The dynamics of the improvising brain: a study of musical creativity using jazz improvisation

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Abstract

One of the defining elements of jazz is the ability to improvise. The neuroscience of jazz improvisation has shown promising results for understanding domain-specific and domain-general processes of creativity. However, until date no previous studies have examined how different modes of improvisation (musical creativity) evolve over time and which cognitive mechanisms are responsible for different stages of musical creation. Here, we used fMRI to measure for the first time the dynamic neural substrates of musical creativity in 16 skilled jazz pianists while they improvised freely *(iFreely*), and by melody (*iMelody*), and contrasted with resting-state. We used the leading eigenvector dynamics analysis (LEiDA) to explore the whole-brain dynamics underlying spontaneous musical creation. Our results reveal a substate comprising areas of the dorsal default mode (DMN), the left executive control (ECN), the anterior salience, language and precuneus networks with significantly higher probability of occurrence in *iFreely* than in *iMelody*. In addition, *iFreely* is also linked to an increased prevalence and dynamic attachment to this substate and to a "global" substate. Such indicates that a more free mode of improvisation (*iFreely*) requires an increased dynamic convergence to networks comprising brain areas involved in processes linked to creativity (generation, evaluation, prediction, and syntactic processing). *iMelody*, a more constrained mode of improvisation involves a higher recurrence of brain regions involved in auditory and reward processes. This study brings new insights into the large-scale brain mechanisms supporting and promoting the complex process of creativity, specifically in the context of music improvisation in jazz.

Introduction

"Jazz is not just music, it´s a way of life, it´s a way of being, a way of thinking." – Nina Simone

Listening to jazz musicians improvise is a spellbinding experience. Jazz musicians are able to spontaneously generate novel pieces of music in a short time frame, creating musical pieces which are both aesthetically and emotionally rewarding[1]. They must balance several simultaneous processes, involving generating and evaluating melodic and rhythmic sequences, coordinating their own performance with fellow musicians, and executing fine motor movements, all in real-time[2,3]. Jazz musicians have been found to show greater openness to experience and higher divergent thinking on personality assessments, even when compared to musicians who don't practice jazz[4]. This phenomenal feat of human improvisation and creativity has been of great interest to neuroscientists who wish to understand the dynamics of the improvising brain, and more specifically the brain dynamics underlying the creative process.

Creativity is often defined as "the act of creating something new and useful" [5], but novelty or unpredictability may not be enough. Boden comments instead on how "constraints and unpredictability, familiarity and surprise, are somehow combined in original thinking." This distinction is important as creative music must also be aesthetically congruent with the physical constraints of the known musical range – it cannot be simply unpredictable or completely surprising. Martindale[6,7] posited that individual differences in the breadth or narrowness of the internal attentional selection of conceptual representations may also relate to creativity. For instance, a broad focus upon conceptual concepts would activate more remote 'nodes' in memory. This is important as it suggests that the most creative are those who can access associative mnemonic content in a broader way, thereby widening the constraints attached to their musical production and allowing for more unpredictable and surprising content, while the content is still familiar by its association. Therefore, predictive, or top-down processing using mnemonic content to inform future outcomes is a key process in creativity. One study that has shown assent for this suggestion asked participants to divergently generate ideas for uses of a brick. If the participants had been primed with a visual task to focus perceptual attention broadly, they generated more original uses[8].

Creativity can be measured by convergent and divergent thinking tasks. Convergent thinking consists of a single solution to a given problem, whereas divergent thinking is the generation of several different ideas to solve a given problem[9,10]. It can be observed in numerous domains, such as in science, engineering, education and art[9,11]. The neural signatures underlying creative thought have been investigated using diverse tasks such as drawing, musical improvisation, and idea generation or 'divergent thinking'. Overall, the majority of the studies have used divergent thinking and creative problem solving, and only a few studies (7.6%) have used musically creative tasks to assess creative thought more generally[12,13]. The neuroscience of jazz improvisation has thus far shown promising results for understanding not only domain-specific creative thought, but also domain-general processes of creativity[1–3,14,15]. Jazz improvisation is well-suited for studying creativity due to its reliance upon known neural and cognitive processes, and it is thus useful for understanding domain-general processes such as motor control, syntactic processing and creativity.

Interestingly, studies of creativity in domains such as divergent thinking (a domain-general creative process) and musical improvisation (domain-specific), using different experimental tasks have still reported similar patterns of brain activity and connectivity underlying the creative process. There is a consensus about the involvement of prefrontal brain regions, such as the pre-supplementary motor area (pre-SMA), medial prefrontal cortex (mPFC), inferior frontal gyrus (IFG), dorsolateral PFC (dlPFC), and the dorsal premotor cortex (dPMC) in creative thought[2,16]. Other brain regions which are also found to be involved in creative thought have been associated with different cognitive processes, such as attention and executive control, motor sequence generation, voluntary selection, sensorimotor integration, multimodal sensation, emotional processing and interpersonal communication[15,17,18].

The brain is an organ of inference, which actively constructs explanations for the future and external stimuli beyond its sensory epithelia[19]. This is often referred to as predictive coding, which has become a dominant model in cognitive neuroscience[20]. Within the predictive coding framework, there are predictions of the incoming perceptual content (known as first-order predictions), and predictions of the precision (i.e., confidence or certainty) that are ascribed to first-order predictions (known as second-order predictions)[21]. When jazz musicians improvise, they engage in both types of prediction – they need to predict the incoming musical features, such as the subsequent melody or harmony, but also need to make a prediction about that prediction (i.e. how likely is that tone). A high precision (otherwise

known as low entropy or low uncertainty) means that the musical feature is generally predictable.

In jazz musicians who improvise and create new musical sequences, the typical predictive coding model may be somewhat different, and the repertoire of predictions may be greater. According to the free energy principle[20], in standard perceptual processes, predictions with low precision are typically ignored as we expect them to be unreliable. Here, however, jazz musicians may be relying upon predicting what is *unpredictable* in order to create new melodies or harmonies. The jazz musician will be drawing significantly upon long-term memory of musical syntax and the likelihood of both regularity *and* irregularity. Improvisation also relies heavily upon the element of surprise or musical prediction errors, which are known to paradoxically generate a pleasure response in listeners due to the resolution of uncertainty[21]. However, the improvised musical piece is at the same time constrained by certain factors such as aesthetic and emotional congruence. As Boden's[22] conceptualisation of creativity denotes, this is a delicate balance between unpredictability and constraints, familiarity and surprise, to reach an original product.

Another important issue are the strategies that jazz musicians use for improvisation. The most common strategy is to improvise *freely* but according to a chord scheme belonging to the specific tune they are playing[16]. Here, jazz musicians use their skills and practiced melodic and harmonic material as building blocks with the aim of creating musical lines that are novel and engaging[23,24]. Consequently, this approach may entail brain processes similar to the ones underlying divergent thinking[2]. Another, often used strategy is to use the melody as starting point for the improvisation[24]. Here the outcome usually becomes less complex, and more 'hummable' and may as such be more related to emotional processing which is known to be associated with the perception of songs. Many jazz musicians who are proficiently using this approach are known to accompanying their instrumental improvisation with vocalization (such as Keith Jarrett)[25]. Since this approach involves a goal-oriented task it may be closer related to convergent thinking than free improvisation.

Previous studies have shown that creativity is a result of a dynamic interplay between different brain networks [2,26,27], however none have yet explored the brain functional dynamics of spontaneous musical creativity through jazz improvisation. Here we propose to explore, for the first time, the whole-brain dynamics underlying spontaneous musical creation in jazz pianists, using the Leading Eigenvector Dynamics Analysis (LEiDA)[28–31]. LEiDA captures

the instantaneous BOLD phase signal and uses leading eigenvector decomposition to find the recurrent functional connectivity patterns (or brain substates). In this study, we quantified the differences in terms of probability of occurrence and switching probabilities, using two complementary tasks during fMRI (two different modes of musical improvisation: one constrained by melody and one by freely), and we also measured the resting state during the same MRI session (rs-fMRI) as a baseline.

We hypothesised that given how musical creativity is a rich and complex dynamic process, we would find corresponding signatures of brain dynamics (recurrent FC metastable substates) that are significantly altered when compared to a baseline condition (resting state). We further hypothesised that different connectivity patterns would be associated with the process of music creation in different stages – idea generation, revision and evaluation – during improvisation, and that these connectivity patterns would be different when improvising freely (*iFreely*), which has a higher level of freedom, than when improvising constrained by the melody (*iMelody*).

Material and methods

Participants

The total sample consisted of 24 right-handed male musicians with normal hearing and no history of neurological disease. Eight participants were excluded from the analyses: 2 found out that they were claustrophobes and 6 were excluded due to excessive head movement. Our final sample resulted in 16 participants (mean 28.0 ± 8.71 SD). All participants were proficient in jazz piano playing (with at least 5 years of experience), and they declared to practice on average 1.9 ± 0.9 SD hours per day, and 22 ± 7.7 days of practicing per month. All participants gave written consent to participate in the study. The study was approved by the local ethics committee and it was undertaken in accordance with the Helsinki declaration.

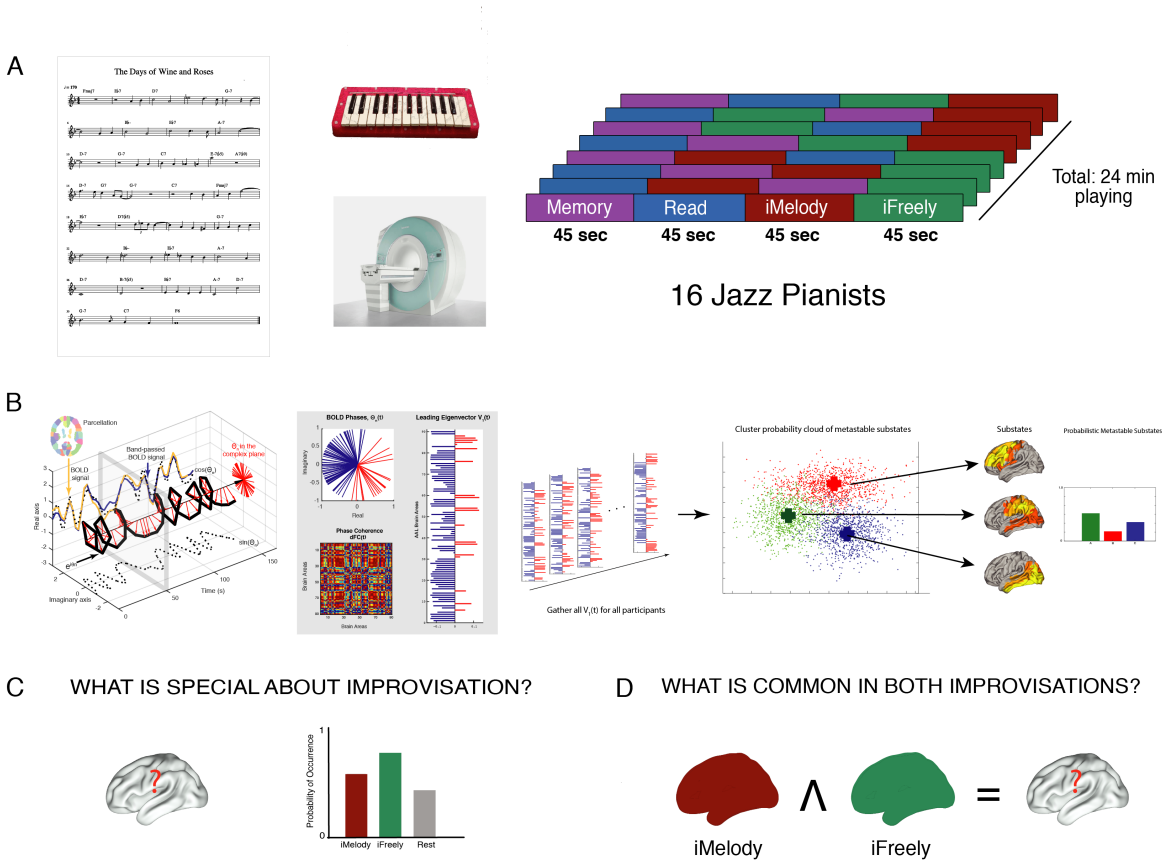

Figure 1. The dynamics of the improvising brain: experimental protocol and methods. *A) Experimental design: participants were asked to play four different conditions inside of the MRI scanner using a 25 keys MRI-compatible keyboard. The four different conditions were: play by memory (Memory), play from a score sheet (Read), improvise by melody (iMelody) and freely improvise (iFreely). B) LEiDA (Leading eigenvector dynamics analysis) captures the coherence based connectivity of the system focusing on the dominant FC pattern captured by the leading eigenvector of dynamic FC matrices. C) Our goals were to understand what is special about the process of improvisation, and D) what different modes of improvisation have in common.*

Stimuli and procedure

We acquired functional MRI while participants were playing on an MRI compatible keyboard in four different conditions in a pre-defined randomized order, while listening to the chords of the jazz standard "The days of wine and roses" (DWR). Participants were asked to a) play the melody of DWR by memory (Memory); b) play from a score sheet (Read) which was a alternative melody composed specifically for this experiment on the chord scheme of DWR; c) improvise on the melody (*iMelody*), i.e. play melodically as if they were to create a new

melody for the chord scheme of DWR and; d) improvise freely on the chord scheme for DWR (*iFreely*). Each condition lasted 45 seconds, and participants had to play it 8 times. In total each participant played 24 minutes (6 minutes for each condition) (Figure 1-A). For the sake of clarity we will here only analyse the improvisation conditions compared to baseline (resting state), whereas the results from conditions a) and b) will be reported elsewhere.

To ensure no image artifacts, we used a custom-made MR-compatible fiber optic piano keyboard [32]. The keyboard, consisting of 25 full size keys, covered two full octaves, and its lightweight and slim design allowed it to be positioned on the participants' laps, such that all keys could be reached by moving only the forearm. Participants were instructed to only play with their right hand. Output from the keyboard was interpreted into a MIDI signal by a microcontroller outside of the scanner room. Piano sounds were generated by a Roland JV-1010 hardware synthesizer based on this MIDI signal. The piano sound from the synthesizer was subsequently mixed together with a backing track, and delivered to the participants through OptoACTIVE noise cancelling headphones.

The instructions for each condition were controlled by a PsychoPy [33] script on a laptop computer. A MR compatible screen was used to project the instructions and participants viewed it using a mirror that was attached to the head coil. Participants were instructed about the conditions before going inside of the scanner, and they were allow to play 2 times the score sheet outside the scanner, to make sure they would understand that they needed to read from a score inside the MR scanner. Inside the scanner participants received the information about which condition they should play through the screen.

Image acquisition and processing

All participants underwent the same imaging protocol using a 32-channel head coil in a Siemens 3 T Trim Trio magnetic resonance scanner located at Aarhus University Hospital, Denmark. Whole-brain T1-weigthed and task-based fMRI images were acquired for each participant.

Anatomical scan acquisition

The 3D T1-weigthed sequence was performed with the following parameters: sagittal orientation; 256 x 256 reconstructed matrix; 176 slices; slice thickness of 1 mm; echo time (TE) of 3.7 ms; repetition time (TR) of 2420 ms; flip-angle (α) of 9.

fMRI Acquisition

A multi-echo EPI-sequence was acquired with a total of 371 volumes and with the following parameters: voxel size of 252 x 252 x 250 mm; 54 slices; slice thickness of 2.50 mm; multi-echo time: TE1= 12 ms, TE2= 27.52 ms, TE3= 43.04 ms, TE4= 58.56 ms; repetition time (TR) of 1460 ms; flip-angle (α) of 71. Only the second echo was used in our analysis.

fMRI Processing

The fMRI data was processed using MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components)[34] part of FSL (FMRIB´s Software Library, www.fmri.ox.ac.uk/fsl). The default parameters of this imaging pre-processing pipeline were used for all the 16 participants: motion correction using MCFLIRT [35]; non-brain removal using BET [36]; spatial smoothing using a Gaussian kernel of FWHM 5 mm; grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor and high pass temporal filtering (Gaussian-weighted least-squares straight line fitting with sigma = 50 seconds). FSL tools were used to extract and average the time courses from all voxels within each cluster in the AAL-90 atlas [37].

Dynamic Functional Connectivity Analysis

We applied a recent method to capture patterns of functional connectivity from fMRI data at single TR resolution with reduced dimensionality, the Leading Eigenvector Dynamics Analysis (LEiDA). On a first stage, the BOLD signals in the N=90 brain areas were band-pass filtered between 0.02 Hz and 0.1 Hz and subsequently the phase of the filtered BOLD signals was estimated using the Hilbert transform [28,38]. The Hilbert transform expresses a given signal x as x(t) = A(t)*cos(θ(t)), where A is the time-varying amplitude and θ is the time-varying phase (see Figure 1B left). Given the BOLD phases, we computed a dynamic FC matrix (dFC, with size NxNxT) based on BOLD phase coherence where each entry dFC(n,p,t) captures the degree of synchronization between areas n and p at time t, given by the following equation:

$$dFC(n,p,t) = cos(\theta(n,t) - \theta(p,t)), \quad \text{with } n,p = 1,\ldots,N.$$

To characterize the evolution of the dFC matrix over time with reduced dimensionality, we considered only its leading eigenvector, $V_1(t)$, which is a $Nx1$ vector that captures, at time t, the projection of the BOLD phase in each brain area into the main *orientation* of BOLD

phases over all areas (Figure 1B, second panel from the left). When all elements of $V_1(t)$ have the same sign, all BOLD phases project in the same direction with respect to the orientation determined by $V_1(t)$. If instead the first eigenvector $V_1(t)$ has elements of different signs (i.e., positive and negative), the BOLD signals project into different directions with respect to the leading eigenvector, which naturally divides the brain into distinct modes (colored in red and blue in Figure 1B second panel from the left). Previous studies using LEiDA have shown that the subset of brain areas whose BOLD signals appear temporally phase-shifted from the main BOLD signal orientation reveal meaningful functional brain networks [28–31].

Recurrent FC Substates

In this work, we aimed to investigate the existence of specific patterns of functional connectivity, or FC substates, associated with musical creativity. To do so, we first searched for recurrent connectivity patterns emerging in each of the four experimental conditions, and compared their probabilities of occurrence to a common resting-state baseline. Recurrent connectivity patterns, or substates, were detected by applying a k-means clustering algorithm to the set of leading eigenvectors, $V_1(t)$, associated to the fMRI volumes acquired during each condition over all participants, as well as the fMRI volumes recorded during a baseline period of 542 seconds (the same baseline was used for all 4 experimental conditions). The k-means algorithm clusters the data into an optimal set of k clusters, where each cluster can be interpreted as a recurrent FC substate.

While resting-state fMRI studies have revealed the existence of a reduced set of approximately 5 to 10 functional networks that recurrently and consistently emerge during rest across participants and recording sites [28,39–41], the number of FC substates emerging in brain activity during a task is undetermined, and depends on the level of precision allowed by the spatial and temporal scales of the recordings. In the current study, we did not aim to determine the optimal number of recurrent FC substates detected in a given condition, but instead to detect FC substates whose probability of occurrence was significantly modified by the experimental condition with respect to the baseline. In that direction, we ran the k-means algorithm varying k from 3 to 15 and, for each k, statistically compared the occurrence of the resulting FC substates between the resting-state baseline and the four experimental conditions.

Probability of Occurrence

Recurrent substates were compared in terms of their probabilities of occurrence in both modes of improvisation (by melody and freely) with respect to their probabilities of occurrence during the resting-state baseline, using a permutation-based paired t-test to assess the statistical differences. The significant thresholds were corrected to account for multiple comparisons as *0.05/k*, where *k* is the number of substates (or independent hypothesis) tested in each partition model [29–31].

Comparison with resting-state networks

We used the large-scale resting-state networks (RSNs) described by Shirer and colleagues [42] to quantify the representation of each RSN in each of the five substates. Intersection of each of the 14 RSNs with the 90 AAL brain regions was computed. Quantification of each RSNs representation was then calculated dividing the results of the intersection between RSNs and 90 AAL by the total number of voxels of each RSNs intersected with the 90 AAL regions (Figure SupMaterial 1).

Results

In this study, we investigated the dynamic nature of the jazz musician's brain while improvising by melody and freely, by characterising the most recurrent patterns of whole-brain functional connectivity arising during the six minutes of each condition.

Detection of the Substates

The repertoire of metastable substates depends upon the number of clusters determined by the k-means clustering algorithm, where higher number of clusters usually results in less frequent and more fine-grained substates [31]. In this study, we did not aim to determine the optimal number of substates but rather to search for the substates, which significantly and recurrently characterize musical improvisation, using resting-state as a baseline. Figure 2 illustrates the p-values obtained from a permutation-based comparison between-conditions in terms of probability and duration (lifetimes) of the substates for each clustering model.

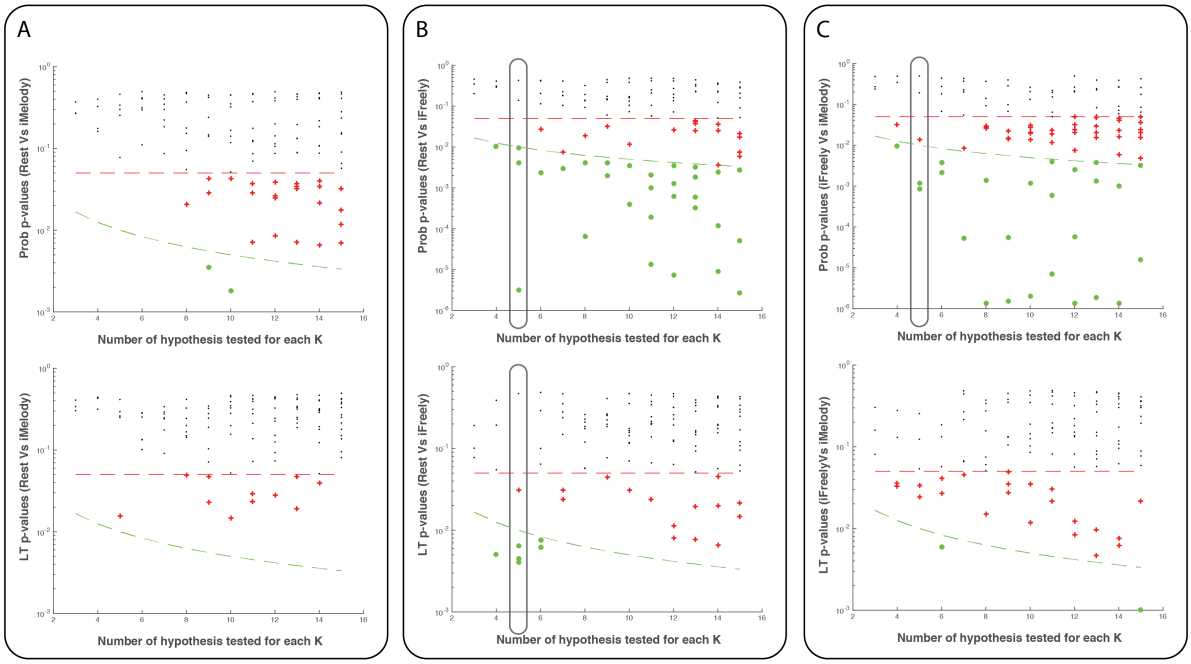

Figure 2. Differences between-conditions in FC substate probability of occurrence and duration (lifetimes, LT) as a function of k. *For each model of k ranging from k= 3 to 15 FC substates p-values are presented for: Top: probability, and Bottom: lifetimes (duration) between A) rest and iMelody; B) rest and iFreely; C) iFreely and iMelody. P-values for the probabilities of occurrence and lifetimes/duration are shown with respect to the standard threshold of 0.05 (red dashed line) and the threshold correcting for multiple comparisons, which divides by the number of independent hypothesis tested (green dashed line). The p-values marked as a red crosses pass the standard threshold but only the green circles survive the correction for multiple comparisons within each partition model. A cluster of k=5 was selected for revealing the highly significant contrasts between conditions (lower p-values) while falling within the typical range of 5 to 10 resting-state functional networks reported in the literature* [28,40].

We selected the partition into five (k=5) FC substates, as it returned five FC substates where highly significant differences were found both in terms of probability of occurrence and lifetime between the three conditions (Figure 2). The partition into five substates is in accordance with the literature, where 5 to 10 functional networks emerge during rest [28,40]. Statistical significance in terms of probabilities of occurrence and lifetimes is corrected for false positives using a Bonferroni correction.

Repertoire of recurrent FC substates

In line with previous studies using LEiDA [28–31], the most probable state of BOLD phase coherence is a global substate, where all BOLD signal are synchronized. The remaining four recurrent substates were found to overlap with typical RSNs reported in the literature [41,42].

Probabilities of occurrence – what is special about improvisation?

We found a recurrent substate, substate 3, with significantly higher probability of occurrence, and longer duration (lifetime) for *iFreely* compared to *iMelody*, and for *iFreely* compared to rest (Figure 3). This FC substate includes the bilateral: ventromedial prefrontal cortex (vmPFC), medial prefrontal cortex (mPFC), medial orbital frontal cortex (mOFC), olfactory cortex, middle temporal poles (TPOmid), anterior (ACC) and posterior cingulum (PCC); the left: angular gyrus (ANG), inferior frontal gryus – orbital (ORBinf) and the middle temporal gyrus (MTG). These nodes are part of the dorsal default mode network (dDMN), language network (LangN), left executive control network (ECN), the anterior salience network (antSN) and precuneus network (Figure 3).

Brain substate-switching probabilties in Jazz Improvisation

We explored the transition profiles between substates for the selected partition model ($k=5$), by calculating the probability of being in a given substate and transitioning to any other substates. In figure 4-A, we show the differences of switching probabilities for both modes of improvisation in a matrix and respective (threshold of 25%) chord diagram. Figure 4-B illustrates the trends of directionality for each mode of improvisation (i.e. within-task), i.e. the tendency for a preferred (>10%) transition direction between pairs of substates. Figure 4-C reveals the most significantly differences in probability of transition between modes of improvisation (i.e. between-task). Differences in probabilities of switching between conditions were statistically assessed using a permutation-based paired t-test with Bonferroni correction (p-corrected<0.05). We highlight the existence of three significant group differences in the probability of substate transitioning between *iMelody* and *iFreely*. The transitions from substate 3 to the 'global' substate 1 and substate 5 to substate 3, were found to have significantly higher probability of switching in *iFreely*. On the other hand, our results reveal that *iMelody* is characterized by a significantly higher probability of switching from substate 5 to substate 2.

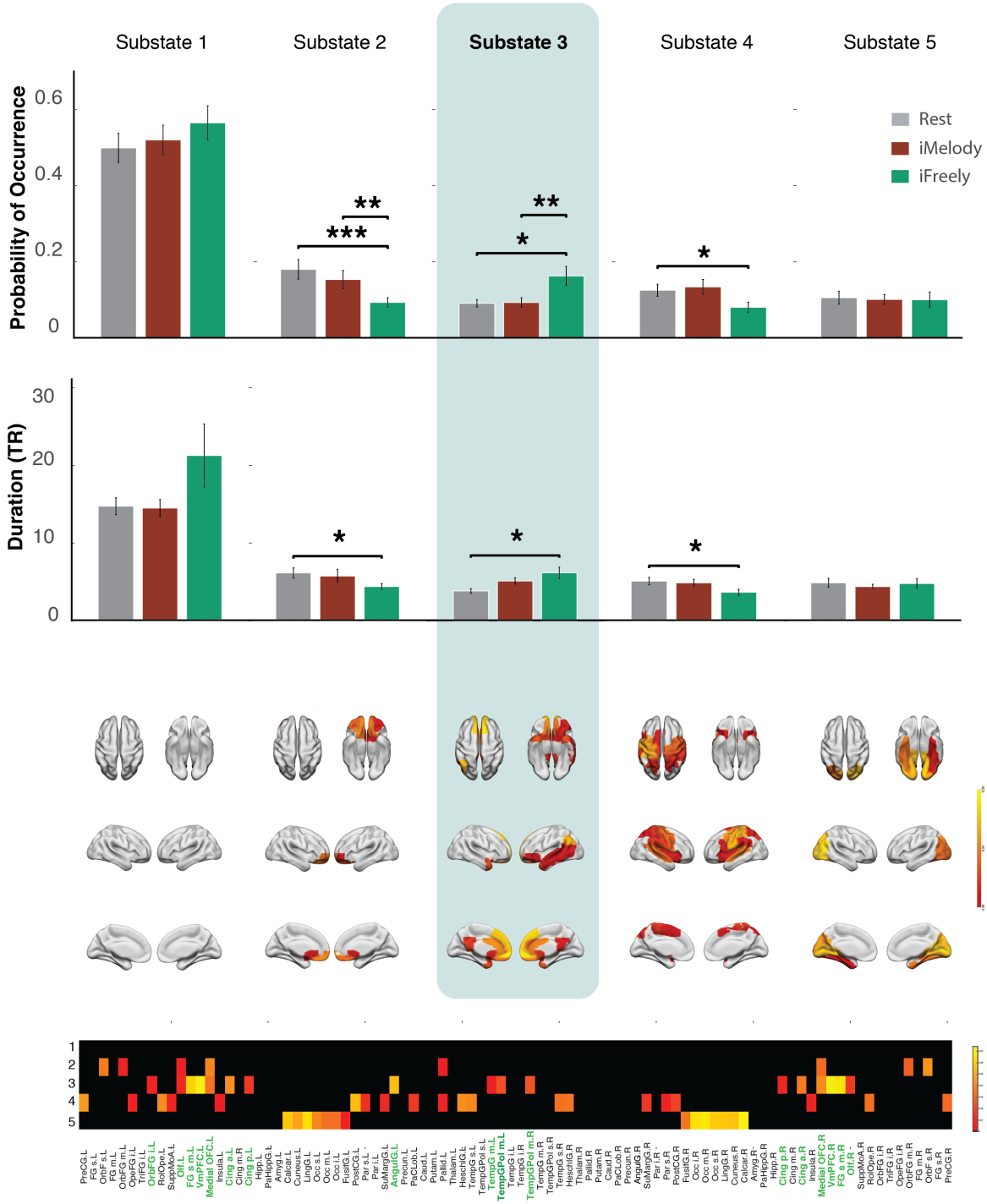

Figure 3. Signature of Domain-General Creativity. *Repertoire of metastable substates during jazz improvisation and the resting-state.* ***A)*** *probability of occurrence (POc) of each of the five brain substates estimated using LEiDA, during improvisation within melody (red), improvisation freely (green) and rest (grey). Substate 3 was found to have significantly (p<0.05; Bonferroni-corrected) higher POc in iFreely than in iMelody and in resting-state.* ***B)*** *duration of each of the five brain substates.* ***C)*** *3D rendering of the brain for the five substates.* ***D)*** *participation and connection weight*

of AAL regions in each substate. Our analysis revealed five recurrent FC substates, one global (substate 1) and four recurrent substates, reflecting: reward and predictions (substate 2), a complex array of functions that support improvisation and creativity more generally (substate 3), an auditory network (substate 4), and a visual network (substate 5).

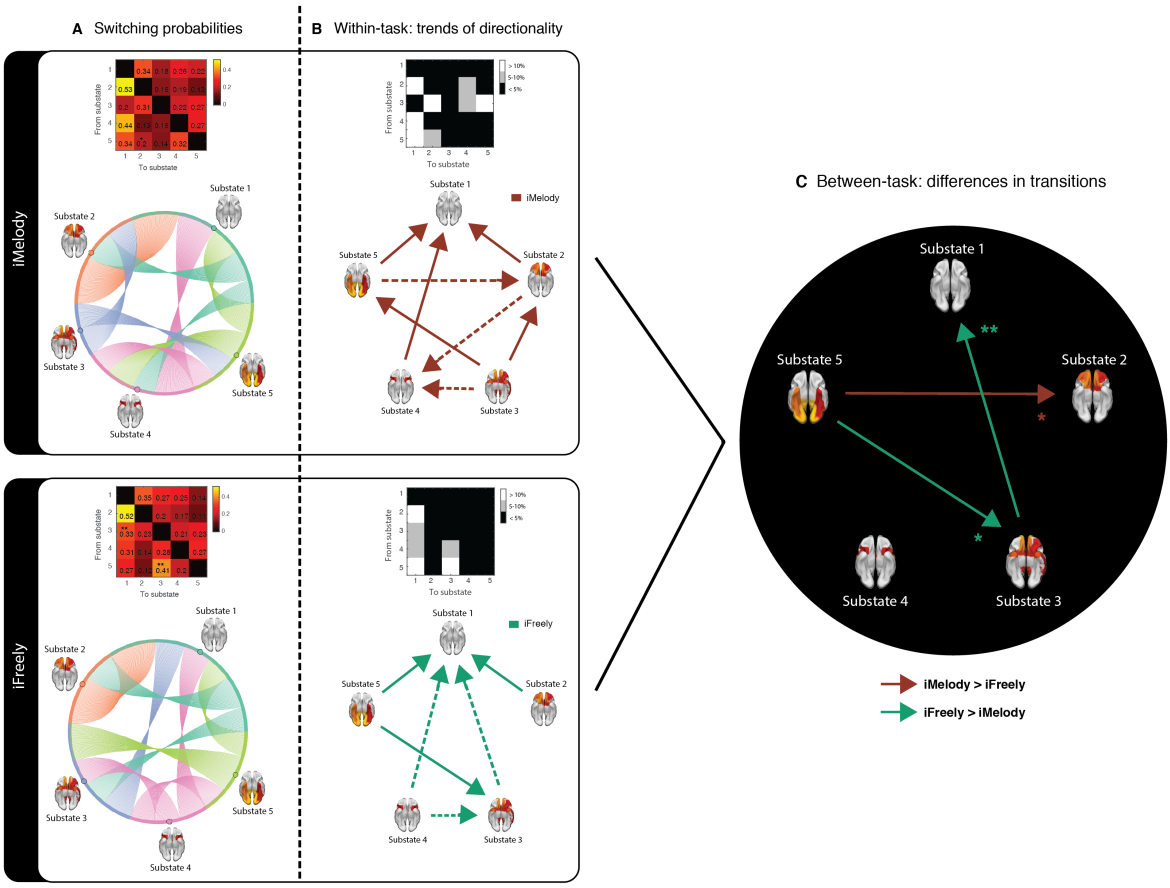

Figure 4. Switching profiles of improvisation. A) *Probabilities of transitions represented as chord diagrams and matrices. On top of each panel, the matrix shows the probability of each substate transitioning in improvisation by melody (iMelody; top panel) and improvisation freely (iFreely; bottom panel). Differences in substate transitioning between conditions were assessed using permutation testing and corrected for false positives with Bonferroni. Statistically significant differences between improvisation modes are marked with '*'. Bellow each matrix, a chord diagram shows all transitions with value higher than 25% of probability of occurrence, with thickness of the chords indicating its strength. B) Within-task trends of directionality of transitions, i.e. transitions with a clear tendency of occurrence with a preferred direction. On top, of each panel, a matrix shows which pairs of substates involve a transition with preferred direction, at 2 different threshold levels – between 5-10% and above 10% (percentage indicating the total probability of transition between a substate and each of the other substates, i.e. for each substate, the sum of the probability of transitioning to all other substates is 100%). Below, the network diagram with solid and dashed*

arrows indicating transition directionality for the higher (>10%) and lower (5-10%) threshold respectively, for both iMelody (top panel; red) and iFreely (bottom panel; green). ***C)*** *Significant task differences (iMelody Vs. iFreely; '*' for p<0.05, and '**' for p<0.005, Bonferroni corrected) in the probability of substate transition. Three significant group differences in the probability of substate transitioning between iMelody and iFreely were found. The transitions from substate 3 to the 'global' substate 1 and substate 5 to substate 3, were found to have significantly higher probability of switching in iFreely. The transitions from substate 3 to the 'global' substate 1 and substate 5 to substate 3, were found to have significantly higher probability of switching in iFreely. On the other hands, our results reveal that iMelody is characterized by a significantly higher probability of switching from substate 5 to substate 2.*

Discussion

The present study investigated the whole-brain dynamics underlying musical improvisation in a group of jazz pianists. A novel analytic method – LEiDA – was used to estimate the metastable brain substates (i.e. recurrent patterns of brain functional connectivity) in which the brain is characterized during two types of musical improvisation: freely and by melody, as well as at rest. Our dynamic analyses show a recurrent substate – "improvisation mode" – characterised by a significantly higher probability of occurrence and duration in *iFreely*, when compared to *iMelody* (as well as rest). This substate comprises areas of the dorsal default mode (DMN), the left executive control (ECN), the anterior salience (SN), language, and precuneus networks. Our results also suggest that *iFreely*, a more free mode of improvisation, involves processes closely linked to core features of creativity, such as generating and evaluating creative ideas, predicting and monitoring sensory input, and syntactic processing through linguistic mechanisms.

In sum, jazz improvisation relies strongly on the use of multiple brain substates (each, represented by a network combining multiple fundamental brain mechanisms), recursively, when they improvise in order to create music, which is novel, surprising, aesthetically balanced and emotionally rewarding. Moreover, we provide the first comprehensive characterization of the FC brain networks involved in musical creativity, as well as the changes in their dynamic fingerprint (i.e. probability of occurrence and switching transitions) compared to the resting-state (our baseline condition).

Here, we describe our findings in terms of the differences in dynamic structure, by first characterizing the five brain substates that best describe both rest and the two modes of

musical improvisation, second, by exploring the probability of occurrence of these substates, and third, by assessing the switching profiles between substates. Lastly, we muse upon how the concordance in brain activity between both modes of improvisation reflects upon domain-general processes of creativity.

We selected the model reflecting five functional substates, as it suggested significant differences in the probability of occurrence and switching probabilities between the three conditions of interest. Our partition model of five substates is in accordance with the literature, where 5 to 10 functional networks emerge during rest [28,40]. Our results revealed, in line with previous studies using LEiDA [28–31], a global substate (substate 1), but also other four recurrent substates which overlap with RSNs reported in the literature [41,42]. These four recurrent substates reflect: reward and predictions (substate 2), a complex array of functions that support improvisation and creativity more generally – "improvisation mode" – in substate 3, an auditory and sensorimotor network in substate 4, and a visual network – planning – in substate 5.

Our dynamic analysis revealed that substate 3 had a significantly higher probability of occurrence, and duration, for *iFreely* compared to *iMelody* (and compared to rest). This substate comprises brain regions including the bilateral: ventromedial prefrontal cortex (vmPFC), medial prefrontal cortex (mPFC), medial orbital frontal cortex (mOFC), olfactory cortex, middle temporal poles, anterior and posterior cingulum; the left: angular gyrus, inferior frontal gryus – orbital, and the middle temporal gyrus. These areas, which are part of the dorsal default mode network (DMN), language network (LangN), left executive control network (ECN), the anterior salience network (SN), and precuneus network have been previously related to the creative musical process [18].

These results are in line with previous research, where DMN (responsible for spontaneous and self-generated thought) and ECN (responsible for cognitive control in more goal-directed cognitive processes) are shown to cooperate in order to generate and evaluate ideas during the creative process [26,27]. The *iFreely* condition corresponds closely to the unconstrained improvisation performed by jazz musicians in a natural playing situation, whereas the *iMelody* leads to more constrained improvisation indicating more convergent thinking. The coupling of DMN with ECN has been suggested to cooperate during creativity tasks (divergent thinking tasks and improvisation)[2,26], and this coupling together with perceptual and action initiation from auditory-motor regions are believed to be responsible for

implementing the different steps involved in musical creation [15]. The salience network has also been suggested to play a role in coordinating the interplay of these two networks (DMN-ECN) in order to identify candidate ideas during idea creation [43].

The medial PFC has been associated with autobiographical narrative [44], self-generated actions, internally-focused attention, internally motivated behaviour [3,45], episodic past and future thinking [46] and self-referential processing [47]. The medial PFC has thus been suggested to play a role in coordinating and expressing internally-motivated behaviours [3], as well as retrieval of episodic processes in creativity [48]. The ACC has also been found to be active in improvisation studies [49,50] and is suggested to play a key role in voluntary selection and decision making during the production of music in real-time. Berkowitz and Erkkinen have also suggested that the ACC may be important for error detection and monitoring errors in the predictions made [18]. The middle temporal gyrus, has been suggested to be related to novel association, and access and storage of conceptual knowledge [46,51]. Resting-state studies have found increases of functional connectivity between medial PFC and the middle temporal gyrus [44], and between the medial PFC and the PCC [52] to be associated with creativity. The authors suggested that these increases might help facilitate the generation of novel ideas and memory retrieval.

Interestingly, the left IFG, one of the most important language regions, also known to be involved in lexical selection and controlled retrieval of conceptual knowledge [53], has been found active in different studies of improvisation [3,27,49,50,54–57]. It has been suggested to play different roles in music improvisation, such as involvement in the generation of novel musical phrases [50], the generation and selection of motor sequences [49], syntactic processing of music and speech [54] and in the generation and evaluation of candidate ideas from memory retrieval [2,18]. The angular gyrus has been related to states of defocused attention, mind-wandering, and memory retrieval, and its function in improvisation may be related with classifying the stimuli as predicted. Limbic regions are also found to be involved in improvisation, potentially reflecting the need for improvised music to remain emotionally compatible with preceding musical elements, and perhaps also due to the musician's emotional investment in the process of improvisation.

In sum, the regions belonging to substate 3 describe an interaction between different cognitive processes such as idea generation (where attention, memory retrieval and mind-wandering are needed), selection, production, evaluation and reward, which may reflect the

increased spontaneous creative processing. We found this substate to have a significantly higher probability of occurrence in *iFreely* than in *iMelody*, which shows that different improvisational strategies may rely upon different cognitive process. Melodic improvisation involves a goal-specific task of arranging the notes in a certain order trying to create a new melody that bears resemblance to the original, in this case a known musical song (DWR). However, the free improvisation on a chord scheme allows for the use of a larger repertoire of melodic and rhythmic material. The constellation of brain regions in this network linked to free improvisation strengthens evidence for the model of improvisation proposed by Pressing, where improvisation is described to be a dynamic interplay of generation, evaluation and execution of novel motor sequences [58].

The bilateral superior, medial, and middle orbitofrontal cortex, the pallidum and the left olfactory cortex comprise substate 2. These regions cluster bilaterally around the orbitofrontal cortex, a region known to be involved as a nexus for sensory integration, prediction-monitoring, and reward [59]. Both visual and auditory information projects to the orbitofrontal cortex, via the superior temporal sulcus and the temporal pole, and is then projected back to regions including the amygdala, anterior cingulate cortex, and basal ganglia[60]. The connectivity of substate 2 therefore leaves it in an important position for integrating the sensory features of incoming musical stimuli, and the rewarding elements of improvisation – both monitoring and predicting the reward value of musical features, and subjective enjoyment.

In addition to the differences found in terms of probabilities of occurrence between the two modes of improvisation (substate 2 and 3), differences in the switching profiles between improvisations were also found in substate 5. Substate 5 is a network encompassing bilateral calcarine fissure, cuneus, lingual gyrus, inferior, medial and superior occipital gyrus, and fusiform gyrus. The gray matter density of posterior regions has previously been associated with divergent thinking and creativity [60,61]. Regions such as the lingual gyrus and precuneus have been linked to the generation of novel associations, necessary for creative thought [62]. Occipital networks support visual mental imagery [63], which may be active during musical improvisation due to the visualisation of melodic and harmonic structures involved in planning what to play [64]. This sensory network parallels the auditory and sensorimotor network that are included in substate 4 and is to be expected in tasks of a musical nature.

Analysis of the similarities and differences in trends of directionality between *iFreely* and *iMelody*, reveals that for *iMelody*, substate 5 has a significantly higher probability of transitioning to substate 2, whereas for *iFreely* substate 5 has a higher probability of going to substate 3. This means that a substate of planning and imagery is more often followed by a substate that involves reward processing, when you are improvising on the melody. For listeners, music which is easily sung is more likely to rouse affect and create pleasure than instrumental music [65]. Hence, for improvising with the goal of creating a melody, it appears that our brains need to draw on similar emotional resources to those of the listeners. In comparison, the iFreely condition yields improvisations, which are less easily sung, but on the other hand allows for more creative ideas to emerge. In this condition, the planning substate is more often followed by substate 3 ("the improvisation mode"), a network which has been associated with divergent thinking tasks, hence a core network for creativity. Studies in domain-general creativity have shown the involvement of the visual network[61,66]. Its involvement may explain the fact that many musicians self-report the use of musical imagery to be necessary to plan and execute their performance [67].

Furthermore, for the *iFreely* condition, the substate 3 is more often followed by the global state (substate 1). This is also reflected in the probabilities of occurrence, with *iFreely* spending more time in the "improvisation mode" and the global substate, and *iMelody* spending more time within substates 2 and 4, associated with listening and reward (Figure 3). The improvising brain may, in the case of *iFreely*, have to spend longer within the improvising mode, only being distracted by direct deviations to and from the global state, in order to complete the task successfully.

As Boden[22] suggests, creativity is a delicate balance between unpredictability and constraints, familiarity and surprise, with the end-point being an original output, which is both aesthetically and emotionally rewarding. As such, real-time musical creativity, such as jazz improvisation, requires a constant retrieval of prior knowledge and anticipation of both predictable and unpredictable musical features and components, and the ability to generate auditory-motor sequences[1]. Substate 3 therefore seems a fitting match for the creative process. In respect to creativity more generally, our results suggest that given the substantial overlap between duration of activity in substate 3 for both *iFreely* and *iMelody*, substate 3 appears to be a good candidate for a domain-general network supporting creativity. As previously suggested, *iFreely* may have higher prevalence of substate 3 due to greater

demands upon the creative process. The switching profiles are also of great interest to an understanding of the creative process more generally, as it may elucidate the spatial and temporal sequence of the dynamic processes (i.e. brain substates, or functional sub-networks), which compose the neural harmony underlying creativity.

A limitation in this study is that we can but make inferences about domain-general creativity. Future studies will need to compare improvisation in different modalities – perhaps verbal (divergent thinking), auditory (music), visual (art), and kinaesthetic (dance) to confirm whether the network herein does indeed support domain-general creativity. For future work in this area, we would suggest that extending this novel approach, LEiDA, to parcellation schemes with a higher number of areas than AAL, for example to Shen and colleagues' [68] or Glasser and colleagues' [69] parcellation schemes, could also reveal more fine-grained substates.

In summary, this study provides a novel approach to studying the brain dynamics of musical creativity. Jazz improvisation reflects a complex and multifaceted set of cognitive processes that have correspondingly complex functional network dynamics. Here, we attempted for the first time to unravel the dynamic neural cognitive processes involved in musical improvisation over time. We found that improvising on the melody and improvising freely on a harmonic progression shared a common fingerprint of brain substates underlying the process of musical creation. However, the act of improvising more freely was characterized by the brain spending more time within the improvising mode and global substate compared to improvisation under melodic constraints. This may reflect functions such as generating and evaluating creative ideas, predicting and monitoring sensory input, and syntactic processing through linguistic mechanisms. In comparison, melodic improvisation was linked to the functional role of auditory and reward networks. These results show the benefit of using novel methods and musical paradigms to investigate the large-scale brain mechanisms involved in the complex process of musical creativity.

References

1. McPherson, M. & Limb, C. J. Difficulties in the neuroscience of creativity: jazz improvisation and the scientific method: Difficulties in the neuroscience of creativity. *Ann. N. Y. Acad. Sci.* **1303**, 80–83 (2013).

2. Beaty, R. E. The neuroscience of musical improvisation. *Neurosci. Biobehav. Rev.* **51**, 108–117 (2015).
3. Limb, C. J. & Braun, A. R. Neural Substrates of Spontaneous Musical Performance: An fMRI Study of Jazz Improvisation. *PLoS ONE* **3**, (2008).
4. Benedek, M., Borovnjak, B., Neubauer, A. C. & Kruse-Weber, S. Creativity and personality in classical, jazz and folk musicians. *Personal. Individ. Differ.* **63**, 117–121 (2014).
5. Stein, M. I. Creativity and Culture. *J. Psychol.* **36**, 311–322 (1953).
6. Martindale, C. *Cognition and consciousness*. (Homewood, IL: Dorsey Press, 1981).
7. Martindale, C. & Dailey, A. Creativity, primary process cognition and personality. *Personal. Individ. Differ.* **20**, 409–414 (1996).
8. Friedman, R. S., Fishbach, A., Förster, J. & Werth, L. Attentional Priming Effects on Creativity. *Creat. Res. J.* **15**, 277–286 (2003).
9. Abraham, A. *The Neuroscience of Creativity*. (Cambridge: Cambridge University Press., 2018). doi:10.1017/9781316816981.
10. Runco, M. A. Creativity. *Annu. Rev. Psychol.* **55**, 657–687 (2004).
11. Csikszentmihalyi, M. *Creativity: Flow and the psychology of discovery and invention.* (HarperCollins Publishers, 1996).
12. Abraham, A. The neuropsychology of creativity. *Curr. Opin. Behav. Sci.* **27**, 71–76 (2019).
13. Benedek, M., Christensen, A. P., Fink, A. & Beaty, R. E. Creativity assessment in neuroscience research. *Psychol. Aesthet. Creat. Arts* **13**, 218–226 (2019).
14. Boccia, M., Piccardi, L., Palermo, L., Nori, R. & Palmiero, M. Where do bright ideas occur in our brain? Meta-analytic evidence from neuroimaging studies of domain-specific creativity. *Front. Psychol.* **6**, (2015).
15. Loui, P. Rapid and flexible creativity in musical improvisation: review and a model: Creativity in musical improvisation. *Ann. N. Y. Acad. Sci.* (2018) doi:10.1111/nyas.13628.
16. Vuust, P. & Kringelbach, M. L. Music Improvisation. in *The Routledge Companion to Music Cognition* (eds. Ashley, R. & Timmers, R.) 265–275 (Routledge, 2017). doi:10.4324/9781315194738-22.
17. Loui, P. & Guetta, R. *Music and Attention, Executive Function, and Creativity*. vol. 1 (Oxford University Press, 2018).
19. Friston, K. Does predictive coding have a future? *Nat. Neurosci.* **21**, 1019–1021 (2018).

20. Friston, K. The free-energy principle: a unified brain theory? *Nat. Rev. Neurosci.* **11**, 127–138 (2010).
21. Koelsch, S., Vuust, P. & Friston, K. Predictive Processes and the Peculiar Case of Music. *Trends Cogn. Sci.* **23**, 63–77 (2019).
22. Boden, M. *Creativity and Art: three Roads to Surprise.* (Oxford University Press, Oxford., 2010).
23. Norgaard, M. How Jazz Musicians Improvise: The Central Role of Auditory and Motor Patterns. *Music Percept.* **31**, 271–287 (2014).
24. Sawyer, K. Improvisational Creativity: An Analysis of Jazz Performance. *Creat. Res. J.* **5**, 253–263 (1992).
25. Watson, C. How Musicians Develop the Ability to Improvise : A Cross-cultural Comparison of Skill Development in the Egyptian , Hindustani Classical , and Jazz Traditions School of the Arts and Media University of New South Wales This thesis is presented for the degr. (2012).
26. Beaty, R. E., Benedek, M., Silvia, P. J. & Schacter, D. L. Creative Cognition and Brain Network Dynamics. *Trends Cogn. Sci.* **20**, 87–95 (2016).
27. Pinho, A. L., Ullén, F., Castelo-Branco, M., Fransson, P. & de Manzano, Ö. Addressing a Paradox: Dual Strategies for Creative Performance in Introspective and Extrospective Networks. *Cereb. Cortex* **26**, 3052–3063 (2016).
28. Cabral, J. *et al.* Cognitive performance in healthy older adults relates to spontaneous switching between states of functional connectivity during rest. *Sci. Rep.* **7**, 5135 (2017).
29. Lord, L.-D. *et al.* Dynamical exploration of the repertoire of brain networks at rest is modulated by psilocybin. *NeuroImage* (2019) doi:10.1016/j.neuroimage.2019.05.060.
30. Stark, E. A. *et al.* The power of smiling: The adult brain networks underlying learned infant temperament. *Cerebral Cortex* (2020).
31. Figueroa, C. A. *et al.* Altered ability to access a clinically relevant control network in patients remitted from major depressive disorder. *Hum. Brain Mapp.* **40**, 2771–2786 (2019).
32. Jensen, M. S., Heggli, Ole Adrian, Alves Da Mota, Patricia & Vuust, Peter. A low-cost MRI compatible keyboard. *Proc. New Interfaces Music. Expr.* (2017).
33. Peirce, J. *et al.* PsychoPy2: Experiments in behavior made easy. *Behav. Res. Methods* **51**, 195–203 (2019).

34. Beckmann, C. F. & Smith, S. M. Probabilistic Independent Component Analysis for Functional Magnetic Resonance Imaging. *IEEE Trans. Med. Imaging* **23**, 137–152 (2004).
35. Jenkinson, M., Bannister, P., Brady, M. & Smith, S. Improved Optimization for the Robust and Accurate Linear Registration and Motion Correction of Brain Images. *NeuroImage* **17**, 825–841 (2002).
36. Smith, S. M. Fast robust automated brain extraction. *Hum. Brain Mapp.* **17**, 143–155 (2002).
37. Tzourio-Mazoyer, N. *et al.* Automated Anatomical Labeling of Activations in SPM Using a Macroscopic Anatomical Parcellation of the MNI MRI Single-Subject Brain. *NeuroImage* **15**, 273–289 (2002).
38. Glerean, E., Salmi, J., Lahnakoski, J. M., Jääskeläinen, I. P. & Sams, M. Functional Magnetic Resonance Imaging Phase Synchronization as a Measure of Dynamic Functional Connectivity. *Brain Connect.* **2**, 91–101 (2012).
39. Beckmann, C. F., DeLuca, M., Devlin, J. T. & Smith, S. M. Investigations into resting-state connectivity using independent component analysis. *Philos. Trans. R. Soc. B Biol. Sci.* **360**, 1001–1013 (2005).
40. Damoiseaux, J. S. *et al.* Consistent resting-state networks across healthy subjects. *Proc. Natl. Acad. Sci.* **103**, 13848–13853 (2006).
41. Thomas Yeo, B. T. *et al.* The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *J. Neurophysiol.* **106**, 1125–1165 (2011).
42. Shirer, W. R., Ryali, S., Rykhlevskaia, E., Menon, V. & Greicius, M. D. Decoding Subject-Driven Cognitive States with Whole-Brain Connectivity Patterns. *Cereb. Cortex* **22**, 158–165 (2012).
43. Beaty, R. E. *et al.* Robust prediction of individual creative ability from brain functional connectivity. *Proc. Natl. Acad. Sci.* **115**, 1087–1092 (2018).
44. Wei, D. *et al.* Increased resting functional connectivity of the medial prefrontal cortex in creativity by means of cognitive stimulation. *Cortex* **51**, 92–102 (2014).
45. Raichle, M. E. & Gusnard, D. A. Intrinsic brain activity sets the stage for expression of motivated behavior. *J. Comp. Neurol.* **493**, 167–176 (2005).
46. Abraham, A., Schubotz, R. I. & von Cramon, D. Y. Thinking about the future versus the past in personal and non-personal contexts. *Brain Res.* **1233**, 106–119 (2008).
47. Hassabis, D., Kumaran, D. & Maguire, E. A. Using Imagination to Understand the Neural Basis of Episodic Memory. *J. Neurosci.* **27**, 14365–14374 (2007).

48. Benedek, M. & Fink, A. Toward a neurocognitive framework of creative cognition: the role of memory, attention, and cognitive control. *Curr. Opin. Behav. Sci.* **27**, 116–122 (2019).
49. Berkowitz, A. L. & Ansari, D. Generation of novel motor sequences: The neural correlates of musical improvisation. *NeuroImage* **41**, 535–543 (2008).
50. de Manzano, Ö. & Ullén, F. Activation and connectivity patterns of the presupplementary and dorsal premotor areas during free improvisation of melodies and rhythms. *NeuroImage* **63**, 272–280 (2012).
51. Ellamil, M., Dobson, C., Beeman, M. & Christoff, K. Evaluative and generative modes of thought during the creative process. *NeuroImage* **59**, 1783–1794 (2012).
52. Takeuchi, H. *et al.* The Association between Resting Functional Connectivity and Creativity. *Cereb. Cortex* **22**, 2921–2929 (2012).
53. Abraham, A. Creative thinking as orchestrated by semantic processing vs. cognitive control brain networks. *Front. Hum. Neurosci.* **8**, (2014).
54. Donnay, G. F., Rankin, S. K., Lopez-Gonzalez, M., Jiradejvong, P. & Limb, C. J. Neural Substrates of Interactive Musical Improvisation: An fMRI Study of 'Trading Fours' in Jazz. *PLoS ONE* **9**, e88665 (2014).
55. Liu, S. *et al.* Neural Correlates of Lyrical Improvisation: An fMRI Study of Freestyle Rap. *Sci. Rep.* **2**, (2012).
56. McPherson, M. J., Barrett, F. S., Lopez-Gonzalez, M., Jiradejvong, P. & Limb, C. J. Emotional Intent Modulates The Neural Substrates Of Creativity: An fMRI Study of Emotionally Targeted Improvisation in Jazz Musicians. *Sci. Rep.* **6**, 18460 (2016).
57. Pinho, A. L., de Manzano, O., Fransson, P., Eriksson, H. & Ullen, F. Connecting to Create: Expertise in Musical Improvisation Is Associated with Increased Functional Connectivity between Premotor and Prefrontal Areas. *J. Neurosci.* **34**, 6156–6163 (2014).
58. Pressing, J. *Improvisation: Methods and models.In Generative processes in music: The psychology of performance, improvisation, and composition.* (Clarendon Press/Oxford University Press, 1988).
59. Kringelbach, M. L. The human orbitofrontal cortex: linking reward to hedonic experience. *Nat. Rev. Neurosci.* **6**, 691–702 (2005).
60. Jung, R. E. *et al.* Neuroanatomy of creativity. *Hum. Brain Mapp.* NA-NA (2009) doi:10.1002/hbm.20874.
61. Fink, A. *et al.* Creativity and schizotypy from the neuroscience perspective. *Cogn. Affect. Behav. Neurosci.* **14**, 378–387 (2014).

62. Luo, J. *et al.* Neural Basis of Scientific Innovation Induced by Heuristic Prototype. *PLoS ONE* **8**, e49231 (2013).
63. Kosslyn, S. M., Thompson, W. L., Klm, I. J. & Alpert, N. M. Topographical representations of mental images in primary visual cortex. *Nature* **378**, 496–498 (1995).
64. Zatorre, R. J., Chen, J. L. & Penhune, V. B. When the brain plays music: auditory–motor interactions in music perception and production. *Nat. Rev. Neurosci.* **8**, 547–558 (2007).
65. Brattico, E. *et al.* A Functional MRI Study of Happy and Sad Emotions in Music with and without Lyrics. *Front. Psychol.* **2**, (2011).
66. Benedek, M. *et al.* To create or to recall original ideas: Brain processes associated with the imagination of novel object uses. *Cortex* **99**, 93–102 (2018).
67. Herholz, S. C., Halpern, A. R. & Zatorre, R. J. Neuronal Correlates of Perception, Imagery, and Memory for Familiar Tunes. *J. Cogn. Neurosci.* **24**, 1382–1397 (2012).
68. Shen, X., Tokoglu, F., Papademetris, X. & Constable, R. T. Groupwise whole-brain parcellation from resting-state fMRI data for network node identification. *NeuroImage* **82**, 403–415 (2013).
69. Glasser, M. F. *et al.* A multi-modal parcellation of human cerebral cortex. *Nature* **536**, 171–178 (2016).