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ORIGINAL ARTICLE

Brain Network Reconfiguration and Perceptual Decoupling During an Absorptive State of Consciousness

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Abstract

Trance is an absorptive state of consciousness characterized by narrowed awareness of external surroundings and has long been used—for example, by shamans—to gain insight. Shamans across cultures often induce trance by listening to rhythmic drumming. Using functional magnetic resonance imaging (fMRI), we examined the brain-network configuration associated with trance. Experienced shamanic practitioners (n=15) listened to rhythmic drumming, and either entered a trance state or remained in a nontrance state during 8-min scans. We analyzed changes in network connectivity. Trance was associated with higher eigenvector centrality (i.e., stronger hubs) in 3 regions: posterior cingulate cortex (PCC), dorsal anterior cingulate cortex (dACC), and left insula/operculum. Seed-based analysis revealed increased coactivation of the PCC (a default network hub involved in internally oriented cognitive states) with the dACC and insula (control-network regions involved in maintaining relevant neural streams). This coactivation suggests that an internally oriented neural stream was amplified by the modulatory control network. Additionally, during trance, seeds within the auditory pathway were less connected, possibly indicating perceptual decoupling and suppression of the repetitive auditory stimuli. In sum, trance involved coactive default and control networks, and decoupled sensory processing. This network reconfiguration may promote an extended internal train of thought wherein integration and insight can occur.

Key words: brain networks, eigenvector centrality, functional connectivity, shaman, trance

Introduction

Trance is an altered state of consciousness characterized by a narrowed awareness of external surroundings. The absorptive state in trance relates to the hyper-focused immersive experience of flow (Csikszentmihalyi 1990) and has been cultivated in many musical and contemplative traditions (Harner 1990; Becker 2004; Walsh 2007). Various methods can induce trance-like states including hypnosis, chanting, dancing, taking

psychoactive substances, and drumming (Becker 2004; Vaitl et al. 2005). Repetitive drumming is a powerful method to alter consciousness and has been used since ancient times in many shamanic traditions (Harner 1990; Krippner 2000).

Shamanism is humanity's most ancient spiritual and healing tradition, and exists in remarkably similar forms across cultures (Harner 1990; Winkelman 2010). Shamans play an important role in their community as healers, and they voluntarily enter a trance-like state to gain insight to a specified problem. In these altered states, shamans may experience "journeying" to other realms filled with vivid imagery, spirits, and symbols (Rasmussen 1929; Eliade 1964; Harner 1990; Walsh 2007). To induce trance, shamans often listen to repetitive drumming while lying down with their eyes closed (Harner 1990). This limits sensory input to highly predictable auditory stimuli, and promotes an absorptive state wherein they disengage from the sensory environment. Highly similar trance-inducing techniques, such as fast quasi-isochronous drumming (~240 beats per min or ~4 Hz), exist in shamanic traditions from unconnected cultures (Harner 1990; Vitebsky 1995). The striking commonalities across cultures suggest that these practices evolved convergently (Harner 1990) and likely have a common biological basis (Winkelman 2010).

Despite shamanism's long-standing tradition, powerful phenomenology, and cross-cultural ubiquity, little is known about the neural correlates of the altered consciousness in its trance state (Vaitlet al. 2005; Walsh 2007). A great deal of neuroscience research has examined other contemplative practices such as meditation, but almost no neuroscience research has examined the neural underpinnings associated with shamanic states of consciousness or trance (Vaitl et al. 2005; Walsh 2007). Experienced shamanic practitioners are highly accomplished and proficient at altering consciousness and entering trance states, and we are not aware of previous neuroscience studies on trance in shamanic practitioners. Because the shamanic trance is characterized by a state of absorption involving deliberate withdrawal from external stimuli, it is reasonable that it is accompanied by alterations in functional networks of the brain.

Coherent correlated activity among brain regions enables large-scale neural integration, and the network configuration can reflect the current mental state (Varela et al. 2001; Leopold et al. 2003; Fox et al. 2005; Buckner et al. 2008; Sporns 2010). Prominent networks include the default mode network (DMN), which is involved in internally directed tasks such as autobiographical planning, self-reference, and stimulus-independent thought (Buckner et al. 2008; Christoff et al. 2009; Spreng et al. 2010; Kucyi et al. 2013), and the dorsal attention network, which is involved in externally directed tasks such as visual attention (Corbetta and Shulman 2002; Fox et al. 2006). Anatomically interposed between these networks are control-related networks (Vincent et al. 2008; Power and Petersen 2013), including related (but dissociable) networks such as the fronto-parietal control network (Vincent et al. 2008; Yeo et al. 2011), and the salience (Seeley et al. 2007; Menon and Uddin 2010) and cingulo-opercular networks (Dosenbach et al. 2008; Power and Petersen 2013). Control-related networks generally support goal-directed processes by allocating attentional resources to relevant events, maintaining task information, and preventing reorienting to distracting events (Seeley et al. 2007; Corbetta et al. 2008; Dosenbach et al. 2008; Menon and Uddin 2010; Power and Petersen 2013). Control network regions can couple with default mode regions to help maintain an internally directed cognitive state (Spreng et al. 2010), and maintaining an internally directed state is further assisted by dampened sensory processing (Smallwood et al. 2012). Dampened processing in the auditory pathway (or perceptual decoupling) could result from highly predictable and repetitive stimulus presentation, such as drumming. Based on this recent neuroscience research, we hypothesize that a network configuration supporting internally oriented thought and perceptual decoupling may be associated with absorptive shamanic

In this study, we examine the functional brain-network profiles of experienced shamanic practitioners during trance-like states of consciousness. Experienced shamanic practitioners listened to rhythmic drumming with their eyes closed, and either entered a trance-like state or remained in a nontrance state, during 8-min functional magnetic resonance imaging (fMRI) scans. Our analysis focused on network configuration using eigenvector centrality mapping (ECM). ECM is a data-driven analysis that calculates each voxel's connectivity and hierarchy within the whole-brain network, and thus can localize the centrality or strength of hubs in the brain (Lohmann et al. 2010). This data-driven analysis was accompanied by more traditional seed-based functional connectivity analyses to investigate hypotheses regarding the connectivity of a central default-network hub with other networks, as well as connectivity within the auditory pathway.

Materials and Methods

Overview

The experimental session consisted of four 8-min scans, alternating between trance and nontrance conditions (order counterbalanced across participants). Participants were instructed to keep their eyes closed, and to go into trance on the trance runs, and not go into trance or think of anything in particular on the nontrance runs. In addition to the fMRI data, we collected simultaneous electroencephalogram (EEG) data (described in Supplementary Material). After the final experimental run, we removed the EEG cap, and acquired anatomical scans (T1 and FLAIR). Total time in the scanner was approximately 1 h. Preparation (including instructions, a mock scanner session, and EEG preparation) lasted approximately 1 h. A post-test interview addressing their experience lasted approximately 30 min.

Participants

Participants were 15 experienced shamanic practitioners (mean age \pm SD, 50.2 ± 8.3 years; range 38-65; 11 female). They were from Germany and Austria and had been involved with shamanic practices for an average of 9.3 years (± 5.0; range = 4-20). Participants had received training in "core shamanism," a system of techniques developed and codified by Michael Harner (1990) based on cross-cultural commonalities among shamanic traditions. Participants were recruited through the German-language newsletter of the Foundation of Shamanic Studies and by word of mouth. They provided informed consent and received remuneration for their time.

Experimental Procedure and Materials

Prior to the experiment, participants were briefed on the experiment and engaged in a practice session in a mock scanner. In the experiment, rhythmic drumming was presented over headphones (MR Confon, Magdeburg, Germany) during the trance and nontrance runs. The audio consisted of a low-pitched hand drum taken from a shamanic drumming CD (Michael Harner's

Solo Drumming). In the trance condition, the drumming was a relatively isochronous pulse with some natural timing fluctuations (mean interonset interval (IOI) = 236 ms [4.24 Hz]; SD of IOI = 6.7 ms). In the nontrance condition, the drumming sequence consisted of the same sounds but with slightly more irregular timing (mean IOI was also 236 ms; SD of IOI = 16.5 ms), to decrease the likelihood that participants inadvertently enter a trance-like state during the nontrance runs. The experiment was self-paced, and participants started each run with a button press when they were ready. After 8 min of repetitive drumming, each track concluded with a distinct 20 s "callback" rhythm that signaled the end of the run as is customary in core shamanism practice. During this callback, the scanner stopped.

After each run, participants answered 6 questions about their experience on a 7-point Likert scale via a button box. The first questions addressed whether the subjects kept their eyes closed during the entire run. The second question asked if they would "describe their experience as a deep shamanic journey." The other questions were from the Phenomenology of Consciousness Inventory (Pekala 1991) and assessed body image, time sense, meaning/altered state, and absorption (see Supplementary Material for details).

Data Acquisition and Preprocessing

MRI data were acquired on a Siemens Verio 3 T scanner with a 12channel head coil. Functional scans (gradient EPI) contained 30 axial slices covering the whole brain (time repetition = 2000 ms, time echo = 24 ms, $3 \times 3 \times 4$ mm³ resolution). This scanning sequence sounds like a relatively constant noise floor, rather than a potentially interfering rhythm. The middle 2 scans were the experimental runs. The first scan was intended to familiarize participants with the MRI environment, and a fourth scan was collected in case participants required more than one scan for familiarization (which was not the case). Preprocessing was completed with LIPSIA software (Lohmann et al. 2001), and included motion correction, temporal filtering, spatial smoothing (7 mm FWHM), and normalization to the MNI305 space.

Eigenvector Centrality Mapping Analysis

To identify systematic changes in the functional network architecture when undergoing the trance state, we used a node centrality measure called ECM (Lohmann et al. 2010). ECM is an assumption-free, data-driven approach that does not use predefined seed regions, but rather uses voxels from the whole brain including the cerebellum as nodes (~50 000 total voxels). With ECM, each voxel in the brain receives a centrality value that depends on the voxel's connectivity and the hierarchy within the network. Voxels that are strongly correlated with many other voxels that are themselves central within the network will have high centrality values. As is customary in ECM, after applying a high-pass filter at 0.01 Hz, the ECM algorithm calculates linear correlations for each voxel to every other voxel, rescales the correlations to positive values, and weights these values based on their degree of connection within the network (for additional details, see Lohmann et al. 2010).

We computed an eigenvector centrality map for each run. For the statistical analysis, we compared the centrality map from the trance run and nontrance run using a (voxel-wise) paired t-test over all subjects. The results were corrected for multiple comparisons using cluster-size corrections based on Monte-Carlo simulations, using a voxel-wise z threshold of 2.33 with a significance level of P < 0.05 on cluster level (Forman et al. 1995; Poline et al. 1997).

Seed-Based Functional Connectivity Analysis

ECM can establish differences in centrality of a brain region, but does not indicate to what regions an area is more or less connected. For this, we used seed-based functional connectivity, which highlights the strength of correlation between a seed region and other regions (e.g., Biswal et al. 1995). For the seedbased connectivity analyses, a temporal filter between 0.1 and 0.01 Hz was applied, and the 6 motion parameters were regressed out. We performed 2 seed-based analyses. We first calculated the correlation coefficients between a seed region of interest (ROI) in the posterior cingulate cortex (PCC) (defined from the ECM analysis and shown in Fig. 2) and all other voxels. As before, we computed a pairwise t-test on the correlation maps of the trance and nontrance runs, and corrected for multiple comparisons using cluster-size inference based on Gaussian random fields inference as implemented in SPM8 (Wellcome Trust Centre for Neuroimaging-UCL, London). In seed-based analyses, additional nuisance signals such those extracted from white matter and cerebrospinal fluid are typically regressed out, whereas this is not customary in ECM (e.g., Lohmann et al. 2010). To keep the underlying data similar across our analyses and to better understand the source of the ECM results, we did not regress out additional physiological signals for the seedbased analyses. However, for completeness, we performed a supplemental analysis that included additional denoising by regressing out signal from the white matter and cerebrospinal fluid. Results with additional denoising were highly consistent with those reported here. We used a voxel-wise threshold of P < 0.001 and a cluster threshold of P < 0.05 to correct for multiple comparisons.

The second seed-based analysis investigated functional connectivity within the auditory pathway. Four ROIs in the auditory pathway were defined a priori (based on anatomy and published auditory seeds [Mühlau et al. 2006]) as 3-voxel-diameter spheres in each hemisphere: The brainstem's superior olivary complex (right and left hemisphere spheres centered at Montreal Neurological Insitute (MNI) coordinates ± 6, -37, -40); the midbrain's inferior colliculus (± 6 , -33, -11); the medial geniculate nucleus of the thalamus (± 17 , -24, 2), and the primary auditory cortex $(\pm 48, -16, 2)$. We visually checked the location of a priori ROIs in the structural and blood oxygen level-dependent (BOLD) data of individual participants. While partial volume effects cannot be avoided at standard acquisition resolutions and with spatial smoothing, we confirmed seed placement and that inclusion of ventricle or nonbrain tissue was unlikely. We computed pairwise t-tests on the z-transformed Pearson correlations from the trance and nontrance runs, and averaged results across hemispheres.

Head Motion

We compared head motion between conditions, as head motion has been shown to influence measures of functional connectivity (Power et al. 2012; Van Dijk et al. 2012). To quantify head motion, we used the translation and rotation parameters from the rigid body correction of head motion. The displacement and rotation of each brain volume compared with the previous volume was calculated as the root mean square of the 3 single-dimension parameters (e.g., total displacement = $\sqrt{(x^2 + y^2 + z^2)}$). These volume-to-volume changes were averaged for each participant and compared between trance and nontrance in paired t-tests. Results showed no differences in head motion between conditions (Ps > 0.5; see Supplementary Material for further details).

Results

Self Report

First, we assessed whether participants subjectively experienced a trance-like state while inside the scanner. In response to the critical question, "would you describe your experience as a deep shamanic journey?" (1 = not at all; 7 = very much so), participants consistently reported experiencing a deep shamanic journey in the trance condition (mean response = 6.20; SD = 0.86), but not in the nontrance condition (M = 1.33 \pm 0.90), $t_{(14)}$ = 15.13, P < 0.001. Post-test interviews corroborated that participants were able to journey in the scanner and their experience was similar (in phenomenological content and depth) to journeys outside the scanner.

Eigenvector Centrality Mapping

Whole-brain ECM analysis of the fMRI scans revealed higher eigenvector centrality during trance than nontrance in 3 distinct clusters: Stronger hubs were located in the PCC, the dorsal anterior cingulate cortex (dACC), and the left anterior insula/operculum (Fig. 1). The PCC is a major hub of integration in the DMN, and is associated with internally directed mental states (Buckner et al. 2008). The dACC and insula/operculum are core regions in control-related networks (Vincent et al. 2008; Power and Petersen 2013) and help maintain task goals (Dosenbach et al. 2008; Menon and Uddin 2010).

The only cluster with significantly lower eigenvector centrality during trance was in the brainstem. The cluster was centered in the caudal pons, which is consistent with the superior olivary complex in the auditory pathway.

Seed-Based Functional Connectivity of the PCC

In addition to the global connectivity measures provided by ECM, we assessed seed-based functional connectivity from a PCC-seed region. In the trance condition, the PCC had significantly higher connectivity with the dACC, the bilateral insula, the cerebellum (lobules VI and VIII), bilateral inferior parietal lobule (IPL), and bilateral dorsolateral prefrontal cortex (dlPFC), (Fig. 2) [The specific cingulate region in Fig. 1b and 2c can be referred to as the dorsal anterior cingulate (dACC) or as the anterior midcingulate cortex (aMCC), a subregion involved in cognitive control (Shackman et al. 2011)]. All these additional regions are part of modulatory control networks (Vincent et al. 2008; Buckner et al. 2011; Yeo et al. 2011). These results indicate that control-network regions were more coactive with the PCC default hub during trance. The parallel-coordinate plots in Figure 3 show the relative consistency across participants for increased PCC connectivity with the dACC and the left insula during trance.

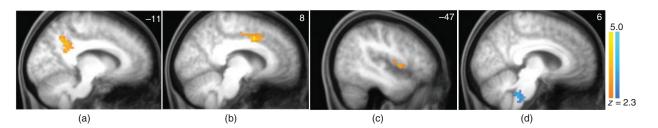


Figure 1. Eigenvector centrality differences between trance and nontrance. Significantly stronger hubs during trance occurred in (a) the PCC, (b) the dACC, and (c) the left anterior insula/operculum. Significantly lower centrality during trance occurred in (d) the caudal pons of the brainstem. Results are corrected for multiple comparisons (cluster thresholded at P < 0.05), and the X-coordinates for the sagittal slices are displayed in MNI space.

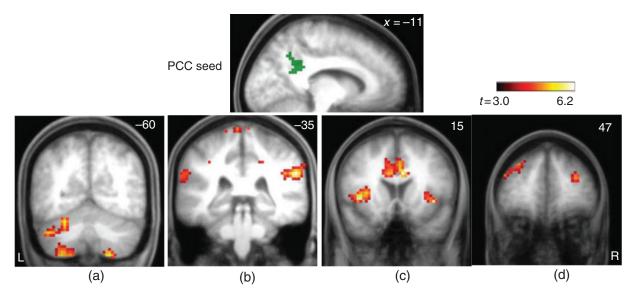


Figure 2. The PCC-seed region had higher connectivity during trance than nontrance with the following regions: (a) the cerebellum (lobules VI and VIII); (b) bilateral inferior parietal lobule; (c) the dACC and bilateral insula; and (d) bilateral dorsolateral prefrontal cortex. Y-coordinates for the coronal slices are displayed in MNI space.

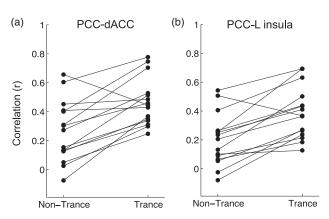


Figure 3. Increased PCC connectivity with the (*a*) dACC and (*b*) left insula during trance. The scatterplots depict each subject's PCC connectivity with 3 voxel-diameter spheres in (*a*) the dACC (centered at x = 9; y = 11; z = 44), and (*b*) the left insula (centered at x = -30; y = 11; z = 14).

Functional Connectivity Within the Auditory Pathway

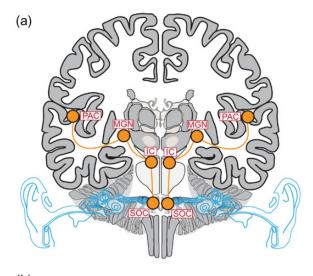
We assessed the functional connectivity between 4 α priori defined anatomical regions in the auditory pathway. During the trance condition, the superior olivary complex (brainstem) had significantly lower functional connectivity with the inferior colliculus (P = 0.034), medial geniculate nucleus (P = 0.008), and the primary auditory cortex (P = 0.004) (Fig. 4). Connectivity between other auditory pathway seeds did not differ significantly between trance and nontrance conditions (Ps > 0.1).

Discussion

Network Centrality

Connectivity in brain networks during shamanic trance journeys was examined using fMRI. Large-scale network connectivity of shamanic practitioners generally increased during trance. Eigenvector centrality increased during trance in 3 distinct and important brain regions: the PCC, dACC, and insula/operculum. The PCC, a default-network region, is a central hub of integration where many interconnected subsystems converge, and is commonly active when not engaged with the external environment (Fox et al. 2005; Buckner et al. 2008; Margulies et al. 2009). Increased PCC centrality during trance supports its importance in internally directed mental states, and suggests that shamanic trance involves increased large-scale neural integration in this key hub.

The dACC and insula/frontal operculum are regions in the control-related networks (Vincent et al. 2008; Power and Petersen 2013) and constitute the core regions of the closely related salience (Seeley et al. 2007; Menon and Uddin 2010) and cingulo-opercular (Dosenbach et al. 2008; Power and Petersen 2013) networks. These network regions have been shown to monitor and identify the most salient and relevant external and internal events (Menon and Uddin 2010). Depending on the task demands, these regions play a critical role in selecting the relevant stream of neural activity (Menon and Uddin 2010), and amplify the task-relevant stream to maintain the task goals (Dosenbach et al. 2008). Increased centrality of these network regions during the trance condition (i.e., increased connectivity with other large-scale network hubs), suggests that trance involves more sustained task maintenance. Moreover, higher eigenvector centrality of the dACC, insula, and the PCC suggests increased coupling among these 3 regions, which could help maintain an



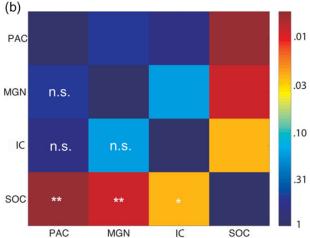


Figure 4. (a) Schematic depiction of the seeds in the auditory pathway. Primary auditory cortex (PAC); medial geniculate nucleus (MGN); inferior colliculus (IC); and superior olivary complex (SOC). (b) T-test results comparing trance and nontrance connectivity between seeds in the auditory pathway. The heat bar displays the P-values on a log scale. n.s.= nonsignificant; P < 0.05; P < 0.01.

internally directed cognitive state. We examined this hypothesis using seed-based functional connectivity.

Co-Activation of Default and Control Network Regions

The PCC-seed connectivity analysis indicated increased coactivation of the PCC hub with modulatory control-network regions during trance. The PCC seed showed increased functional connectivity with core salience and cingulo-opercular network regions (the dACC and insula), and with other areas including the inferior parietal lobule, the dorsolateral prefrontal cortex, and parts of the cerebellum (lobules VI and VIII). These additional areas are all included in control-related networks (Vincent et al. 2008; Buckner et al. 2011; Yeo et al. 2011). The control networks are most commonly reported to respond to salient external events and to engage externally oriented attention systems while disengaging the DMN regions (e.g., Sridharan et al. 2008). Here, we observed increased connectivity of control-network regions with the PCC default hub during trance, which indicates that the behaviorally relevant stream to be maintained is the internally oriented stream.

Recent studies indicate that control-network regions can flexibly couple with the dorsal attention network during externally oriented tasks, or with DMN regions during internally directed tasks such as autobiographical planning (Spreng et al. 2010; Spreng 2012). Efficient allocation of limited neuronal resources likely drives competition between internal and external streams (Smallwood et al. 2012), and this competition is mediated by the modulatory control network (Spreng et al. 2010). While focused engagement with external stimuli is often important, the ability to sustain an internally directed stream of thought is crucial in activities such as planning and processing information from memory not immediately available in the environment (e.g., Smallwood et al. 2012). To sustain an internal stream of thought over an extended period, control regions must amplify relevant internally oriented streams, and at the same time disengage and suppress irrelevant sensory streams (e.g., Corbetta et al. 2008). This disengaging of cognition from perception has been termed perceptual decoupling (Smallwood et al. 2012).

Perceptual Decoupling

Functional connectivity in the auditory pathway was lower during trance. The auditory brainstem seed was less connected with regions higher in the auditory pathway (the inferior colliculus, medial geniculate nucleus, and primary auditory cortex). Decreased connectivity in the auditory pathway could suggest perceptual decoupling and that the repetitive auditory information is suppressed and does not reach cortex as readily during trance. Perceptual decoupling or sensory gating would limit disruptions from irrelevant stimuli and help sustain an absorptive internally directed train of thought. Auditory decoupling, closed eyes, and a still body would help close down the external sensory world, and facilitate transfer to the internal world of shamanic journeying.

Shamanic drumming is monotonous and highly predictable; regular beats occur about 4 times per second (240 beats per min) (Harner 1990). We initially considered that the drum's ~4 Hz rhythm might drive a similar ~4 Hz (theta) rhythm in the brain, since such "auditory driving" of brain rhythms had been proposed as a mechanism for inducing trance (Neher 1962). However, the current data did not support auditory driving of cortex: theta power in the EEG was comparable in both conditions (see Supplementary Material). Rather than "opening up" and allowing the auditory rhythm to drive or entrain wide swaths of cortex, we observed something of the opposite: the system might "close down" or suppress the highly predictable auditory input, as possibly reflected in the decreased functional connectivity in the

Highly predictable sensory information could be gated or attenuated, and this resonates with predictive coding approaches to perception. According to such views, higher-level processing regions generate predictions that attempt to "explain away" bottom-up signals; only unpredicted sensory events cascade up the processing hierarchy (as prediction error) and necessitate more processing (e.g., Rao and Ballard 1999; Friston 2005). When events are highly predictable, cortical areas might be less dependent on the actual sensory signal, which could result in decreased connectivity and/or less activation (as in repetition suppression, Grill-Spector et al. 2006). Isochronous auditory stimuli produce an attenuated response (lower P50 auditory evoked response) compared with auditory stimuli that are temporally unpredictable (Schwartze et al. 2013). Here, the slightly less predictable stimulus timing in the nontrance condition could curtail auditory gating. Complementary to gating of predictable

events, an unpredicted rhythmic shift is commonly used to end the shamanic journey and helps disengage from the trance and reengage with the sensory world.

Evidence for perceptual decoupling has been observed when people are not engaged with the external environment. For example when participants inadvertently disengage from a perceptual task and mind wander, their sensory-evoked responses are attenuated (Smallwood et al. 2008; Kam et al. 2011) and their default network regions (i.e., PCC) are decoupled from primary sensory regions (Christoff 2012). In trance, shamans purposefully disengage from the external environment and this is likely facilitated by predictable sensory input. The present study along with evidence from several convergent lines of research establishes the deliberate use of a predictable external stimulus to (somewhat paradoxically) facilitate decoupling from the external environment.

Shamanic Trance and its Relation to Other Research Areas

The brain-network signatures in the trance condition (i.e., increased coactivation of the PCC and control networks, and decreased connectivity within the auditory pathway) are consistent with the absorptive states experienced during shamanic trance: Shamanic trance is characterized by heightened focus and decreased awareness of the environment (Walsh 2007). Listening to monotonous drumming with eyes closed and lying immobile would reduce reorienting to unexpected auditory, visual, and somatosensory events, and in turn facilitate an uninterrupted internally directed state (Winkelman 2010). During this extended absorptive state, shamanic practitioners often experience another layer of reality filled with imagery, spirits, and symbols. In the shamanic journey, there is an openness to whatever arises, and the symbols can lead to insight or better understanding of a problem specified prior to the journey. In this sense, the shamanic journey is a goal-directed exploratory state, wherein nascent and previously disparate mental contents can be simulated, evaluated, and integrated. The shaman's "integrative mode of consciousness" (Winkelman 2010) resonates with the DMN's proposed role in generating mental simulations of events beyond the immediate environment (e.g., Buckner et al. 2008) and its role in moving the system through attractor state space to explore potential network configurations (Deco et al. 2011).

The neural signatures of shamanic trance relate to recent neuroimaging studies of dreaming, insight, meditation, and hypnosis. Dreaming parallels shamanic trance as an immersive, visually dominated exploratory state with high PCC activation, but conversely, is associated with decreased control-related activity (Fox et al. 2013). The difference in control-related regions makes sense in that dreaming is typically experienced as a haphazard "exploratory" state beyond one's control, whereas the shamanic trance is often experienced as a lucid dream with meta-awareness and insight. In a recent study of creativity, which plays a role in insight problem solving, creative idea generation and evaluation were associated with similar increases in functional connectivity between default-network regions (including the PCC) and control-network regions (including the dACC and dlPFC) (Ellamil et al. 2012).

Similar changes in large-scale network connectivity have been observed in meditation (e.g., Hasenkamp and Barsalou 2012; Josipovic et al. 2012). Experienced mindfulness meditators had increased functional connectivity between the PCC and dACC (Brewer et al. 2011). While DMN regions are sometimes implicated in maladaptive mind wandering, the functional connectivity between default and control regions could also indicate cooperation to support internally directed or stimulusindependent thought (Spreng et al. 2010; Christoff 2012). A meditation practice highly relevant to shamanic techniques is mantra-based meditation, which also uses repetitive sounds and is associated with decreased awareness of the environment. Mantra-based meditation has been associated with brain patterns suggestive of decreased processing of sensory information (Lutz et al. 2007) and possibly a general gating of cortical activity (Berkovich-Ohana et al. 2015).

Finally, the shamanic trance resembles the intense absorption in a hypnotic state. Hypnosis, like shamanic trance, is characterized by focused attention and dissociation from competing thoughts (Spiegel 2013). However, they differ in the orientation of attention: in shamanic trance, attention is directed away from the external environment, whereas hypnotic trance is associated with suggestibility and enhanced response to external social cues (Oakley 2008; Spiegel 2013). A recent study found that highly hypnotizable individuals had higher resting state functional connectivity between the dlPFC and dACC control-related network regions (Hoeft et al. 2012). How neural connectivity during a hypnotic trance or during mundane internally directed tasks compares with a shamanic trance remains to be determined.

Limitations

Several methodological limitations should be mentioned. First, our study examined experienced shamanic practitioners in and out of trance states, and did not include naïve controls, so the generalizability of the effects to the wider population is unclear. In this first study, we wanted to investigate an experienced group who could reliably enter a trance state (in the MR environment). A recent behavioral study, however, showed that repetitive drumming with shamanic instructions altered conscious states and increased dreamlike experiences in novices (Gingras et al. 2014), and another study showed that drumming-induced trance states were deeper in more hypnotizable naïve subjects (Maurer et al. 1997). These studies suggest the viability of studying neural correlates (and individual differences) in naïve subjects, and how they change with training. Second, the current evidence for auditory gating stems from decreased connectivity of the brainstem, while other imaging research suggests that auditory gating is mediated by regions including the auditory cortex and thalamus (Mayer et al. 2009). The brainstem nuclei are small and brainstem registration is imperfect due in part to movement (Beissner et al. 2011), and we could be getting partial volume effects from other brainstem regions (which have also shown connectivity differences related to alterations of consciousness [e.g., Boveroux et al. 2010; Gili et al. 2013]). More sophisticated techniques such as ultra-high spatial resolution MRI (e.g., at 7 T) with less partial volume effects and brainstem-specific coregistration to an atlas could help localize the functional role of specific brainstem nuclei (e.g., Satpute et al. 2013), and is needed to substantiate the role of brainstem-nuclei connectivity in auditory gating. Additionally, we used the generic techniques of core shamanism developed by Harner (1990), but active techniques such as chanting and dancing can induce stronger trance states in certain circumstances (e.g., Friedrich and Buddruss 1955). However, core shamanism afforded consistency among the participants, and since these techniques have been taught in similar forms for decades throughout the world, many accomplished practitioners are

available for replication and extension. Future work could examine and contrast different techniques. Despite these considerations, the effects in this study should open doors for future investigations.

Conclusion

In sum, shamanic trance involved cooperation of brain networks associated with internal thought and cognitive control, as well as a dampening of sensory processing. This network configuration could enable an extended internal train of thought wherein integration and moments of insight can occur. Previous neuroscience work on trance is scant, but these results indicate that successful induction of a shamanic trance involves a reconfiguration of connectivity between brain regions that is consistent across individuals and thus cannot be dismissed as an empty ritual. By uncovering neural signatures associated with shamanic states, we hope to inspire further rigorous research into shamanic practices and alterations of consciousness. These first indications of the brain-network signatures underlying shamanic trance, along with shamanism's cross-cultural ubiquity, convergent evolution of techniques, enduring influence, and current resurgence suggest that shamanism might capture something fundamental about our human experience and the capabilities of the mind. These practices and their transformative potential deserve a deeper understanding.

Supplementary Material

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

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Notes

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