruited from the Israeli Insight Society (http://www.tovana.co.il) and the Newman Society (http://www.metta.org.il) and 12 controls. All the meditation practitioners have been practicing mindfulness according to the Satipathana and Theravada Vipassanā traditions. The mindfulness practitioners were divided into three groups ($n = 12$ each), on the basis of accumulated hours of formal practice: Short-term mindfulness (5 females; mean experience in hours: 894 ± 450 h, range 180–1430 h; and experience in years: 5.7 ± 0.9 years), Intermediate-term mindfulness (3 females; 2570 ± 471 h, 1740–2860 h; 9.6 ± 1.5 years), and Long-term mindfulness practitioners (2 females; 7556 ± 5027 h, 3870–23,000 h; 13.8 ± 2.2 years). Meditation expertise was calculated using a self-report of the practitioners of all the retreats they attended (for each retreat, they were questioned as to its length in days and number of hours with formal practice), as well as accumulated weekly personal practice (to their best of memory, counting separately for the different periods since the beginning of their practice, if their practice changed over time). To control for possible age effects, the meditator groups (mean ages in years: short-term: 41.6 ± 13.3; intermediate-term: 37.9 ± 10.4; long-term: 45.6 ± 10.6) were age-matched with the control group (5 females; mean age in years, 41 ± 12.5). In addition, in order to reduce possible self-selection effects caused by interest in meditation being higher in the meditation groups, the control group composed only of participants who scored "meditation interest" > 5 on a scale between 0 and 10. The study took place in Bar-Ilan University, Israel. Participants were tested at least 3 h after their last meditation session, to enable studying long-term, trait effects of practice. The research was approved by the Bar-Ilan University Institutional Ethical Committee, and informed consent was obtained from participants.

Procedure

Creativity was measured with the Alternate Uses (AU) task. EEG was then recorded during resting state (2.5 min eyes open and then 2.5 min eyes closed) prior to a battery of tasks designed to measure temporal and spatial perception, and attentional skills, as well as a meditation/relaxation session of 15 min. The task battery was applied again after the meditation/relaxation session. As the participants had to sit with the EEG cap as long as 1 h (we had a battery of tasks before and after a 15-min meditation session), we attempted to reduce the length of this inconvenience. Thus, as the AU task did not require EEG measurements simultaneously, we performed it before the EEG session. Given that the time required to place the EEG net was around 30 min, the immediate effect of the AU task on the resting-state activity can be considered negligible. Given that our aim here is to study the relationship between resting-state EEG, mindfulness meditation expertise effects and creativity, only resting-state EEG data and AU scores from the pre-meditation condition will be reported, based on our previous reports with this cohort of participants (Berkovich-Ohana et al. 2012, 2013).

Measures

The Alternative Uses (AU) task is a test of divergent thinking which requires participants to generate as many and unusual uses of conventional, everyday objects (Guilford 1968). In a previous study with the aim of examining changes in creativity following training (reported in Ben-Soussan et al. 2013), we clustered a 908-word database (developed by Levy-Drori and Henik 2006) using hierarchical cluster analysis and grouped those words having similar ratings of concreteness, availability of context, and familiarity assigned by Levy-Drori and Henik. We then chose 18 words from the three largest clusters for which the level of concreteness, similarity on familiarity, and availability features were highest (see Table S1). These 18 words were divided into two groups (nine words in each group) and tested on 60 pilot participants. The words were then divided into six sets of three words so that each set had a similar availability, familiarity, and concreteness (Table S1). Yet, there was a significant difference between the six sets in terms of fluency, stemming from a higher number of uses in set 4. However, we show (detailed in the supplementary information) that all the reported results maintain significance when correcting the potential bias created by using set 4.

In the current study, one set of three words was shown sequentially on a computer screen before the meditation/relaxation session, with a response interval of 1 min allocated for each item. The participants were asked to name as many uses as they can think of for this item. Presentation order of these sets was counterbalanced across a larger set of participants ($n = 59$ meditators and $n = 38$ control participants), as a part of the PhD dissertation of the first author (Berkovich-Ohana 2010). However, after exclusion of participants who did not meet criteria for inclusion in this study (not age-matched, medicated, and left-handed), as well as after dividing the meditation participants into three groups of expertise, the counter-balancing scheme was infringed. Table S2 presents complete data regarding which set was presented to the different participants of each group in the resting state (pre-meditation/relaxation), as analyzed in this paper.

From the AU, we calculated two measures: ideational fluency (*Fluency*, the number of uses generated), as well as cognitive flexibility (*Flexibility*, the number of categories employed). The *Fluency* score was defined as the mean of the total number of uses given by the participant for the three items in each session (Snyder et al. 2004). The *Flexibility* score was defined as the average number of different categories used by the participant for these three items (Russ 1998). Hence, all responses for a given item were first divided into different independent categories (i.e., using an item as a musical instrument or as a weapon were two independent categories). For example, alternative uses given by a participant for the word "ladder" may include "climb," "stand on," "reach high places," "hang for decoration," "make a bridge," "attach an enemy," or "burn to warm," in which case the Fluency = 7 (total items), and the Flexibility = 4 categories (category 1 is "common uses," including the first three uses; category 2 is "decoration" for the 4th use; category 3 is "rebuilding" for the 5th use; category 4 is "weapons" for the last use). Since *Flexibility* is a subjective measure, two independent raters scored the test. The inter-rater correlation was very high [$r = 0.915$, $p < .01$, $n = 48$], so the average score was used in the statistical analyses. The data of one control participant is missing due to technical problems.

EEG was recorded with a 65-channel geodesic sensor net (Electrical Geodesics Inc., Eugene, USA), sampled at 500 Hz and referenced to the vertex (Cz), with analog 0.1–200 Hz band-pass filtering. AC noise was removed by a 50-Hz digital notch filter, and impedance was kept under 40 kΩ (Ferree et al. 2001). The data were referenced offline to average reference and then visually screened for artifacts. Whenever electrodes were affected in a widespread distribution by artifacts, we excluded their data from the analysis. Whenever several channels exhibited noisy recording due to local high impedance (>40 kΩ, mean of three electrodes per epoch, in ~10% of the epochs), the corrected values were calculated offline by using spherical spline interpolation (Perrin et al. 1989).

Data Analyses

From the initial closed-eyes resting state, the first 16 non-overlapping, artifact-free epochs of 1024 sample points (2.048 s duration) were extracted for analysis. The power (μV^2) spectral distribution was calculated by first multitapering the raw data (using the Chronux toolbox)), then applying a fast Fourier transform (0.5 Hz resolution, 1024 point block-size, Hanning window, 0.5–46 Hz). For each electrode, the absolute spectral power was first grouped into frequency bands, including theta (3.5–7.5 Hz), alpha (7.5–13 Hz), and gamma (25–45 Hz), then log-transformed, and averaged across the 16 epochs. Electrodes were collapsed into regions of interest (ROIs), and mean log spectral power was calculated for each ROI separately. Here, we report the results of left and right frontal (F) and midline (M) (Fig. 1), previously related to DMN activity.

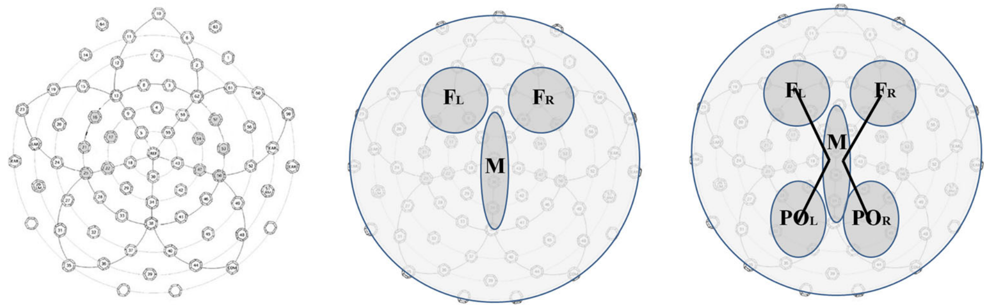

Fig. 1 Electrode net configuration (*left*), ROIs used for power calculations (*center*), and ROIs used for mean phase coherence calculations as well as intra-hemispheric long-range connections used for further analyses (*right*)

Functional connectivity was measured using a mean phase coherence (MPC, Mormann et al. 2000) index, appropriate for non-linear and non-stationary data, as is the case in EEG signals. MPC is a measure of how the relative phase is distributed over the unit circle. If two signals are phase-synchronized, the relative phase will occupy a small portion of the circle and MPC approaches the value of 1—meaning strong phase functional connectivity, and vice versa—for uncorrelated signals MPC is close to zero (Pereda et al. 2005) (for further details, see Supplementary in Berkovich-Ohana et al. 2013). As MPC is independent of frequency, the raw EEG signal was filtered into the different frequency bands prior to the calculation of MPC values for each electrode pair (a total of $(65 \times 64)/2 = 2080$ electrode pairs). The MPC values were Fisher *z*-transformed and averaged across the 16 epochs.

In order to reduce the dimensionality of the data, mean MPC of different ROIs was calculated as the mean MPC value of all the possible pairwise connections between the two ROIs. As our previous report identified DMN activity reflected as inter-hemispheric gamma functional connectivity, we focused here only on inter-hemispheric connections. Moreover, as we were interested in the major DMN connections, we selected four classical electrode connections, chosen to capture activity covering the DMN: bilateral F-M and PO-M (Fig. 1).

As this report focuses on gamma activity, a cautious stance is warranted. Cortically induced gamma activity is known to be at possible risk of contamination with muscular activity (Whitham et al. 2007) or saccade-related spike potentials (SP) due to eye movements (Yuval-Greenberg and Deouell 2009). Thus, we employed several measures to minimize these risks, including (1) using only eyes-closed conditions to eliminate saccade-related artifacts, as the SP is elicited at the onset of small saccades occurring during eyes-open fixation (Martinez-Conde et al. 2004); (2) using lower gamma frequencies (25–45 Hz) to minimize muscle artifacts, habitually peaking at 70–80 Hz (Cacioppo et al. 1990); (3) excluding circumference electrodes from statistical analyses, to minimize eye, neck, and face muscle artifacts (Whitham et al. 2007); and (4) we assessed the reliability of gamma power using the coefficient of variation (Fingelkurts et al. 2006), showing high within-subjects internal-consistency reliability (detailed in Berkovich-Ohana et al. 2012).

Results

We examined whether both *Flexibility* and *Fluency* were distributed normally, which they were [kurtosis = .568 and −.004; skewness = .484 and −.650, respectively]. We then conducted a MANOVA, for *Flexibility* and *Fluency*, which uncovered significant group differences [$F(6, 84) = 2.84$, $p = .014$, $\eta_p^2 = .169$, obs. Power = .865]. The follow-up ANOVA showed significant differences both for *Flexibility* [$F(3, 46) = 5.51$, $MSE = 169.54$, $p < .005$, $\eta_p^2 = .278$, obs. Power = .919] and for *Fluency* [$F(3, 46) = 4.14$, $MSE = 224.28$, $p < .01$, $\eta_p^2 = .224$, obs. Power = .817], as hypothesized, stemming from higher scores for the intermediate and long-term mindfulness groups compared to the controls and short-term mindfulness group (Fig. 2a).

To study the relationship between creativity and DMN activity, we tested the effect of gamma power and gamma functional connectivity, previously shown to correspond to DMN activity (Berkovich-Ohana et al. 2012, 2013) on Alternative Uses scores, in several steps.

First, to reduce the number of comparisons, we computed mean gamma power, having first checked the reliability of the three ROI values (Left F, Right F, and Midline, $\alpha = .90$). Similarly, we computed mean gamma MPC, having first checked the reliability of the four ROI values (bilateral PO-M and F-M, $\alpha = .85$). Second, we conducted a hierarchical regression analysis, with the three predictors (mean gamma power, mean gamma MPC, mindfulness expertise [in hours]) being entered in a stepwise manner. To test the possible effect of age on the reported results, we conducted the same hierarchical regression analysis same as above, but with age of the participants being forced into the equation (detailed in the supplementary information). This analysis showed that age was not a significant predictor for Fluency and Flexibility. We identified one control participant as an outlier, having mean gamma MPC = 0.89 (excluded from Fig. 2b–c). To test the effect of this outlier on the reported results, we conducted the hierarchical regression analysis again without this participant. The results generally remained the same for *Flexibility* (old vs. new: *Coefficient* = −21.5* vs.

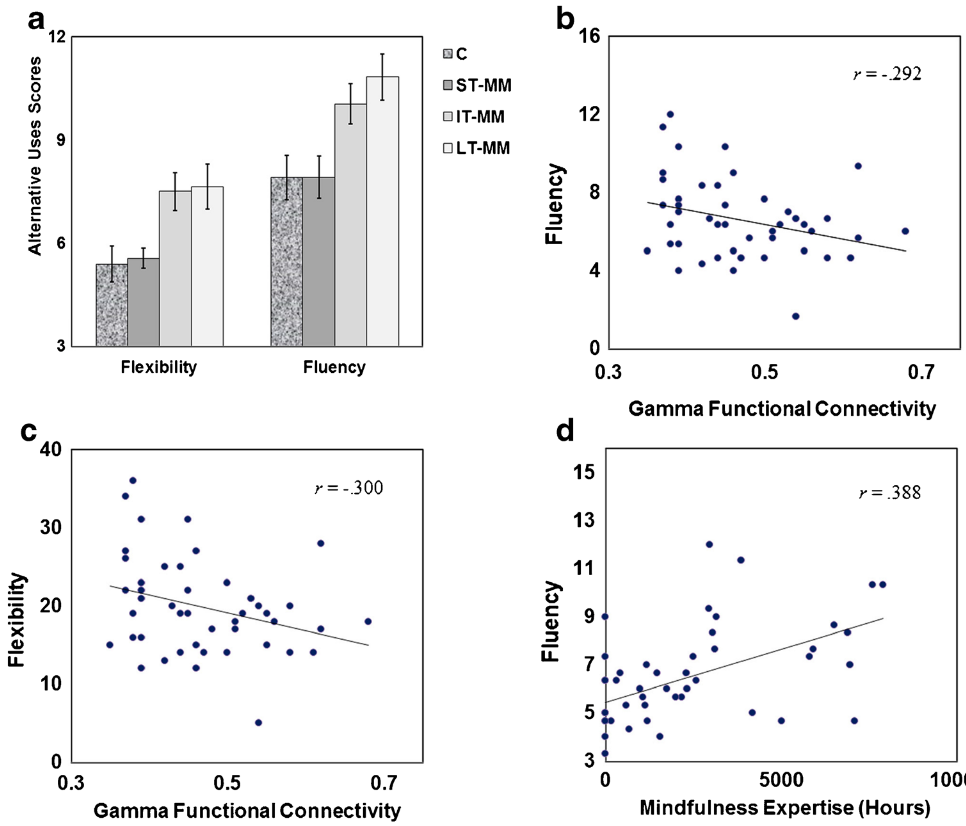

Fig. 2 **a** The significant group differences in creativity, showing Alternative Uses scores of Flexibility and Fluency (M ± SEM); MM mindfulness meditation; ST, IT, and LT short, intermediate, and long-term, respectively; $^{**}p < .01$; $^{***}p < .0005$; **b**, **c** Two scatterplots showing a significant negative correlation between gamma functional connectivity (mean MPC) and Fluency scores [$r = -.292$, $p < .05$], or Flexibility scores [$r = -.300$, $p < .05$], respectively. The trend line accounts for all participants ($n = 45$, one outlier excluded). **d** A scatterplot showing the significant correlation between Fluency scores and mindfulness expertise [$r = .388$, $p < .05$] ($n = 35$. One long-term meditator with 23,000 h of expertise and Fluency score of 12 was excluded for better visualization)

−23.24*, respectively; $R^2 = .125$ vs. .101; *Adjusted* $R^2 = .104$ vs. .081). Similarly, for *Fluency*, the results are similar, but weaker, emphasizing the limitation of this study in terms of group size, as one reviewer noted (old vs. new: *Coefficient* = −24.7* vs. −23.5 [only marginally significant with $p = .057$], respectively; $R^2 = .262$ vs. .231; *Adjusted* $R^2 = .226$ vs. .194).

For both *Fluency* and *Flexibility*, it was mean gamma MPC that was negatively correlated with these indices of creativity (Fig. 2b, c). We further note that the regression was much stronger for *Fluency* than for *Flexibility*, as indicated by the R^2 values. In addition, mindfulness meditation expertise was a significant predictor of *Fluency* (Fig. 2d). Mean gamma power, in contrast, was not a significant predictor.

Discussion

Mindfulness Meditation Practice Increases Divergent Thinking

We showed that long-term mindfulness practitioners score significantly higher compared to controls in both *Flexibility* and *Fluency* (Fig. 2a). We also reported a significant correlation between mindfulness expertise and *Fluency* (Fig. 2d). These results are generally consistent with the contention that the practice of meditation supports creativity (Horan 2009).

Our results support the Open Monitoring (mindfulness)—divergent thinking hypothesis (Colzato et al. 2012). Furthermore, our results reveal an expertise effect, as shown in other Open Monitoring studies (reviewed by Tomasino et al. 2012), but has been missing in the context of meditation-related creativity research (Capurso et al. 2013, p. 2). At first sight, it seems that our results contradict another study (Colzato et al. 2014), which recently reported that meditation training does not provide long-term benefits for divergent thinking. This was based on the observation that while divergent thinking benefited more from Open Monitoring meditation than from Focused Attention meditation, the same effect was found for both novices and a group of 20 practitioners. However, Colzato et al. (2014) examined meditation practitioners with an average of 3.3 years' experience. Similarly, our short-term mindfulness group, with expertise of approximately 5 years, showed no difference from the control group, in accord with Colzato et al. (2014). However, the other groups in our study (expertise > 5 years) demonstrated enhanced Fluency and Flexibility compared to controls. Thus, our results significantly contribute to the accumulating data concerning the question of the expertise effect by showing that it is only above 5 years of practice that the long-term effect of meditation is revealed in divergent thinking (see Fig. 2a).

Divergent Thinking Is Negatively Correlated with Gamma Functional Connectivity, Reflecting DMN Activity

We have found that both *Fluency* and *Flexibility* negatively correlate with resting-state gamma functional connectivity (Fig. 2b–c). However, the creativity measures did not significantly correlate with gamma power. These results are aligned with a previous study that reported a similar relationship with other frequency bands during resting-state EEG. In the Jaušovec and Jaušovec (2000) study, divergent thinking scores showed a very weak positive correlation with power (mainly within the upper alpha—lower beta bands (10.6–23.5), aligned with other EEG studies (Mok 2014), as well as showing predominantly a negative correlation with functional connectivity, as seen by probability maps over the entire scalp (found for all tested frequency bands, from delta (1.5–3.5 Hz) up until the beta3 (23.6–31.5 Hz)). Indeed, power and functional connectivity carry different information: while power is a measure of the local summation of electrical activity of a given region, functional connectivity is a dynamical interaction characterized by synchrony (precise phase locking) relationships between the activities of two neuronal populations (Florian et al. 1998; Varela and Thompson 2003).

In our results, the negative correlation was found with mean resting-state gamma functional connectivity, calculated within the bilateral F-M and PO-M. Considering the fact that connectivity reflects coordinated electrophysiological activity, one can assume that increases in functional connectivity indicate closer cooperation of the two regions in question in the respective frequency band, and vice versa, as shown by others in cognitive studies (e.g., Bhattacharya and Petsche 2005; Petsche 1996). Thus, our results suggest that reduced gamma coordinated activity over the frontal-midline and posterior-midline hubs of the DMN correlate negatively with divergent thinking. While the fractionation of the DMN into sub-components is yet to be studied, it was suggested that the midline core (posterior cingulate and anterior medial prefrontal cortex) is active when people make self-relevant, affective decisions (Andrews-Hanna et al. 2010). Thus, we speculate that the less self-focused one is during the resting state, the more creative one will be during a divergent thinking task.

We need to cautiously emphasize that our population for the correlation analyses comprised mainly mindfulness meditation practitioners, who were previously shown in the literature to exhibit functional and structural alterations, including within the DMN, compared to control groups (Chiesa and Serretti 2010; Fox et al. 2014; Tang et al. 2015). Thus, the results reported here cannot reflect on the general population. Nevertheless, these results support the general notion suggested by Jung et al. (2013) that creativity appears to depend, at least in part, on reduced activity within the DMN.

Why should divergent thinking increase with reduced trait DMN activity? A possible explanation is based on the creative-action theory of creativity, postulating that creative thought is always causally dependent on non-perceptual creatively generated action-schemata (Carruthers 2007, 2011). Whenever an action-schema is activated, commands are sent to muscles necessary to control the action, and efferent copies are simultaneously used to generate a representation of the visual and proprioceptive perception. This, in turn, lies at the bottom of any type of imagery transformation. In this way, the non-conceptual mental rehearsal of an action-schema will give rise to an imagistic thought representing the action in question and thus to a conceptual verbal creative thought (Carruthers 2007, 2011). Turning back to the mindfulness practitioners, using fMRI, it has been recently found that their eyes-closed resting-state mentation exhibits significantly less DMN activation and more extrinsic (visual) activation compared to controls (Berkovich-Ohana et al. 2016). Such a trait activity pattern can support less conceptual reasoning, as a trait, and increased activity in networks related to action-schemata. This, in turn, might explain the higher divergent thinking scores in mindfulness practitioners, as well as the negative rest DMN activity and divergent thinking connection. At the same time, it was shown using fMRI for long-term mindfulness practitioners that during meditation the DMN-Executive network functional connectivity increases (Brewer et al. 2011). According to Mok (2014), this "correspond to the capacity to achieve, on a moment to moment basis, optimal balance between control network activity and default network activity, and optimal coordination between these respective networks and other brain regions involved in content processing" (p. 3), and creative processing emerges from this optimal balance. Taken together, these explanations raise the question if the results are unique to the meditation practitioners' population in this study. Definitely, a replication in the regular population is highly warranted.

Implications for the Disinhibitory Notion of Divergent Thinking

Our results might be interpreted as arguing against the common disinhibitory notion of creativity, so it seems warranted to discuss this issue in some detail. The disinhibitory notion of creativity emphasizes reduced inhibitory frontal activity as the underlying mechanism of divergent thinking (Dietrich 2004). This is based on Martindale's (1977) low arousal theory of creativity, arguing that the production of original ideas more likely occurs in states of lower cortical arousal, i.e., increased alpha activity during the creative tasks. This theory was based on the findings of Martindale and Mines (1975), reporting that highly creative individuals displayed comparatively low cortical arousal while performing the Alternative Uses task, while medium and low creative subjects were strongly cortically aroused. Similarly, in Martindale and Hasenfus (1978), highly creative individuals showed lower levels of cortical arousal than low creative participants during an inspirational phase (i.e., thinking of a story) but not during an elaboration phase (i.e., writing down the story).

The disinhibitory notion of creativity has clear predictions concerning the DMN activity *during* creative tasks. Indeed, it was suggested that the DMN could serve as a system which operates disinhibitory mental simulation processes, namely divergent thinking, whereas cognitive control networks, which rely on excitatory processes, would initiate selection processes and refine ideas, namely convergent thinking (Jung et al. 2013; Mok 2014). More specifically, divergent thinking—which relies on primary processes (Martindale and Mines 1975)—is related to reduced dorsolateral prefrontal cortex (DLPFC) executive control activity and concomitant increased DMN activity.

Accumulating data supports the notion that increased DMN activity underlies divergent thinking. For example, increased mind wandering was shown to increase creative problem solving (Baird et al. 2012). Others studied musicians using fMRI and have found that spontaneous improvisation was associated with widespread deactivation of the DLPFC along with simultaneous activation of the frontal DMN region, the medial prefrontal cortex (Limb and Braun 2008; Liu et al. 2012). Similarly, another study showed that a decrease in cortical excitability of the lateral frontal cortex, induced by transcranial magnetic stimulation, improved performance on a divergent creativity task (Chrysikou et al. 2013). Another recent study showed that exposure to high inhibition demands led to enhanced fluency in a divergent thinking task, but no such changes occurred in a convergent thinking task (Radel et al. 2015). These findings suggest that when resources for inhibition were lacking, the frequency and the originality of ideas was facilitated. In addition, direct fMRI evidence shows diverse DMN regions to activate during divergent thinking tasks, including the left lateral posterior parietal cortex—specifically, the angular gyrus (Bechtereva et al. 2004; Kleibeuker et al. 2013) and the posterior cingulate cortex (Beaty et al. 2015).

Importantly, the disinhibitory notion of creativity predicts an increase in DMN activity *during* divergent thinking tasks, and the reviewed studies above indeed support such a *state* effect. But, is there a clear prediction concerning the relationship between DMN resting state and divergent thinking?

A hypothesis termed "spontaneous trait reactivation" suggests that the resting-state spontaneous activity reflects subtle individual differences in neuro-cognitive "traits," or past accumulating effects (Harmelech and Malach 2013). A number of studies appear to be compatible with this hypothesis (e.g., Harmelech et al. 2013). According to the spontaneous trait reactivation hypothesis, if DMN activity increases during a divergent thinking task, then individuals with higher scores should exhibit also an increased resting-state DMN activity level. However, when reviewing the literature, the evidence is inconclusive.

An early electrophysiological study (Martindale 1977) reported no consistent relationship between creativity and resting-state EEG alpha power, an EEG measure which was shown by several studies to be positively related to DMN activity (Chen et al. 2008, 2013; Laufs et al. 2003; Mantini et al. 2007). Yet, in a later study, resting-state EEG alpha power was only weakly positively correlated with divergent thinking scores, while coherence measures in all frequency bands—including alpha—negatively correlated with divergent thinking scores (Jaušovec and Jaušovec 2000). Two later fMRI resting-state functional connectivity studies revealed that higher creativity scores of divergent thinking were associated with increased rest functional connectivity within the DMN. In the first study, divergent thinking scores significantly and positively correlated with rFC between the medial prefrontal cortex and the posterior cingulate cortex (Takeuchi et al. 2012), while Wei et al. (2014) found a positive correlation of rest functional connectivity between the left medial prefrontal cortex and the left middle temporal gyrus with divergent thinking scores. However, rest functional connectivity cannot be taken as a measure of the DMN activity per se, as it reflects correlation structures, i.e., the co-activation of regions comprising fundamental networks that are activated or suppressed simultaneously (Fox et al. 2006; Smith et al. 2009). A direct measure for DMN activity was studied by Takeuchi et al. (2011), reporting regional resting-state cerebral blood flow in the precuneus, a posterior DMN node, to significantly and negatively correlate with a divergent thinking task. Indirectly, assuming a widely accepted positive function-structure relationship (Honey et al. 2009), a few anatomical findings support a positive DMN-creativity relationship, by showing divergent thinking scores to positively correlate with gray matter volume within the DMN, including medial prefrontal cortex and precuneus (Kühn et al. 2014) and lesions in the medial prefrontal cortex to involve profound impairment in originality (Shamay-Tsoory et al. 2011).

In contrast, other studies support a negative DMN-creativity relationship (reviewed by Jung et al. 2013). The first is a structural MRI study by Jung et al. (2010), which utilized three different divergent thinking tasks to create a composite creativity index and showed it to correlate with decreased cortical thickness within several regions, including the left cuneus and inferior parietal, both of which are DMN regions. Another anatomical study showed a positive correlation between originality scores and left posterior parietal lesion area (Shamay-Tsoory et al. 2011). Loss of function in the anterior temporal lobes as a result of frontotemporal dementia was found to lead in several cases to the "facilitation" of visual artistic skills (Miller et al. 1998). In a functional study, regional resting-state cerebral blood flow in the precuneus was significantly and negatively correlated with a measure of divergent thinking (Takeuchi et al. 2011). Taken together, the above studies provide initial support that decrease in structural integrity and resting-state functional reductions, as well as lesions within the DMN, positively correlate with creativity measures.

The evidence in the literature is thus inconclusive for the creativity—trait (resting-state) DMN activity connection, and more evidence is needed to conclude whether resting-state DMN activity follows the intuitive positive relationship with divergent thinking laid forth by the disinhibitory notion of creativity, or whether a counter-intuitive negative relationship may be the case. In this light, our results, which can be interpreted as arguing against the common disinhibitory notion of creativity, contribute new evidence to this open scientific question.

Limitations

The results reported here stem from a large group of mindfulness meditation practitioners. This limits the generalization of the results to the wider population. Another limitation raised by one of the reviewers refers to the study design, where the AU results were acquired before the EEG resting-state session, thus might have affected the resting state. While not highly likely, this possibility is slightly plausible, and the design should be reversed in further studies.

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