Resting-state networks of believers and non-believers: An EEG microstate study

Kyle Nash*, Tobias Kleinert, Josh Leota, Andy Scott, Jeff Schimel

Department of Psychology, University of Alberta, Edmonton AB T6G 2R3, Canada

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A B S T R A C T

Atheism and agnosticism are becoming increasingly popular, yet the neural processes underpinning individual differences in religious belief and non-belief remain poorly understood. In the current study, we examined differences between Believers and Non-Believers with regard to fundamental neural resting networks using EEG microstate analysis. Results demonstrated that Non-Believers show increased contribution from a resting-state network associated with deliberative or analytic processing (Microstate D), and Believers show increased contribution from a network associated with intuitive or automatic processing (Microstate C). Further, analysis of resting-state network communication suggested that Non-Believers may process visual information in a more deliberative or top-down manner, and Believers may process visual information in a more intuitive or bottom-up manner. These results support dual process explanations of individual differences in religious belief and add to the representation of non-belief as more than merely a lack of belief.

Non-belief in deities is on the rise in Western societies (Pew research center, 2019a, 2019b; Phillips, Curtice, Phillips & Perry, 2018). Psychologically, non-belief appears to be more than just an ‘absence’ of belief. Non-belief (at least partially) constitutes or involves a distinct ideology, with psychological costs and benefits comparable to religious belief (Galen, 2015; Galen & Kloet, 2011; Preston & Shin, 2017). However, the origin of and psychological processes underlying individual differences in non-belief remain unclear. Though prior research has primarily focused on characterizing individual differences in religious belief (Inzlicht, McGregor, Hirsh & Nash, 2009; Kay, Gaucher, McGregor & Nash, 2010), the limited research on non-belief has been interpreted according to dual process models. Specifically, research suggests that non-belief is associated with more deliberative or analytic reasoning, whereas religious belief is associated with more intuitive and heuristic reasoning (Gervais & Norenzayan, 2012; Pennycook, Cheyne, Seli, Kohler & Fugelsang, 2012; Pennycook, Ross, Koehler & Fugelsang, 2016; Shenav et al., 2012). Here, we used a neural trait approach to examine if religious disbelief and belief are associated with distinct neural networks related to dual processes.

The neural trait approach involves indexing quantifiable, brain-based characteristics and examining whether these indices predict affective, cognitive, and behavioral processes (Leota, Kleinert, Tran & Nash, 2021; Nash et al., 2015; Nash & Knoch, 2016; Schiller, Gianotti, Nash & Knoch, 2014; Schiller, Gianotti, Baumgartner & Knoch, 2019; Schiller, Kleinert, Teige-Mocigemba, Klauser & Heinrichs, 2020). This approach is task-independent and adds a level of analysis that supplements and is informed by existing task-dependent analyses of neural and psychological processes (for further discussion on the benefits of task-independence, see Berking & Falk, 2013). Further, neural traits are objective—unalterated by personal biases and demand characteristics. In the current study, we measured resting-state activity with EEG to index dispositional differences in neural functioning. Resting-state EEG measures demonstrate strong test–retest reliability (Dünki et al., 2000; Napflin et al., 2007), heritability (De Geus, 2010; Smit, Stam, Posthuma, Boomsma & De Geus, 2008; van’t Ent, Van Soelen, Stam, De Geus & Boomsma, 2009; Zietsch, Hansen, Hansell, Gelfen, Martin & Wright, 2007), and distinctiveness (Napflin et al., 2007), supporting the view that these measures reflect a kind of ‘neural fingerprint’ (Gianotti, Nash, Baumgartner, Dahinden & Knoch, 2018).

We used resting-state microstates to index heterogeneity in neural network activation. Research on EEG microstates has proliferated in recent years, with investigations of clinically relevant microstate differences (e.g., da Cruz et al., 2020; de Bock, Mackintosh, Maier, Borgwardt, Riecher-Rossler & Andreou, 2020; Lehmann et al., 2005; Murphy et al., 2020; Murphy & Öngür, 2020), associations of microstates with social behavior or personality (Schiller et al., 2020; Schlegel, Lehmann, & Stober, 2014; Schiller, Gianotti, Baumgartner & Knoch, 2019; Schiller, Kleinert, Teige-Mocigemba, Klauser & Heinrichs, 2020).
Based on combined EEG and fMRI studies, it has been found that Microstate A is associated with brain activity in the temporal cortex and the left insula, indicating a role in phonological processing (Britz et al., 2010; Custo, Van De Ville, Wells, Tomescu, Brunet & Michel, 2017). Microstate B is associated with areas of the occipital cortex, indicating a role in visual processing (Britz et al., 2010; Custo et al., 2017). This view is supported by increased contribution of Microstate B in eyes-open EEG compared to eyes-closed EEG (Seitzman, Abell, Bartley, Erickson, Bolbecker & Hetrick, 2017). Though more difficult to characterize, Microstate C has been associated with default mode and task-negative networks as evidenced by brain activity in the anterior and posterior cingulate cortex, inferior frontal gyrus, insula, and precuneus (Britz et al., 2010; Custo et al., 2017). These results indicate that Microstate C is a task-negative network with a role in more intuitive or automatic (bottom-up) processing (Gronchi & Giovannelli, 2018; Jilka et al., 2014; Menon & Uddin, 2010; Vatansever et al., 2017). This view is supported by decreased activity of Microstate C during a serial subtraction task requiring top-down executive control (Seitzman et al., 2017), increased activity during initial bottom-up encoding of visual stimuli compared to later top-down retrieval (D’Croz-Baron, Bréchet, Baker & Karp, 2021), and decreased activity during fluid reasoning tasks involving spatial relationships and visualization (Zappasodi et al., 2019). Conversely, Microstate D is associated with brain activity in right-lateralized areas of the frontal and parietal cortex, namely the inferior parietal cortex, the right middle and superior frontal gyri, and the insula (Britz et al., 2010; Custo et al., 2017), indicating that Microstate D has a role in deliberative or analytic (top-down) processing (Damoiseaux et al., 2006; Mantini, Perrucci, Del Gratta, Romani & Corbetta, 2007). This view is supported by increased activity of Microstate D during a serial subtraction task requiring top-down executive control (Seitzman et al., 2017), increased activity during the preparation of a top-down directed decision process (D’Croz-Baron et al., 2021), and increased activity during a fluid reasoning task involving spatial relationships (Zappasodi et al., 2019).

Microstate analysis of resting EEG is thus ideally suited to examine differences between Believers and Non-Believers with regard to fundamental neural networks related to deliberative (Microstate D) and intuitive reasoning (Microstate C).

In the current research, we examined how Believers and Non-Believers differ with regard to neural network activation at rest. In particular, we expected that Non-Believers would be characterized by increased contribution of Microstate D to the resting-state EEG, indicating increased activation of a neural network associated with deliberative or controlled (top-down) processing. Conversely, we expected that Believers would be characterized by increased contribution of Microstate C to the resting-state EEG, indicating increased activation in a neural network associated with more intuitive or automatic (bottom-up) processing.
1.3. EEG Recording and Preprocessing

Continuous resting-state EEGs were recorded using a 64 Ag-AgCl channel ActiCHamp EEG system (Brain Products GmbH, Munich, Germany), positioned according to the 10/10 system and digitized at a sampling rate of 500 Hz (24 bit precision; bandwidth: 0.1–100 Hz). During the baseline recording, signals were referenced to TP9 electrode positioned over the left mastoid. All EEG data was preprocessed offline using Brain Vision Analyzer (Version 2.1.0.327; Brain Products GmbH, Munich). A notch filter (50 Hz) and a band-pass filter of 1.5–20 Hz were applied to the resting-state EEG data. Ocular artifacts were identified and removed using a semi-automatic independent component analysis for each participant. EEG channels that were defective or heavily affected by artifacts were interpolated using neighboring electrodes. Remaining artifacts were automatically identified (Min./max. threshold: −100 to +100 μV, maximum voltage step: 50 μV, lowest allowed voltage difference [maximum—minimum] in intervals of 100 ms: 0.5 μV) and removed from the signal. This automatic procedure was manually inspected and, if necessary, corrected, resulting in artifact-free EEG signals for microstate analysis. Then, the signal was re-referenced to an average (whole-head) reference. Finally, artifact-free epochs with durations of at least two seconds were exported for microstate analysis (also see Khanna et al., 2014; Koenig, Lehmann, Merlo, Kochi, Hell & Koukkou, 1999).

1.4. Resting-State Microstates

Resting-state microstate analyses were conducted using a software plugin for EEGLAB (Delorme & Makeig, 2004) by Koenig (Koenig, 2017; for procedures, see Lehmann et al., 1987; Strik & Lehmann, 1993). To obtain individual electric potential field maps of the scalp, artifact-free EEG data from all available channels were extracted for each participant at time points of maximum global field power (GGP; Koenig et al., 2002). Extracting data at GGP-peaks only instead of using data from the whole epoch ensures an optimal signal-to-noise ratio (Koenig et al., 2002). In each participant, microstate maps from all GGP-peaks in the EEG recording were then submitted to an atomize-agglomerate hierarchical cluster analysis (AAHC) to identify the four most prevalent microstate-maps (Michel, Koenig, Brandeis, Gianotti & Wackermann, 2009; Murray et al., 2008). Table 1

| Microstate | A | B | C | D |
|------------|---|---|---|---|
| Map        | ![Map A](image1) | ![Map B](image2) | ![Map C](image3) | ![Map D](image4) |

Table 1
Grand-mean microstates maps.

$N = 104$. Grand-mean maps of resting-state microstates A-D. Note that the maps closely resemble the canonical microstate types A, B, C and D known from the literature (Koenig et al., 2002).

In order to examine the links between Believers and Non-Believers in resting-state neural network functioning, we first calculated the contribution (% of the total resting-state) of microstates C and D during resting-state (eyes-closed) as the dependent variables. Contribution is based on the values of microstate duration (average length of each microstate in milliseconds) and occurrences (total number of instances with reference to previous findings on the functional significance of the four prototypical microstate types A, B, C and D. We included the full EEG sample in this step ($N = 104$) instead of including only Believers and Non-Believers ($N = 69$) in order to obtain more reliable grand-mean microstate maps for the back-fitting. Note that grand-means obtained from the whole sample and grand-means obtained from Believers and Non-Believers show no noticeable differences, and closely resemble the four canonical resting-state microstate types A, B, C and D known from the literature (see Table 1 and Table S1 in the supplementary material; for reviews, see Khanna, Pascual-Leone, Michel & Farzan, 2015; Michel & Koenig, 2018). Based on spatial correlations with the four grand-mean microstate maps obtained from our own data ($N = 104$), the four most prevalent microstate-maps of each individual participant were then assigned to the best-fitting grand-mean microstate type A, B, C or D. Next, individual potential field maps from GGP peaks were assigned to the best fitting of the four most prevalent microstate maps in each participant, resulting in a continuous temporal stream of microstates. Finally, we extracted average durations in milliseconds, average numbers of occurrences per second, and percentage contributions to the EEG signal (duration x occurrence) for each microstate type and each subject.

We also extracted transitions involving the microstates C and D (transitions from any other microstate type to these microstates and transitions from these microstates to any other microstate type). Transitions between microstates are calculated as the observed number of transitions relative to the expected number of transitions based on the occurrence of a network. For example, the transition from microstate B to D shows how much more often B switches to D per second (on average) than one would expect based on occurrences of microstate B. Thus, considering baseline occurrences of microstate B controls for the fact that switches from network B to any other network are more likely if B occurs very frequently (for details, see Lehmann et al., 2005). Note that transitions between microstate maps extracted from GGP-peaks (as was performed in our microstate analysis) might differ from transitions between microstate maps extracted from the whole EEG recording, as microstates between GGP-peaks are not considered (Michel & Koenig, 2018). This remains a matter of controversy in the current literature with further research needed (e.g., Koenig & Brandeis, 2016).

1.5. Statistical Analyses

In order to examine the links between Believers and Non-Believers in resting-state neural network functioning, we first calculated the contribution (% of the total resting-state) of microstates C and D during resting-state (eyes-closed) as the dependent variables. Contribution is based on the values of microstate duration (average length of each microstate in milliseconds) and occurrences (total number of instances with reference to previous findings on the functional significance of the four prototypical microstate types A, B, C and D. We included the full EEG sample in this step ($N = 104$) instead of including only Believers and Non-Believers ($N = 69$) in order to obtain more reliable grand-mean microstate maps for the back-fitting. Note that grand-means obtained from the whole sample and grand-means obtained from Believers and Non-Believers show no noticeable differences, and closely resemble the four canonical resting-state microstate types A, B, C and D known from the literature (see Table 1 and Table S1 in the supplementary material; for reviews, see Khanna, Pascual-Leone, Michel & Farzan, 2015; Michel & Koenig, 2018). Based on spatial correlations with the four grand-mean microstate maps obtained from our own data ($N = 104$), the four most prevalent microstate-maps of each individual participant were then assigned to the best-fitting grand-mean microstate type A, B, C or D. Next, individual potential field maps from GGP peaks were assigned to the best fitting of the four most prevalent microstate maps in each participant, resulting in a continuous temporal stream of microstates. Finally, we extracted average durations in milliseconds, average numbers of occurrences per second, and percentage contributions to the EEG signal (duration x occurrence) for each microstate type and each subject.

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of each microstate/sec) in the resting-state.

We conducted a one-way MANCOVA with belief group as the independent variable (Non-Believers vs Believers) and contribution of microstates C and D as the dependent variables, and the average microstate duration and occurrence across all four microstates entered as covariates to ensure that any differences between groups are associated with the specific microstate and not a general microstate stability. We then followed up with separate one-way ANCOVAs for each dependent variable, with the same covariates. To determine if duration or occurrences are driving any contribution differences between groups, we next conducted separate MANCOVAs with duration and occurrences of microstates C and D as the dependent variables. We then again followed up with separate one-way ANCOVAs for each dependent variable. Again, to control for a general microstate stability, we entered mean duration in the duration-specific analyses, and total occurrences in occurrence-specific analyses, as covariates. Finally, we used a MANOVA and follow-up t-tests to test for group differences between Believers and Non-Believers in microstate transitions involving the microstates C and D.

2. Results

2.1. Resting-State Microstates

On average, there were 106.34 s of artifact-free resting-state EEG data available for microstate analyses (SD = 7.33; range: 79.13–112.41). AAHC-analyses resulted in an average variance-translation of the EEG-signal of 74.89% (SD = 4.37; range: 59.53–84.43). This value is closely in line with previous research and demonstrates that four microstate clusters fit our EEG data well (see Table 1 for grand-mean microstate maps). On average, participants showed a contribution of microstate C of 27.26% (SD = 5.69; range: 12.09–37.92) and a contribution of microstate D of 25.00% (SD = 4.84; range: 11.34–35.32). These microstate characteristics as well as transitions involving microstates C and D were normally distributed (all KS-tests p > .844). For descriptive statistics of demographic data and microstate characteristics for the whole sample used in the study (N = 69), Believers (n = 43), Non-Believers (n = 26) and Non-Responders (N = 35) see Table S2 in the supplementary material.

2.2. Resting-State Microstates in Believers and Non-Believers

In our initial MANOVA test, there was a statistically significant difference in microstate contribution to resting-state activation based on religious belief, F(2, 64) = 3.85, p = .026; Wilk’s Λ = 0.893, partial η² = 0.107 (for details on all main analyses of the study, see Table S3 in the supplementary material). Controlling for age, gender, self-reported Math Ability, Openness to Experience, social status, Neuroticism and trait anxietyness (Behavioral Inhibition) as separate or joint covariates resulted in highly comparable results (group remained significant as a predictor in all of these analyses (p = .021 to.028), and with similar effect-sizes (partial η² = 0.107 to 0.116; see Table S4 in the supplementary material for these analyses as well as all subsequent analyses including these covariates, all reported effects of this study remained stable in these analyses).

In our follow-up analyses, a one-way ANCOVA revealed that Non-Believers demonstrated reduced contribution of Microstate C to the resting-state (M = 25.52, SD = 6.36), compared to Believers (M = 28.31, SD = 4.81), F(1, 65) = 4.15, p = .046, partial η² = 0.060. A second one-way ANCOVA revealed that Non-Believers demonstrated increased contribution of Microstate D to the resting-state (M = 26.60, SD = 5.49), compared to Believers (M = 24.63, SD = 4.18), F(1, 65) = 5.16, p = .026, partial η² = 0.074. (Fig. 1).

Next, we examined if the contribution effects are due to either duration or occurrences differences, or both. In the MANOVA test examining duration, there was a no significant difference in microstate duration based on religious belief, F(2, 66) = 1.49, p = .232; Wilk’s Λ = 0.956, partial η² = 0.044, and no significant differences in follow-up ANCOVA analyses (both p's >.017; partial η² < 0.044). However, In the MANOVA test examining occurrences, there was a significant difference in microstate occurrences based on religious belief, F(2, 66) = 4.57, p = .014; Wilk’s Λ = 0.878, partial η² = 0.123. Follow-up ANCOVA analyses revealed that Non-Believers demonstrated reduced occurrences of Microstate C (M = 5.69, SD = 1.42), compared to Believers (M = 5.97, SD = 1.70), F(1, 67) = 5.40, p = .032, partial η² = 0.076. Non-Believers also demonstrated increased occurrences of Microstate D (M = 6.06, SD = 2.33), compared to Believers (M = 5.47, SD = 1.49), F(1, 67) = 6.99, p = .010, partial η² = 0.096. Thus, contribution effects were primarily driven by differences in microstate occurrences.

Finally, we explored individual differences in transitions between networks in the resting-state, focusing on transitions involving Microstates C and D (i.e., ten separate transition variables). Results showed that, in a one way MANOVA test, there was again a statistically significant difference in transitions to and from Microstate C and D based on religious belief, F(10, 58) = 2.07, p = .042; Wilk’s Λ = 0.737, partial η² = 0.263. This multivariate effect appeared to be entirely driven by two variables. Non-Believers demonstrated fewer transitions from Microstate B to Microstate C (M = −0.001, SD = 0.006) than Believers (M = 0.002, SD = 0.006), t(67) = 2.05, p = .044. Additionally, Non-Believers demonstrated more transitions from Microstate B to Microstate D (M = −0.003, SD = 0.007) than Believers (M = −0.002, SD = 0.005), t(67) = 2.09, p = .004. There were no other significant differences between groups on microstate transitions.

3. Discussion

Initial research suggests that religious non-belief may reflect a different kind of belief system, rather than a lack of one (Farias, Newheiser, Kahane & de Toledo, 2013). However, little research has directly examined Non-Believers. Here, we applied a neural trait approach to better understand the neural origins of individual differences in religious belief. Neural traits are objective, stable, brain-based measures capable of revealing sources of heterogeneity in affective, cognitive, and behavioral processes (Leota et al., 2021; Nash et al., 2015; Nash & Knoch, 2016; Schiller et al., 2014, 2020; Schiller, Gianotti, et al., 2019). Broadly, our results support dual process explanations of individual differences in religious belief. Research has shown that religious belief is related to more intuitive and heuristic reasoning and non-belief is related to more deliberative and analytic reasoning (Gervais & Normazyan, 2012; Pennycook et al., 2012, 2016; Shenav et al., 2012). Consistent with this, we demonstrate that Non-Believers are
characterized by neural resting networks associated with deliberative reasoning, whereas Believers are characterized by neural resting networks associated with intuitive reasoning.

Specifically, microstate analyses revealed that Non-Believers demonstrated increased contribution from Microstate D and decreased contribution from Microstate C to the resting-state EEG compared to Believers. Further, these microstate contribution effects were primarily driven by the number of occurrences of the respective microstate. Because Microstate D is associated with deliberative or analytic (top-down) processing, and Microstate C is associated with more intuitive or automatic (bottom-up) processing (Britz et al., 2010; Custo et al., 2017; Seitzman et al., 2017), these findings support dual process models of religious belief, which suggest that Non-Believers are characterized by increased deliberative and analytic reasoning, whereas Believers are characterized by increased intuitive or automatic reasoning (Gervais & Norenzayan, 2012; Pennycook et al., 2012, 2016; Shenhav et al., 2012).

Analysis of microstate transitions suggests that the contribution findings may be related to individual differences in resting-state network communication. Non-Believers showed more transitions from Microstate B to Microstate D, whereas Believers showed more transitions from Microstate B to Microstate C. Given that Microstate B is associated with visuo-spatial processing (Britz et al., 2010; Custo et al., 2017; Koenig et al., 2002; Seitzman et al., 2017), these results suggest that Non-Believers may process visual information in a more deliberative, top-down manner, and Believers may process visual information in a more intuitive, bottom-up manner.

Several previous microstate studies investigated bottom-up and top-down processing at rest. For example, it was found that believers in paranormal activity showed increased bottom-up visual processing (i.e. increased contribution of Microstate B) compared to skeptics (Schlegel et al., 2012), supporting the general idea of increased bottom-up processing in believers. However, note that microstate maps of believers and skeptics in paranormal activity systematically differed from each other, indicating that the two groups might differ with regard to microstate topography rather than their temporal dynamics. As microstate maps of Believers and Non-Believers were extremely similar in our research (see Table S1 in the supplementary material), an advantage of our study is that group differences can be clearly deduced on the temporal dynamics of microstate maps (i.e., contributions of Microstates C and D and transitions from Microstate B to D and from B to C). In another study, intranasal application of the hormone and neuropeptide oxytocin led to increased contribution of Microstate D and decreased contribution of Microstate C compared to controls, a similar pattern of microstate dynamics as identified in our group of Non-Believers. As oxytocin is well-known for its anxiolytic effects (e.g., Yoshida et al., 2009; for a review, see Meyer-Lindenberg, Domes, Kirsch & Heinrichs, 2011), and religious belief has been found to show complex associations with anxiety (e.g., Laurin et al., 2008; for a review, see Kay et al., 2010), we speculate that temporal dynamics of resting networks related to top-down and bottom-up processing at rest might be related to individual levels of anxiety. Future research could therefore aim to investigate differences between people high and low in anxiety with regard to Microstate C and D, or the impact of manipulating anxiety on these parameters.

Overall, our results add to the idea that non-belief is more than merely a lack of belief. Rather, in addition to research on the psychological function of non-belief, Non-Believers here were associated with different neural networks. Furthermore, we note that neural traits, though highly stable, are not immutable. Various techniques, including neurofeedback, meditation, and repeated task training, can effect changes to cortical volume or cortical baseline activation in targeted brain regions (Ghaziri et al., 2013; Lazar et al., 2005; Takeuchi et al., 2010; Taya, Sun, Babiloni, Thakor & Bezerianos, 2015). As such, future research could further explore if these techniques can also effect changes in EEG microstate function (see also Hernandez, Rieger, Baenninger, Brandeis & Koenig, 2016, 2018). As the number of Non-Believers increase, a better understanding of the associated capabilities and shortcomings, as well as ways in which to improve on negative outcomes, may become increasingly important.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.biopsycho.2022.108283.

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