


SPECIAL ISSUE ARTICLE

New Trends in the Empirical Study of Consciousness: Measures and Mechanisms

Electrophysiological (EEG) microstates during dream-like bizarre experiences in a naturalistic scenario using immersive virtual reality

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Abstract

Monitoring the reality status of conscious experience is essential for a human being to interact successfully with the external world. Despite its importance for everyday functioning, reality monitoring can systematically become erroneous, for example, while dreaming or during hallucinatory experiences. To investigate brain processes associated with reality monitoring occurring online during an experience, i.e., perceptual reality monitoring, we assessed EEG microstates in healthy, young participants. In a within-subjects design, we compared the experience of reality when being confronted with dream-like bizarre elements versus realistic elements in an otherwise highly naturalistic real-world scenario in immersive virtual reality. Dream-like bizarreness induced changes in the subjective experience of reality and bizarreness, and led to an increase in the contribution of a specific microstate labelled C'. Microstate C' was related to the suspension of disbelief, i.e. the suppression of bizarre mismatches. Together with the functional interpretation of microstate C' as reported by previous studies, the findings of this study point to the importance of prefrontal meta-conscious control processes in perceptual reality monitoring.

KEYWORDS

bizarreness, conscious experience, EEG microstates, immersive virtual reality, perceptual reality monitoring

Abbreviations: AAHC, Atomize and Agglomerate Hierarchical Clustering Algorithm; ACC, anterior cingulate cortex; ANOVA, analysis of variance; CON, cingulo-opercular control network; EEG, electroencephalography; EOG, electrooculography; fMRI, functional magnetic resonance imaging; FMS, Fast Motion Sickness Scale; GFP, global field power; HMD, head-mounted display; ICA, independent component analysis; LSHS-R, Launay-Slade Hallucination Scale - revised; NREM, non-rapid eye movement; SN, saliency network; TANOVA, topographic analysis of variance; UE4, Unreal Engine 4; VR, virtual reality; 3D, three-dimensional.

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1 | INTRODUCTION

Through conscious experience, a human being becomes aware of the external world and the self (Laureys, 2005; Vanhaudenhuyse et al., 2011). For a successful interaction between the self and the external world, it is highly relevant to differentiate whether an experience has been caused by external sensory stimuli, such as seeing a cat, or by internal, stimulus-independent mentation, such as imagining a cat (Dijkstra et al., 2022; Vanhaudenhuyse et al., 2011). Monitoring whether the entity of a current experience corresponds to internal or external causes is based on the meta-quality of the experience, which is to feel real (like when seeing) vs. not real (like when imagining; Dijkstra et al., 2022). Given the importance of monitoring the reality status of conscious experience online during the experience, also called ‘perceptual reality monitoring’ (Dijkstra et al., 2022; Lau et al., 2022), it is intriguing that such monitoring can become erroneous on a systematic basis. Most frequently, a vivid and complex experience during sleep while dreaming is erroneously attributed as being real, despite the absence of corresponding external sensory signals (Nir & Tononi, 2010). Similar erroneous attribution may occur during the transition from wakefulness to sleep in hypnagogic hallucinations (Waters et al., 2016). Further, during wakefulness in states such as psychosis, vivid hallucinatory experiences are judged as real in the absence of corresponding external stimuli (Waters et al., 2021). Additionally, experiences during dreams and psychotic hallucinations are not only judged as real, but also as non-bizarre, despite the potential presence of bizarre elements (e.g. semantically incongruent elements, violations, or discontinuities in the stream of events; Rosen, 2018; Scarone et al., 2008). Furthermore, the erroneous attribution of an experience as something unreal in the presence of adequate external sensory signals can occur during dissociative states such as derealization or depersonalization (Simeon et al., 2008). Nevertheless, the fact that the source of the experience was erroneously misattributed can reach conscious awareness. States like hallucinations in Charles Bonnet syndrome can occur with insight, that is, the patient knows about the erroneous feeling of realness (Pang, 2016), or in lucid dreams, the dreamer becomes aware of the dream, although it feels real (Baird et al., 2019). Hence, monitoring the reality status of an experience depends on at least two processes: the more implicit feeling of being real, i.e., experience of reality, and the more explicit knowledge of realness, i.e., reality judgement (Dijkstra et al., 2022). So far, reality monitoring specifically of memory has been studied before (Johnson & Raye, 1981; Simons et al., 2017), focusing on the “offline” judgement

about whether the source of a certain memory is internal or external. However, there is little insight into when and why “online” perceptual reality monitoring during an experience fails. Thus, a deeper understanding of the basic mechanisms underlying perceptual reality monitoring integral to conscious experience will aid in explaining the role of erroneous reality monitoring in health (e.g. dreaming) and disease (e.g. psychotic hallucinations).

Any conscious experience is supposed to be associated with a certain type of brain activity (Nani et al., 2013). This view has given rise to several neuroscientific theories of consciousness (Boly et al., 2017; Frith, 2021). In short, what they have in common is that experience depends on the synchronized activity of large-scale brain networks, mainly including frontal and frontoparietal networks (Global Neuronal Workspace Theory, Dehaene et al., 2003; Higher-Order Theories, Lau & Rosenthal, 2011), as well as their long-range connectivity and/or integration (Integrated Information Theory, Tononi, 2008). However, while processes such as meta-cognition and attention are considered within these current theories (Boly et al., 2017; Frith, 2021), only one of them specifically accounts for perceptual reality monitoring processes (Lau, 2019). Therefore, the aim of this work is to investigate empirically the synchronized brain network dynamics underlying the monitoring of the reality status of conscious experience.

Synchronized large-scale brain networks and their temporal dynamics can be reliably assessed using EEG microstates. Microstates are defined by a limited set of successive scalp potential field topographies that remain semi-stable for approximately 80 ms before transitioning into another state (Michel & Koenig, 2018). Each microstate represents a global functional state of the brain (Khanna et al., 2015). Interestingly, the same few canonical microstate topographies (typically labelled A to D or higher) were replicated by multiple studies, explained approximately 80% of the variance, and could be associated with resting state networks identified by fMRI research (Michel & Koenig, 2018). The original four canonical topographies were associated with the auditory network (microstate A), the visual network (microstate B), the default mode network (microstate C) and the dorsal attention network (microstate D; cf. Michel & Koenig, 2018). Recently, a fifth microstate showing a high spatial correlation with microstate C has been considered as well, which has been associated with a frontal network overlapping with frontal control and saliency networks (microstate C'/F; cf. Custo et al., 2017; also called microstate E). Thus, EEG microstates are able to capture the current global functional state of large-scale brain networks, which makes them a suitable tool for

investigating conscious experience and involved reality monitoring processes.

EEG microstates have previously been used to investigate states of experience associated with altered reality monitoring. However, only one recent study directly assessed the experience of reality as part of reflective consciousness or reflective awareness, which relates to higher cognitive control processes. Diezig et al. (2022) investigated natural variance in reflective awareness during the transition to sleep. During this transition, reflective awareness, including reality monitoring, gradually fades while phenomenal awareness persists (Revonsuo et al., 2009; Yang et al., 2010). This dissociation can lead to hallucinatory experiences called hypnagogic hallucinations. The authors found that with less reflective awareness, the percentage of time covered and the mean duration of a microstate similar to C' increased, and those of a microstate similar to B decreased. Another study investigated altered conscious experience during dreaming but did not explicitly assess experience of reality (Br chet et al., 2020). The contrast in this study was experience vs. no experience during NREM sleep, where the altered experience of reality can only occur during sleep with experience. With reported dreaming experience during NREM sleep, there was an increase in the global explained variance of a microstate similar to C, and a decrease in the global explained variance of a microstate similar to D. In addition, several studies have shown changes in the temporal dynamics of microstates in patients with psychopathological conditions including hallucinatory experiences. Kindler et al. (2011) directly assessed experience with vs. without auditory hallucinations in frequently hallucinating patients. They observed a shortening of microstate D during hallucinatory experiences. Further, a meta-analysis on resting state microstate dynamics in patients with schizophrenia compared to healthy controls showed that microstate C contribution and duration were increased in patients, while microstate D contribution and duration were reduced (Rieger et al., 2016). These findings were replicated by da Cruz et al. (2020). Common to these microstate findings is an increase in the temporal parameters of microstate C and a decrease in those of microstate D. Thus, these two microstates are promising candidates to reflect processes associated with perceptual reality monitoring of an experience. Note that in this work, we use the term "contribution" while it has also been called "coverage" (c.f. Michel & Koenig, 2018).

Furthermore, potential neural correlates of perceptual reality monitoring, being theoretically derived by meta-cognition research, have been suggested to be in anterior regions of the medial prefrontal cortex (Dijkstra et al., 2022). The anterior region of the medial prefrontal cortex was again reported to be involved in the reality

monitoring of memory (Simons et al., 2017). Additionally, the potential role of the prefrontal cortex in perceptual reality monitoring is supported by neurophysiological similarities between altered states like dreams and hallucinations. Both phenomena are accompanied by reduced connectivity of prefrontal brain areas (Waters et al., 2016, 2021). Additionally, during lucid dreaming compared to non-lucid dreaming, increased activity and functional connectivity of areas including the prefrontal cortex were observed (Baird et al., 2019). Interestingly, inverse solutions of resting state EEG microstates estimated the medial prefrontal cortex as a source being active, especially in C and D (Custo et al., 2017). Thus, EEG microstates are a useful tool to investigate neural correlates of perceptual reality monitoring and to clarify the potential role of the prefrontal cortex.

1.1 | Investigating EEG microstates associated with reality monitoring in immersive virtual reality

Most of the presented studies were conducted in spontaneously occurring states, such as sleep or psychosis, which cannot be controlled well in an experimental setting. Further, some studies compared physiologically different states such as sleep onset vs. wakefulness, or disease vs. healthy control, which makes it difficult to separate the effects of experience from the effects of vigilance or psychopathology. Moreover, none of the reported microstate studies directly investigated the contrast between altered and unaltered monitoring of reality experience. Thus, we propose to systematically induce naturalistic changes in the experience of reality during normal wakefulness by using highly immersive virtual reality technology. Immersive VR provides a global experience in an ecologically valid scenario, and, at the same time, it allows for precise manipulation of the content of sensory input; especially for creating content, which is usually not possible in the physical world. Furthermore, it allows for a VR illusion, which leads to the feeling of being located in the virtual environment and that virtual events are actually happening (Slater, 2009); as well as to the willingness to suspend disbelief in the virtual character of the environment (de Gelder et al., 2018). This in turn leads to natural and realistic behaviour in VR (Slater, 2009, 2018). With this approach, it is possible to induce a global change in the experience of reality during the same vigilance state in the same healthy participant, and simultaneously record changes in EEG microstates. In short, this approach allows for the assessment of perceptual reality monitoring processes in real-time and specifically at the feeling-level, i.e., the experience of reality.

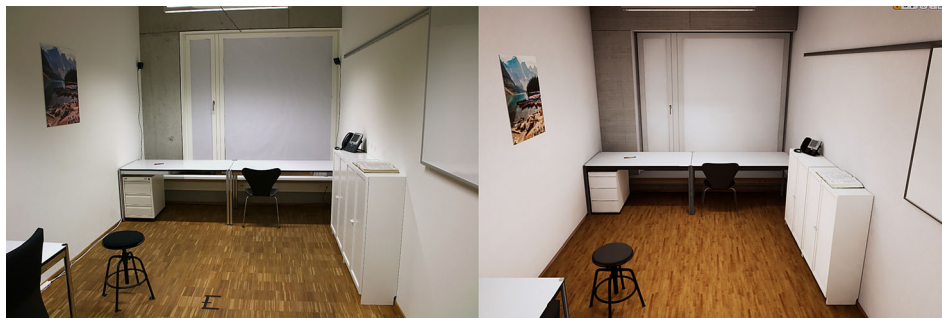


FIGURE 1 Real office room (left) vs. exact virtual copy (right). Figure reprinted from Denzer et al. (2022) under the CC BY 4.0 license.

By combining mobile EEG and immersive virtual reality, we tested a healthy and awake population in two conditions: a state of induced altered experience of reality and a state of normal experience of reality.

Experience of reality is influenced by bizarre elements, such as during lucid dreams, where the presence of bizarre elements can elicit bizarre experiences, which in turn reduces the experience of reality, which can trigger the awareness of the experience being a dream (Gott et al., 2021). Therefore, we used dream bizarreness as a model for naturally occurring alteration in reality. To induce changes in the experience of reality, we manipulated the presence of dream-like bizarre elements (cf. Figure 2) in a highly naturalistic virtual copy of the actual experimental room (cf. Figure 1, based on the principles of substitutional reality, cf. Simeone et al., 2015), and reported behavioural outcomes of this approach in previous work (Denzer et al., 2022). We demonstrated that, during wakefulness, the spontaneous presentation of bizarre elements elicited higher values of reported experienced bizarreness, and bizarreness was negatively correlated with reported experience of reality. Presenting bizarre elements, however, did not change the high level of spatial presence ratings, i.e., the feeling of actually being located in the environment, which is an indicator of how real the environment itself is perceived. Further, in the bizarre condition, ratings for experienced reality were reduced but still high compared to the realistic control condition without bizarre elements. This indicates that the bizarre condition induced a state of altered reality monitoring such that, despite bizarre content in a realistic environment, the experience was rated as more realistic than expected for processing during normal wakefulness.

In the present work, we analysed microstates in the EEG data, which were recorded while participants explored the two virtual environment conditions in the study by Denzer et al. (2022). The analysis of EEG microstates in an eyes-open, task-active and mobile setup other than the eyes-closed resting state has been validated before using different cognitive tasks (Milz et al., 2016; Seitzman et al., 2017; Zanesco et al., 2021) and in a mobile helicopter setup (Deolindo et al., 2021). Furthermore, the

feasibility of combining mobile EEG and immersive VR has been demonstrated before (cf. Banaei et al., 2017; El Basbasse et al., 2023; Klug & Gramann, 2021; Stolz et al., 2019). To our knowledge, this is the first study to analyse EEG microstates during a mobile, dynamic and ecologically valid immersive virtual environment.

In sum, to investigate neural correlates of perceptual reality monitoring, we assessed EEG microstates during induced changes in the experience of reality in a healthy and awake population within a mobile naturalistic VR scenario. We expected that differences in the experience of reality induced by the BizarreVR paradigm (reported in Denzer et al., 2022) would be accompanied by differences in EEG microstate dynamics. More specifically, based on the reliability of EEG microstates across studies and their validity in eyes-open, task-active conditions, we expected the microstate topographies to be highly correlated with those reported in previous literature. Moreover, given the consistency of findings across studies investigating EEG microstates in conditions with altered reality monitoring, such as dreaming or psychosis, and the theoretically proposed neural correlates of perceptual reality monitoring, we hypothesized that the temporal characteristics of microstates resembling classes C and D would differ between the realistic and the bizarre condition.

2 | MATERIALS AND METHODS

2.1 | Participants

Of the 47 participants enrolled into the study, 39 participants (29 female; mean age of 23.45 years; SD = 4.62 years; age range 19–39 years; one left-handed) were eligible for analysis (two dropouts, which did not take part in the second of two sessions, and six exclusions due to technical problems during the experiment). This sample satisfied a beforehand sample size estimation with an assumed medium effect size, significance level of .05 and power of 0.85, which revealed 38 participants. Participants were students at the University of Bern or external students. They were native speakers of German,

had normal or corrected to normal vision and had a regular sleep rhythm to exclude the influence of sleepiness on experience. Exclusion criteria were nausea in VR (FMS > 11; Fast Motion Sickness Scale; Keshavarz & Hecht, 2011), implanted medical devices including hearing aids, hearing problems, severe tinnitus, history of neurological or psychiatric disorders, current intake of psychoactive substances or cardiovascular agents and an EEG-incompatible hairstyle. All participants gave their written informed consent prior to participation. As compensation for participation, undergraduate psychology students received course credit. This study was conducted in accordance with the ethical principles as stated in the Declaration of Helsinki and was approved by the Ethics Committee of the University of Bern (approval no. 2019-07-00003).

2.2 | BizarreVR setup and stimuli

In the following section, we summarize the combined VR and EEG setup and the implementation of the bizarre elements (details are described in Denzer et al., 2022). The virtual environment was built using Unreal Engine 4, version 4.21 (UE4, Epic Games, 2018). Virtual scenes were presented using the HTC Vive Eye Pro head-mounted display (HMD) with a display resolution of 1440×1600 pixels per eye in combination with the HTC Vive Wireless Adapter. Four HTC Vive SteamVR Base Stations 2.0, fixed at the four corners of the room, enabled full room-scale tracking to walk naturally across the real office room and thus across the exactly aligned virtual office room. 3D content was built using Maya 2018 (Autodesk Inc., 2018), and Blender, version 2.79b (Blender Foundation, 2017), or assets from the UE4 Epic Store.

Although the VR system was wireless, the EEG system was wired. Since the presence of the EEG cable while navigating in VR could have influenced the experience in VR, participants wore a hiking backpack containing the EEG amplifiers and battery pack to allow a maximum of free-range movements despite the required glass fibre wires of the EEG system. Moreover, a slide rail mounted on the ceiling of the room (Appendix A.1) served as guidance to keep the cable away from the participant, the VR equipment and the EEG backpack at any time.

The BizarreVR paradigm included two conditions RealisticVR and BizarreVR, which took place in the virtual office environment, an exact virtual copy of our experimental room including all objects (see Figure 1). The only difference between conditions was that six objects were transformed into dream-like bizarre elements in the BizarreVR condition. Between conditions, participants could sit and rest in a virtual resting environment, which was a

plain world containing only a simple floor and a black stool. Prior to the experiment, participants were trained for the task in a virtual training environment, which was a plain world containing only a simple floor, three white walls (two opposite walls aligned with the two longer walls of the real room), a black stool and two geometric figures as example objects on top of rectangular pedestals. A white beam was painted on the floor.

Six bizarre elements related to the place and objects of the virtual office room were manipulated based on a common definition of dream bizarreness (Williams et al., 1992). Bizarre transformations of the objects were designed within the three levels 'discontinuity', 'incongruency' and 'vagueness' of the stated dream bizarreness definition. The target objects and places were selected based on 1470 dream reports, from which the most frequent office-related objects or places were extracted (for details, see Denzer et al., 2022). Three examples of bizarre transformations are depicted in Figure 2. Bizarre transformations were implicitly self-elicited upon approach (< 1.5 m) and fixation of the object. The transformation started with a delay of 1 s and took 2 s to complete. Every transformation remained active until the end of the condition such that at the end, all six transformations were visible. The 3D representation of all bizarre elements is provided in Appendix A.2.

2.3 | Procedure

The experiment consisted of two sessions: the screening and the experimental session. The screening took place approx. one week before the experiment, with a mean delay of 6.77 days ($SD = 3.71$). The screening lasted approx. 50 min and included a check for eligibility and information regarding the study. After consent to the study was given, participants performed a short VR training. The VR training included a test for VR sickness, training for natural movement within the test environment and training for the experimental task. Finally, to control for individual differences between participants, they rated their tendency towards hallucinatory experiences on a desktop screen ('Launay-Slade Hallucination Scale', LSHS-R; Lincoln et al., 2009). For all participants, the experimental session started at 9 am and lasted approx. 3.5 h including all preparation and follow-up procedures. Participants were told to refrain from caffeine and nicotine one hour before the experiment and to get a sufficient and regular amount of sleep the night before. For the combined VR and EEG setup, participants were first prepared with a 64-channel EEG cap and the EEG backpack before putting on the HMD (Appendix A.3). Both the fit of the HMD and backpack were adjusted to be functional and

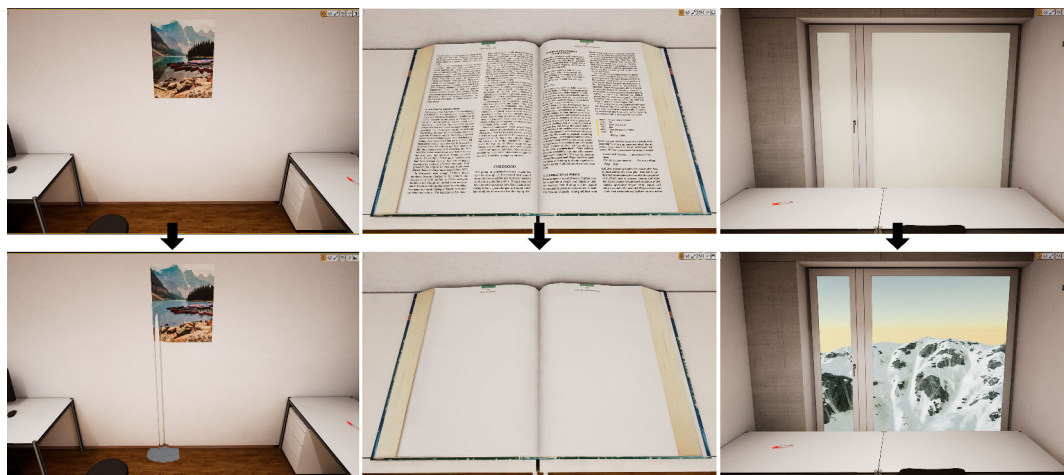


FIGURE 2 Dream-like bizarre elements. 3D objects in the RealisticVR condition (top). Transformed objects containing bizarre elements in the BizarreVR condition (bottom). Picture, (bottom left): water starts draining out of the depicted lake onto the floor. Book (bottom middle): text disappears. Window (bottom right): white cover disappears; appearance of a panoramic view from above on mountain peaks indicates shift of room location. All bizarre objects transformed upon approach and fixation. Figure adapted from Denzer et al. (2022) under the CC BY 4.0 license.

comfortable. Simultaneous to preparation, participants received written instructions about the subsequent task, which were confirmed orally to ensure that the participant understood the task. Until the start of the experimental task, participants remained naïve to the fact that the virtual environment was a copy of the real environment.

The experimental procedure consisted of two blocks representing the two conditions, RealisticVR and BizarreVR, with a counterbalanced order of conditions (cf. Appendix A.4). Before the start of each block, participants were guided to the same starting point in the real room. They were reminded of the instructions, which were to explore the subsequent virtual environment carefully, to look at all the objects and parts of the room and to remember them for questions at the end (pseudo-task). Additionally, they were told to move close to all visible objects, to avoid fast (head) movements and to explore thoroughly as long as they wanted. Finally, they were instructed to finish their exploration by sitting on the black virtual stool (which corresponded to a real stool) after being sure of having seen and approached all visible objects. After the instruction, participants started exploration immediately after the virtual office room appeared on the HMD. Throughout the VR task, the experimenter stopped any interaction with the participant, avoided physical contact and remained quiet to prevent a disruption of the participants' immersion and presence in VR.

After the VR task, participants were asked to rate their subjective experience during both conditions on a desktop screen. We asked for ratings regarding the experience of reality (Reality Judgement Questionnaire, Baños et al., 2000), experience of bizarreness (adapted version of

Subjective Experiences Rating Scale; Kahan & LaBerge, 2011) and spatial presence as a measure of VR illusion (subscales 'Self Location' and 'Suspension of Disbelief' from Spatial Presence Questionnaire; Vorderer et al., 2004) for each condition. Regarding the Reality Judgement Questionnaire, unfortunately, this scale's name is confusing, because it includes the term "judgement", although it actually asks for "experience" of reality, i.e. the more implicit level of reality monitoring. Details and results of all subjective experience ratings were previously reported by Denzer et al. (2022).

2.4 | EEG recording

EEG was recorded throughout the experiment using a 64-channel system with slim active electrodes (ActiCAP snap, Brain Products, Gilching, Germany). The electrodes were placed according to the extended 10–20 system and referenced against the electrode at position FCz. Active electrodes were best suited for our mobile EEG setup because they have a low centre of gravity and lower weight, both reducing motion artefacts. The signal was sampled at 250 Hz using two 32-channel A/D amplifiers (BrainAmp DC, Brain Products) and impedances were below 20 kΩ. Since participants were wearing an HMD on top of the EEG cap, we added small pieces of latex foam in the empty areas around the electrodes at locations where the HMD strip exerted pressure on the electrodes and moved the ground to another position. By doing so, we reduced the impact of the HMD on the EEG signal and increased the comfort of wearing the HMD.

2.5 | EEG preprocessing

EEG data pre-processing was performed using MATLAB R2018b (Mathworks Inc. Natick, MA, USA), EEGLAB version 2019 (Delorme & Makeig, 2004) and BrainVision Analyzer 2.2 (Brain Products). To construct an independent component analysis (ICA)-based spatial artefact filter, the EEG of each participant was first filtered using a 2–100 Hz band pass and a 50 Hz notch filter. In addition, a 90 Hz notch filter was applied to remove the potential impact of the VR frame rate. Severe channel or pressure artefacts were manually marked. Data were cleaned from eye and movement artefacts via ICA using the AMICA algorithm (version 1.5.1, Palmer et al., 2011). We ran the AMICA with one model and a maximum of 2000 iterations per participant. Next, for each obtained independent component, we computed a dipole model using the DIPFIT plugin (version 3.3) and the probability of being an artefact vs. a brain source using the ICLabel plugin for EEGLAB (version 1.2.5, Pion-Tonachini et al., 2019). The most probable brain components were selected based on two criteria (relative residual variance of the dipole model $rv < .250$ and ICLabel probability for brain $p_{brain} > .375$). The remaining components were further reduced based on the activity power spectrum (low at higher frequencies and high at approx. 1–10 Hz) and the calculated dipole position (located within the brain). On average, 18.05 IC components related to brain activity were retained per participant. We filtered the raw data of each participant using an individual spatial filter based on the remaining components.

2.6 | Microstate analysis

Microstate analysis was performed using the Microstates plugin for EEGLAB (version 1.2, Thomas Koenig, available at <http://www.thomaskoenig.ch>) following the standard procedure. For each participant and condition, the spontaneous EEG during the VR exploration task was selected, marked artefacts were removed and artefact-free epochs were concatenated. Data were re-referenced to the average reference and filtered between 2–20 Hz. For each participant and condition, the electric potential field topographies at the peaks of the Global Field Power (GFP) of the normalized EEG data were clustered using the Atomize and Agglomerate Hierarchical Clustering (AAHC) algorithm (for a comparison of algorithms see von Wegner et al., 2018). The polarity of the topographies was ignored. Since we based our hypotheses on the four canonical microstates and used mobile EEG, introducing slightly more complexity to the recorded data, we chose a four-cluster solution, i.e., four microstates. This allows

a comparison with and replication of the previous microstate literature while reducing complexity. Within each condition, the mean across participants' individual cluster topographies was calculated. Next, the grand mean of cluster topographies of the two conditions was calculated, which served as the microstate template for both conditions. The grand mean microstates were sorted manually according to the common microstate topographies reported in the literature. Finally, the sorted grand mean microstates were fitted back to the original EEG data of the individual participants and the temporal parameters were calculated for each microstate. Potentially truncated microstates occurring at the borders of artefact-free epochs were excluded. Temporal parameters included occurrence (mean number of microstate occurrences per second), duration (mean duration of all microstate occurrences), contribution (percentage of time spent in a microstate) and meanGFP (average GFP of all time points assigned to a microstate).

2.7 | Statistical analysis

To analyse spatiotemporal differences in the obtained microstate classes between the two conditions, we conducted a within-subject ANOVA with the two within-subject factors Condition (BizarreVR vs. RealisticVR) and Microstate Class (class 1, class 2, class 3, class 4) for each of the four temporal characteristics. To test for further differences in the individual microstates, post-hoc paired t-tests were performed. Findings were reported with the Benjamini-Hochberg ('false discovery rate') correction for multiple testing (Benjamini & Hochberg, 1995). To check whether there was a confounding effect of our counterbalanced within-subject design, we added Start-Condition of each participant as a between-subjects factor. Effect sizes were reported as *partial* η^2 . To test for differences in the topographies between conditions, we performed a topographic analysis of variance (TANOVA). To determine how well our results correspond to the literature, we calculated the similarity of our topographies with other studies. Spatial similarity was calculated as spatial correlation using the Pearson correlation coefficient. Available topography templates from other studies were obtained from the Microstate Template Explorer (Koenig et al., 2024). In a post-hoc analysis to examine the relationship between subjective experience and the relevant significant microstate parameters, we performed a multiple regression by fitting a linear mixed model using the lme4 package for R (Bates et al., 2015), predicting the significant *microstate class parameter* with *Reality Judgement*, *Experienced Bizarreness*, the *LSHS* score, *Self Location*, *Suspension of Disbelief* and *Condition* as fixed

effects. The model included *Participants* as random effect. The significance level was set at $\alpha = 0.05$. All statistical analyses were performed using RStudio version 1.2.5033 (RStudio, Inc., 2019) with R version 3.6.2 (R Core Team, 2019) except for the TANOVA, for which the RAGU plugin (Habermann et al., 2018) for MATLAB was used.

3 | RESULTS

The resulting four microstate class topographies (grand mean over two conditions, Figure 3, top), as identified by the cluster analysis, explained 80.97% of the variance in the EEG at GFP peaks of all participants (RealisticVR = 80.95%, BizarreVR = 80.99%). Topographies were highly similar between conditions ($r = .898$, Figure 3, middle & bottom). Moreover, microstate topographies did not significantly differ between conditions (all $p > .440$), and none of the obtained microstate topographies resembled a typical ICA-extracted EOG topography (maximal shared variance 32%). We compared the similarity of our microstate topographies with those reported in a large normative study (Custo et al., 2017). Our microstate class 3 topography was most similar to the microstate F topography ($r = .954$) in Custo et al. (2017). The authors described microstate F as C' due to its high similarity with microstate C. The topographies of our other three microstates showed as well high similarity with the respective microstates reported by Custo et al. (2017), such that microstate class 1 was similar to A ($r = .870$), microstate class 2 similar to B ($r = .856$) and microstate class 4 similar to D ($r = .909$).

Furthermore, we observed differences between conditions in the temporal dynamics of the four microstates (see Table 1). For contribution, there was a significant interaction effect of *Condition* \times *Microstate Class* ($F[3,114] = 3.114$, $p = .029$, $\eta_p^2 = .076$). A main-effect of *Condition* cannot be expected because values for contribution always add up to 100% across microstate classes. Post-hoc analysis revealed a difference in the contribution of microstate C' between conditions ($F[1,38] = 9.53$, $p_{adj} = .016$, $\eta_p^2 = .201$), such that the contribution of microstate C' was higher in BizarreVR than in RealisticVR. Thus, in BizarreVR, the mean percentage of time covered by microstate C' increased. For microstate A, there was only a trend for differences between conditions ($F[1,38] = 4.74$, $p_{adj} = .072$, $\eta_p^2 = .111$), with higher contribution in RealisticVR than in BizarreVR. No difference was observed between conditions for the other two microstates ($p_{adj} > .100$). Figure 4 shows the mean difference in contribution for the BizarreVR minus RealisticVR condition.

For meanGFP, we found no main effect of *Condition* ($F[1,38] = 2.267$, $p > .100$), but a significant interaction effect of *Condition* \times *Microstate Class* ($F[2.13,80.94] = 3.291$, $p = .039$, $\eta_p^2 = .080$). Post-hoc analysis revealed only a trend for a difference between conditions in meanGFP for microstate C' ($F[1,38] = 6.28$, $p_{adj} = .068$, $\eta_p^2 = .142$) and microstate D ($F[1,38] = 4.76$, $p_{adj} = .070$, $\eta_p^2 = .111$). Regarding duration and occurrence, we did not find a significant effect of *Condition* nor an interaction effect of *Condition* \times *Microstate Class*.

Adding *StartCondition* as a between-subjects factor to the analysis did not alter the significance of the results.

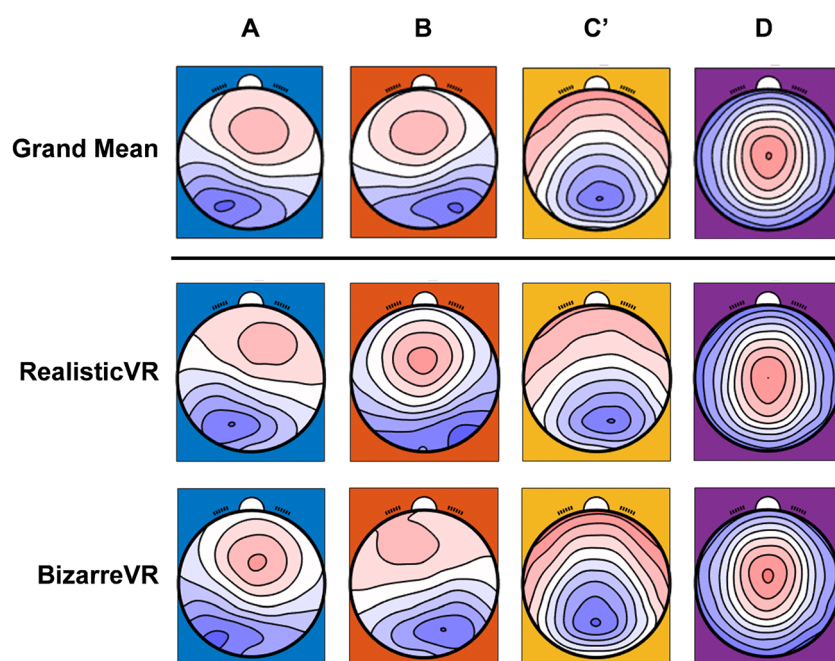
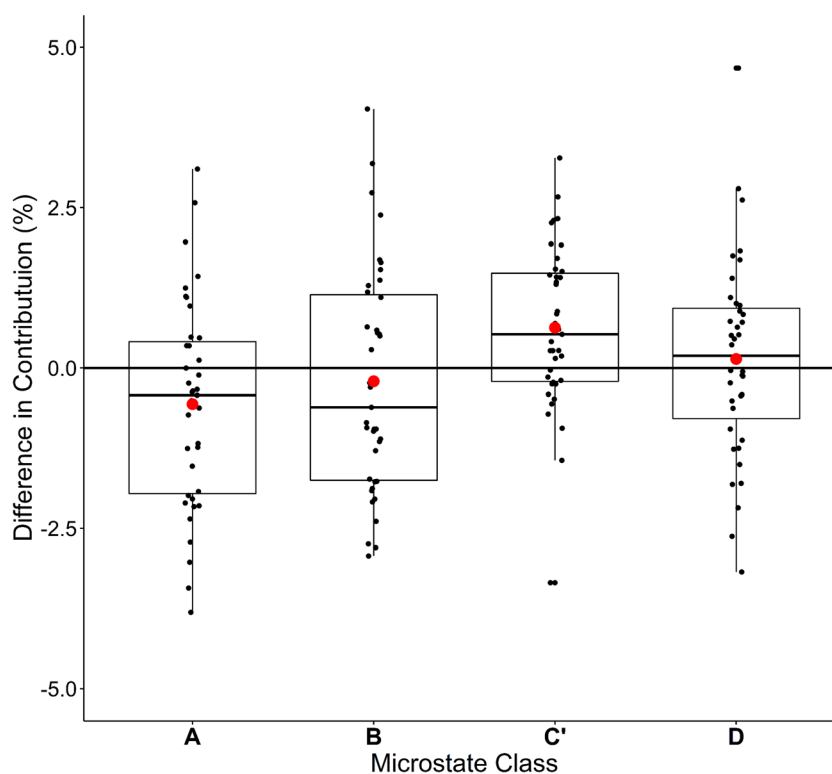


FIGURE 3 Microstate class topographies. Topographies for each condition (middle, bottom) and the grand mean over conditions (top). Individual topographies are shown in appendix A.5.

TABLE 1 Mean values and standard deviation of the temporal parameters and mean global field power (meanGFP) in each condition and microstate (MS) class. Data to support these values is shown in Table S1.

MS class	Condition	Occurrence (Hz)		Duration (ms)		Contribution (%)		meanGFP (μ V)	
		M	SD	M	SD	M	SD	M	SD
A	BizarreVR	3.66	0.79	63.07	5.92	23.28	6.30	3.21	0.63
	RealisticVR	3.70	0.78	63.78	6.24	23.84	6.29	3.20	0.65
B	BizarreVR	3.85	0.72	63.00	5.52	24.37	5.32	3.31	0.65
	RealisticVR	3.86	0.70	63.38	5.35	24.58	5.50	3.29	0.69
C'	BizarreVR	4.26	0.50	63.82	7.62	27.23	5.00	3.34	0.61
	RealisticVR	4.18	0.51	63.22	7.19	26.60	5.32	3.29	0.64
D	BizarreVR	4.02	0.43	62.16	8.02	25.12	4.85	3.25	0.59
	RealisticVR	4.02	0.43	61.77	8.04	24.98	5.03	3.22	0.60

FIGURE 4 Mean difference in contribution between the conditions BizarreVR minus RealisticVR. Boxes represent the 25–75 percentile of the distribution; whiskers represent the non-outlier range. Horizontal bars within the boxes indicate median values; red dots indicate mean values; black dots represent individual values of participants.



Contribution: A significant interaction effect of *Condition* \times *Microstate Class* ($F[3,111] = 3.048$, $p = .032$, $\eta_p^2 = .076$). **MeanGFP:** No effect of *Condition*, but a significant interaction effect *Condition* \times *Microstate Class* ($F[2,14,79.10] = 3.164$, $p = .044$, $\eta_p^2 = .079$). Post-hoc analysis for each microstate class was not significant between conditions. **Duration and Occurrence:** No significant main effect of *Condition* nor interaction effect of *Condition* \times *Microstate Class*.

As microstate class C' contribution significantly differed between conditions, we investigated the functional relationship of microstate C' with subjective experience in an additional post-hoc analysis. We conducted a

multiple regression to predict the *contribution of microstate C'* with *Reality Judgement*, *Experienced Bizarreness*, *LSHS*, *Self Location*, *Suspension of Disbelief* and *Condition* as fixed effects and *Participant* as random effect. The model's total explanatory power is substantial (conditional $R^2 = 0.98$). Within this model, the effect of *Reality Judgement* showed a trend for statistical significance, which was negative, with $\beta = -0.41$, 95% CI of $[-0.83, 0.01]$, and $t(37.57) = -1.86$, $p = .071$. This trend indicates that the contribution of microstate C' increased with lower ratings for experience of reality. Further, the effect of *Suspension of Disbelief* was statistically significant and positive with $\beta = 0.66$, 95% CI $[0.21, 1.11]$, t

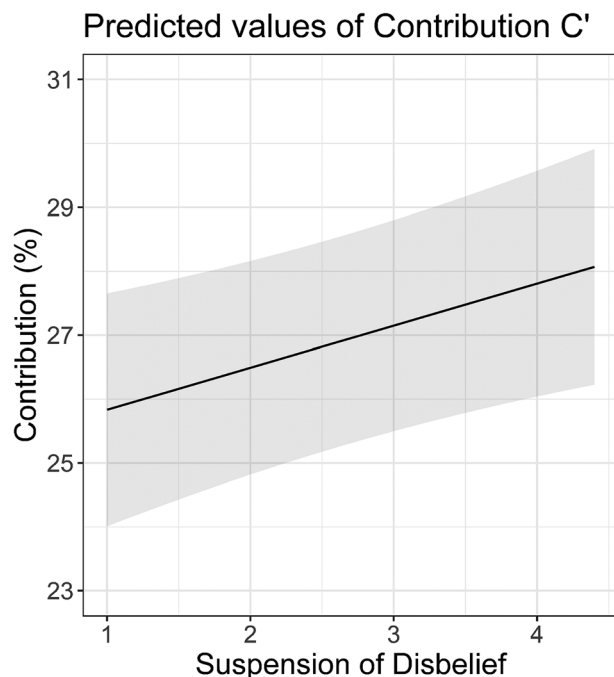


FIGURE 5 Predicted values of contribution of microstate C' by suspension of disbelief. The model to predict contribution of C' included reality judgement, experienced bizarreness, LSHS, self-location, suspension of disbelief and condition as fixed effects and participant as random effect.

(37.59) = 2.75, $p = .009$. This indicates that the contribution of microstate C' significantly increased with higher ratings of Suspension of Disbelief (cf. Figure 5), i.e., the intention to belief in the virtual reality by the suppression of bizarre mismatches. All other effects, including condition, were not significant ($p > .475$).

4 | DISCUSSION

Based on a mobile EEG-VR setup, we investigated brain network dynamics by means of EEG microstates underlying the induced changes in the experience of reality during normal wakefulness. As a proof of concept for our combined mobile EEG and immersive VR setup, we found four microstates that resembled the common microstates reported in the existing resting state literature. With induced alteration in experience of reality, we observed an increase in microstate C' contribution. This partially confirms our hypothesis that changes in the experience of reality would be accompanied by changes in the temporal dynamics of microstate C since the topographies of microstates C' and C were shown to have a high spatial correlation (Custo et al., 2017). However, they differed regarding the associated network (Custo et al., 2017). When performing a multiple regression, the

contribution of C' was associated with suspension of disbelief and as a trend with experience of reality. We did not find changes in the temporal parameters of microstate D, indicating that immersion into BizarreVR did not elicit the full spectrum of brain states associated with psychosis or dreaming. In the following sections, we discuss the functional role of microstate C' based on previous literature. Furthermore, we put our findings in the context of perceptual reality monitoring.

4.1 | Functional role of microstate C'

We found that a high value of contribution of microstate C' is associated with a state in which suspension of disbelief is high, i.e. the intention to disregard mismatches between the current sensory experience in the virtual reality and prior expectations, and thus the suppression of bizarre mismatches in the virtual environment. This special state of acceptance is different from presence in VR and can coexist with the knowledge that virtual bizarre events are not real (de Gelder et al., 2018). Furthermore, we found a trend for a negative relation between experience of reality and the contribution of microstate C'. This fits our previous finding that, in the BizarreVR condition with increased microstate C' contribution, values for experience of reality were indeed lower, but still high relative to the rating scale (cf. Denzer et al., 2022). Thus an increase in microstate C' contribution seems to reflect a state where bizarre breaks are disregarded more than usual and these breaks reduce the experience of reality, but less than usual.

Further evidence for the functional role of microstate C' is coming from recent studies. One study associated microstate C' with a dream-like experience during the transition to sleep. Diezig et al. (2022) found an increase in the duration, occurrence and contribution of a microstate similar to C', which was associated with less reflective awareness during sleep onset. Since reflective awareness includes processes like situational awareness and reality monitoring (Kahan & LaBerge, 2011; Revonsuo et al., 2009), this finding puts microstate C' into the context of reality monitoring. Another study reported findings regarding microstate C' in the broader context of situational awareness (Deolindo et al., 2021), as part of reflective awareness. In a complex emergency situation in a real flying helicopter requiring heightened situational awareness and reality monitoring, the contribution of C' was decreased. In this study, microstate C' was discussed to be associated with the control of stimulus-saliency. Further, the presence of microstate C' was reported to increase during moderate sedation in propofol-induced anaesthesia (duration, Artioni

et al., 2022; Lapointe et al., 2023; contribution, occurrence, Shi et al., 2020). Like sleep onset, the transition to anaesthetic sedation comes with the gradual loss of higher-order cognitive processes (MacDonald et al., 2015), which includes reality monitoring. In sum, these studies suggest that the presence of microstate C' is associated with a reduction of meta-conscious processes like reflective awareness and meta-cognitive control. Nonetheless, an effect of decreased presence of microstate C' has also been reported in other contexts such as somatic awareness (Tarailis et al., 2021) or mind wandering (Zanesco et al., 2021; cf. review by Tarailis et al., 2024).

The network of microstate F as reported by Custo et al. (2017) consisted of areas such as the dorsal anterior cingulate cortex (ACC), middle and superior frontal gyrus and insula, which are predominantly in the medial prefrontal cortex. Considering the high spatial similarity with our microstate C' ($r = .954$), areas in the medial prefrontal cortex are likely to be involved in our microstate C' as well. The medial prefrontal cortex as a source for microstate C'/F was also reported by Deolindo et al. (2021) and Br chet et al. (2019). Again, the spatial correlation between our microstate C' and the microstate F in Deolindo et al. (2021) was high ($r = .905$). A recent study involving patients with lesions in the medial prefrontal cortex also reported a link between microstate C' and the middle frontal gyrus (Zhao et al., 2023). Further, Diezig et al. (2022) found parts of the medial prefrontal cortex but additionally of the parietal cortex as a source for their microstate C', indicating a somewhat different network for sleep onset (spatial correlation $r = .790$). The dorsal ACC, middle and superior frontal gyrus and the insula are key areas of the cingulo-opercular control network (CON; Dosenbach et al., 2008) as well as the saliency network (SN; Seeley, 2019). The CON provides extended maintenance of task control (Christoff et al., 2016; Dosenbach et al., 2008) as well as the integration of error information (Cocchi et al., 2013). The saliency network integrates internal autonomic feedback with external environmental demands to evaluate the most relevant stimuli (Seeley, 2019). Thus, both networks are highly interrelated and provide plausible mechanisms for detecting bizarre elements, either in the form of an error or as a salient stimulus. Such a functional association of error monitoring and stimulus saliency with the microstate C' network further supports the assumption that microstate C' is involved with meta-conscious control processes such as reality monitoring.

Most of the presented studies report an inhibitory functional role of microstate C'. This implies a local inhibition instead of facilitation of the network associated with the microstate (cf. Milz et al., 2016, 2017; Zulliger

et al., 2022). However, based on the mere topography, an inhibitory or facilitating effect of a microstate cannot be concluded. Therefore, the presence of microstate C' in BizarreVR might reflect either an inhibition or a facilitation. An inhibitory effect would imply that increased contribution indicates a reduction of meta-conscious control in the face of a persisting mismatch between dream-like bizarreness and a strong VR illusion, by lowering the role of pre-existing expectations in the evaluation of the current experience. However, a facilitating effect is equally possible, in which increased contribution would indicate an active suppression of mismatching stimuli and enhanced meta-conscious control demand in the face of the discrepancy between expectations and experience. Future work is needed to investigate factors that determine whether the presence of a microstate has an inhibitory or facilitating effect.

4.2 | Implications for the two levels of reality monitoring

Considering our findings in the context of a neural correlate for monitoring the reality status of an experience, we showed that changes in the experience of reality are accompanied by a change in microstate C' contribution. In a review by Dijkstra et al. (2022), two levels for perceptual reality monitoring were proposed: a more implicit lower-order feeling of reality versus a more explicit higher-order judgement about the reality status, which might be mapped onto different parts of the prefrontal cortex. More specifically, the lower-order feeling has been suggested to be realised by activity in medial prefrontal areas like the pregenual ACC, whereas the higher-order judgement about reality has been thought to be related to the frontopolar cortex (Dijkstra et al., 2022). Given the reported sources underlying microstate C', it is thus reasonable that the findings of our study reflect perceptual reality monitoring on the feeling-level of an experience. One potential conclusion could be that activity in the anterior medial prefrontal cortex (as represented by microstate C') can predict whether perceptual reality monitoring on the feeling-level of an experience will be adequate or erroneous. However, future work is needed to clarify the relationship between microstate C' and the two levels of perceptual reality monitoring.

4.3 | Limitations and future experiments

Although we focused on inducing a global change in experience and excluded or controlled several confounding factors in our study design, there are still some

limitations. First, one potential limitation is that we investigated the experience of reality in virtual reality. Participants were, to a certain degree, aware of the virtual nature of the experience. However, in our previous evaluation of the paradigm, participants showed a high and comparable level of spatial presence, i.e. VR illusion, during both conditions (Denzer et al., 2022). This indicates that during the two conditions, they were under a sufficiently high illusion of realness, i.e. the feeling of being actually located in the environment, and were able to temporarily suspend their knowledge about the virtual origin. Therefore, experience in our study can be compared to natural experience, such as, for example, in a lucid dream. Furthermore, analysing EEG data in mobile and dynamic environments comes at the cost of artefacts, which might have affected our results. However, it has been shown that artefact removal using a combination of an AMICA decomposition and a high pass filter of 2 Hz was functional for mobile EEG recorded in immersive VR (Klug & Gramann, 2021). This combination was also proposed by Gorjan et al. (2022). Moreover, as a feasibility check for our data, the obtained microstate topographies showed a high spatial correlation with those in the literature. In sum, this speaks against a systematic effect of remaining movement artefacts in the data.

Furthermore, there might be other explanations for the differences between conditions. For example, the transformation animation of the 3D objects was present only in the bizarre condition, which might have resulted in an increase in attention or vigilance in the bizarre condition. However, previous work associated attentional processes with microstate D (Michel & Koenig, 2018), for which we did not observe an effect in the present data. Differences in vigilance can be excluded due to a control variable asking for sleepiness before each condition (Karolinska Sleepiness Scale, Kaida et al., 2006; scale range 1 to 10, with 5 = “neither alert nor sleepy”). The reported sleepiness was not significantly different between conditions ($p > .100$) with a mean value of $M = 5.36$ ($SD = 1.44$) in the BizarreVR condition and $M = 4.95$ ($SD = 1.60$) in the RealisticVR condition. Further, we used a counterbalanced study design and included “starting condition” as a covariate in our analysis to exclude the effect of sequence. Finally, in a post-hoc analysis, we found a relationship between microstate C' and subjective experience ratings for suspension of disbelief and experience of reality, which supports our interpretation. In addition, potential differences in movement might play a role in the observed difference between conditions. However, such motor-related activity would present with a different topography (cf. Borràs et al., 2022), which speaks against the effect of movement. Taken together, the observed difference in

microstate C' contribution between conditions most likely reflects processes related to the bizarreness-induced changes in the experience of reality as one level of perceptual reality monitoring.

Within our BizarreVR setup, a future study could investigate other populations, such as patients with schizophrenia, participants with increased sleep pressure, or participants under the influence of psychoactive substances known to induce altered experiences. In these other populations, it would be interesting to see whether there are similar changes in microstate class C' and whether the observed effects are stronger or weaker. Such additional data will allow investigation of the interaction between different populations (psychotic vs. healthy wake) and bizarre experiences (bizarre elements present vs. absent), which would aid in finding a general mechanism underlying perceptual reality monitoring. Future studies should also clarify the role of microstate C' in perceptual reality monitoring by considering its two levels of feeling vs. judgement. A systematic approach could be to define states with alteration in either of the levels, resulting in four categories (feeling-1/ judgement-1; feeling-0/ judgement-1; etc.; with 1 = intact, 0 = erroneous). Lucid dreaming would be an example of erroneous feeling but intact judgement, while psychotic hallucinations would be an example of erroneous feeling and erroneous judgement. A systematic comparison of EEG microstates recorded during states within each category could help to disentangle the two levels of perceptual reality monitoring as well as the roles of microstates C' and C, as both have been reported during states with altered reality monitoring. Moreover, with some adaptations, our paradigm is suitable for investigating the processing of bizarre mismatches in a time-locked analysis. With approx. 30 bizarre vs. realistic elements, which are no longer presented in a free exploration task but in a standardized and randomized study design, an event-related microstate analysis could provide further information about the specific processing of bizarre stimuli and how this changes over trials. Finally, to further investigate the involvement of anterior medial prefrontal areas in the feeling-level of perceptual reality monitoring, a future study could use non-invasive brain stimulation techniques to experimentally inhibit these areas to determine whether the experience of reality changes, e.g. when seeing bizarre elements.

5 | CONCLUSION

This study is the first to systematically investigate EEG microstates associated with changes in the global experience of reality in a healthy wake state using immersive

VR. The contribution of microstate C' increased during a bizarre experience, which was similar to a lucid dream. A similar increase in microstate C' has been found in other states related to altered experience of reality, such as sleep onset or anaesthesia. The results support the interpretation of a functional relationship of microstate C' with the experience of reality and suspension of disbelief, i.e. the suppression of bizarre mismatches in the virtual environment. This puts the feeling-level of perceptual reality monitoring in the context of meta-conscious control. With that, our findings contribute to the understanding of a general mechanism underlying perceptual reality monitoring. Future studies should investigate the relationship between microstate C' and both levels of perceptual reality monitoring processes. Finally, this study adds evidence regarding the feasibility of microstate analysis in an eyes-open, non-resting state, using a mobile EEG and immersive VR setup.

AUTHOR CONTRIBUTIONS

Simone Denzer: Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing—original draft; writing-review and editing. **Sarah Diezig:** Conceptualization; writing—review and editing. **Peter Achermann:** Methodology; supervision; writing—review and editing. **Fred W. Mast:** Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing—review and editing. **Thomas Koenig:** Conceptualization; formal analysis; funding acquisition; methodology; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ejn.16530>.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made available under a formal data sharing agreement requiring that data will be shared with scientific researchers who intend to use them for scientific research only.

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