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RESEARCH REPORT

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Dopamine dysregulation in Parkinson's disease flattens the pleasurable urge to move to musical rhythms

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Abstract

The pleasurable urge to move to music (PLUMM) activates motor and reward areas of the brain and is thought to be driven by predictive processes. Dopamine in motor and limbic networks is implicated in beat-based timing and music-induced pleasure, suggesting a central role of basal ganglia (BG) dopaminergic systems in PLUMM. This study tested this hypothesis by comparing PLUMM in participants with Parkinson's disease (PD), age-matched controls, and young controls. Participants listened to musical sequences with varying rhythmic and harmonic complexity (low, medium and high), and rated their experienced pleasure and urge to move to the rhythm. In line with previous results, healthy younger participants showed an inverted U-shaped relationship between rhythmic complexity and ratings, with preference for medium complexity rhythms, while age-matched controls showed a similar, but weaker, inverted U-shaped response. Conversely, PD showed a significantly flattened response for both the urge to move and pleasure. Crucially, this flattened response could not be attributed to differences in rhythm discrimination and did not reflect an overall decrease in ratings. For harmonic

Victor Pando-Naude and Tomas Edward Matthews shared first authorship.

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complexity, PD showed a negative linear pattern for both the urge to move and pleasure while healthy age-matched controls showed the same pattern for pleasure and an inverted U for the urge to move. This contrasts with the pattern observed in young healthy controls in previous studies, suggesting that both healthy aging and PD also influence affective responses to harmonic complexity. Together, these results support the role of dopamine within cortico-striatal circuits in the predictive processes that form the link between the perceptual processing of rhythmic patterns and the affective and motor responses to rhythmic music.

KEYWORDS
basal ganglia, dopamine, harmony, music-induced pleasure, Parkinson's disease, predictive processes, rhythm

1 | INTRODUCTION

When listening to rhythmic music, we often feel an automatic and pleasurable urge to tap our feet or bob our heads along with the underlying beat or pulse of the rhythm. This pleasurable urge to move to music (PLUMM) is a key component of groove (Câmara & Danielsen, 2018; Duman et al., 2022; Janata et al., 2012; Madison, 2006; Senn et al., 2019; Witek et al., 2014) and highlights the deep connection between music, movement and pleasure. In a recent neuroimaging study, we showed that PLUMM is associated with greater activity in dorsal and ventral striatal regions within the basal ganglia (BG), along with cortical regions associated with the motor and limbic cortico-striato-thalamo-cortical circuits (Alexander et al., 1986; Matthews et al., 2020) (henceforth, cortico-striatal circuits). This aligns with previous work implicating these loops in the predictive processes thought to drive both rhythm perception and music-induced pleasure, along with motor timing and reward processes more generally (Pando-Naude et al., 2021). For example, the motor cortico-striatal circuit is consistently engaged during rhythm and beat perception and production (Bengtsson et al., 2009; Chen et al., 2008; Grahn & Rowe, 2009, 2013; Kasdan et al., 2022; Schubotz et al., 2000), whereas the limbic cortico-striatal circuit is implicated in music-induced pleasure (Blood et al., 1999; Blood & Zatorre, 2001; Cheung et al., 2019; Gold et al., 2019; Salimpoor et al., 2011, 2013; Shany et al., 2019). Within cortico-striatal circuits, dopamine seems to have a functional role in both beat-based (Biswas et al., 2016; Cameron et al., 2016; Geiser & Kaelin-Lang, 2011; Grahn & Brett, 2009; Hsu et al., 2022) and motor timing (Jahanshahi et al., 2010), as well as music-induced pleasure (Ferreri et al., 2019; Gebauer et al., 2012; Salimpoor et al., 2011). This confluence of musically relevant timing, motor and reward processes suggests a key role of dopamine in PLUMM (Matthews et al., 2020). To directly test this, we compared ratings of pleasure and the urge to move in two groups of participants with Parkinson's disease (PD), as well as age-matched and younger healthy controls.

Dopamine is thought to be necessary for the predictive processes that are fundamental to motor timing and reward mechanisms (Meck, 2006; Schultz et al., 1997; Tomassini et al., 2016), likely via separate pathways within motor and limbic cortico-striatal circuits. The motor cortico-striatal circuit, including the putamen, premotor cortex and supplementary motor area, encompasses the nigrostriatal dopaminergic pathway, wherein dopaminergic cells in the substantia nigra pars compacta project to the dorsal striatum, including the putamen and caudate. Nigrostriatal dopamine is implicated in timing processes in the hundreds of milliseconds range that are necessary for sensory anticipation and motor preparation (Behroozmand & Johari, 2019; Coull et al., 2012; Jones & Jahanshahi, 2014; Meck, 2006). The limbic cortico-striatal circuit, including the nucleus accumbens and medial prefrontal cortices, encompasses the mesolimbic dopaminergic pathway, wherein cells in the ventral tegmental area project to the ventral striatum including the nucleus accumbens. Longstanding models suggest that mesolimbic dopamine encodes reward prediction errors, indicating whether a reward was better or worse than expected (Schultz et al., 1997). Recent empirical and theoretical work suggest an expansion of the role of striatal dopamine to include sensory prediction errors (when sensory outcomes deviate from predictions), as well as the certainty of sensorimotor, state or value representations (Friston et al., 2014, 2012; Gershman & Uchida, 2019).

Predictive processes are crucial to the perception and production of music, as well as affective responses including PLUMM. Music is often highly structured both in time and tonal space. Embellishments on or deviations from this structure can elicit prediction confirmations or errors and, in turn, affective and motor responses within listeners (Huron, 2006; Koelsch et al., 2019; Meyer, 1956; Salimpoor et al., 2015; Vuust et al., 2022; Zald & Zatorre, 2011). In terms of PLUMM, there is an inverted U-shaped relation between rhythmic complexity (predictability) and ratings of both the urge to move and pleasure, as the highest ratings are elicited by rhythms that are neither too simple (predictable) nor too complex (Matthews et al., 2019, 2022; Sioros et al., 2014; Spiech et al., 2022; Stupacher, Wrede, & Vuust, 2022; Witek et al., 2014). A predictive processing account suggests that this pattern is driven by both the number of rhythm-based temporal prediction errors and the certainty of the antecedent predictions (Koelsch et al., 2019; Vuust et al., 2018, 2022; Vuust & Witek, 2014). According to this framework, predictions arise from an internal model based on prior experience. In the case of rhythmic music, the model is the meter, which, in western musical traditions, is the pattern of strong beats (when a note is very likely to occur) and weak beats (when a note is less likely). Therefore, moderately complex, high-PLUMM rhythms are regular enough to enable relatively precise metrical predictions and complex enough to challenge them. Recently, harmonic complexity was also shown to influence PLUMM via its effect on pleasure, in contrast to rhythmic complexity which directly affects both the urge to move and pleasure (Matthews et al., 2019). This suggests that the urge to move and pleasure can be at least partially disentangled via the differential effects of rhythm and harmony.

The role of dopamine in temporal and reward-related predictive processes is well established (Hollerman & Schultz, 1998; Nomoto et al., 2010); however, it has yet to be linked to PLUMM. A recent theoretical model suggests that nigrostriatal dopamine plays a key role in probabilistic representations of the musical beat and thus supports beat-based motor and perceptual timing (Cannon & Patel, 2020). This is consistent with studies involving participants with PD, which is characterized by cell loss in the substantia nigra leading to dysregulated dopamine in the nigrostriatal pathway and thus problems with motor timing (e.g., dysfunctional gait and bradykinesia). Specifically, PD show poorer performance and altered brain activity during perceptual and motor tasks that rely on beat-based timing (Bellinger et al., 2017; Benoit et al., 2014; Biswas et al., 2016; Breska & Ivry, 2018; Cameron et al., 2016; Elsinger et al., 2003; Geiser & Kaelin-Lang, 2011; Grahn & Brett, 2009; Hsu et al., 2022; Jones et al., 2008; Merchant et al., 2008; O'Boyle et al., 1996; Vikene et al., 2019a, 2019b). There is evidence that neural oscillations at the beat frequency and the beta frequency range (13–30 Hz) are involved in beat and meter perception and synchronization and thus may provide a neural mechanism underlying beat-based predictive processes (Large & Snyder, 2009). Intriguingly, participants with PD show weaker entrainment of beta-range neural oscillations to rhythmic stimuli (te Woerd et al., 2017), suggesting that beta entrainment may mediate the link between dopamine dysregulation and beat-based timing. More generally, one study showed that participants with PD had a reduced urge to engage with music via dancing or singing compared with healthy controls (Morris et al., 2019), suggesting a weakened link between music and movement. Finally, rhythmic auditory stimulation, for example, cueing participants' gait with a metronome, improves motor deficits in participants with PD (Bella et al., 2017; Lei et al., 2019; Pau et al., 2016; Thaut et al., 1996), further supporting the link between dopamine and predictive motor timing.

The BG and dopamine are also implicated in music-induced pleasure (Ferreri et al., 2019; Gebauer et al., 2012; Salimpoor et al., 2011). Activity in the limbic cortico-striatal circuit, as well as functional and structural connectivity within this loop, and between the striatum and auditory cortex, are associated with music liking (Blood et al., 1999; Blood & Zatorre, 2001; Salimpoor et al., 2013), music wanting (i.e., the money one is willing to spend on a given piece; Salimpoor et al., 2013) and music reward sensitivity (Martinez-Molina et al., 2019; Martínez-Molina et al., 2016). Activity in the nucleus accumbens has also been linked to the predictive processes thought to underlie music-derived pleasure (Cheung et al., 2019; Gold et al., 2019; Seger et al., 2013; Shany et al., 2019). Evidence of a causal role for striatal dopamine in music-induced pleasure more generally comes from two parallel lines of research showing that modulations in BG activity or dopamine availability results in corresponding modulations in liking and wanting of music (Ferreri et al., 2019; Mas-Herrero et al., 2018). However, many of these studies have focused on harmonic predictions rather than the temporal predictions that dominate in PLUMM (Matthews et al., 2019).

Given the role of dopamine within cortico-striatal circuits in both rhythm-based predictive timing and music-derived pleasure, we investigated the link between dopamine and PLUMM by comparing the urge to move and pleasure in PD along with healthy older and younger controls. We hypothesized that the inverted U-shaped relation between rhythmic complexity, urge to move and pleasure would differ in PD compared with controls but

that the relationship between harmonic complexity and PLUMM would be unaffected. Aging has also been linked to changes in neural and behavioural correlates of rhythm (Al Jaja et al., 2020; Henry et al., 2017; Krampe et al., 2001, 2002, 2005; Sauvé et al., 2019; Turgeon & Wing, 2012) and reward processing (Chowdhury et al., 2013; Eppinger et al., 2013; Schott et al., 2007; Vink et al., 2015). Therefore, the inclusion of both healthy older and younger controls also allowed us to examine any age-related changes in overall PLUMM response.

2 | MATERIAL AND METHODS

2.1 | Participants

The study was conducted at the Center for Music in the Brain, Aarhus University, Denmark. A total of 112 participants performed the experiment. Data from 101 of these participants were analysed after 11 PD were excluded from the analysis due to incomplete data. Table 1 shows a summary of demographic data.

PD participants (age 46–80) were diagnosed with idiopathic PD, in early- to mid-stages based on the Hoehn and Yahr scale (Di Biase et al., 2017; Hoehn & Yahr, 1967). They were diagnosed by a certified neurologist according to the Movement Disorder Society (MDS) diagnostic criteria (Postuma et al., 2015). PD whose symptoms exceeded stage III on the Hoehn and Yahr scale (Hoehn & Yahr, 1967) were excluded from the analysis to avoid confounding effects of cognitive impairments associated with late-stage PD. Additionally, PD were excluded if they were in treatment with DBS or if they suffered from severe walking and balance problems, had important uncontrolled metabolic problems (e.g., diabetes and hypertension), hearing loss or any other neurological or psychiatric disorders. PD were instructed to maintain their regular medication regimen which included levodopa for all PD except for three who were only taking a dopamine agonist. Dopamine agonist medication is often taken in combination with levodopa and the combination can lead to disruptions in motivation and reward processes (Cools & D'Esposito, 2011). To test for these effects, the PD were divided into two groups, those who were taking dopamine agonist medications (PD_{DA}; $n = 23$) and those who were not (PD_{nonDA}; $n = 24$). There were two groups of healthy controls: age-matched older adults (HC_{old}; age 47–77; $n = 27$) and younger adults (HC_{young}; age 21–33; $n = 27$). Both PD and HC were excluded if they had important uncontrolled metabolic problems (e.g., diabetes and hypertension), hearing loss or any other neurological or psychiatric disorders. The metabolic syndrome has been linked to cognitive dysfunction and brain abnormalities, with insulin resistance-induced impairment in cerebrovascular reactivity being a key mechanism (Yates et al., 2012). All participants in the HC_{old} group and in both PD groups reported their nationality as Danish.

TABLE 1 Demographics and behavioural questionnaires.

	HC_{young}	HC_{old}	PD_{DA}	PD_{nonDA}
Participants (n)	27	26	23	24
Gender (females)	14	21	4	10
Age (years)	24.9 ± 3.2	65.7 ± 8.2	68.2 ± 4.8	66.8 ± 9
Education (years)	18.2 ± 2.1***	14.7 ± 2.3	14.9 ± 2.9	14.9 ± 3.5
Musical training (years)	4.5 ± 6.4**	2.6 ± 5.9	.3 ± .9	2 ± 5.4
Music time (h/week)	22 ± 14	19 ± 15	18 ± 18	16 ± 15
MDI	3.1 ± 3**	5 ± 6*	8.4 ± 4.6	8.1 ± 5.7
MoCA	29 ± 1.1	29 ± 1.2	28 ± 1.4	28 ± 1.5
PD diagnosis (years)	-	-	6.6 ± 4.7	5.6 ± 4.9
MDS-UPDRS-III	-	-	29.7 ± 11	25.2 ± 12.3
Hoehn and Yahr[a]	-	-	2 (2–2)	2 (1–2)
MET: Melody	36.7 ± 5.8	34 ± 5.6	31.5 ± 4	32.4 ± 5.4
MET: Rhythm	38 ± 5.5	34 ± 5.7	32.7 ± 3.9	32.3 ± 3.9

Abbreviations: MDI, major depression inventory; MDS-UPDRS-III, motor part of the Movement Disorder Society Unified Parkinson's Disease Rating Scale; MET, Musical Ear Test; MoCA, Montreal cognitive assessment.

[a]Median (IQR).

*Significantly different than PD_{DA}.

**Significantly different than both PD groups.

***Significantly different than all other groups.

Nineteen participants in the HC_{young} group reported their nationality as Danish while the remaining participants reported their country of nationality as Poland, German, Egypt, the Philippines, the Netherlands, the United Kingdom, Turkey and Brazil (all were international exchange students at Aarhus University).

All participants gave their consent verbally and in written form before the experiment. The study was conducted in accordance with the Declaration of Helsinki and approved by the Internal Review Board at the DNC (*Dansk Neuroforskningscenter*), Aarhus University Hospital, Aarhus, Denmark. PD received no compensation for participating in the study, but the costs of transportation were covered. Healthy controls received 200 DKK, in compensation for their participation in the 2-h experiment.

2.2 | Behavioural questionnaires and Musical Ear Test (MET)

Participants filled out an initial background questionnaire which included variables such as age, gender, years of education, years of musical training, preferred musical genre, and number of hours spent per week interacting with music. Such musical interaction included active music listening or playing, or passively using music as background. Specifically for PD, we asked for a list of current medication prescribed by their neurologist. All participants filled out the Major Depression Inventory (MDI) to exclude depression (Olsen et al., 2003) and the Montreal Cognitive Assessment (MoCA) to exclude dementia (Nasreddine et al., 2005). PD filled out the MDS-Unified Parkinson's Disease Rating Scale (MDS-UPDRS-III) to ensure PD diagnosis (Goetz et al., 2008). Authorization to use materials owned by the International Parkinson and MDS was granted to author V.P.-N., for research purposes only. Additionally, rhythm and melody discrimination ability was assessed in all participants via the MET (Wallentin et al., 2010). Table 1 shows a summary of questionnaire and MET data.

2.3 | PLUMM rating paradigm

Participants listened to and rated their experienced pleasure and urge to move for rhythmic stimuli (see Figure S1 for musical notation of an example stimuli). The stimuli were selected from previous studies conducted in our lab (Matthews et al., 2019, 2020, 2022; Pando-Naude et al., 2023; Stupacher, Wrede, & Vuust, 2022; Stupacher, Matthews, et al., 2022) and varied in their degree of rhythmic complexity, which was measured using the syncopation index (Fitch & Rosenfeld, 2007). The index quantifies the extent to which a pattern deviates from the standard 4/4 m. There were three levels of rhythmic complexity (low, medium and high) with three different rhythms in each level. The medium complexity rhythms consisted of the son and rumba claves along with an experimenter-created rhythm in a clave style. These claves are five-onset patterns that originate in Afro-Cuban music but are commonly used in many musical genres. The low complexity rhythms followed similar patterns but with nearly all onsets falling on strong beats, thus removing nearly all syncopations. The high complexity rhythms also followed similar patterns, but only the first of the five onsets fell on a strong beat while the remaining four onsets were shifted to off-beat positions. In this way, all rhythmic patterns had the same number of onsets and followed a similar general pattern, differing only in terms of syncopation.

The rhythmic patterns were made up of piano chords (six notes spanning four octaves in D major) with a single chord repeating to generate the rhythm. These chords varied across three levels of harmonic complexity, with three different chords per level. Harmonic complexity corresponded to the degree to which the chords deviated from the D major key and was quantified as roughness using the MIR Toolbox in Matlab (Lartillot et al., 2007; Plomp & Levelt, 1965; Sethares, 2004). The rhythmic patterns and chords were combined into 54 stimuli, which were a subset of the 81 possible rhythm-chord combinations. Each stimulus also included an isochronous hihat (corresponding to eighth notes) which provided a metrical context. The rhythmic patterns were repeated four times, were presented at 96 bpm and lasted 10 s. See Figure S2 for a schematic of all rhythmic patterns used and Figure S3 for musical notation of all chords used.

At the start of the task, participants listened to two musical sequences that were not part of the experiment, to adjust the volume to a comfortable level. Participants listened to each sequence and rated pleasure/urge to move on a 5-point Likert scale (1 = *not at all/none*, 5 = *very much/a lot*), by using numbers on the computer keyboard to select their rating. The ratings were made according to the following questions: (a) To what extent does this rhythm make you want to move? and (b) How much pleasure do you experience listening to this rhythm? Following stimulus presentation, participants were given 5 s to make their rating. Ratings were made for all 54 stimuli in two consecutive sessions, urge to move then pleasure, to avoid influences of one rating on the other. Within each session, each musical sequence was presented in a fully randomized order. Participants listened via Beyerdynamic DT 770 Pro headphones.

2.4 | Statistical analysis

Only data from participants who completed all questionnaires and all trials of the PLUMM rating paradigm were analysed. Therefore, the analyses described below are implemented on a complete data set with no missing values ($n = 101$).

2.4.1 | Behavioural questionnaires and MET

Descriptive and inferential statistics of data were performed using R (version 4.1.1) in RStudio (R Core Team, 2020). Non-parametric (Kruskal–Wallis rank sum) tests were used to check for differences in demographic, cognitive, motor and depression questionnaire responses between groups. Post hoc analyses were conducted using the Dunn test of multiple comparisons corrected with the Bonferroni method.

The MET results showed a normal distribution; therefore, a one-way ANOVA was conducted to compare the groups. Post hoc analyses were conducted using the Tukey HSD multiple comparisons of means test with a 95% family-wise confidence level.

2.4.2 | Urge to move and pleasure ratings

The correlation between pleasure and urge to move ratings was high but not so high as to be considered colinear (Spearman $r(99) = .68$, 95% CI [.56, .77]); therefore, the rating types were analysed separately. Effects of group, rhythmic and harmonic complexity, and their interactions, on the urge to move and pleasure ratings, were investigated using two separate regression models, one for each type of rating. Data from all four groups (HC_{old}, HC_{young}, PD_{DA} and PD_{nonDA}) were included in these models. As there were between-group differences in years of education, years of formal music training and MDI score, these variables were included as covariates. To account for inter-individual variability, as well as variability between versions of stimuli (items) within the same complexity levels, the regression models were estimated using linear mixed effects models on the raw pleasure and urge to move ratings using lme4 (Bates et al., 2015) and afex (Singmann et al., 2013) packages. Random effects structures were determined following the recommendations of Bates et al. (2015) and Matuschek et al. (2017). For both models, this resulted in by-participant random intercepts and random slopes for both rhythmic and harmonic complexity, as well as by-item random intercepts. Correlations between by-participant random slopes and intercepts were included for the analysis of urge to move ratings but not pleasure ratings. Diagnostic plots of residuals indicated no violations of assumptions in either model.

The two models were submitted to separate type III sum of squares analysis of variance (ANOVA) to test for main effects and interactions. Since the interactions were our primary interest, we report these first, and only mention significant main effects if relevant. If the ANOVA showed a significant three-way interaction, F tests were used to test for a rhythm by harmony interaction simultaneously in all groups. Second-order polynomial and pairwise contrasts were used to test quadratic and linear effects of rhythmic and harmonic complexity and to compare these effects between groups, using the emmeans package (Lenth et al., 2021). These follow-up comparisons focused on the effects between PD groups and HC_{old}, and between HC_{old} and HC_{young}. Effects in HC_{young} were not compared to those in the PD groups. For the ANOVAs, the degrees of freedom were estimated using the Satterthwaite method. For the follow-up contrasts, degrees of freedom were estimated using the Kenward–Roger method, and the multivariate t method was used to correct for multiple comparisons.

Finally, we tested correlations between the ratings and PD motor symptom severity in PD_{DA} and PD_{nonDA} and age and MET scores in PD_{DA}, PD_{nonDA} and HC_{old}. A summary measure capturing the pattern of ratings (Medium − (Low + High)/2), calculated on estimated ratings from the models were used in the correlations. False discovery rate was used to correct for multiple correlations.

3 | RESULTS

3.1 | Demographic and behavioural questionnaires

Demographic and questionnaire data are presented in Table 1. Kruskal–Wallis tests indicated that PD_{DA}, PD_{nonDA} and HC_{old} were not significantly different in terms of age ($\chi^2(2) = 1.21$, $p = .55$) and MoCA scores ($\chi^2(3) = 7.03$, $p = .07$). Dunn tests showed no significant differences between PD_{nonDA} and PD_{DA} in years since PD diagnosis ($p = .25$), UPDRS ($p = .23$) or Hoehn and Yahr scale ($p = .24$). The groups differed in terms of gender ratio, with the HC_{old} identifying predominantly as female and the PD groups as predominantly male. The groups also differed in years of education ($\chi^2(3) = 25.66$, $p < .001$), with HC_{young} having more education than all other groups (all $p < .001$). A significant effect of group on musical training ($\chi^2(3) = 12.99$, $p = .004$) was driven by HC_{young} having more years of musical training than both

PD groups (both $p < .05$) but not HC_{old}. There was no significant effect of group on hours spent interacting with music ($\chi^2(3) = 3.98$, $p = .26$). There was a significant effect of group on MDI scores ($\chi^2(3) = 25.05$, $p < .001$) driven by significantly lower scores in HC_{old} and HC_{young} compared with PD_{DA} (both $p < .05$) and HC_{young} compared with PD_{nonDA} ($p = .001$). As there were between-group differences in years of education, years of formal music training and MDI score, these variables were included as covariates in the regression models.

A significant effect of group on the rhythm version of the MET ($\chi^2(3) = 17.37$, $p < .001$) was driven by significantly better performance in HC_{young} compared with all other groups (all $p < .05$). A significant effect of group on the melody version of the MET ($\chi^2(3) = 12.48$, $p = .006$) was driven by better performance in HC_{young} compared with PD_{DA} ($p = .006$), with a near-significant difference between HC_{young} and PD_{nonDA} ($p = .05$) but not HC_{old} ($p = .65$).

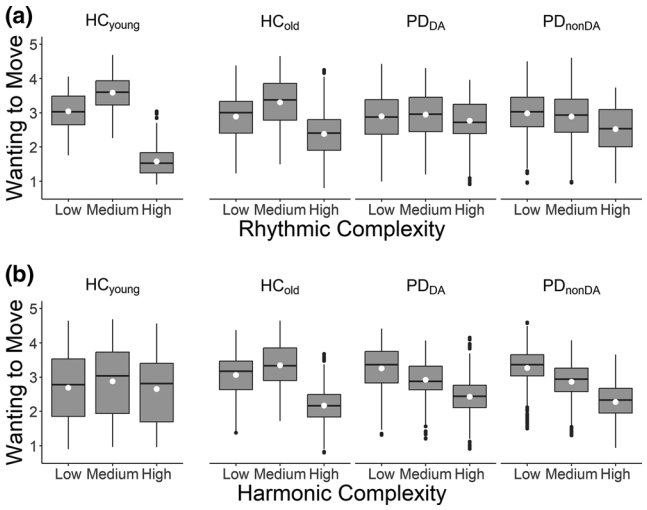

FIGURE 1 The effects of (a) rhythmic and (b) harmonic complexity on urge to move ratings across groups. Values are estimated ratings from regression model. Centre line, median; box limits, upper and lower quartiles; whiskers, 1.5× interquartile range; white points, means; black points, outliers.

3.2 | Urge to move ratings

3.2.1 | Rhythmic complexity by group interaction

The ANOVA showed a significant group by rhythmic complexity interaction (Table S1). Follow-up tests showed a significant quadratic effect in both HC_{young} and HC_{old}, with HC_{young} showing a stronger effect compared with HC_{old} ($b(97) = -1.216$, 95% CI [−1.840, −.589]; Table S2 and Figure 1a). The quadratic effect was significantly stronger in HC_{old} compared with both PD_{nonDA} ($b(97) = -1.066$, 95% CI [−1.821, −.312]) and PD_{DA} ($b(97) = -1.113$, 95% CI [−1.876, −.349]). PD_{nonDA} showed a significant negative linear effect which was driven by significantly higher ratings for low compared with high complexity rhythms ($b(85.3) = .468$, 95% CI [.091, .845]). PD_{DA} showed a relatively flat pattern of ratings as reflected in no significant linear or quadratic effects. The difference in linear effects between PD_{nonDA} and PD_{DA} was not significant.

3.2.2 | Harmonic complexity by group interaction

The ANOVA also showed a group by harmonic complexity interaction (Table S1). Follow-up tests showed that both HC_{old} and HC_{young} showed a significant quadratic effect and that this effect was stronger in HC_{old} compared with HC_{young} ($b(97) = 1.043$, 95% CI [.593, 1.490]; Table S3 and Figure 1b). HC_{old} also showed a stronger quadratic effect compared with both PD_{nonDA} ($b(97) = -1.261$, 95% CI [−1.801, −.720]) and PD_{DA} ($b(97) = -1.289$, 95% CI [−1.836, −.742]). As can be seen in Figure 1b, both PD_{nonDA} and PD_{DA} showed significant negative linear effects. This was reflected by significant low–medium (PD_{nonDA}: $b(89.2) = .403$, 95% CI [.153, .653]; PD_{DA}: $b(90.1) = .333$, 95% CI [.078, .589]) and medium–high (PD_{nonDA}: $b(89.0) = .593$, 95% CI [.343, .842]; PD_{DA}: $b(90.0) = .495$, 95% CI [.241, .749]) contrasts. There were no significant differences in these effects between PD_{nonDA} and PD_{DA}.

3.2.3 | Rhythmic complexity by harmonic complexity interaction

The ANOVA also showed a significant rhythmic by harmonic complexity interaction and a near-significant three-way interaction (Table S1). Given that the three-way interaction was near significant, and each group showed such different patterns of ratings, F tests on the rhythmic by harmonic complexity interaction were performed per group. These revealed a significant rhythmic complexity by harmonic complexity interaction in HC_{old} ($F(4, 4908.05) = 4.38$, $p = .002$) and a near-significant interaction for HC_{young} ($F(4, 4908.05) = 2.11$, $p = .077$) but not for PD_{DA} or PD_{nonDA} (both $p > .2$). Follow-up contrasts in HC_{old} showed that the quadratic effect of rhythmic complexity was significantly stronger, here reflecting a more peaked inverted U, for medium

complexity chords compared with both low ($b(4908) = -.611$, 95% CI [−1.177, −.045]) and high ($b(4908) = -.833$, 95% CI [−1.400, −.267]) complexity chords (see Figure S6). Unlike HC_{old}, HC_{young} showed no significant differences in the quadratic effect of rhythmic complexity between medium and low or medium and high complexity chords.

3.2.4 | Main effects

The ANOVA showed that the main effect of group was not significant ($F(3, 94.1) = .78$, $p = .508$). Therefore, although the groups showed different patterns in their ratings, there was no overall difference when averaging over rhythmic and harmonic complexity. There were no significant main effects of the control variables (years of education, years of musical training, and MDI).

3.2.5 | Correlations between Urge to Move ratings, UPDRS and MET scores

In PD, correlations between UPDRS and the contrast estimates for both rhythmic ($r(47) = -.24$, 95% CI [−.52, .09]) and harmonic complexity were not significant ($r(47) = -.24$, 95% CI [−.52, .09]). Correlations with MET scores were also not significant (all $p > .09$).

3.3 | Pleasure ratings

3.3.1 | Rhythmic complexity by group interaction

The ANOVA showed a significant group by rhythmic complexity interaction (Table S4). Follow-up tests showed a stronger quadratic effect in HC_{young} compared with HC_{old} ($b(98.5) = -1.128$, 95% CI [−1.87, −.389]) and no significant quadratic effects in HC_{old}, PD_{nonDA} and PD_{DA} (Table S5 and Figure 2a). PD_{nonDA} showed a significant negative linear effect ($b(119.6) = -.602$, 95% CI [−1.077, −.127]) driven by higher ratings in medium compared with high complexity rhythms ($b(117.5) = .565$, 95% CI [.091, 1.039]). The same contrast was also significant in HC_{old} ($b(113.3) = .512$, 95% CI [.060, .964]). There were no significant differences in the linear effect between groups. As can be seen in Figure 2a, both HC_{old} and PD_{nonDA} show similar ratings for low and medium complexity rhythms, then a drop-off for high complexity rhythms. Conversely, PD_{DA}'s ratings are relatively flat across all levels.

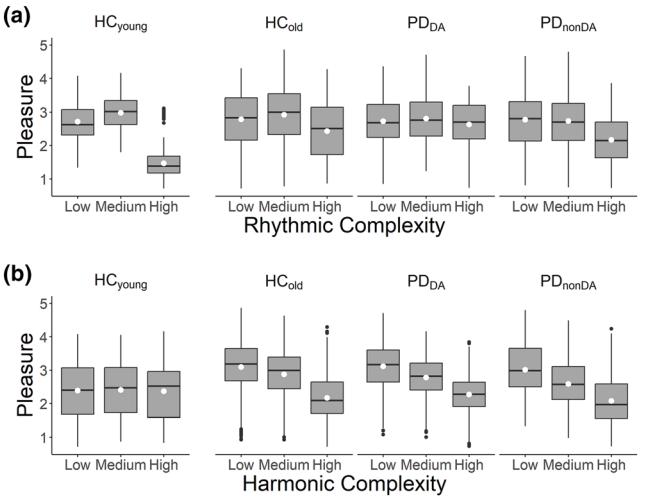

FIGURE 2 The effects of (a) rhythmic and (b) harmonic complexity on pleasure ratings across groups. Values are estimated ratings from regression model. Centre line, median; box limits, upper and lower quartiles; whiskers, 1.5× interquartile range; white points, means; black points, outliers.

3.3.2 | Harmonic complexity by group interaction

The ANOVA also showed a significant group by harmonic complexity interaction (Table S4). Follow-up tests indicated that HC_{old} showed greater linear ($b(103) = -.93$, 95% CI [−1.320, −.541]) and quadratic ($b(103) = -.44$, 95% CI [−.850, −.030]) effects compared with HC_{young}, for whom neither effects were significant. As can be seen in Figure 2b, HC_{old}, PD_{nonDA} and PD_{DA} all show a negative linear pattern as supported by a significant linear contrast in these groups (Table S6). These three groups showed significant differences between low and medium and medium and high complexity chords. However, HC_{old} showed a smaller difference between low and medium chords leading to the significant quadratic effect. Follow-up test showed a significant quadratic effect in HC_{old} and significant negative linear effects for both PD_{nonDA} and PD_{DA}. There were no significant differences between HC_{old}, PD_{nonDA}, and PD_{DA} groups in either the quadratic or linear contrasts.

3.3.3 | Rhythmic complexity by harmonic complexity interaction

The ANOVA also showed a significant three-way interaction (Table S4, Figure S7). Comparing HC_{young} and HC_{old}, F-tests showed that this interaction was significant in HC_{young} ($F(4, 4914.92) = 4.464$, $p = .001$) but not in

HC_{old} ($F(4, 4914.92) = .422$, $p = .793$). Follow-up contrasts showed that the quadratic effect of rhythm in HC_{young} was stronger for low compared to high complexity chords ($b(4915) = -.735$, 95% CI [−1.300, −.170]). There were no differences in the quadratic effect of rhythm between low versus medium and medium versus high complexity chords.

PD_{DA} and HC_{old} did not show a significant or near-significant interaction (both $p > .16$), while PD_{nonDA} showed a near-significant rhythmic complexity by harmonic complexity interaction ($F(4, 4914.92) = 2.245$, $p = .061$). There was no significant difference between medium and low complexity rhythms at any level of harmonic complexity. Together, these results suggest that the three-way interaction was driven by differences between HC_{young} and the other groups.

3.3.4 | Main effects

The ANOVA also showed a main effect of group (Table S4). HC_{old} showed higher ratings overall compared to HC_{young} ($b(94) = .453$, 95% CI [.141, .765]). There were no significant differences between PD_{nonDA}, PD_{DA} and HC_{old}. There were no significant main effects of the control variables (years of education, years of musical training, and MDI).

3.3.5 | Correlations between pleasure ratings, UPDRS and MET scores

In PD, there was a significant negative correlation between UPDRS and rhythmic complexity contrast estimates ($r(47) = -.37$, 95% CI [−.62, −.05]; Figure 3) but not harmonic complexity contrast estimates ($r(47) = -.03$, 95% CI [−.35, .30]). This indicates that as PD symptoms worsen, the quadratic effect of rhythmic complexity flattens out and/or becomes more linear. No other correlations were significant.

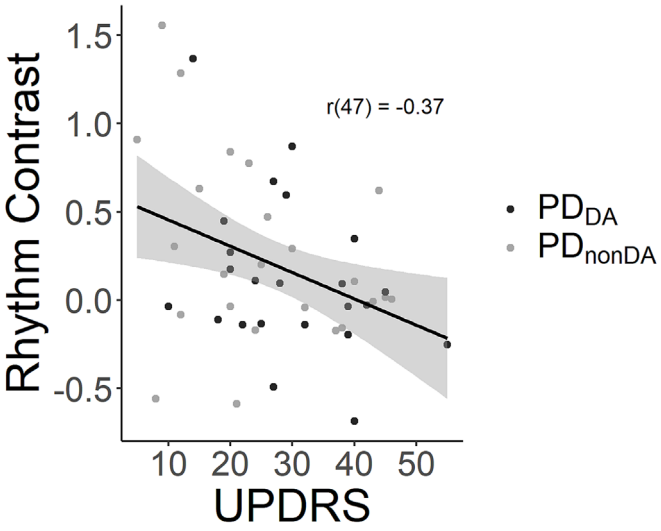

FIGURE 3 Correlation between severity of PD-related motor symptoms (UPDRS) and contrast estimates (medium − (low + high)/2) from the effect of rhythmic complexity on pleasure.

4 | DISCUSSION

Our results support the hypothesis that dopamine within cortico-striatal circuits play a crucial role in the PLUMM (Matthews et al., 2020; Stupacher, Matthews, et al., 2022). Both PD groups showed a flattening of the U-shaped relation between rhythmic complexity and the urge to move compared with healthy age-matched controls. In addition, the severity of motor symptoms in PD was associated with a flatter effect of rhythmic complexity on pleasure. The inverted U-shaped relation was significantly weaker in healthy older compared with younger adults, suggesting that aging also influences the effect of rhythmic complexity on PLUMM. In addition, both PD groups showed a strong negative linear effect of harmonic complexity for both pleasure and the urge to move whereas healthy older adults showed a negative linear effect for pleasure and a quadrative effect for the urge to move. Importantly, PD did not differ from age-matched controls on a test of rhythm discrimination and did not show overall lower ratings for the urge to move and pleasure but rather a difference in the pattern of ratings. These results indicate that the flattening of the PLUMM response cannot easily be attributed to deficits in rhythm perception or a general inability to experience PLUMM. Finally, PD taking a dopamine agonist in addition to the standard levodopa regime generally showed a similar flattening effect to the PD_{nonDA} group. Taken together, these findings indicate that the chronic dysregulation of dopamine associated with PD flattens the typical U-shaped relationship between rhythmic complexity and PLUMM. We propose that this points to the crucial involvement of dopamine in the beat- and meter-based predictive processes thought to drive PLUMM.

4.1 | Rhythmic complexity

The flattened response to rhythmic complexity in PD supports a role of dopamine in the effects of rhythm on both the urge to move and pleasure. The motor cortico-striatal circuit is part of a core timing network, along with prefrontal and cerebellar regions (Coull et al., 2011; Matell &

Meck, 2004; Teghil et al., 2019) and is implicated in relative or beat-based timing in particular (Bengtsson et al., 2009; Breska & Ivry, 2018; Chen et al., 2008; Cheng et al., 2022; Cope et al., 2014; Grahn & Rowe, 2009, 2013; Kasdan et al., 2022; Kung et al., 2013; Merchant et al., 2015; Schubotz et al., 2000; Teki et al., 2012; Thaut et al., 2008). This is consistent with a role of the motor system in driving temporal predictions in the context of auditory perception and attention more generally (Arnal, 2012; Morillon et al., 2015; Nobre & van Ede, 2018; Rimmele et al., 2018; Schubotz, 2007). Involvement of the motor cortico-striatal circuit implies a role of nigrostriatal dopamine. However, studies on beat perception and perceived rhythmic complexity in PD show mixed results (Benoit et al., 2014; Biswas et al., 2016; Cameron et al., 2016; Geiser & Kaelin-Lang, 2011; Grahn & Brett, 2009; Hsu et al., 2022; Vikene et al., 2019c). Conversely, many of these same studies show deficits in rhythm discrimination in PD (Benoit et al., 2014; Biswas et al., 2016; Cameron et al., 2016; Geiser & Kaelin-Lang, 2011; Grahn & Brett, 2009; Hsu et al., 2022), which could suggest that the flatter pattern of ratings seen here may be due to reduced ability to distinguish the stimuli. However, HC_{old}, PD_{nonDA} and PD_{DA} significantly differed in their patterns of ratings but not in their rhythm discrimination ability, as measured by the MET. Further, there were no significant associations between MET scores and the patterns of ratings or between MET scores and the severity of PD-related motor symptoms (UPDRS). Conversely, higher UPDRS was associated with a flatter effect of rhythmic complexity on pleasure. Therefore, our results suggest that PD disrupts the beat and meter-based predictive processes that form the link between perceptual processing of rhythmic patterns and the affective responses to rhythmic music.

According to predictive processing accounts of PLUMM, strongly weighted prediction errors, in the form of syncopations, drive the inverted U-shaped relation between rhythmic complexity and both the urge to move and pleasure (Koelsch et al., 2019; Vuust et al., 2018, 2022; Vuust & Witek, 2014). In this context, strongly weighted syncopations drive the urge to move, either directly to reinforce the metrical model or indirectly via covert adjustments to that model. In terms of pleasure, by challenging our metric models, these syncopations potentiate model improvement (Stupacher, Matthews, et al., 2022), which is itself intrinsically rewarding (Oudeyer et al., 2016; Schmidhuber, 2010). The weight of prediction errors due to syncopations depends on both the rhythmic context (Lumaca et al., 2019) and the strength of the listener's metrical model (Vuust et al., 2005). According to a recent theoretical model (Cannon & Patel, 2020), nigrostriatal dopamine underlies both the timing and certainty of beat-based predictions. Therefore, one interpretation of our results is that disrupted dopamine in PD results in a weaker metrical model and more uncertain predictions, reducing pleasure and the urge to move for moderately complex rhythms. Similarly, high complexity rhythms are less disruptive to an already weak model and are thus less aversive, leading to a flatter pattern of ratings overall. Support for the role of metric model strength in PLUMM comes from studies comparing musicians and non-musicians. Behavioural and neural evidence suggests that musicians show stronger and/or more refined metrical models compared with non-musicians (Drake et al., 2000; Geiser et al., 2010; Jongsma et al., 2004; Palmer & Krumhansl, 1990; Perna et al., 2018; Vuust et al., 2005, 2009) and that musicians have a sharper U-shaped pattern of PLUMM ratings and greater preference for higher levels of complexity (Matthews et al., 2019, 2022). In the current study, healthy aging was also linked to a flatter effect of rhythmic complexity, particularly for pleasure ratings. Like PD, healthy aging is associated with differences in the neural correlates of predictive rhythmic pattern perception (Henry et al., 2017), an effect that is also linked to dopamine (Al Jaja et al., 2020). Therefore, metrical model strength, supported by dopaminergic signalling, may provide a common mechanism underlying the effects of PD, aging and musicianship on the shape and location of the inverted U relation between PLUMM and rhythmic complexity.

Neuroimaging evidence suggests that neural oscillations in the beta range (13–30 Hz) may encode the metrical model within the motor cortico-striatal circuit and thus may provide a potential neural mechanism underlying the altered link between rhythm perception and affective responses in PD. Beta dysfunction within the BG is a hallmark of PD (Hammond et al., 2007) suggesting a functional link between dopamine and beta activity. One proposal is that, by encoding the certainty (or salience) of state, sensorimotor or value representations (e.g., rhythmic context; Friston et al., 2014), dopamine signals the need for motor preparation or resource allocation which are governed by beta modulations (Jenkinson & Brown, 2011). Crucially, cortico-striatal beta activity is linked to beat and meter representations (Bauer et al., 2015; Fujioka et al., 2012, 2015; Graber & Fujioka, 2019; Iversen et al., 2009) and is sensitive to musical training (Doelling & Poeppel, 2015; Fujioka & Ross, 2017). Further, PD show weaker beta entrainment in motor regions during rhythmic auditory and multimodal perceptual tasks (te Woerd et al., 2017, 2018), an effect that is reversed following treatment with levodopa and DBS (Gulberti et al., 2015). Finally, the degree of beta dysfunction in cortico-striatal circuits is correlated with

the severity of motor symptoms in PD (Kühn et al., 2009) which aligns with the association between severity of motor symptoms and the flattening of the effect of rhythmic complexity on pleasure ratings seen here. Together, these results point to a functional link between dopamine, beta activity, metrical model strength and PLUMM; however, further work is necessary to solidify and clarify this link.

An alternative interpretation for the flattened effect of rhythmic complexity on PLUMM ratings in PD is that, rather than weakening the metrical model, dopamine dysregulation disrupts the signalling of syncopation-related prediction errors, thus reducing the urge to move and pleasure thought to result from these prediction errors. However, (reward) prediction errors are associated with mesolimbic dopamine (Schultz et al., 1997) while PD primarily affects nigrostriatal dopamine, at least in early and mid-stages of the disease (Dauer & Przedborski, 2003). One challenge is that the effects on metrical model strength would also be expected to affect the prediction errors, as the certainty of the meter-based prediction is thought to directly relate to the weight of the prediction error. Future work should use behavioural (Palmer & Krumhansl, 1990; Perna et al., 2018) and/or computational methods to explicitly test whether metrical representations do in fact differ between PD and healthy controls matched in age and musical training.

Interestingly, both PD groups showed a very similar pattern of ratings, aside from a drop in the urge to move and pleasure in PD_{nonDA} for high complexity rhythms. This constitutes an internal replication and suggests that dopamine agonist medication does not have a strong effect on PLUMM over-and-above the general dopamine dysregulation and counteracting effects of levodopa present for all PD. To further delineate the role of dopamine, future work should compare PLUMM in both PD and healthy controls on and off levodopa medication.

4.2 | Harmonic complexity

Contrary to our hypothesis, and in contrast to the pattern of ratings in young healthy adults shown here and elsewhere (Matthews et al., 2019, 2020), PD showed greater pleasure and urge to move for low complexity chords, while healthy older adults showed the same pattern for pleasure and an inverted U for the urge to move. Recent work suggests that musicianship is associated with an altered pattern liking responses as a function of harmonic complexity (Matthews et al., 2019; Witek et al., 2023). Specifically, non-musicians preferred low complexity chords to medium, high or octave chords, while musicians preferred medium complexity chords (Witek et al., 2023). Therefore, as with rhythmic complexity, PD, aging and (lack of) musical training seem to a similar influence on chord preferences. Further, previous studies using the same type of stimuli showed that medium harmonic complexity enhances the effect of moderately complex rhythms and that this may depend on musical training (Matthews et al., 2019; Matthews et al., 2020). In the current study, this effect was only seen for the urge to move in healthy older adults. Therefore, PD may also dampen the influence of harmonic complexity on rhythmic complexity. Younger healthy controls also showed an interaction between harmonic and rhythmic complexity, but only for pleasure ratings and this was not the expected pattern as low harmonic complexity enhanced the quadratic effect of rhythm. This group had more years of musical training compared with both PD groups. However, years of musical training was included as a control nuisance variable in all analyses, which, in addition to controlling for group differences, may have also reduced its influence on the effects of harmonic complexity.

PD and healthy older adults may also have an altered association between the complexity of a single chord and the emotion evoked or referenced by this chord. For example, PD show differences in the ability to recognize emotions expressed in music (Gothwal et al., 2022), which is relevant as chords of varying complexity are often used to convey different emotions. However, the specific nature of this effect is so far inconclusive, as some studies show deficits in recognizing happiness and peacefulness in PD (Lima et al., 2013) and others show deficits in recognizing fear and anger (van Tricht et al., 2010). Other factors including changes to listening habits and genre preferences that come with aging may also have influenced the pattern of ratings seen here; however, research into these effects is lacking. Therefore, further work is necessary to disentangle the relative contributions of musical training, age and PD to the effects of harmonic complexity and its interaction with rhythmic complexity.

5 | CONCLUSION

Overall, our results are consistent with models implicating cortico-striatal circuits and dopamine in PLUMM (Matthews et al., 2020; Stupacher, Matthews, et al., 2022) and provide insight into the function of dopamine within these circuits more generally. We propose that dopamine depletion within the motor cortico-striatal circuit disrupts beat- and meter-based predictive processes that are supported by beta modulations and are crucial for the

affective response to rhythmic music. Beyond music, this proposal aligns with and complements theoretical and empirical work suggesting that premotor beta modulations transmit top-down predictive signals that temporally structure auditory perception, for example, in the context of speech (Abbasi & Gross, 2020; Arnal, 2012; Arnal & Giraud, 2012; Morillon et al., 2015; Rimmele et al., 2018). Importantly, the current results better our understanding of dopamine's role in linking temporal predictions and reward processing which can be leveraged to improve treatments for PD and other dopamine-related disorders.

AUTHOR CONTRIBUTIONS

Victor Pando-Naude: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; visualization; writing—original draft; writing—review and editing. **Tomas Edward Matthews:** Conceptualization; formal analysis; writing—original draft; writing—review and editing. **Andreas Højlund:** Conceptualization; methodology; supervision. **Sebastian Jakobsen:** Data curation; investigation. **Karen Østergaard:** Conceptualization; supervision. **Erik Johnsen:** Investigation; supervision. **Eduardo A. Garza-Villarreal:** Conceptualization; supervision. **Maria A. G. Witek:** Conceptualization; supervision. **Virginia Penhune:** Conceptualization; supervision; writing—review and editing. **Peter Vuust:** Conceptualization, supervision, writing—review and editing, supervision, funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest for this work.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data supporting the findings of this study is freely available at the Open Science Framework (OSF) website: https://osf.io/fszqe/?view_only=cffadc85e4004c8789ca5cf604f172c7.

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SUPPORTING INFORMATION

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