Exploring the neural networks of temporal expectations in rhythm with fMRI: SMA processes pattern-based expectations

Boer, Joris de

Citation

Boer, J. de. (2026). *Exploring the neural networks of temporal expectations in rhythm with fMRI: SMA processes pattern-based expectations*.

Exploring the neural networks of temporal expectations in rhythm with fMRI: SMA processes pattern-based expectations

Joris de Boer

Research Master Thesis *Cognitive Neuroscience*

Date: 15/05/2026

Student number: s4240618

Supervisor: Fleur Bouwer

Second reader: Bryant Jongkees

Abstract

Temporal expectations (e.g., predicting “when”) are a key element of musical rhythms, which makes these rhythms an excellent way of looking at temporal expectations in the brain. Temporal expectations can be based on regular, periodic beats, or on predictable patterns with varying interval lengths (e.g., the morse code of the rhythm). However, it is unknown whether beat-based and pattern-based expectations utilize different or shared neural networks. In an fMRI study, 45 participants listened to rhythms and rated their complexity. We used computational models of periodicity (quantifying beat-based expectations) and predictability (quantifying pattern-based expectations) to select rhythms that maximally differed on these aspects. Behaviorally, the absence compared to the presence of beats and patterns both independently increased the perceived complexity of rhythms. Whole-brain and ROI analyses revealed that the cerebellum and the SMA showed increased activity for unpredictable compared to predictable rhythms, which is not in line with previous research. Additionally, contrary to previous studies, there was no change in activity in the medial temporal lobes and basal ganglia based on periodicity and predictability differences. Furthermore, multivariate analyses revealed different activity patterns in the left caudate based on periodicity. However, contrary to previous research, this was not true for the right caudate, SMA, and putamen. Additionally, in line with previous absolute time interval research, the cerebellum and MTL both showed different activity patterns based on predictability differences. However, this was also true for the caudate, putamen, and SMA. These results especially question the role of the SMA in processing temporal expectations, suggesting that beat-based and pattern-based expectations may have been confounded in previous research with factors, such as complexity task demands, and on-beat tones.

Introduction

The brain uses the temporal structure within sensory input to make predictions about when something is going to happen in our environment (Nobre & Van Ede, 2018). In this way, we can deal with sensory input in a flexible and proactive fashion (Rimmele et al., 2018). These temporal expectations are a key element of musical rhythms. Thus, musical rhythms are an excellent way of researching temporal expectations. This research shows that sensory processing is improved for events that are aligned with rhythmic temporal expectations (Bouwer et al., 2020; Bouwer & Honing, 2015; Herbst et al., 2022; Morillon et al., 2016; Snapiri et al., 2023; Solli et al., 2025). Furthermore, rhythmic temporal expectations are also influential for movement (Damm et al., 2020), perception (Nobre & Van Ede, 2018), memory, and social reward (Fiveash et al., 2023).

Temporal expectations can be based on different types of environmental structural input. Namely, they can be based on a regular, periodic beat ("beat-based"), but also on predictable rhythmic patterns ("pattern-based") (Bouwer et al., 2020, 2023). The beat is the constant underlying pulse in music, which is what you would tap along to when listening to it. A pattern is a sequence with differing predictable intervals, which is sort of the morse code of rhythm. Schwartze and Kotz (2013) propose that these temporal expectations ("when") are processed separately from formal structure, which are the identifiable features of the sound ("what"). However, they do not distinguish between beat-based and pattern-based temporal expectations for this processing. Thus, from this it is unclear if these types of temporal expectations have shared or different mechanisms. Additionally, there is quite some research looking at the neural mechanisms of beat-based expectations (Hoddinott & Grahn, 2024; Kasdan et al., 2022; Teghil et al., 2019; Teki et al., 2011), but there is less research that looks directly at the neural mechanisms of pattern-based expectations. Namely, most research into the neural networks of pattern-based expectations has been done using single interval paradigms (Breska & Ivry, 2016; Paquette et al., 2017; Teki et al., 2011; Teki & Griffiths, 2016). Here, it is argued that this represents pattern-based expectations, because these expectations rely on the memorization of these inter-onset interval timings. However, Bouwer et al. (2026) found that the forming of pattern-based expectations might not rely on precise representations of these absolute inter-onset intervals. Thus, it remains unclear what neural networks are involved for pattern-based expectations and whether beat-based and pattern-based expectations rely on shared or separate neural networks.

Some researchers argue that the processing of these beat-based and pattern-based expectations relies on a shared neural network. Rimmele et al. (2018) propose that higher order top-down and motor systems are utilized to prepare sensory information to process it in a flexible and proactive manner by anticipating its timing. Importantly, they argue that this is done through a top-down phase reset of neural oscillations for both periodic beats and aperiodic patterns. There is some EEG research to back up the shared processing of beat-based and pattern-based expectations. Namely, Cappotto et al. (2023) found that violations of beat-based and pattern-based expectations were both associated with similar spatiotemporal patterns of electroencephalogram (EEG) evoked activity modulations. Furthermore, these were both linked to connectivity increases at late stages of cortical processing.

On the other hand, other research seems to suggest that beat-based and pattern-based expectations might rely on separate networks. Namely, beat-based and pattern-based expectations separately and differently affect performance on behavioral tasks. Bouwer et al. (2020) showed improved detection of targets that were in line with either beat-based or pattern-based expectations. However, they found that pattern-based expectations improved target detections even when events were in line with beat-based expectations. Furthermore, the presence of beat-based expectations decreased off-beat target detection, even when these targets were in line with pattern-based expectations. Thus, it seems that beat-based and pattern-based expectations influence target detection with partially separate mechanisms, which would suggest some separate neural processing. Additionally, Bouwer et al. (2023) looked at whether learned beat-based expectations and pattern-based expectations affected ratings of how well probes fitted in rhythms. These probes were during a silent period after the rhythm was heard. They showed that on-beat probe tones were rated as better fitting than off-beat probe tones in rhythms that contained beat-based expectations. Furthermore, they found that pattern-aligned probes were rated as better fitting compared to pattern-unaligned probes in rhythms with pattern-based expectations, but only for early probes. However, these effects of beat-based expectations lasted longer than the effects of pattern-based expectations. Thus, beat-based and pattern-based expectations differently affected performance on this task. This suggests that these effects may be reliant on different mechanisms.

Additionally, other research shows differing EEG activity for beat-based and pattern-based expectations, also suggesting that they rely on separate neural mechanisms. Bouwer et al. (2020) found that at expected time points, beat-based and pattern-based expectations resulted in weaker P1 and N1 responses regardless of whether the expectations were task-relevant. However, beat-based expectations uniquely led to an increased N1 responses at events at unexpected times. Furthermore, Bouwer et al. (2023) found increased spectral power at beat frequency when listening to, and during a silence after, rhythms with beat-based expectations. This increased spectral power was also found at pattern frequency when listening to rhythms with pattern-based expectations, but not during the silence after the rhythms. This difference in spectral power between beat-based and pattern-based expectations during the silence period suggests that these temporal expectations use different neural mechanisms during that time. Additionally, Solli et al. (2025) found an increased P3b amplitude for predictable compared to unpredictable rhythms. However, only periodic rhythms induced an entrained modulation pattern. This again shows differing EEG effects based on beat-based and pattern-based expectations. Lastly, Breska and Deouell (2017) found that beat-based and pattern-based expectations lead to similar phase concentration enhancement and anticipatory change in alpha activity. However, only beat-based expectations led to a depression of preparation-related premotor brain activity when on-beat events are omitted. They used a single interval discrimination task, so it is unclear whether this is based on the actual processing of pattern-based expectations. Nevertheless, these studies taken together suggest that beat-based and pattern-based expectations may rely on a shared neural mechanism for earlier processing stages in the auditory cortex, but that they do require different mechanisms at later processing stages.

For beat-based expectations, research seems to suggest that these later processing stages are in a striato-cortical network consisting of the basal ganglia and supplementary motor area (SMA). The action simulation for auditory processing prediction (ASAP) hypothesis theorizes about how these beat-based expectations are processed. This hypothesis posits that periodic movement is simulated in motor planning regions. This simulation leads to a neural signal that helps the auditory system predict upcoming beats through connections with motor planning regions and the parietal cortex (Patel & Iversen, 2014). Cannon and Patel (2021) propose that this motor planning occurs through neural timekeeping in the SMA, where activity is tuned to the inter-beat intervals and updated based on auditory cues. This SMA activity is then orchestrated by the basal ganglia, which selects and disinhibits units of SMA activity based on contextual input from motor and sensory cortices. If these neural processes are of a consistent duration, then it would create a self-sustaining cycle of activity that creates beat-based expectations for auditory processing. Studies using fMRI seem to confirm the involvement of the SMA and the basal ganglia for processing beat-based expectations. Teki et al. (2011) found an increased BOLD response in the SMA for beat-based rhythms compared to rhythms without a beat when participants compared the duration of two time intervals. Furthermore, a meta-analysis of fMRI studies found that the SMA and basal ganglia are involved in processing temporal expectations (Teghil et al., 2019). They do not distinguish between beat-based and pattern-based expectations, but most of the research they included was based on beat-based expectations. Therefore, this paper probably indicates that these areas are involved in beat-based expectation processing. Another meta-analysis that did specifically look at beat-based expectations corroborates the involvement of the SMA and the basal ganglia for beat-based expectations (Kasdan et al., 2022). Newer research looking at multi-voxel activity patterns also points to a striato-cortical network for beat-based expectations. Hoddinott and Grahn (2024) found that strong beat rhythms, as opposed to non-beat rhythms, led to different multi-voxel activity patterns in the SMA and basal ganglia. Furthermore, they found that this dissimilarity was associated with beat strength models. Lastly, EEG research into basal ganglia lesions also indicates the involvement of this brain region for beat-based expectations. Namely, Criscuolo et al. (2025) found that basal ganglia lesions led to disruptions in delta-band oscillations whilst focusing on periodic rhythms. Overall, it seems that there is a striato-cortical network for processing beat-based expectations.

A different cerebellar-hippocampal network consisting of the cerebellum and the medial temporal lobes (MTL) seems to be involved in processing interval timing within rhythms, which is thought to be indicative of processing pattern-based expectations. An fMRI study found an increased BOLD response in the cerebellum whilst participants compared the duration of two time intervals in rhythms without a beat compared to beat-based rhythms (Teki et al., 2011). Furthermore, Teki and Griffiths (2016) showed an increased BOLD response in the cerebellum as a function of increased jitter in time intervals. They also found that gray matter volume in the cerebellum was positively associated with precision on more jittered trials. Additionally, Paquette et al (2017) found a positive association with interval discrimination and gray matter volume in the cerebellum. Breska and Ivry (2016) also show that the cerebellum seems to be necessary to time discrete intervals, but only if there is not a beat present. These results indicate that the cerebellum is involved when time intervals differ more and are not aligned with a beat. This also seems to be true for the medial temporal lobes (MTL). Indeed, the MTL also has a larger BOLD response as jitter increased between time intervals (Teki & Griffiths, 2016). This might indicate that the cerebellum and MTL are involved for pattern-based expectation, because these expectations rely on processing the differing intervals between tones. Lee et al. (2020) did find some more direct evidence for the involvement of the MTL in pattern-based processing. In a meta-analysis, they found that the MTL is involved in memorizing duration within a sequence of events, such as rhythms. This is, in essence, memorizing patterns. Therefore, this indicates the processing of pattern-based expectations. Altogether, this indicates a cerebellar-hippocampal network for processing pattern-based expectations. However, it is still unknown if actual rhythmic patterns, and not just single interval timings, are processed in this cerebellar-hippocampal network.

To summarize, EEG studies show mixed results about whether beat-based and pattern-based expectations rely on shared or different neural networks. On the other hand, fMRI research seems to indicate separate networks. Although, it is also unclear whether the single interval results will generalize to complete pattern-based expectations. Therefore, the current study aims to find the separate or shared neural networks of beat-based and pattern-based expectations.

For beat-based expectations, I hypothesize that the previously discussed striato-cortical network processes this type of temporal expectations. Furthermore, I hypothesize that the discussed cerebellar-hippocampal network processes pattern-based expectations. This is based on the evidence found from fMRI studies. To find this out, participants will listen to rhythms varying in periodicity and predictability outside and inside an MRI scanner. They will also rate how complex they find these rhythms. This MRI data will be analyzed using whole brain analyses and univariate region-of-interest (ROI) analyses. Thus, I expect there to be a larger BOLD response during periodic rhythms compared to aperiodic rhythms in the SMA and the subparts of the basal ganglia (putamen and caudate). Additionally, I expect there to be a larger BOLD response during predictable rhythms compared to unpredictable rhythms in the cerebellum and MTL.

Additionally, the current study will look at the activity patterns for temporal expectations in the striato-cortical and cerebellar-hippocampal networks. To date, Hoddinott and Grahn (2024) has been the only study to look at activity patterns during temporal expectations as far as I am aware. I expect to reproduce their findings. Thus, I hypothesize that activity patterns will differ in the striato-cortical network based on whether beat-based expectations are present. On the other hand, no research has performed multivariate pattern analyses (MVPA) to study pattern-based expectations to the best of my knowledge. However, previous research seems to indicate that the cerebellar-hippocampal network is involved in processing pattern-based expectations. Accordingly, I hypothesize that activity patterns will differ in the cerebellar-hippocampal network based on whether pattern-based expectations are present. To find this out, the same data as in the whole brain and univariate ROI analyses will be used. This same data will be analyzed using MVPA. Thus, I expect that the areas in the striato-cortical network will be able to decode periodic and aperiodic rhythms above chance-level (50%). Furthermore, I expect that the areas in the cerebellar-hippocampal network will be able to decode predictable and unpredictable rhythms above chance-level (50%).

Methods

Participants

We used a G*Power analysis to calculate the desired sample size. This analysis was based on a meta-analysis by Kasdan et al. (2022) of neuroimaging studies that examined rhythm processing. They reported standardized effect sizes ranging from -0.36 to 1.08 for contrasts looking at rhythm complexity and beat presence. A minimum standardized effect size of 0.46 was found in these contrasts for the putamen, cerebellum, and supplementary motor area (SMA), which are some of our ROIs. The primary planned analysis was a dependent samples t-test with an effect size of 0.46, an alpha of 0.05, and a required power of 0.8. This analysis resulted in a required sample size of 40. Therefore, we aimed to get 48 participants for our analyses. To account for data loss, we wanted to get 52 participants in total.

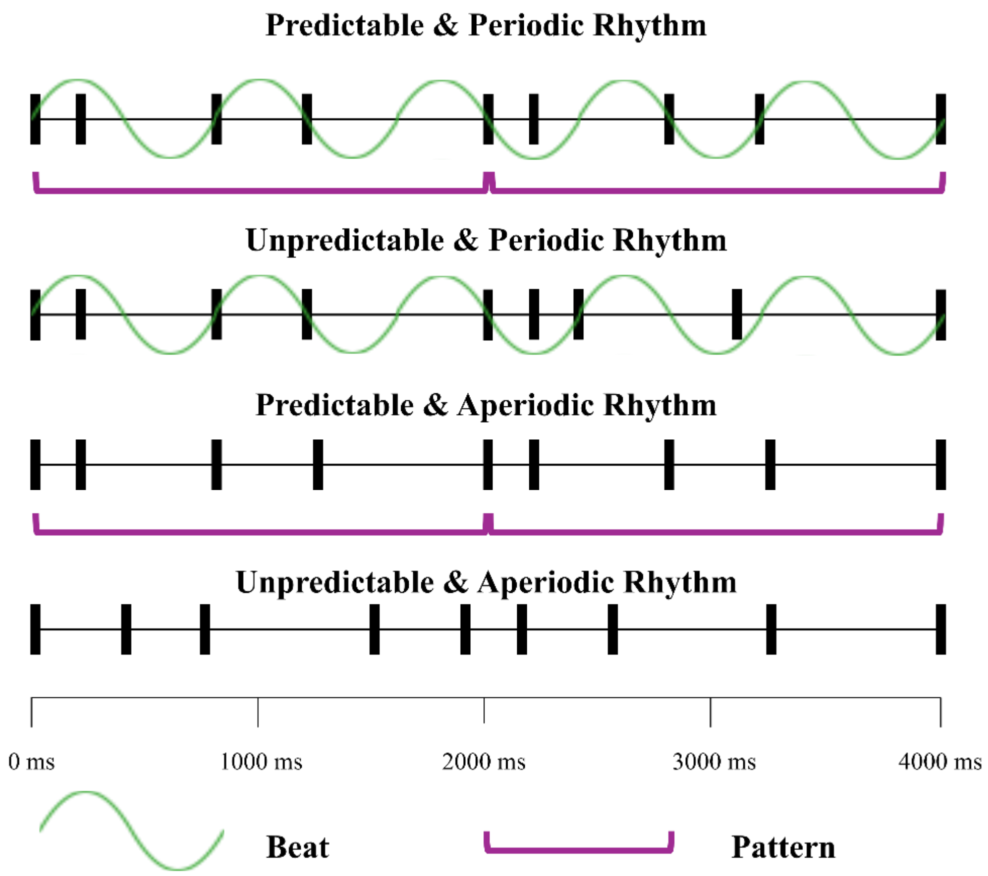
52 healthy adults participated in this study. Of those, 1 was excluded due to excessive movement in the MRI scanner, 2 were excluded due to technical issues with the headphones inside the MRI scanner, 2 were excluded because they did not complete the task in the MRI scanner, and 2 were excluded due to other technical issues. Thus, 45 participants were included in our analyses (M*age* = 22.96, S*age* = 3.12; 13 males, 31 females, 1 other). Participants were included if they reported no hearing impairments, no history of neurological or psychiatric disorders, and normal or corrected-to-normal vision. Furthermore, participants were included if they were eligible to undergo fMRI testing. This means that the participants, for example, did not have metal implants or had no previous adverse reaction to an MRI scan. The participants were recruited via SONA, word-of-mouth, and social media. Furthermore, our goal was to mainly find musically trained participants, because they show larger effect sizes for our measures of interest compared to musical novices. Therefore, we also recruited participants through local orchestras. The participants received 27.5 euros for partaking in the study. Furthermore, the procedures of this study were approved by the Psychology Research Ethics Committee at Leiden University.

Rhythmic stimuli

The rhythms were created to maximally differ in terms of periodicity and predictability (Figure 1). Predictability was computed using a probabilistic model of rhythmic complexity (Pearce, 2018), and periodicity was computed using an entrainment model of rhythmic complexity (Large et al., 2015). The outcomes were 4-second rhythmic stimuli comprised of 8 sine tones with inter-onset-intervals between 200 and 800 ms. These sine tones were 440 Hz, with 5ms rise and fall time. These rhythms were computationally classified as predictable or unpredictable, and as periodic or aperiodic resulting in 2x2 conditions. This resulted in 48 rhythms (12 per condition) which were extracted from a larger set of rhythms.

Figure 1

Visual representation of four rhythm conditions differing in terms of periodicity and predictability, where each thick vertical black line represents a sine tone



Rating task

During the rating task, the participants listened to the 48 rhythms consisting of three concatenated identical 4-second rhythmic patterns. Furthermore, the participants listened to one block of 48 rhythms (12 per condition) outside of the scanner, and three blocks of 48 rhythms (12 per condition) inside the scanner. The order of the rhythms was randomized per participant. For both versions, the participants looked at a fixation cross on a screen while they were listening to the rhythms.

The participants rated the rhythm complexity on a 7-point Likert scale from “extremely simple” to “extremely complex” after each rhythm. Outside the scanner, they rated this on a computer keyboard using the “m” and “n” buttons to navigate a slider from 1-7. Inside the scanner, they rated the rhythm complexity using the same scale, but on random trials and with a button box. This was on average once every 4 rhythms, and so that it was evenly distributed over the 4 conditions. Additionally, they rated each unique rhythm no more than once over all three blocks. They rated this using a button box to navigate a slider from 1-7. For both versions, the participants had 4 seconds to rate the rhythm complexity. Furthermore, to avoid motor preparation, the order of the numbers of the slider were randomly reversed for half the trials.

Image acquisition

Anatomical and functional scans were acquired using a 3T Philips Achieva TX MRI scanner with a 32-channel head coil at the Leiden Institute for Brain and Cognition. T2-weighted echo-planar imaging (EPI) were recorded with a multiband acceleration factor of 4, a 55◦ flip angle, a 800 ms TR, and a 30 ms TE. This EPI data was acquired from 2.500 mm and reconstructed with 2.292 mm isotropic voxels in a matrix of 220 x 220 x 120 mm. T1-weighted anatomical images were recorded using a 8◦ flip angle, a 7.9 ms TR, and a 3.5 ms

TE. This anatomical data was collected from 1.1 mm isotropic voxels in a matrix of 250 x 195.8 x 170.5 mm.

Procedure

Before the start of the study, the participants were informed about the study, gave their consent, and confirmed their eligibility for the study. In the lab, the participants first performed some computer tasks. First, they performed the rating task on a laptop outside the scanner. Before starting the task, the participants did two practice trials to familiarize them with the tasks and to anchor their complexity ratings according to our scale. Next, the participants proceeded with a tapping task. Then, they moved on to The Goldsmith Musical Sophistication Index (GMSI) (Müllensiefen et al., 2014). This questionnaire was done before or after the scanning session based on convenience. The tapping task and GMSI were part of a larger study and will not be discussed further in this paper. Lastly, the participants performed the rating task in the MRI scanner. Overall, the study lasted around 2.5 to 3 hours.

Analyses

Behavioral rhythm complexity ratings

To see how complexity was influenced by beat-based and pattern-based expectations outside and inside the MRI scanner, linear mixed model analyses were performed in R (R Core Team, 2026) using the lmer function, which is part of the lme4 package (Bates et al., 2015). Here, each model predicted the complexity ratings with periodicity, predictability and the interaction effect of these two as the fixed effects. Additionally, to account for repeated measures within participants, a random intercept was included for each participant. This was done separately for the rating task done outside and inside the scanner. We expect similar results for the complexity ratings outside and inside the scanner, which would indicate that they are processed similarly outside and inside the scanner. If any significant main effect was found, then the means of the groups within this main effect would be compared. Furthermore, if any significant interaction effect was found, post-hoc tests would follow to look at the specific differences between the conditions. This was done using the emmeans() function in R, which is part of the emmeans R package (Lenth & Piaskowski, 2026).

Normality for these analyses was checked by inspection of a Q-Q plot of the residuals, multicollinearity was checked by looking at whether there are no VIF values above 10. Furthermore, a residuals versus fitted plot was inspected to see whether there is no distinct non-linear pattern to check for linearity, and the same plot was inspected for equal variances distributed across all points on the horizontal line to check for homoscedasticity (See Appendix A for plots). For this, the check_model() function was used in R, which is part of the performance package (Lüdecke et al., 2021). These inspections revealed no violation of assumptions.

fMRI preprocessing

MRI data was preprocessed using SPM25 (Tierney et al., 2025) in MATLAB 2023b (The MathWorks Inc., 2023). First, fieldmap-based distortion correction was performed by generating voxel displacement maps from dual-echo phase and magnitude images to correct for B0 inhomogeneities. Then, functional images were realigned to the mean functional image using second-degree B-spline interpolation to correct for subject motion. Subsequently, using slice-time correction, functional images were corrected for differences in slice acquisition timing. Next, functional images were coregistered with their anatomical scan using a normalized mutual information cost function for each subject. The anatomical scans were then segmented into gray matter, white matter, and cerebrospinal maps with a segment function and tissue probability maps. Next, coregistered images were normalized to the Montreal Neurological Institute (MNI) template space. Lastly, these normalized images were spatially smoothed with a 5-mm full-width half maximum kernel.

Next, a general linear model (GLM) was estimated. Four regressors were included that corresponded to the four rhythm conditions (predictable-periodic, unpredictable-periodic, predictable-aperiodic, and unpredictable-aperiodic), and three regressors corresponding to the presentation of a fixation cross, the complexity question, and for key presses. Additionally, six motion parameters were added as regressors of no interest.

Whole-brain analyses

Voxel-wise, whole-brain group analysis were performed using SPM25 (Tierney et al., 2025) in MATLAB 2023b (The MathWorks Inc., 2023). For this, a rhythms versus rest contrast was included to check for auditory cortex activity, and to find peak activations that will be used to define the left SMA, and the bilateral cerebellum. We expect to find an increased BOLD response in these brain regions for rhythms versus rest. Additionally, a periodic versus aperiodic, an aperiodic versus periodic, a predictable versus unpredictable, and an unpredictable versus predictable contrast were created. This was to look at the specific brain activations based on periodicity and predictability. For each participant, one contrast image was created per contrast. These first-level contrast images were put into second-level random-effects models to assess population-level effects. For each contrast, a separate second-level model was specified as a one-sample t-test. The contrast images were treated as independent observations. SPM’s classical ordinary least squares approach was used to estimate every model. Next, it was tested whether the group mean contrast value differed significantly from zero with a specified single t-contrast. From this, regions that had a group-level effect could be identified. For the results, a threshold of $p < 0.05$ at the voxel level for family-wise error correction was used to control for multiple comparisons across the whole brain.

Univariate ROI analyses

Region-of-interest (ROI) analyses were performed on the BOLD activity of the left and right putamen, caudate, and hippocampus using SPM25 (Tierney et al., 2025) in MATLAB 2023b (The MathWorks Inc., 2023). These areas were anatomically defined using the 7th version of the Automated Anatomical Labelling Atlas 3 (AAL3), because these areas are anatomically well defined. From this, labels were obtained and brought into the same space as the EPI images obtained during the experiment. These were also resliced to the space of the contrast images, because the voxel dimensions of the contrast maps of the atlas and the subject might differ in voxel dimensions. Thus, labels were obtained from the AAL3 and brought into the same space as the EPI images obtained during the experiment.

Additionally, a supplementary motor area (SMA), and a left and right cerebellum spherical ROI were defined by the peak activation voxel in these regions for the rhythms versus rest contrast. The radius of these ROIs was 8 mm. This method was used for these ROIs, because the SMA is anatomically not that well defined (Hiroshima et al., 2014). Furthermore, the cerebellum is quite large and has many distinct areas with varying functions (Carey, 2024), and with this ROI definition, the specific cerebellar area for rhythm processing can be found.

Within all ROIs, the average beta-weighted contrast value for all voxels within the ROI were extracted from each participant's contrast images. For this, a periodic unpredictable versus rest, an aperiodic predictable versus rest, a periodic unpredictable versus rest, and an aperiodic unpredictable versus rest contrast was created. Thus, there was one beta-weighted contrast value per condition per ROI for every participant. Linear mixed model analyses were performed on the mean beta-weighted contrast values in R (R Core Team, 2026) using the lmer() function, which is part of the lme4 package (Bates et al., 2015). Here, each model predicted the mean beta-weighted contrast values for each ROI with periodicity, predictability and the interaction effect of these two as the fixed effects. Additionally, to account for repeated measures within participants, a random intercept was included for each participant. For each ROI, one linear mixed model analysis was performed. Thus, one analysis for the left SMA, and left and right putamen, caudate, cerebellum and MTL.

If any significant interaction effect was found, post-hoc tests followed to look at the specific differences between the conditions. This was done using the emmeans() function in R (R Core Team, 2026), which is part of the emmeans R package (Lenth & Piaskowski, 2026). The Holm-Bonferroni method (Holm, 1979) was used to account for familywise error rates of multiple testing. This was applied to each main and interaction effect separately over all ROIs.

Normality for these analyses was checked by inspection of a Q-Q plot of the residuals, multicollinearity was checked by looking at whether there are no VIF values above 10. Furthermore, a residuals versus fitted plot was inspected to see whether there is no distinct non-linear pattern to check for linearity, and the same plot was inspected for equal variances distributed across all points on the horizontal line to check for homoscedasticity (See Appendix A for plots). For this, the check_model() function was used in R (R Core Team, 2026), which is part of the performance package (Lüdecke et al., 2021). These inspections revealed no violation of assumptions.

Multivariate pattern analyses.

Multivariate pattern analyses (MVPA) were conducted to examine whether distributed patterns of voxel activity differ based on differences in beat-based and pattern-based expectations. This was performed using SPM12 (Wellcome Centre for Human Neuroimaging, London, UK) in MATLAB 2023b (The MathWorks Inc., 2023). SPM25 was not used, because of compatibility issues with the toolboxes needed to do MVPA. A GLM was estimated using the same regressors as in the univariate analyses. However, the input images were unsmoothed and not normalized. These input images were already made during the preprocessing for the univariate analyses. The condition-, voxel-, and run-wise parameter estimates of this GLM were used for the MVPA.

This MVPA was performed on the beta maps using The Decoding Toolbox (Hebart et al., 2015). A searchlight classifier with a 12 mm radius was trained and tested in 2 different setups using libSVM (ChangChih-Chung & LinChih-Jen, 2011). Firstly, a periodic versus aperiodic rhythms setup was analyzed. Secondly, a predictable versus unpredictable rhythms setup was analyzed. For both analyses, a classifier was trained on 2 out of the 3 runs, and the leftover run was used to test the performance of the classifier. This was repeated 3 times, each time a different run was left out (leave-one-run-out procedure).

All analyses resulted in decoded accuracy maps per subject. These maps were normalized to MNI space to create the inverse normalization matrix. For the generation of anatomy-based regions of interests, which are the same ROIs as in the univariate analyses, we used the AAL3 and peak activations from the rhythms versus rest contrast. These ROIs were created in MNI space and converted to individual brains using the previously created inverse normalization matrix. Activity-based ROIs were created using the SPM-based tool “Marsbar” (Brett et al., 2002).

This resulted in one decoding accuracy score per participant per ROI for both distinguishing periodic versus aperiodic rhythms and predictable versus unpredictable rhythms. One-samples t-tests were performed to test whether the average decoding accuracy per ROI for both distinguishing periodic versus aperiodic rhythms and predictable versus unpredictable rhythms was above chance-level (50%). Thus, 18 one-sample t-tests were performed in total (9 ROIs x 2 setups). This was done using the t.test() function in R (R Core Team, 2026), which is part of the stats package (R Core Team, 2026). The Holm-Bonferroni method (Holm, 1979) was used to account for familywise error rates of multiple testing. This was applied to the periodic versus aperiodic setup and to the predictable versus unpredictable setup separately over all ROIs.

Normality was checked by inspection of a Q-Q plot per ROI for periodicity and predictability (See Appendix B for plots). This was done by using the ggqqplot() function in R, which is part of the ggpubr package (Kassambara, 2026). This inspection revealed no violation of normality.

Results

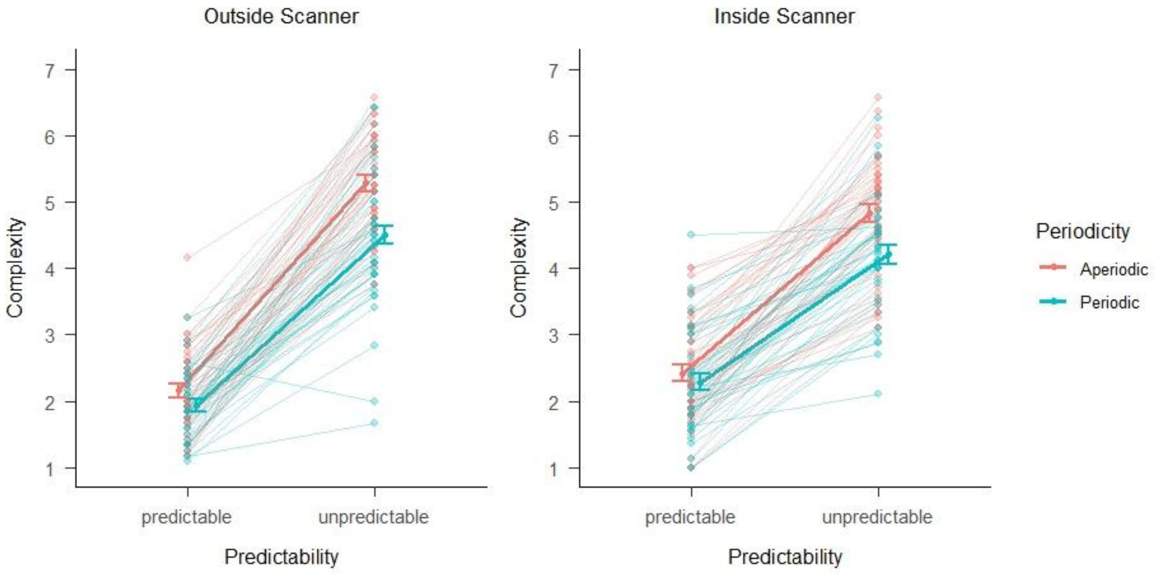
Behavioral rhythm complexity ratings

Linear mixed model analyses revealed that periodicity had a significant effect on complexity ratings of the rhythms outside, $\chi^2(1, N = 45) = 90.28$, $p < .001$, and inside the scanner, χ^2 $(1, N = 45) = 40.20$, $p < .001$. Outside and inside the scanner, aperiodic rhythms (outside: $M = 3.72$, $s = 2.02$, inside: $M = 3.63$, $s = 1.79$) were rated as more complex than periodic rhythms (outside: $M = 3.22$, $s = 1.88$; inside: $M = 3.23$, $s = 1.67$). Furthermore, predictability also had a significant effect on the ratings of the rhythms outside, $\chi^2(1, N = 45) = 2911.53$, $p < .001$, and inside the scanner, $\chi^2(1, N = 45) = 1320.69$, $p < .001$. Outside and inside the scanner, unpredictable rhythms (outside: $M = 4.89$, $s = 1.54$; inside: $M = 4.52$, $s = 1.44$) were rated as more complex than predictable rhythms (outside: $M = 2.04$, $s = 1.14$, inside: $M = 2.35$, $s = 1.27$). Lastly, the interaction effect between periodicity and predictability also had a significant effect on complexity ratings of the rhythms outside, $\chi^2(1, N = 45) = 27.66$, $p < .001$, and inside the scanner, $\chi^2(1, N = 45) = 16.81$, $p < .001$. For both outside and inside the scanner, it seems that periodicity had a larger effect on complexity ratings within unpredictable rhythms than within predictable rhythms (See Figure 2). Outside the scanner, post-hoc pairwise comparisons revealed that within predictable rhythms, aperiodic rhythms were rated significantly higher in complexity than periodic rhythms, with an estimated difference of 0.22 ($SE = 0.07$), $t(2112) = 3.00$, $p = 0.003$. Within unpredictable rhythms, this difference seems to be larger with an estimated difference of 0.78 ($SE = 0.07$), $t(2112) =$

10.44, $p < 0.001$. Inside the scanner, within predictable rhythms, aperiodic rhythms were not rated significantly higher than periodic rhythms, with an estimated difference of 0.14 (SE = 0.08), $t(1574) = 1.60$, $p = 0.111$. Within unpredictable rhythms, this difference is larger and significant with an estimated difference of with an estimated difference of 0.63 (SE = 0.08), $t(1574) = 7.38$, $p < 0.001$. Thus, rhythm type had similar effects on complexity ratings outside and inside the scanner. This indicates that the rhythms were processed similarly outside and inside the scanner.

Figure 2

Mean complexity ratings (general and per participant) outside and inside scanner based on periodicity and predictability with within-subject 95% confidence interval error bars



Whole brain analyses

Consistent with our expectations, rhythms elicited a larger BOLD response in the auditory cortex, the left supplementary motor area (SMA), and left and right cerebellum compared to rest (See Table 1 and Figure 3). This indicates that there was increased auditory and motor processing during rhythms versus rest. Therefore, like the complexity ratings, this confirms that the participants processed the rhythms inside the scanner.

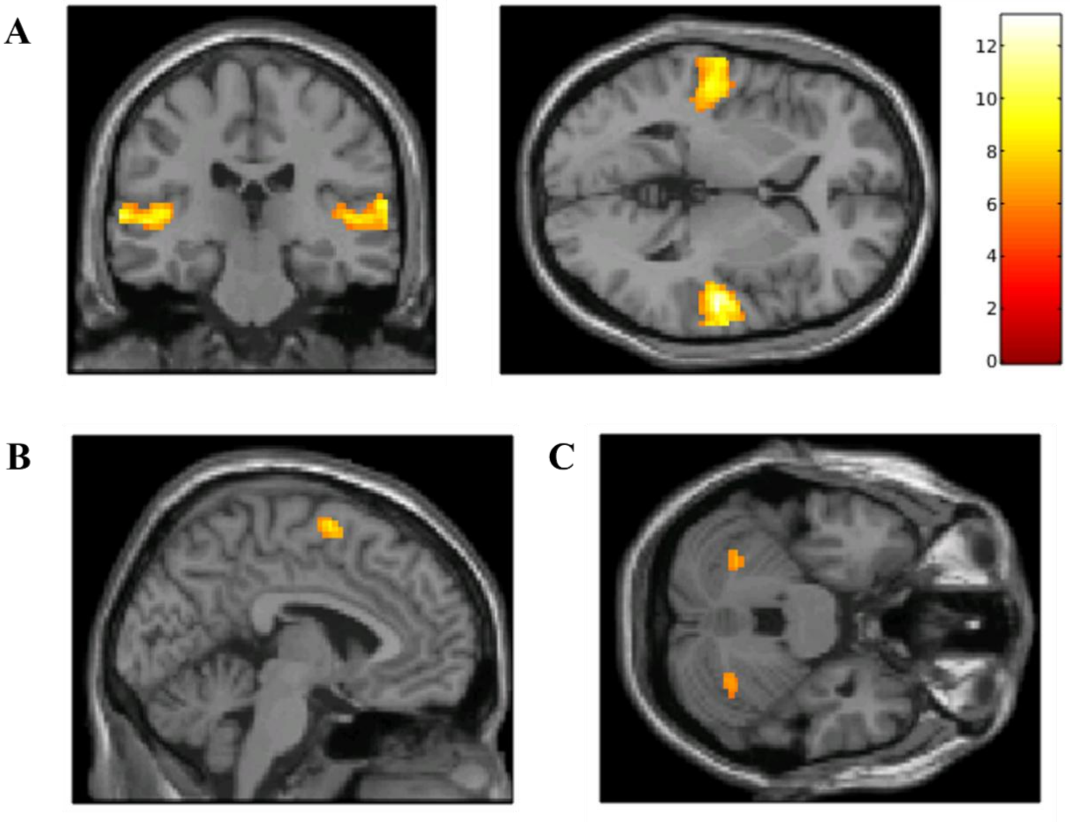
Table 1

Peak voxel activation areas in rhythms versus rest contrast

Brain area	Hemisphere	x	y	z	*t*	*p(FWE corrected)*
Auditory cortex	Right	56	-17	0	13.10	<.001
	Left	-64	-24	5	10.39	<.001
SMA	Left	-4	0	65	8.59	<.001
Cerebellum	Right	33	-60	-30	6.71	0.001
	Left	-27	-60	-28	7.16	<.001
Somatosensory cortex	Left	-50	-7	50	7.43	<.001
Primary motor cortex	Right	53	0	45	5.88	0.019

Figure 3

Rhythms versus rest: (A) Coronal and axial view of increased auditory cortex BOLD response. (B) Sagittal view of increased left SMA BOLD response. (C) Axial view of increased left and right cerebellar BOLD response.



Unexpectedly, the periodicity contrasts revealed no significant differences in BOLD response when comparing periodic and aperiodic rhythms. Here, we would have expected significant increased BOLD responses in the striato-cortical network for periodic compared to aperiodic rhythms. On the other hand, the predictability contrasts did reveal some brain areas that showed an increased BOLD response when comparing predictable and unpredictable rhythms. Here, we found increased BOLD responses in the bilateral cerebellum for unpredictable rhythms compared to predictable rhythms. This contrasts with our expectations, because we expected this increase in the bilateral cerebellum for predictable compared to unpredictable rhythms. Additionally, unpredictable rhythms also showed an increased BOLD response in the left SMA compared to predictable rhythms (see Figure 4). This is also not in line with our expectations, because we would have expected this increase for periodic compared to aperiodic rhythms. Additionally, unpredictable rhythms compared to predictable also showed some increased BOLD responses in other brain regions, most notably the auditory cortex and primary motor cortex (for a full overview see Table 2). Furthermore, predictable compared to unpredictable rhythms did not show increased BOLD responses in the expected cerebellar-hippocampal network. However, this comparison also showed some increased BOLD responses in brain regions that we did not discuss in our expectations, such as the precuneus and supramarginal gyrus (See Figure 5 and Table 3 for an overview).

Figure 4

Unpredictable versus predictable contrast: (A) Sagittal view of the left SMA showing an increased BOLD response. (B) Axial view of the left and right cerebellum showing an increased BOLD response.

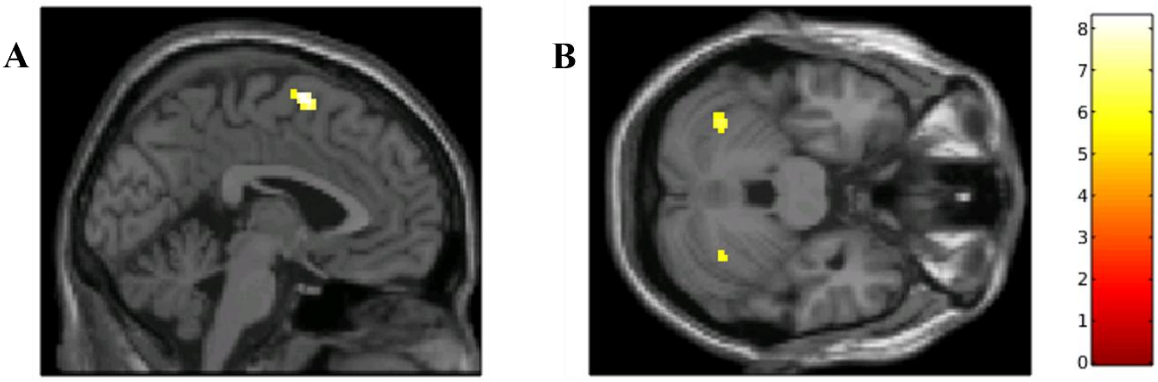


Table 2

Peak voxel activation in unpredictable versus predictable contrast

Brain area	**Hemisphere**	**x**	**y**	**z**	***t***	***p(FWE corrected)***
SMA	left	0	3	65	8.27	<.001
Cerebellum	Left	-34	-62	-28	6.41	0.003
	Right	30	-62	-25	6.10	0.009
Auditory cortex	Right	60	-20	-2	7.39	<.001
	Right	48	-37	8	5.72	0.029
Medial temporal gyrus	Left	-62	-27	2	6.22	0.006
	Left	-64	-17	2	5.53	0.049
Primary motor cortex	Left	-50	0	48	5.96	0.014

Figure 5

Predictable versus unpredictable contrast Unpredictable:: (A) Coronal view of the left inferior temporal gyrus showing an increased BOLD. (B) Coronal view of the left precuneus showing an increased BOLD response. (C) Axial view of the left inferior frontal triangularis showing an increased BOLD response

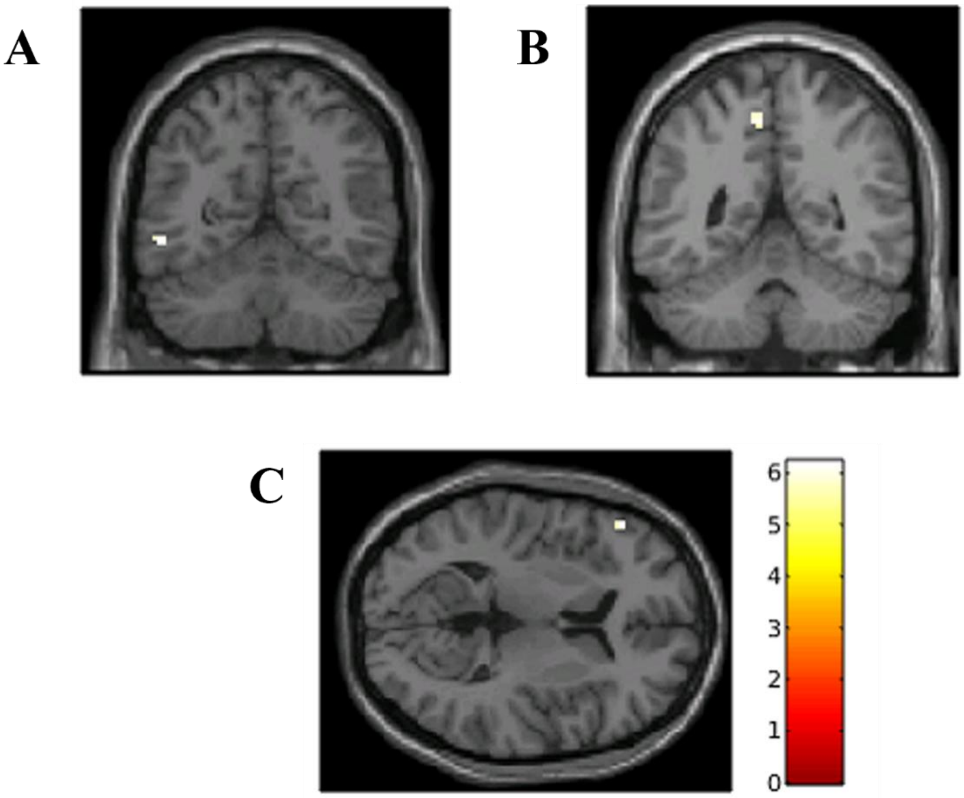


Table 3

Peak voxel activation in predictable versus unpredictable contrast

Brain area	Hemisphere	x	y	z	*t*	*p(FWE corrected)*
Inferior temporal gyrus	Left	-50	-57	-8	6.22	0.006
	Left	-44	-40	-15	5.88	0.018
Precuneus	Left	-7	-50	52	6.03	0.012
	Left	-14	-44	45	5.57	0.043
Supramarginal gyrus	Left	-62	-40	35	6.03	0.012
	Left	-62	-27	35	5.63	0.037
Inferior frontal triangularis	Left	-52	33	8	6.00	0.013
Medial cingulum	Right	3	6	42	5.82	0.021
Insula	Left	-37	0	10	5.59	0.041
Gray matter (near somatosensory cortex)	Left	-20	-37	52	6.16	0.007
	Right	23	-37	55	5.63	0.037

Univariate ROI analyses

Striato-cortical network

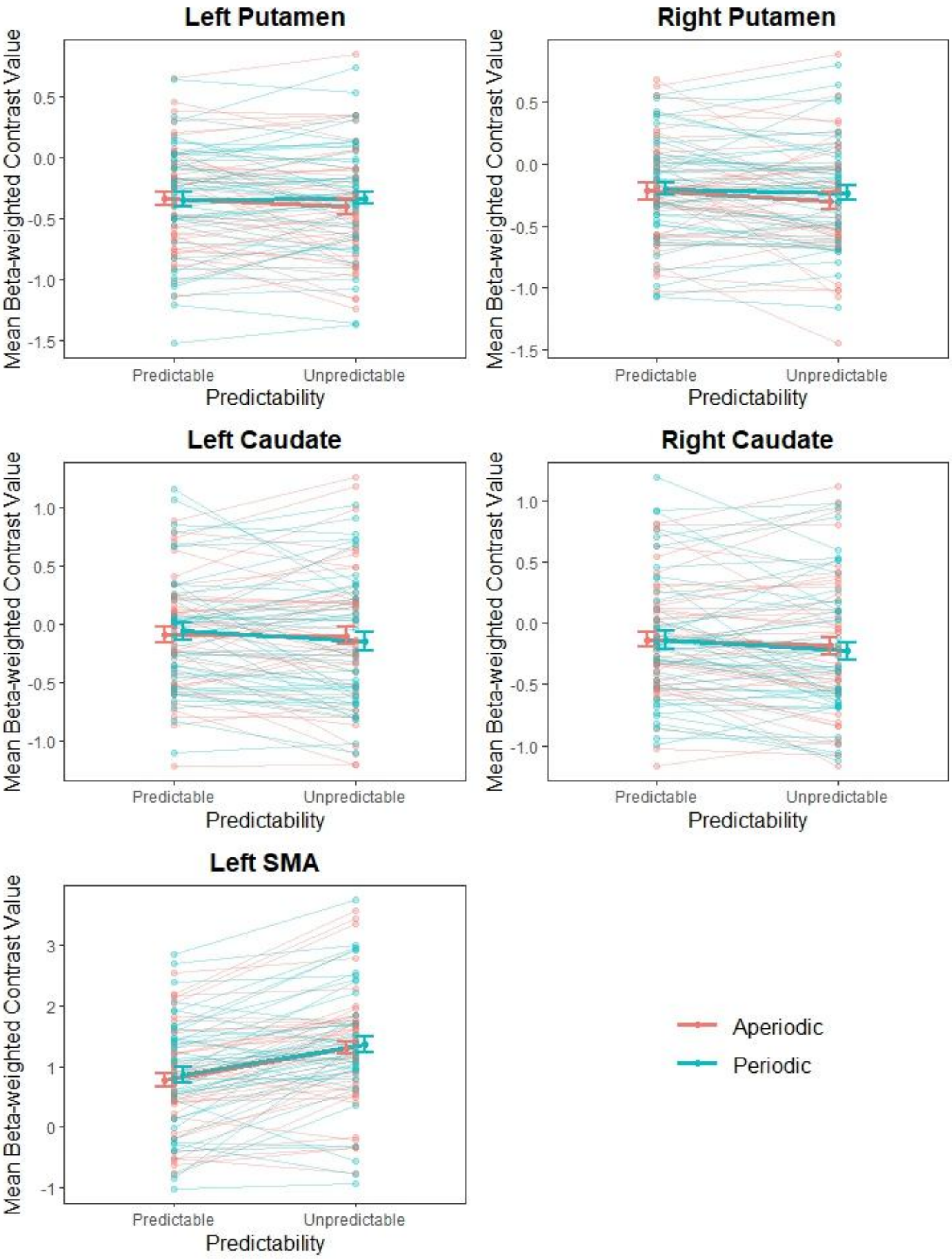
In the putamen, linear mixed model analyses revealed no significant main effect of periodicity (left: $\chi^2(1, N = 45) = 1.01, p = 0.316, p_{adj} = 1.000$; right: $\chi^2(1, N = 45) = 1.74, p = 0.187, p_{adj} = 1.000$), predictability (left: $\chi^2(1, N = 45) = 0.95, p = 0.329, p_{adj} = .986$; right: $\chi^2(1, N = 45) = 3.05, p = 0.081, p_{adj} = 0.403$), and interaction effect between periodicity and predictability (left: $\chi^2(1, N = 45) = 1.53, p = 0.216, p_{adj} = 1.000$; right: $\chi^2(1, N = 45) = 0.62, p = 0.431, p_{adj} = 1.000$) on BOLD response (See Figure 6). We found similar results for the caudate. In the caudate, linear mixed models also revealed no significant main effect of periodicity (left: $\chi^2(1, N = 45) = 0.04, p = 0.842, p_{adj} = 1.000$; right: $\chi^2(1, N = 45) = 0.45, p = 0.500, p_{adj} = 1.000$), predictability (left: $\chi^2(1, N = 45) = 1.59, p = 0.207, p_{adj} = 0.829$; right: $\chi^2(1, N = 45) = 4.15, p = 0.042, p_{adj} = 0.249$), and interaction effect between periodicity and predictability (left: $\chi^2(1, N = 45) = 1.29, p = 0.256, p_{adj} = 1.000$; right: $\chi^2(1, N = 45) = 0.29, p$

= 0.589, p_{adj} = 1.000) on BOLD response (See figure 6). Thus, contrary to our hypothesis, we found no evidence that the putamen and caudate are involved in the processing of beat-based and pattern-based expectations.

In the left supplementary motor area (SMA), a linear-mixed model unexpectedly revealed no significant effects of periodicity and the interaction of periodicity and predictability on BOLD response (periodicity: $\chi^2(1, N = 45) = 1.47$, $p = 0.224$, $p_{adj} = 1.000$; interaction: $\chi^2(1, N = 45) = 0.10$, $p = 0.749$, $p_{adj} = 1.000$). However, there was an unexpected significant main effect of predictability, $\chi^2(1, N = 45) = 71.23$, $p < .001$, $p_{adj} < .001$, on BOLD response in the left SMA. Unpredictable rhythms ($M = 1.33$, $s = 0.97$) had a higher beta-weighted contrast value than predictable rhythms ($M = 0.82$, $s = 0.87$) (See Figure 6). Thus, contrary to our hypothesis, we did not find evidence that the left SMA processes beat-based expectations, but we did find evidence that indicates that it might process the absence of pattern-based expectations.

Figure 6

Mean beta-weighted contrast values per ROI in the striato-cortical network (general and per participant) based on periodicity and predictability with within-subject 95% confidence intervals per condition



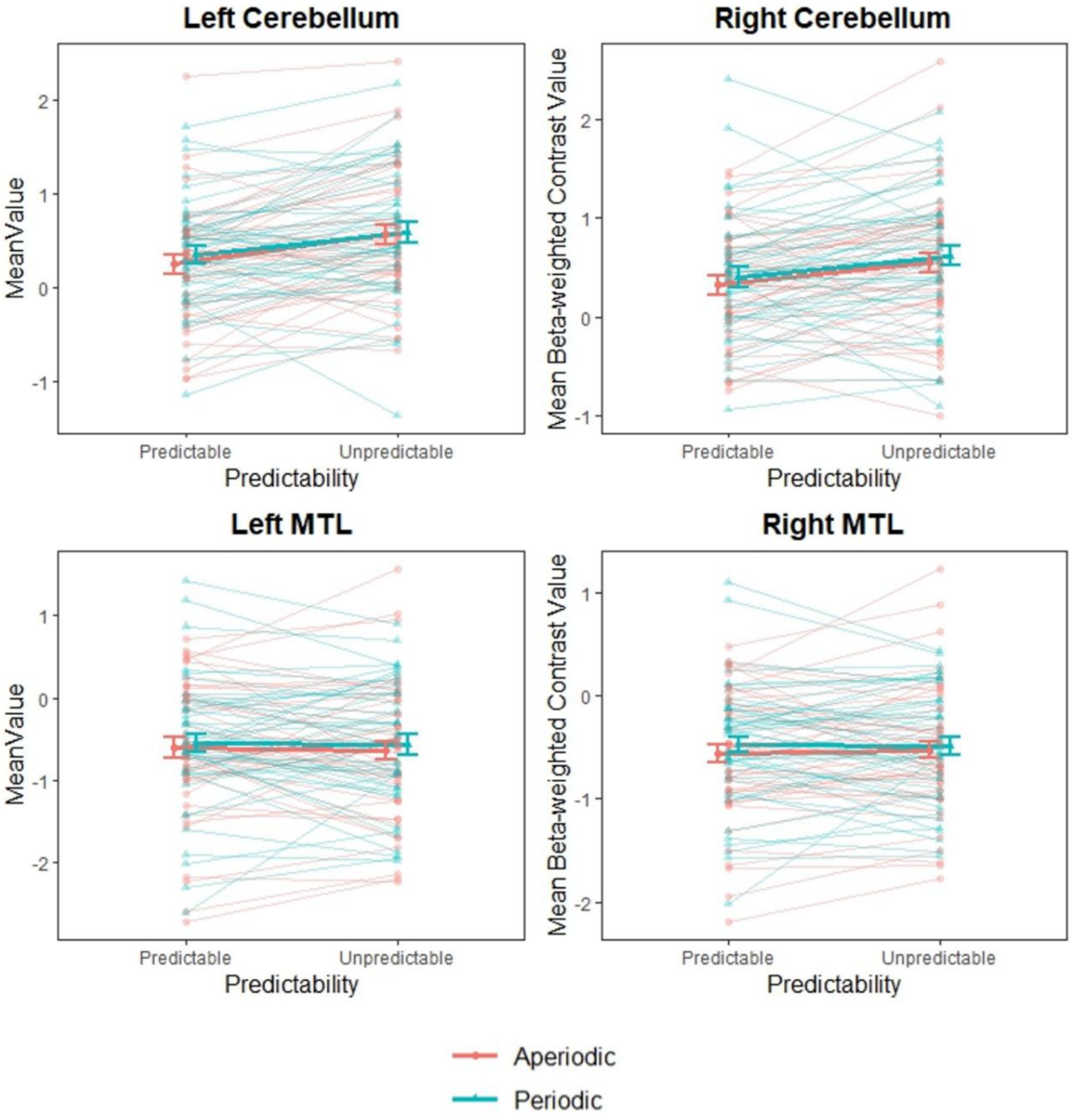
Cerebellar-hippocampal network

In the cerebellum, linear mixed models revealed neither a significant main effect of periodicity (left: $\chi^2(1, N = 45) = 1.44$, $p = 0.230$, $p_{adj} = 1.000$; right: $\chi^2(1, N = 45) = 2.33$, $p = 0.127$, $p_{adj} = 1.000$), nor a significant interaction effect between periodicity and predictability (left: $\chi^2(1, N = 45) = 0.62$, $p = 0.430$, $p_{adj} = 1.000$; right: $\chi^2(1, N = 45) = 0.01$, $p = 0.904$, $p_{adj} = 1.000$). The main effect of predictability was significant in both left ($\chi^2(1, N = 45) = 31.32$, $p_{adj} < .001$) and right ($\chi^2(1, N = 45) = 20.36$, $p < .001$, $p_{adj} < .001$) cerebellum, with higher beta-weighted contrast values for unpredictable compared to predictable rhythms (unpredictable left: $M = 0.58$, $SD = 0.69$, right: $M = 0.58$, $SD = 0.70$; predictable left: $M = 0.30$, $SD = 0.61$, right: $M = 0.36$, $SD = 0.60$) (See Figure 7). Thus, contrary to our expectations, these results might indicate that the cerebellum is involved in processing the absence of pattern-based expectations instead of the presence of these expectations.

In the medial temporal lobes (MTL), linear mixed model analyses revealed no significant main effect of periodicity (left: $\chi^2(1, N = 45) = 1.19$, $p = 0.275$, $p_{adj} = 1.000$; right: $\chi^2(1, N = 45) = 2.40$, $p = 0.121$, $p_{adj} = 1.000$), predictability (left: $\chi^2(1, N = 45) = 0.19$, $p = 0.662$, $p_{adj} = 1.000$; right: $\chi^2(1, N = 45) = 0.08$, $p = 0.779$, $p_{adj} = 1.000$), and interaction effect between periodicity and predictability (left: $\chi^2(1, N = 45) = 0.07$, $p = 0.787$, $p_{adj} = 1.000$; right: $\chi^2(1, N = 45) = 0.27$, $p = 0.601$, $p_{adj} = 1.000$) on BOLD response (See Figure 7). Thus, contrary to our expectations, we did not find evidence that the MTL is involved in processing beat-based and pattern-based expectations.

Figure 7

Mean beta-weighted contrast values per ROI in the striato-cortical network (general and per participant) based on periodicity and predictability with within-subject 95% confidence intervals per condition



MVPA

Striato-cortical network

For distinguishing between periodic and aperiodic rhythms, one-sample t-tests revealed that the left and right putamen, the left SMA, and the right caudate all did not have a significant above chance-level (50%) mean decoding accuracy (for an overview see Table 4 and Figure 8). However, the mean decoding accuracy level for distinguishing between periodic and aperiodic rhythms within the left caudate ($M = 52.82$, $s = 6.15$) was significantly higher than chance-level (50%), $t(44) = 1.35$, $p = 0.004$, $p_{adj} = 0.032$. Thus, in line with our hypothesis, we found evidence that activity patterns differ in the left caudate based on whether beat-based expectations were present or not. However, contrary to our hypothesis, we did not find evidence for this in the left and right putamen, left SMA, and right caudate.

In the putamen, one-sample t-tests revealed that the mean decoding accuracy level for distinguishing between predictable and unpredictable rhythms (left: $M = 57.11$, $s = 8.10$; right: $M = 55.97$, $s = 8.19$) was significantly higher than chance-level (50%) (left: $t(44) = 5.89$, $p < .001$, $p_{adj} < .001$; right: $t(44) = 4.88$, $p < .001$, $p_{adj} < .001$). We found similar results for the caudate. In the caudate, one-sample t-tests revealed that the mean decoding accuracy level for distinguishing between predictable and unpredictable rhythms (left: $M = 53.48$, $s = 6.66$; right: $M = 54.01$, $s = 7.65$) was significantly higher than chance-level (50%) (left: $t(44) = 3.50$, $p = 0.001$, $p_{adj} = 0.004$; right: $t(44) = 3.51$, $p = 0.001$ $p_{adj} = 0.004$). Additionally, the left SMA also shows similar results. In the left SMA, a one-sample t-test revealed that the mean decoding accuracy level for distinguishing between predictable and unpredictable rhythms ($M = 69.45$, $s = 11.67$) was significantly higher than chance-level (50%), $t(44) = 11.18$, $p < .001$, $p_{adj} < .001$ (See Table 5 and Figure 8 for an overview of the mean decoding accuracies for predictability in each ROI). Thus, we unexpectedly found evidence that indicates that the putamen, caudate, and left SMA show different activity patterns based on whether pattern-based expectations are present or not.

Cerebellar-hippocampal network

For distinguishing between periodic and aperiodic rhythms, one-sample t-tests revealed that the left and right cerebellum, and MTL all did not have a significant above chance-level (50%) mean decoding accuracy (for an overview see Table 4 and Figure 8).

Thus, we did not find evidence that the cerebellum and MTL show different activity patterns based on whether beat-based expectations are present or not.

In the cerebellum, one-sample t-tests revealed that the mean decoding accuracy level for distinguishing between predictable and unpredictable rhythms (left: $M = 62.401$, $s = 9.36$; right: $M = 61.79$, $s = 10.87$) was significantly higher than chance-level (50%), (left: $t(44) = 8.61$, $p < .001$, $p_{adj} < .001$; right: $t(44) = 7.27$, $p < .001$, $p_{adj} < .001$). The MTL shows similar results. In the left MTL, one-sample t-tests revealed that the mean decoding accuracy level for distinguishing between predictable and unpredictable rhythms (left: $M = 53.38$, $s = 8.33$; right: $M = 53.90$, $s = 8.15$) was significantly higher than chance-level (50%) (left: $t(44) = 2.72$, $p = 0.009$, $p_{adj} = 0.009$; right: $t(44) = 3.21$, $p = 0.002$, $p_{adj} = .005$) (See Table 5 and Figure 8 for an overview of the mean decoding accuracies for predictability in each ROI). Thus, in line with our expectations, we found evidence that the cerebellum and MTL show different activity patterns based on whether there are pattern-based expectations present or not in rhythms.

Table 4

Descriptive and t-test statistics (to test for above chance-level of 50%) for mean decoding accuracy of distinguishing periodic versus aperiodic rhythms

Brain area	Hemisphere	*M*	*SD*	*t*	*df*	*p*	p_{adj}
Putamen	Left	50.41	6.54	0.42	44	0.679	1.000
	Right	50.87	8.37	0.70	44	0.487	1.000
Caudate	Left	52.82	6.15	3.08	44	0.004^{**}	0.032^{*}
	Right	51.44	6.90	1.40	44	0.170	1.000
SMA	Left	51.26	8.23	1.02	44	0.311	1.000
Cerebellum	Left	51.75	9.32	1.26	44	0.214	1.000
	Right	51.79	8.07	1.49	44	0.144	1.000
MTL	Left	49.96	6.80	-0.04	44	0.970	1.000
	Right	50.81	6.85	0.79	44	0.434	1.000

$* p < .05$, $** p < .01$, $*** p < .001$

Table 5

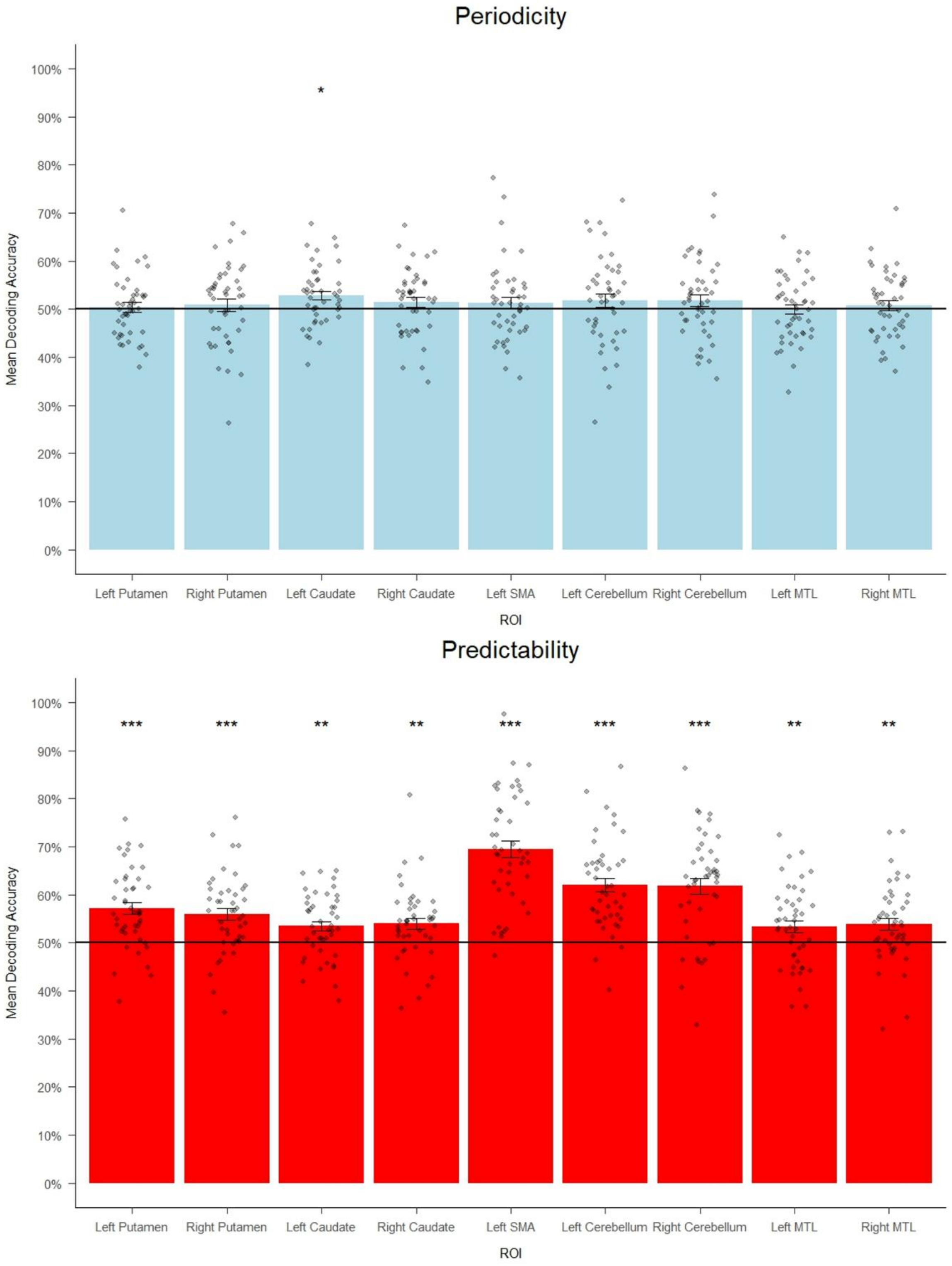
Descriptive and t-test statistics (to test for above chance-level of 50%) for mean decoding accuracy of distinguishing predictable versus unpredictable rhythms

Brain area	**Hemisphere**	***M***	***SD***	***t***	***df***	***p***	p_{adj}
Putamen	Left	57.11	8.10	5.89	44	$< .001^{***}$	$< .001^{***}$
	Right	55.87	8.19	4.88	44	$< .001^{***}$	$< .001^{***}$
Caudate	Left	53.48	6.66	3.50	44	0.001^{**}	0.004^{**}
	Right	54.01	7.65	3.51	44	0.001^{**}	0.004^{**}
SMA	Left	69.45	11.67	11.18	44	$< .001^{***}$	$< .001^{***}$
Cerebellum	Left	62.01	9.36	8.61	44	$< .001^{***}$	$< .001^{***}$
	Right	61.79	10.87	7.27	44	$< .001^{***}$	$< .001^{***}$
MTL	Left	53.38	8.33	2.72	44	0.009^{**}	0.009^{**}
	Right	53.90	8.15	3.21	44	0.002^{**}	0.005^{**}

* $p < .05$, ** $p < .01$, *** $p < .001$

Figure 8

Mean decoding accuracy per ROI (general and dots indicating per participant) compared to chance-level (50%) for periodicity and predictability with one standard error (SE) error bars



** p < .05, ** p < .01, *** p < .001 (Bonferroni-Holm corrected)*

Discussion

In the current study, we aimed to find out whether beat-based and pattern-based expectations relied on shared or separate networks. This was done by looking at BOLD responses and activity patterns in a cortico-striatal and a cerebellar-hippocampal network whilst participants listened to and rated rhythms differing in periodicity and predictability outside and inside an MRI scanner. Behavioral results showed that a lack of periodicity and predictability both increased complexity ratings. Furthermore, periodicity and predictability showed an interaction effect, so that periodicity impacted complexity ratings more in unpredictable rhythms compared to in predictable rhythms. This was true for the complexity rating inside and outside the MRI scanner. Thus, as expected, beat-based and pattern-based expectations were both formed and used to process the rhythms. This is in line with previous research that also shows that beat-based and pattern-based expectations affect behavior and rhythm processing (Bouwer et al., 2020, 2023).

At a neural level, whole brain and univariate analyses both showed no effect of periodicity on BOLD response in any brain area. This is not in line with our hypotheses, because previous studies indicated that a striato-cortical network would be necessary for processing beat-based expectations (Kasdan et al., 2022; Teghil et al., 2019; Teki et al., 2011). On the other hand, both the whole brain and univariate analyses showed that the left SMA, and the bilateral cerebellum showed an increased BOLD response for unpredictable compared to predictable rhythms. However, this is contrary to our hypotheses, because previous research indicated the reversed direction of this comparison for the cerebellum, and showed no indications for the involvement of the SMA for processing pattern-based expectations (Breska & Ivry, 2016; Paquette et al., 2017; Teki et al., 2011; Teki & Griffiths, 2016). Furthermore, the medial temporal lobes (MTL) were also expected to be involved in processing pattern-based expectations (Lee et al., 2020; Teki & Griffiths, 2016), but the whole brain and univariate analyses of the current study did not find this.

For neural activity patterns, multivariate pattern analyses (MVPA) showed that the left SMA, and the left and right putamen, caudate, cerebellum, and MTL all showed an above chance-level (50%) decoding accuracy for predictable versus unpredictable rhythms. Thus, we found evidence that the cerebellar-hippocampal network, but also unexpectedly the striato-cortical network, shows different activity patterns based on differences in pattern-based expectations. For differences in beat-based expectations, this was only true for the left caudate. Thus, we found some evidence that the activity patterns are different in the basal ganglia based on whether beat-based expectations are present or not, which in line with our hypotheses and the study by Hoddinott and Grahn (2024). However, contrary to our hypotheses and previous research, this was not the case for all the parts of the basal ganglia and for the left SMA.

Overall, these results might indicate that beat-based and pattern-based expectations do rely on different neural networks, but not on the ones previous research has indicated. Firstly, the results show some evidence that the left caudate might be involved in the processing of beat-based expectations instead of the expected involvement of the whole striato-cortical network. Additionally, pattern-based expectations do not seem to only rely on a cerebellar-hippocampal network. Namely, the results show strong evidence for the involvement of the left SMA and bilateral cerebellum and some evidence for the involvement of the putamen, caudate, and MTL for processing of pattern-based expectations.

The whole-brain analyses also showed some other brain areas that might be involved in processing pattern-based expectations. Firstly, the increased precuneus activation for predictable compared to unpredictable rhythms might be because this area is an important part of the default mode network (Azarias et al., 2025). This network becomes active during rest. Thus, predictable rhythms might have allowed the participants to rest a bit more, because these were easier to follow. Furthermore, predictable rhythms showed an increased BOLD response in the left inferior temporal gyrus compared to unpredictable rhythms. Mongelli et al. (2017) also found an increased BOLD response in this region whilst reading music annotation compared to rest. This might have activated a mental representation of the pattern in the music, which might have also happened in the current study. Additionally, the increased activation in the supramarginal gyrus might be explained by the repetition of the predictable pattern. Heim et al. (2012) found that the supramarginal gyrus is involved during repetition of speech and motor movement. So, the supramarginal gyrus might also cause some motor responses due to repetition of patterns in predictable rhythms. This might also explain the increased BOLD response in the inferior frontal triangulus for predictable compared to unpredictable rhythms, because this area has also been found to be involved in speech repetition (Thiel et al., 2005). Additionally, there is some bilateral gray matter activation that is near the somatosensory cortex. Thus, it seems that pattern-based expectations also cause some neural motor responses. Lastly, the role of the left insula is a little bit less clear. There is some evidence that shows that the insula processes novel musical information (de Aquino et al., 2019). However, our participants already listened to the same rhythms before going in the scanner, so it is unlikely that they processed the rhythms as novel musical information. Overall, this might indicate that these brain regions process pattern-based expectations by having a repeated mental motor representation of the predictable patterns of these rhythms. Thus, through the recruitment of this mental representation, the brain might predict the upcoming event in the predictable patterns.

Furthermore, unpredictable compared to predictable rhythms also caused increased BOLD responses in brain areas that were not part of our ROIs. Firstly, there was an increased BOLD response in the primary motor cortex. Thus, unpredictable rhythms might elicit some motor responses compared to predictable rhythms. Furthermore, there was a significant increase in the BOLD response in the right auditory cortex for unpredictable compared to predictable rhythms. One explanation for this is that this is due to prediction error, because the tones violate the pattern-based expectations in unpredictable rhythms. Indeed, the auditory cortex processes prediction errors in auditory sequences (Schlossmacher et al., 2022). The role of the left middle temporal cortex for unpredictable versus predictable rhythms is a bit less clear. It might be related to prediction error processing going on in the adjacent auditory cortex. However, Schlossmacher et al. (2022) did not find middle temporal cortex activation in the middle temporal cortex. Additionally, the auditory cortex activation in the current study is also laterally opposite from the middle temporal cortex activation. Rogalsky et al. (2011) did find an increased BOLD response in the left middle temporal cortex for sentences compared to melodies. Thus, the lack of a melody increases left middle temporal cortex compared to a present melody. Since melodies generally contain patterns, this could be seen as the middle temporal cortex processing non-present versus present pattern-based expectations, like in our comparison. Furthermore, language seems to have overlapping rhythmic structure with music (Patel, 2003). Therefore, the sentences from Rogalsky et al. (2011) might have had a similar unpredictable rhythmic structure compared to the rhythms we used. Thus, the middle temporal cortex might be involved in the processing the absence of pattern-based expectations in both music and language. This could mean that there might be some overlapping neural processing between music and language.

The left and right cerebellum also seem to be involved in processing pattern-based expectations, which was expected. However, the BOLD response unexpectedly increased for unpredictable compared to predictable rhythms, instead of the other way around. This might be because previous research looked at how people judged time intervals (Breska & Ivry, 2016; Lee et al., 2020; Paquette et al., 2017; Teki et al., 2011; Teki & Griffiths, 2016), which might not actually indicate processing of pattern-based expectations. For example, they found that the cerebellum volume and activity is associated with increased jitter in time intervals (Teki & Griffiths, 2016), with better interval discrimination (Breska & Ivry, 2016; Paquette et al., 2017), and increased time interval discrimination when there was no beat presence (Teki et al., 2011). On the other, Kasdan et al. (2022) found that more complex compared to less complex rhythms led to more bilateral BOLD response in the cerebellum. Their definition of complexity is based on heterogenous research where complexity is not defined consistently across studies. Yet, they boil it down to less complex rhythms being rhythms with clearer beats indicated by more stable recurring inter-onset intervals, whereas complex rhythms have fewer clear beats with less stable recurring inter-onset intervals. This would then be in line with the single interval discrimination tasks where increased jitters in the inter-onset intervals can be seen as these intervals being less stable. Furthermore, this less versus more complex definition also comes close to how the current study defines predictable versus unpredictable rhythms. Namely, rhythms with stable recurring inter-onset intervals versus rhythms without these. If this is taken into account, then the results of the complexity contrast by Kasdan et al. (2022) are indicative of differences in pattern-based expectations. This supports the results of the current study showing that the cerebellum becomes more involved for unpredictable compared to predictable rhythms.

This might also explain why the left SMA, for which there are also indications that it processes time intervals (Nani et al., 2019), also unexpectedly showed the same pattern of results. Namely, this region also shows increased activity in more complex compared to less complex rhythms (Kasdan et al., 2022). Thus, this could be seen as evidence that the SMA is also more involved for unpredictable compared to predictable rhythms, which is line with the results of the current study.

This might also explain why the current study did not find changes in BOLD responses in the MTL based on difference in processing pattern-based expectations. Namely, Kasdan et al. (2022) did not find any MTL activity differences based on differences in rhythm complexity. This could indicate that the MTL is not involved in processing pattern-based expectations. Another explanation is that the complexity ratings used in the task of the current study did not demand memorization. Lee et al. (2020) found that memorization of the durations within the rhythms is needed for the involvement of the MTL. However, Bouwer et al. (2026) found that humans rely on imprecise representations of patterns within rhythms, and that these representations may be adapted based on what the task demands. Thus, the complexity task used in the current study may not have required precise enough representations of the patterns to warrant memorization, and thus the involvement of the MTL. Therefore, the MTL might only be involved in processing pattern-based expectations when the task demands memorization.

For pattern-based expectations, the MVPA showed a pattern of results that was similar, but also slightly different compared to the univariate analyses. It again showed the involvement of the left and right cerebellum for pattern-based expectations, which was hypothesized. Furthermore, this was also again unexpectedly the case for the left SMA. This is in line with the univariate analyses. However, the MVPA also showed increased above chance-level mean decoding accuracies for the left and right putamen, caudate, and MTL. This was expected for the MTL, but not for the putamen, and caudate. This is also not in line with Kasdan et al. (2022), because they did not find the involvement of these brain regions for more complex rhythms. They did find some involvement of the putamen for less compared to more complex rhythms. So, this region might process the presence of pattern-based expectations. However, the left and right putamen, caudate, and MTL do seem to show a lower above chance-level mean decoding accuracy compared to the left SMA, and the left and right cerebellum (see Table 5). This difference might be because pattern-based expectations require more processing from the cerebellum and left SMA compared to the caudate, putamen, and MTL. This could explain why the cerebellum and left SMA show processing involvement for the univariate and multivariate analyses and the caudate, putamen, and MTL just show this involvement in the multivariate analysis. Thus, the left SMA, and left and right putamen, caudate, cerebellum, and MTL, might all process pattern-based expectations instead of just the cerebellar-hippocampal network.

For beat based expectations, it is unclear why the left SMA is not involved in processing these temporal expectations. One explanation could be that the SMA only shows increased activation for rhythms with beat-based expectations compared to rest and not for rhythms with beat-based expectations compared to rhythms without beat-based expectations. Indeed, this is exactly what Kasdan et al. (2022) found. However, the studies used by Kasdan et al. (2022) for the periodic versus aperiodic contrast showed mixed results for SMA BOLD responses. Furthermore, most studies that did not find an effect of periodicity on the SMA might have possible confounding effects that could have interfered with this effect. Namely, some used beat production instead of perception (De Pretto & James, 2015; Kornysheva & Schubotz, 2011), Grahn and Rowe (2009) manipulated volume, and Geiser et al. (2012) manipulated intensity. On the other hand, the studies that only manipulated periodicity during beat perception did find an increased BOLD response in the SMA for periodic compared to aperiodic rhythms (Araneda et al., 2017; Grahn & Rowe, 2013; Teki et al., 2011). These designs are more in line with the current study where the comparison was also purely based on periodicity during the perception of rhythms. However, these studies that did find an effect do have slightly different periodic rhythms compared to the current study. Namely, in their periodic rhythms, the beat always coincided with a tone, whereas that is not the case for the periodic rhythms in the current study (see Figure 1). Thus, the presence of a tone on each beat might be a requirement for the involvement of the SMA in beat-based expectations, and this might explain why the current study did not find this effect.

This might also explain the lack of hypothesized putamen involvement for processing beat-based expectations. In the studies used by Kasdan et al. (2022), the results were again mixed about the involvement of the basal ganglia in processing beat-based expectations (Araneda et al., 2017; De Pretto & James, 2015; Geiser et al., 2012; Grahn & Rowe, 2009, 2013; Kornysheva & Schubotz, 2011; Teki et al., 2011). However, Kasdan et al. (2022) did find increased activation in the putamen, whereas the current study did not. This discrepancy could again be explained by the fact that most studies in this meta-analysis used rhythms where each beat coincided with a tone and that the current study did not have these kinds of rhythms. These on-beat tones might be necessary for the involvement of the putamen in processing beat-based expectations.

However, Kasdan et al. (2022) did not find increased activation in the caudate, which the current study also did not find. Only a few studies in this meta-analysis found the caudate to be involved in auditory beat-based expectations (Grahn & Rowe, 2009; Teki et al., 2011), but most did not find this (Araneda et al., 2017; De Pretto & James, 2015; Geiser et al., 2012; Grahn & Rowe, 2013; Kornysheva & Schubotz, 2011). Araneda et al. (2017), did find some involvement of the caudate during beat-based expectations, but this was for visual beat-based expectations and not for auditory beat-based expectations. Thus, this might indicate that the caudate is not involved in processing beat-based expectations.

On the other hand, the MVPA did show some involvement of the caudate in processing beat-based expectations. Namely, the left caudate showed a significant above chance-level mean decoding accuracy. However, this was only 2.82 percentage points above chance-level, which is not that big of an effect relative to the increases found for predictability. On the other hand, Hoddinott and Grahn (2024) also found different activity patterns in the caudate based on beat-based expectations, but this was just under the threshold for statistical significance. This might be because the sample size of the current study was almost twice as big as theirs. Thus, their sample size might not have been large enough to find a significant effect of beat-based expectations in the caudate, whereas the current study could find this significant small effect in the left caudate. This indicates that the left caudate might still be involved in processing beat-based expectations.

However, when it comes to activity patterns in the SMA and putamen, the current study did not find that these regions were involved in processing beat-based expectations. On the other hand, Hoddinott and Grahn (2024) did find different activity patterns based on differences in beat-based expectations in the SMA and putamen. One explanation for this is that Hoddinott and Grahn (2024) used a representational similarity analysis, whereas the current study used decoding accuracies. However, these analyses both look at the same activity patterns, thus it would be unlikely that this would cause this difference. An explanation that does seem plausible is task differences. In the current study, the participants listened to the rhythms and then rated the complexity of these rhythms for random trials. Hoddinott and Grahn (2024), on the other hand, used a task where participants listened to two rhythms per trial and were then asked whether a third rhythms was the same or different. They had to make this judgment for every trial. It may be that having to constantly distinguish between rhythms requires a more active processing of beat-based expectations, whereas a sporadic complexity judgment might not require this. There is evidence that task demands can alter the representation of rhythmic patterns (Bouwer et al., 2026), so this might also be true for rhythmic beats. Thus, it might be that the SMA and putamen show different activity patterns for differences in beat-based expectations, only when the task demands enough processing of these beat-based expectations. Another explanation is again that the forming of beat-based expectations requires the presence of a tone on each beat, because Hoddinott and Grahn (2024) also found their results with these kind of rhythms.

These univariate and multivariate results implicate that the interplay between the basal ganglia and the SMA, proposed by Cannon and Patel (2021), might work differently than proposed. This interplay might thus require every beat to coincide with a tone. Hoddinott and Grahn (2024) found evidence for this, as they only found an increased BOLD response and different activity patterns in the putamen for strong beat compared to non-beat rhythms. On the other hand, they did not find this effect for weak beat compared to non-beat rhythms. They found similar results for the SMA, but only for activity patterns and not for the BOLD response. These strong beats did have a tone on each beat, and the weak beats did not. Thus, these differences between the results for strong and weak beats might be due to the difference in the number of beats that coincide with a tone. However, it remains unclear if this is the reason for this. Therefore, future research is needed to see what the role is of beats coinciding with tones for the involvement and interplay of the SMA and the basal ganglia for processing beat-based expectations.

For processing pattern-based expectations in the SMA, we can be quite sure about our activity pattern findings, because the mean decoding accuracy increased quite a lot for this brain region for pattern-based expectations. This is also true for the cerebellum. However, all our other ROIs also showed a significant increase in decoding accuracy based on predictability. On the other hand, this increase was quite small for these other ROIs. Since all ROIs showed this pattern, then this may also be true for other brain regions. Thus, this might indicate that our predictability manipulation caused some general activity pattern changes across larger parts of the brain, which might mean that our manipulation went wrong. For this, it would have been better to have included a dummy-ROI to see if our manipulation was specific to our ROIs. For example, we would not expect our auditory stimuli to influence activity patterns in the visual cortex. Thus, the visual cortex would have been a great candidate to be a dummy-ROI. If we would not find different activity patterns in this region based on predictability, then we would be more confident that our manipulation was specific to our ROIs.

Additionally, in the current study, we did not make sure that the participants actually processed beat-based expectations. This is also the case for pattern-based expectations. It is frequently assumed that most people develop the ability to perceive beat-based expectations (Honing, 2012). However, Bouwer et al. (2023) found that only two-thirds of their participants showed evidence of processing beat-based expectations. This might be mitigated in our study, because we recruited many participants that were musically trained. Bouwer et al. (2023) found that musical training is positively associated with better perception of beat-based expectations. They also found this for pattern-based expectations. Thus, any potential lack of presence of processed pattern-based expectations might also be mitigated. However, the current study did not take musical training into account in the analyses. Therefore, it remains unclear what effect musical training has on the BOLD responses and activity patterns in the striato-cortical and cerebellar-hippocampal network for processing temporal expectations. Future studies should look at this relationship. Kasdan et al. (2022) did find that musicianship does not greatly affect complexity processing in rhythms, where complexity could be indicative of pattern-based expectations. However, it is uncertain whether this is actually indicative of this.

Besides the musically trained people, another strength of the current study is that the participants did not have to respond after each trial in the MRI scanner. In this way, the participants often only listened to the rhythms without having to perform a task. Thus, the rhythms were often the only present stimuli. This may have prevented any confounding variable interfering with our results besides the beat-based and pattern-based expectations within our rhythms. This is unlike many previous studies that did require participants to respond for every trial (Araneda et al., 2017; De Pretto & James, 2015; Geiser et al., 2012; Hoddinott & Grahn, 2024; Teki et al., 2011). On the other hand, the lack of a required response on many trials might also be a limitation. It could be that this causes the participants to pay less attention to the rhythms, which could cause less processing of the temporal expectations. This might be the reason we found some increased activation in the precuneus, which is part of the default-mode network (Azarias et al., 2025), in one of our whole brain analysis contrasts. Grahn and Rowe (2013), also did not require a response on each trial where participants listened to rhythms, and they also found some increased precuneus activation, which was not found in the studies where a response was required for each trial. Furthermore, they found this increased activation for periodic compared to aperiodic rhythms. These periodic beats are likely less complex and easier to process. Thus, it could be argued that the precuneus becomes active during easier trials. This is in line with what was found in the current study, where the precuneus was active for less complex predictable compared to more complex unpredictable rhythms. Thus, it seems important for future studies to make sure that the participants are always paying attention to the rhythms, whilst also trying to limit any confounding effects due to task demands.

Conclusion

In summary, we have provided evidence that beat-based and pattern-based expectations might not rely on the same neural network in unexpected ways. Especially the left SMA showed an unexpected role. It seems that this region processes the absence of pattern-based expectations instead of beat-based expectations. These findings provide novel evidence for how our brain processes rhythmic temporal expectations and indicate that previous research might have confounded temporal expectations with other factors, such as complexity, task demands, and on-beat tones.

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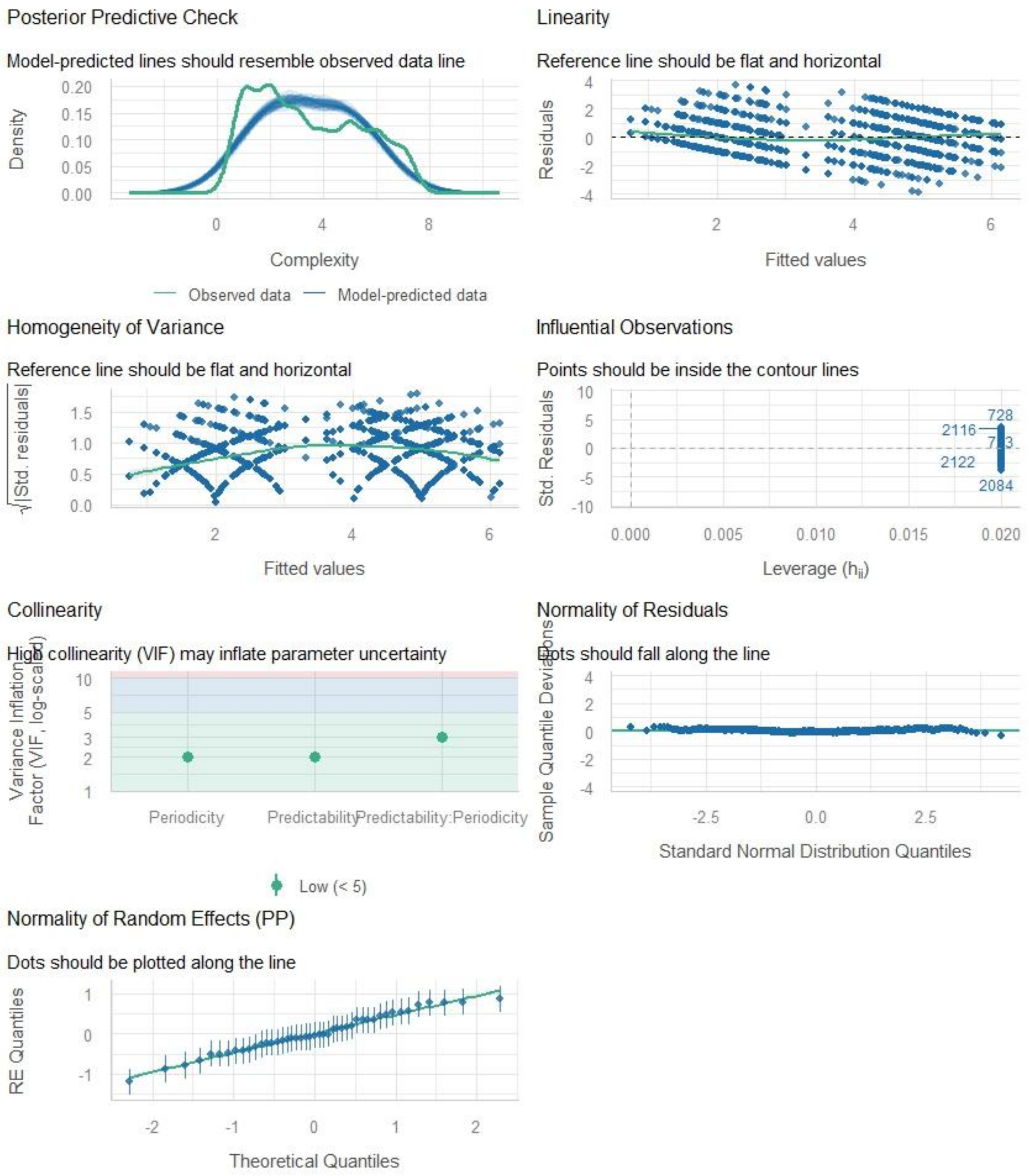
Appendix A

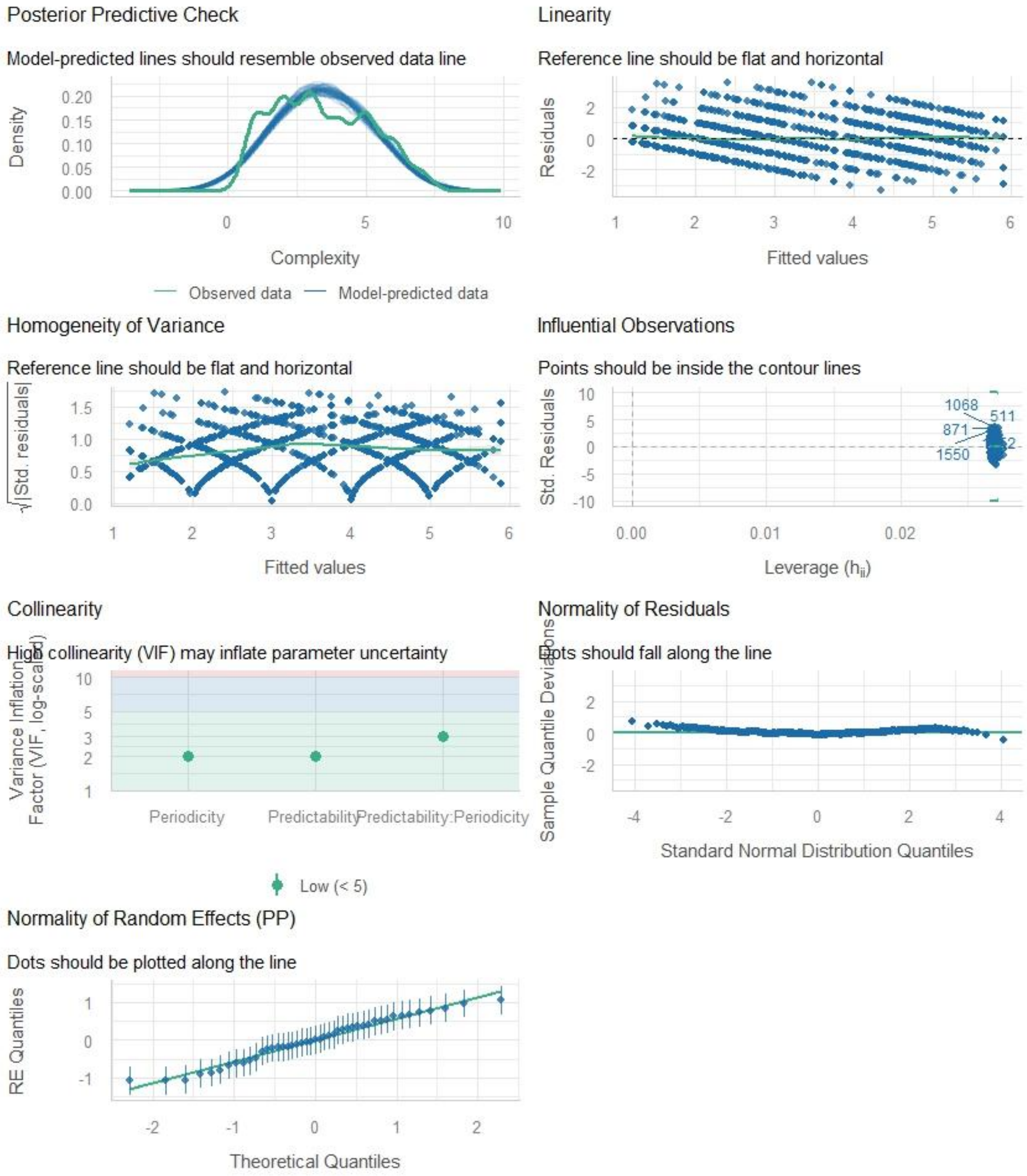
Assumption checks for complexity and univariate analyses

Complexity analyses

Outside scanner

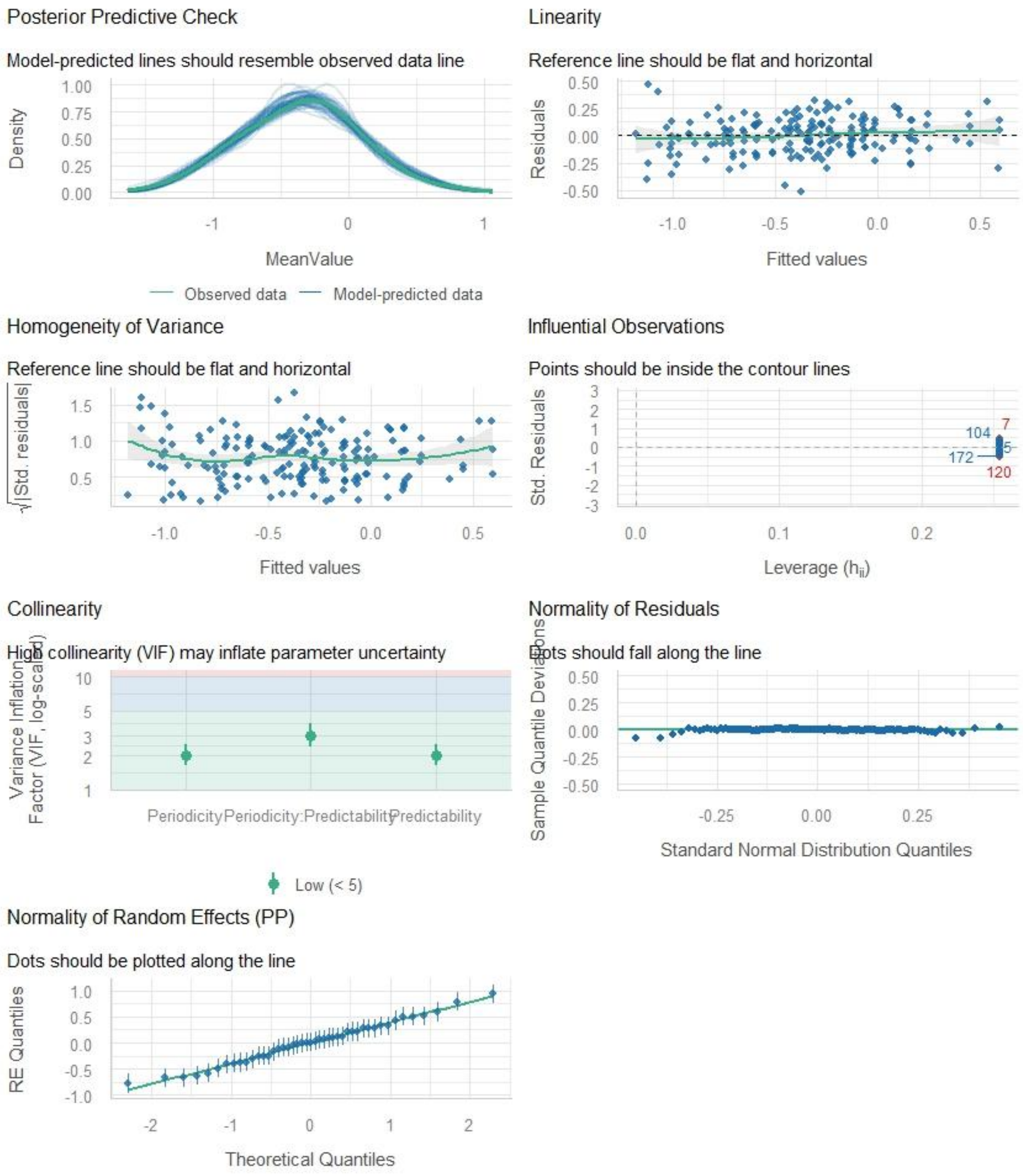


Inside scanner

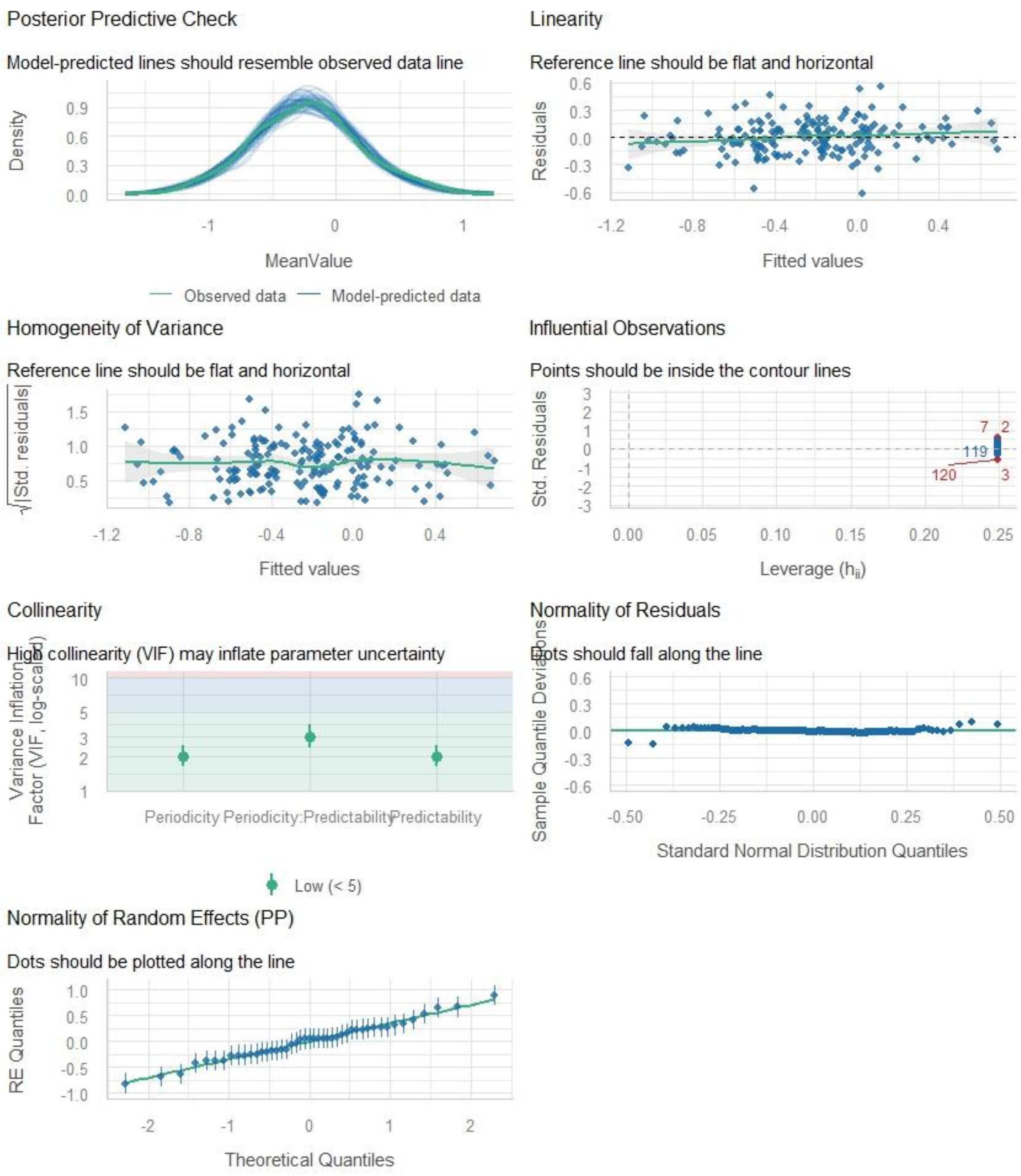


Univariate analyses

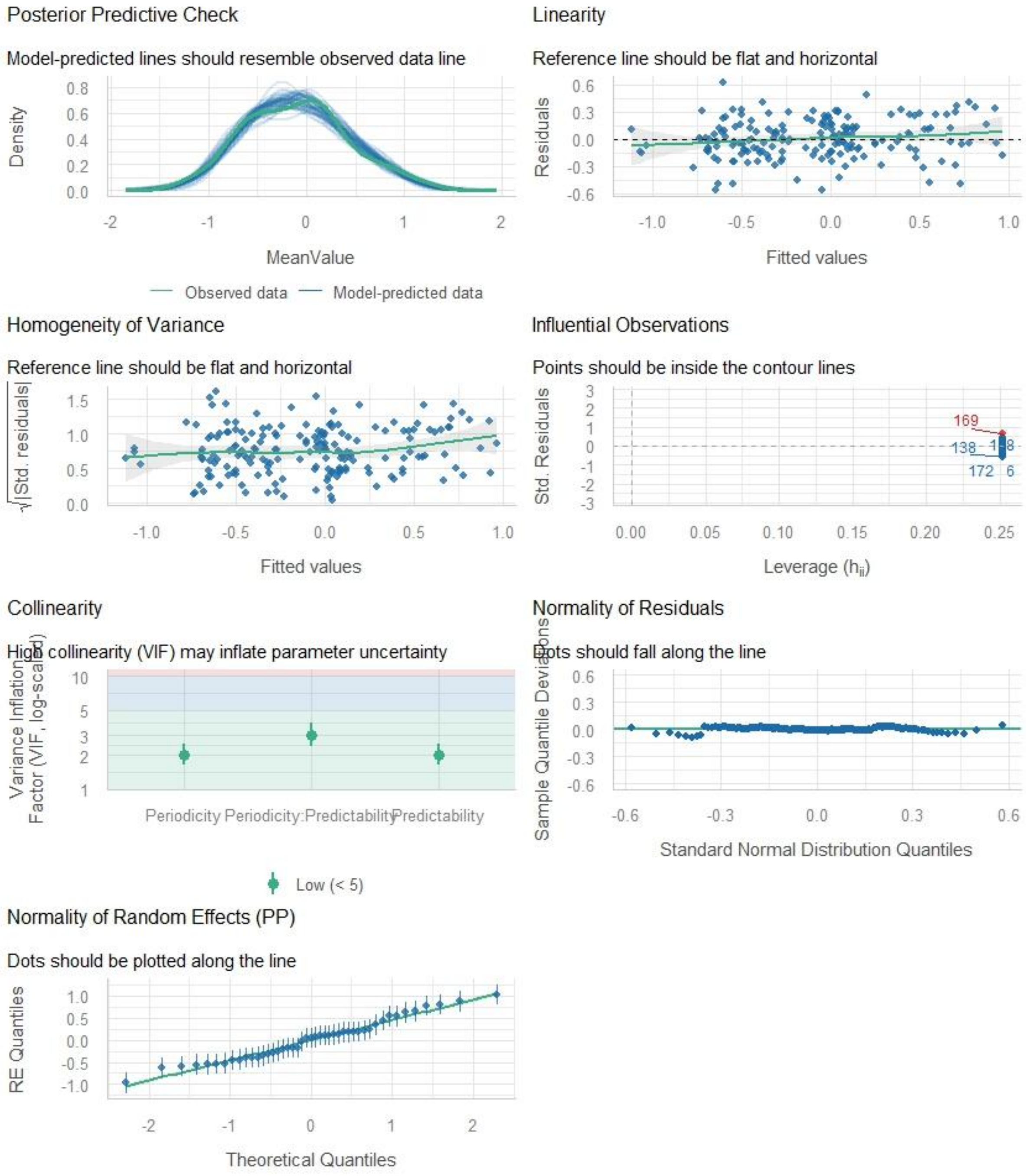
Left putamen



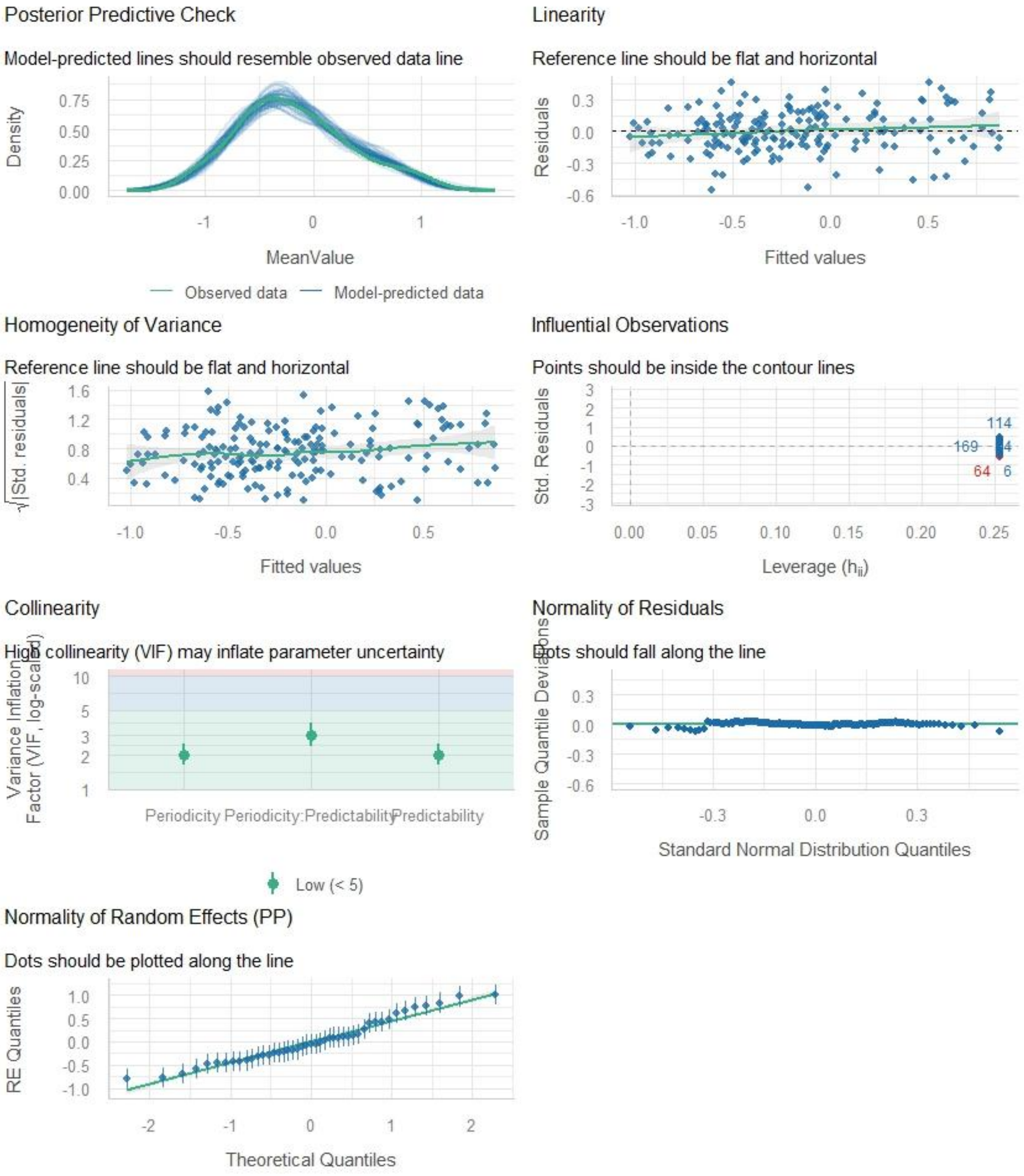
Right putamen



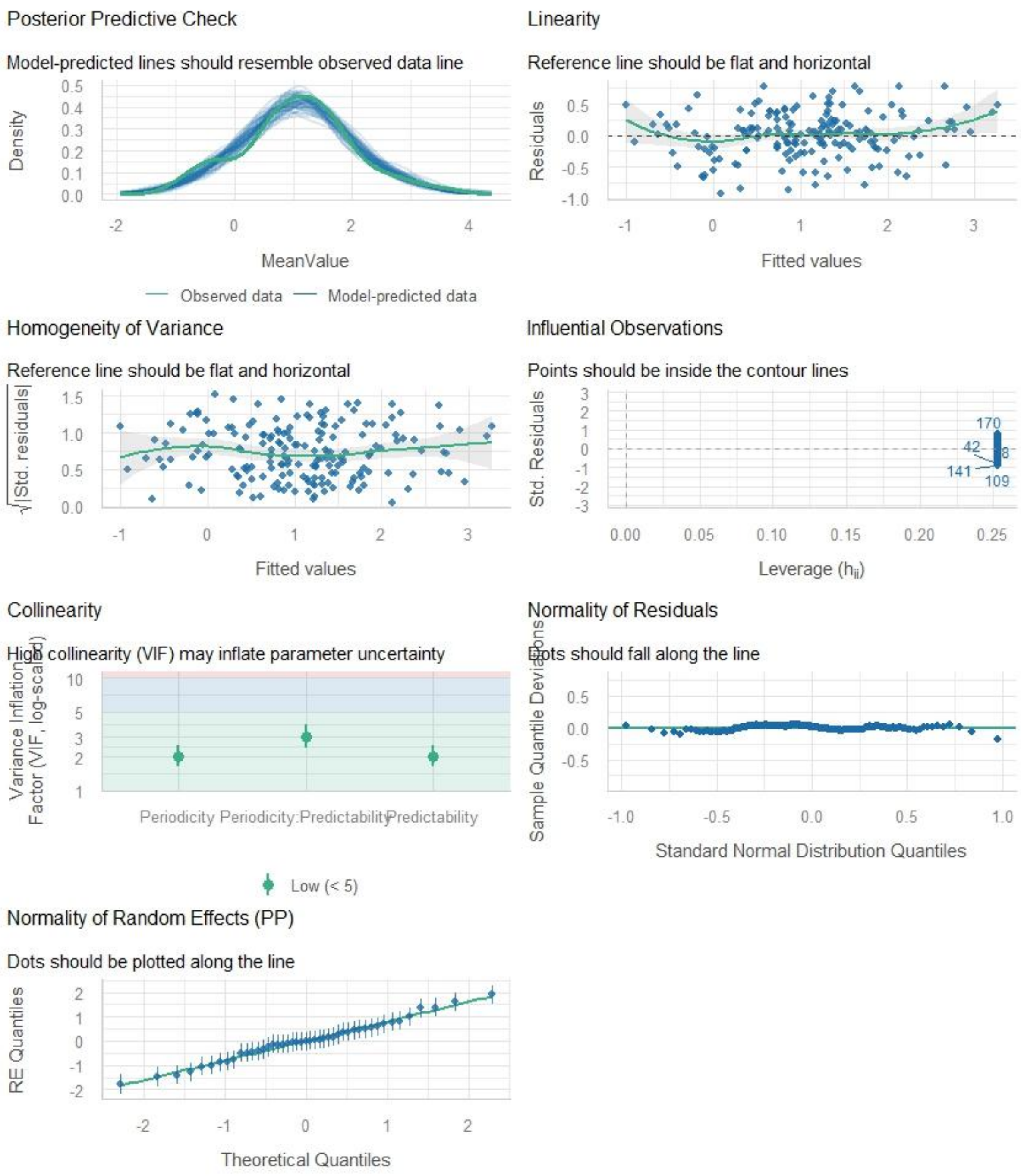
Left Caudate



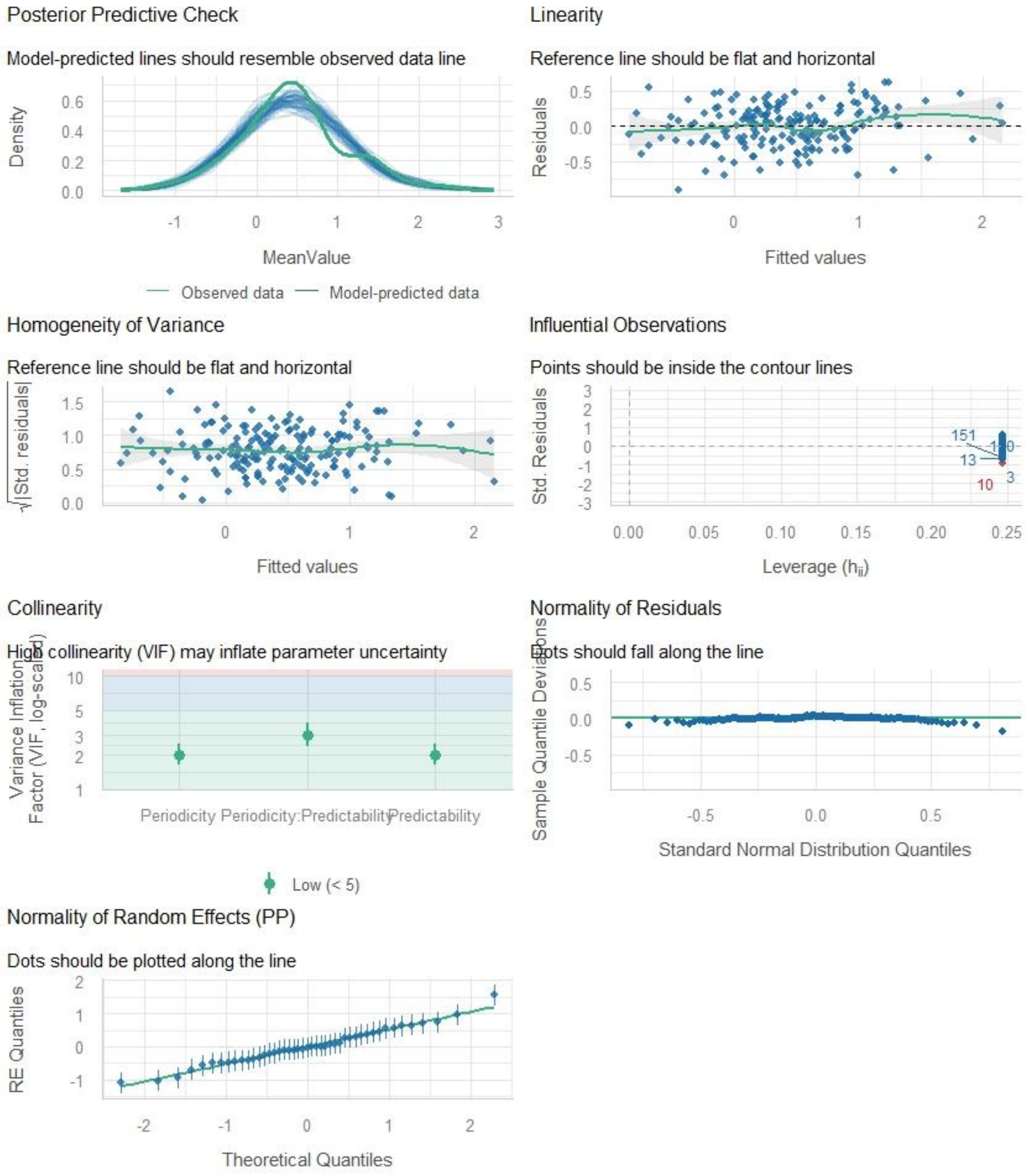
Right Caudate



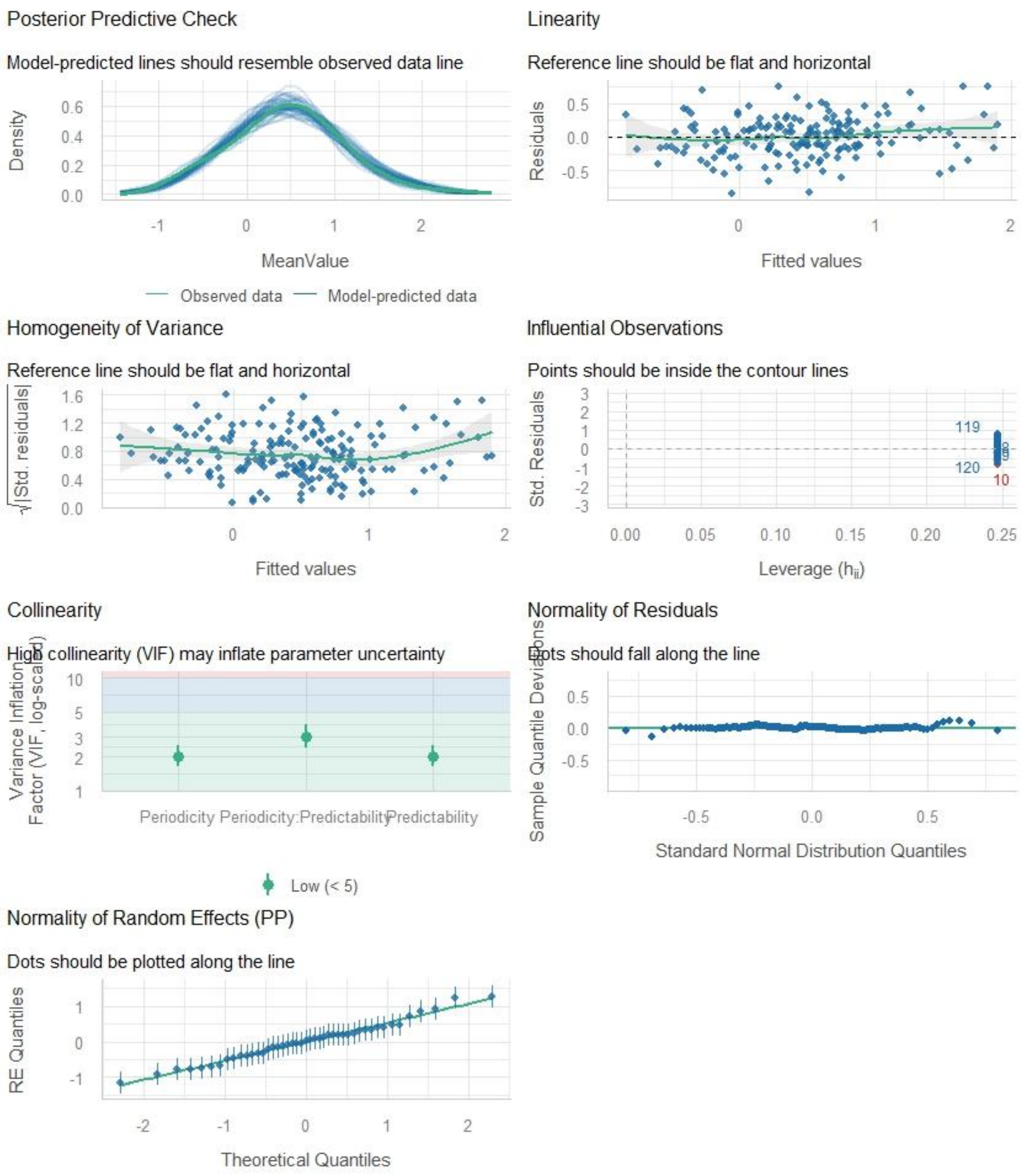
Left SMA


Posterior Predictive Check
Model-predicted lines should resemble observed data line
Density
0.5
0.4
0.3
0.2
0.1
0.0
-2
0
2
4
MeanValue
Observed data
Model-predicted data
Linearity
Reference line should be flat and horizontal
Residuals
0.5
0.0
-0.5
-1.0
-1
0
1
2
3
Fitted values
Homogeneity of Variance
Reference line should be flat and horizontal
√|Std. residuals|
1.5
1.0
0.5
0.0
-1
0
1
2
3
Fitted values
Influential Observations
Points should be inside the contour lines
Std. Residuals
3
2
1
0
-1
-2
-3
170
42
8
141
109
0.00
0.05
0.10
0.15
0.20
0.25
Leverage (h_{ii})
Collinearity
High collinearity (VIF) may inflate parameter uncertainty
Variance Inflation Factor (VIF, log-scaled)
10
5
3
2
1
Periodicity
Periodicity:Predictability
Predictability
Low (< 5)
Normality of Residuals
Dots should fall along the line
Sample Quantile Deviations
0.5
0.0
-0.5
-1.0
-0.5
0.0
0.5
1.0
Standard Normal Distribution Quantiles
Normality of Random Effects (PP)
Dots should be plotted along the line
RE Quantiles
2
1
0
-1
-2
-2
-1
0
1
2
Theoretical Quantiles

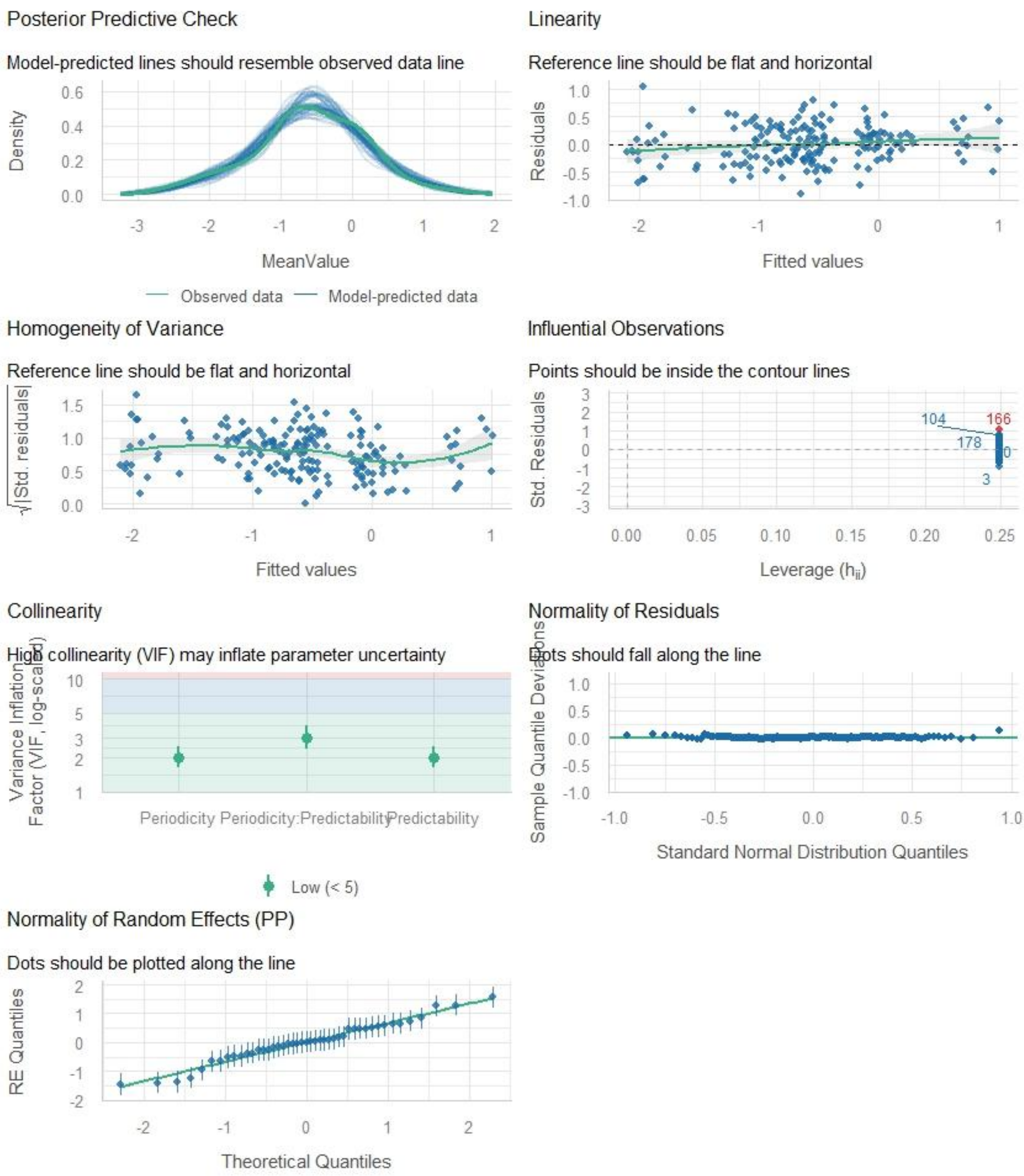
Left Cerebellum



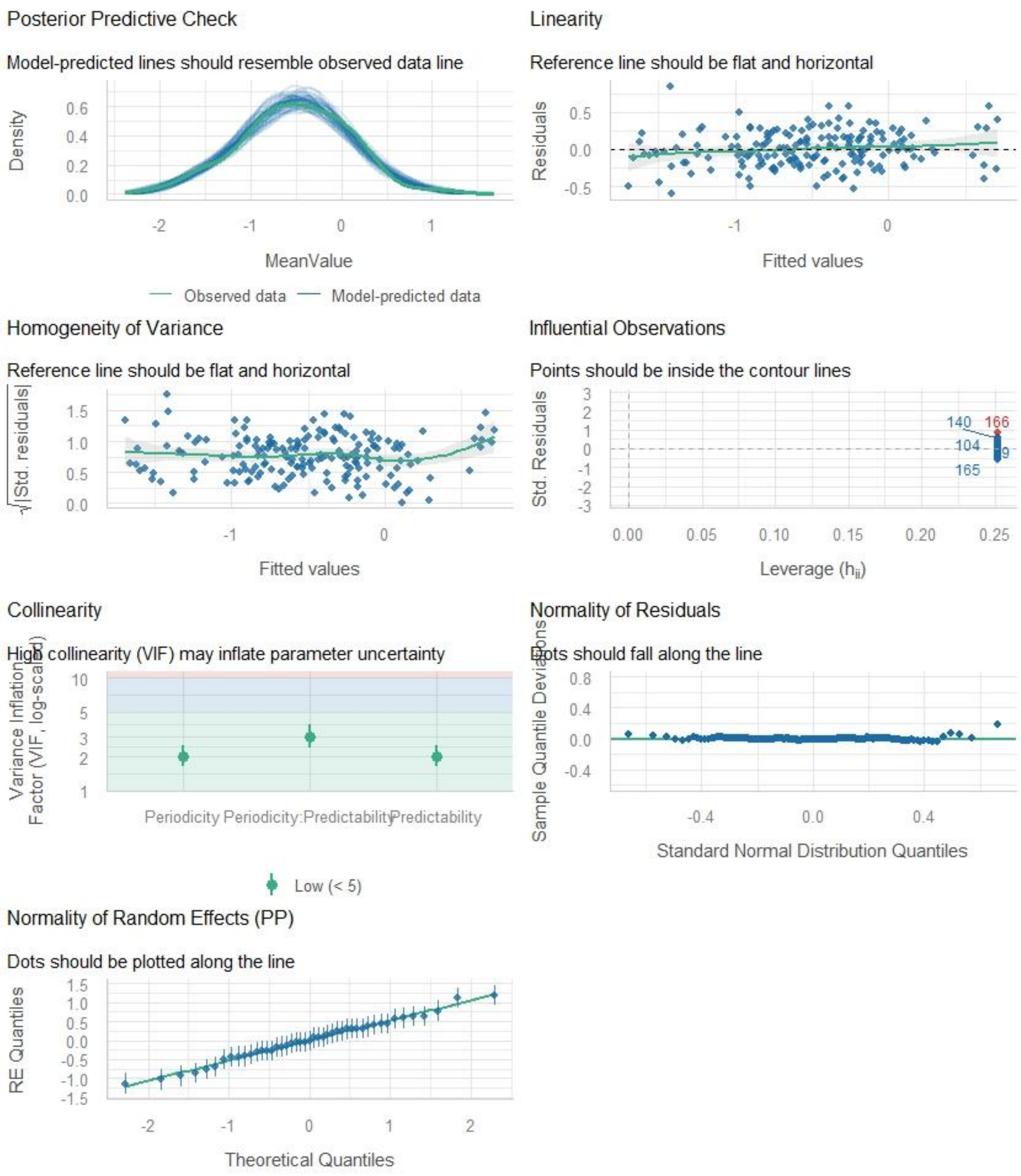
Right Cerebellum



Left medial temporal lobe



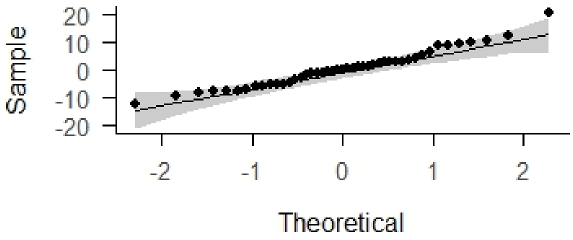
Right medial temporal lobe

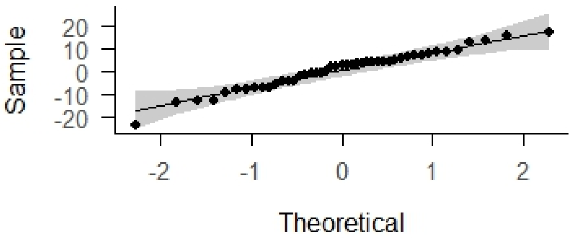


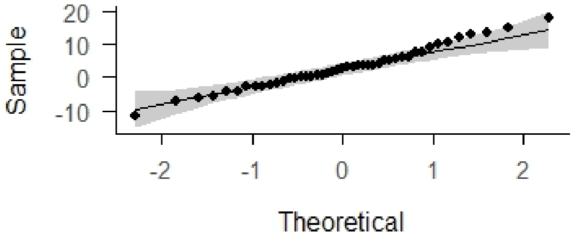
Appendix B

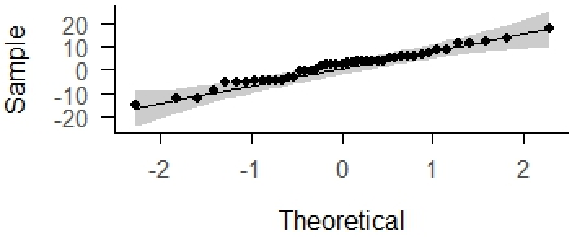
Normality assumption checks for multivariate pattern analyses

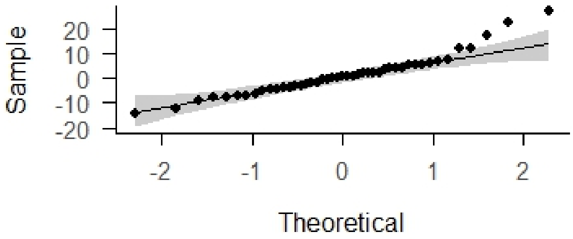
Periodicity

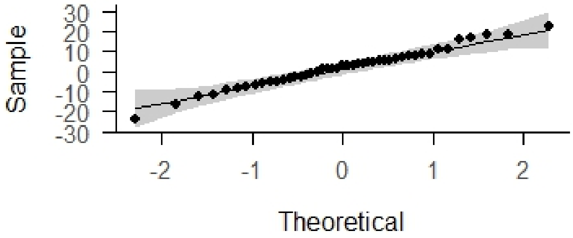

Left Putamen

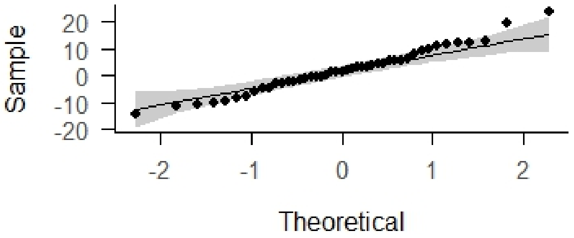

Right Putamen

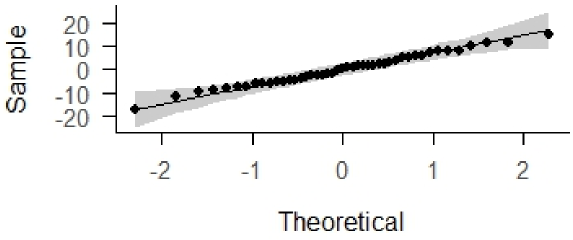

Left Caudate

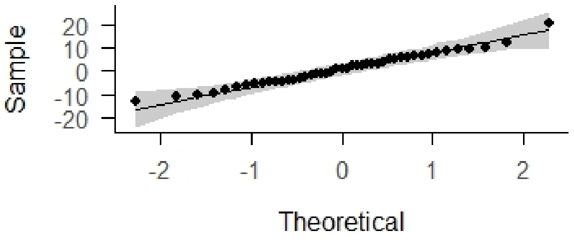

Right Caudate


Left SMA


Left Cerebellum


Right Cerebellum


Left MTL


Right MTL

Predictability