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Got Rhythm? Better Inhibitory Control Is Linked with More Consistent Drumming and Enhanced Neural Tracking of the Musical Beat in Adult Percussionists and Nonpercussionists

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Abstract

■ Musical rhythm engages motor and reward circuitry that is important for cognitive control, and there is evidence for enhanced inhibitory control in musicians. We recently revealed an inhibitory control advantage in percussionists compared with vocalists, highlighting the potential importance of rhythmic expertise in mediating this advantage. Previous research has shown that better inhibitory control is associated with less variable performance in simple sensorimotor synchronization tasks; however, this relationship has not been examined through the lens of rhythmic expertise. We hypothesize that the development of rhythm skills strengthens inhibitory control in two ways: by fine-tuning motor networks through the precise coordination of movements “in time” and by activating reward-based mechanisms, such as predictive processing and conflict monitoring, which are involved in tracking temporal structure

in music. Here, we assess adult percussionists and nonpercussionists on inhibitory control, selective attention, basic drumming skills (self-paced, paced, and continuation drumming), and cortical evoked responses to an auditory stimulus presented on versus off the beat of music. Consistent with our hypotheses, we find that better inhibitory control is correlated with more consistent drumming and enhanced neural tracking of the musical beat. Drumming variability and the neural index of beat alignment each contribute unique predictive power to a regression model, explaining 57% of variance in inhibitory control. These outcomes present the first evidence that enhanced inhibitory control in musicians may be mediated by rhythmic expertise and provide a foundation for future research investigating the potential for rhythm-based training to strengthen cognitive function. ■

INTRODUCTION

Attention and inhibitory control are complementary processes that enable us to pursue goal-driven behaviors while remaining responsive to environmental demands. Attention involves the selection and amplification of relevant signals or actions, whereas inhibitory control provides a mechanism by which competing inputs or actions can be suppressed (e.g., see Wiecki & Frank, 2013). Attention and inhibitory control work in tandem in adults, although inhibitory control emerges later in development (Durstun et al., 2002; Zelazo & Frye, 1998), suggesting somewhat dissociable mechanisms. We recently revealed an inhibitory control advantage in adult percussionists compared with vocalists matched on extent of musical practice (Slater, Azem, Nicol, Swedenborg, & Kraus, 2017). No such advantage was observed in attention performance, suggesting that rhythmic expertise may be of particular relevance to the mechanisms of inhibitory con-

trol. In this study, we investigate the percussionist advantage further by considering relationships between inhibitory control and different aspects of rhythm processing, across a range of rhythmic expertise.

Several studies have demonstrated enhanced inhibitory control in musicians compared with nonmusician peers, both in musically trained adults (Moussard, Bermudez, Alain, Tays, & Moreno, 2016; Moreno, Wodniecka, Tays, Alain, & Bialystok, 2014; Zuk, Benjamin, Kenyon, & Gaab, 2014; Bialystok & Depape, 2009; Bugos, Perlstein, McCrae, Brophy, & Bedenbaugh, 2007) and in children participating in early childhood music programs (Joret, Germeys, & Gidron, 2016). Although these group differences could reflect innate predispositions rather than causal effects of training, they are supported by longitudinal evidence for improved inhibitory control with short-term music training (Moreno et al., 2011). Furthermore, it has been suggested that enhancements in inhibitory control may underlie the transfer of benefits from musical practice to more general cognitive functions (Moreno & Farzan, 2015; Degé, Kubicek, & Schwarzer, 2011). It is therefore of interest to determine which elements of musical experience may lead to these enhancements.

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Studies investigating the potential factors contributing to inhibitory control advantages in musicians have not yielded clear answers: Carey et al. (2015) compared violinists, pianists, and nonmusicians on a range of perceptual and cognitive tasks and found no instrument-based differences on the cognitive measures (Carey et al., 2015). In a study with adult musicians, researchers assessed performance on musical discrimination tasks and inhibitory control but found no relationship between them (Slevc, Davey, Buschkuehl, & Jaeggi, 2016).

There are compelling theoretical reasons why rhythm may be of particular importance to inhibitory control. Inhibitory control relies upon complex predictive processing and conflict detection, because the irrelevant inputs or actions to be suppressed are most often those in conflict with what was predicted or planned (Buschman & Miller, 2014). This complex predictive processing is a hallmark of human cognition and learning (Bubic, Von Cramon, & Schubotz, 2010; Raichle, 2010; Engel, Fries, & Singer, 2001), and there is evidence to suggest that similar predictive mechanisms may be activated by musical rhythm (Grahn & Rowe, 2013; Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009).

Recent research has emphasized the importance of the brain's motor systems as centers of timing and prediction-based processing, because converging evidence suggests that their functions extend beyond the coordination of movement to encompass perceptual and cognitive functions. Brain areas such as the cerebellum, BG, and cortical motor regions are implicated in both cognitive control (Buschman & Miller, 2014; Kotz, Schwartze, & Schmidt-Kassow, 2009; Akshoomoff, Courchesne, & Townsend, 1997; Allen, Buxton, Wong, & Courchesne, 1997; Graybiel, 1997) and rhythm perception, even in the absence of overt movement (Merchant, Grahn, Trainor, Rohrmeier, & Fitch, 2015; Grahn & Rowe, 2009, 2013; Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007). There is evidence to suggest that a lifetime of musical practice may influence these brain structures, for example, researchers found larger cerebellar volume (Hutchinson, Lee, Gaab, & Schlaug, 2003) and increased gray matter in premotor areas (Gaser & Schlaug, 2003) in musicians compared with nonmusician peers. Functionally, there is evidence that expert musicians demonstrate greater left lateralization of rhythm processing than nonmusicians (Limb, Kemeny, Ortigoza, Rouhani, & Braun, 2006; Vuust et al., 2005). Interestingly, the increased left hemisphere activation in musicians includes left parietal areas that are also engaged during temporal attention tasks (Coull & Nobre, 1998). Taken together, these outcomes suggest potential overlap between neural networks that are strengthened in musicians, engaged by musical rhythm and important for cognitive control.

Although all musicians interact with musical rhythm to some degree, irrespective of their chosen instrument, an expert drummer or percussionist is particularly focused on activities that engage motor and reward circuits: first,

through the precise coordination of complex movements "in time," and second, through constant monitoring and maintenance of temporal structure, such as the musical beat. Krause et al. revealed enhanced functional connectivity within motor networks during a sensorimotor task in musicians compared with nonmusicians and showed additional enhancements in drummers, beyond those observed in professional pianists (Krause, Schnitzler, & Pollok, 2010).

Relationships between motor coordination and inhibitory control have not been examined in percussionists, to our knowledge; however, previous research in typically developing adolescents revealed that greater variability in a sensorimotor synchronization task is associated with greater variability in RTs in an inhibitory control task (Rigoli, Piek, Kane, & Oosterlaan, 2012). Impairments in inhibitory control associated with attention-deficit/hyperactivity disorder (ADHD) are also linked with greater variability in motor timing (see Kaiser, Schoemaker, Albaret, & Geuze, 2015, for a review). In contrast, expert percussionists show reduced variability in sensorimotor synchronization compared with nonmusicians and, to a lesser degree, nonpercussionist musicians (see Repp & Su, 2013, for a review). Although it is possible that group comparisons reflect innate abilities in those drawn to pursue music training rather than causal effects, the potential for basic synchronization skills to be improved with music training is supported by evidence from a random assignment training study with elementary school children in which children with 1 year of music class showed more accurate finger tapping than untrained controls (Slater, Tierney, & Kraus, 2013). It is beyond the scope of this study to assess causal effects of training and determine whether variability in synchronization and inhibitory control can be improved together through musical practice. However, we take a first step by assessing relationships between inhibitory control and drumming variability across a range of rhythmic expertise.

The ability to track temporal structure relies upon the dynamic interaction between prediction, conflict-monitoring, and error correction. This adaptive process could be considered a form of online learning and is thought to rely upon dopaminergic signaling within circuitry that integrates the regulatory functions of the frontal cortex, with action selection and feedback mechanisms based in subcortical regions including the BG (e.g., see Graybiel, 2005). In addition to the identification of involved brain regions, ERPs have been used to investigate how the precise timing and amplitude of neural responses to a stimulus can be altered by context and the expectations that context creates. Despite some variation across modalities and tasks, ERP studies have converged upon identifiable neural indices of conflict and error detection. For example, an enhanced negative deflection in the neural response around 300 msec post-stimulus (referred to as the N300, with N indicating a negative amplitude) has been linked with timing error

in the context of reward-based predictive processing (Baker & Holroyd, 2011; Miltner, Braun, & Coles, 1997). This neural index has been observed in response to rhythmic incongruities in speech as well as music (Magne, Jordan, & Gordon, 2016; Magne et al., 2004), suggesting that rhythmic processing may be a point of commonality between the domains. Indeed, amidst the ongoing debate regarding the extent of processing overlap between speech and music, one recent review proposed that cognitive control may be an important area of common ground (Slevc & Okada, 2015), relying on the same mechanisms of predictive processing, conflict detection, and reevaluation of expectations that are important for processing rhythm.

There is also evidence that these neural response components may be influenced by musical experience. For example, children who received musical training showed enhanced cortical potentials relating to auditory discrimination (Putkinen, Tervaniemi, & Huotilainen, 2013; Moreno et al., 2009; Moreno & Besson, 2006), including an increased N300 in response to melodic incongruities (Moreno et al., 2009). Increased amplitude in late negative components has even been observed in adult pianists in response to incongruence between auditory and visual clips that show hands playing the piano (Proverbio, Cozzi, Orlandi, & Carminati, 2017), suggesting that this effect is not limited to processing within a single modality.

Previous work from our lab revealed differences in cortical evoked responses to stimuli presented on versus off the beat of music, in a passive listening paradigm using ecologically valid musical excerpts (Tierney & Kraus, 2013b, 2015b). This study revealed a significant increase in the positive component around 100 msec (P100), when the stimuli were aligned with the beat, and an increased negative amplitude of the N300 component, when stimuli were out of sync with the musical beat, consistent with the role of this late negative component in indexing incongruence or timing error. In this study, we adopted this same protocol to investigate whether these neural indices of beat alignment are enhanced in percussionists and whether they are correlated with inhibitory control performance.

We assessed relationships between inhibitory control, attention, simple drumming skills, and the neural index of beat alignment (based on Tierney & Kraus, 2015b). The drumming measures include paced and continuation drumming, similar to the tapping measures previously linked with sustained attention in adolescents (Tierney & Kraus, 2013a), as well as self-paced drumming, which provides a measure of internal timing consistency in the absence of an external stimulus. Attention and inhibitory control were measured using the Integrated Visual and Auditory Plus Continuous Performance Test (Sandford & Turner, 1994), which is a standard clinical measure of attention and inhibitory control in both auditory and visual domains.

We hypothesized that the development of rhythm skills through musical practice strengthens inhibitory

control in two ways: by fine-tuning motor networks through the precise coordination of movements “in time” and by activating reward-based mechanisms such as predictive processing and conflict monitoring, which are involved in tracking musical rhythm. We predicted that, across a range of rhythmic expertise, better inhibitory control performance would correlate with less variable drumming and enhanced neural tracking of the musical beat. Furthermore, we predicted a greater effect of beat alignment on the cortical evoked responses in percussionists compared with nonpercussionists.

METHODS

Participants were 36 young adults, aged 18–35 years, including percussionists ($n = 16$, four female) and nonpercussionists ($n = 20$, four female) to provide a range of rhythmic skill for correlational analyses. On the basis of our previous finding that percussionists outperformed both vocalists and nonmusicians in inhibitory control (Slater et al., 2017), the nonpercussionist group included vocalists ($n = 7$) and nonmusicians ($n = 13$). Percussionists had been actively playing for at least the past 5 years, with drums/percussion as their primary instrument, based on self-report. Nonpercussionists were either nonmusicians with no more than 3 years of musical experience across their lifetime and no active music-making within the 7 years before the study or vocalists whose primary instrument was voice and who had been singing for at least the past 5 years.

All participants completed an audiological screening at the beginning of the testing session (pure tone thresholds at octave frequencies 0.125–8 kHz) and had normal hearing (any participant with thresholds above 25 dB nHL for more than one frequency in either ear did not continue with further testing). The groups did not differ on age; sex; IQ, as measured by the Test of Nonverbal Intelligence (Brown, Sherbenou, & Johnsen, 1997); handedness; or hearing thresholds (see Table 1 for a summary of group demographics and comparison statistics). No participants had a history of neurological insult or a current diagnosis of ADHD or learning disability. All procedures were approved by the Northwestern Institutional Review Board. Participants provided written consent and were compensated for their time.

Testing Protocol

Attention and Inhibitory Control

Auditory and visual attention were assessed using the Integrated Visual and Auditory Plus Continuous Performance Test (Sandford & Turner, 1994). This is a standard clinical tool used to assess several components of attention performance and is used in conjunction with other diagnostic procedures to screen for attention-related disorders, including ADHD. The participant is asked to

Table 1. Summary of Group Demographics

	<i>Percussionists (n = 16)</i>	<i>Nonpercussionists (n = 20)</i>	<i>Group Comparison Statistic</i>
	<i>M (SD)</i>	<i>M (SD)</i>	
Age (years)	25.6 (6.0)	23.7 (3.8)	$t(34) = -1.167, p = .277, d = 0.378$
Nonverbal IQ	69.5 (20.1)	68.4 (27.7)	$t(34) = -0.131, p = .896, d = 0.045$
Hearing (PTA right/dB HL)	6.8 (4.6)	6.3 (3.2)	$t(34) = -0.400, p = .692, d = 0.126$
Hearing (PTA left/dB HL)	5.2 (3.8)	5.0 (3.5)	$t(34) = -0.171, p = .865, d = 0.055$
Sex	12 male, 4 female	16 male, 4 female	$\chi^2 = 0.129, p = 1.0$
Handedness	15 right, 1 left	18 right, 2 left	$\chi^2 = 0.164, p = 1.0$

click the mouse whenever a “1,” but not a “2,” is seen or heard.

The test was administered in a soundproof booth on a laptop computer placed 60 cm from the participant and includes four sections: warm-up, practice, test, and cool-down. Prerecorded instructions are included in the test to minimize variability in test administration. The auditory track is presented via Sennheiser HD 25-1 headphones with corresponding visual cues presented on the laptop monitor. During the warm-up, participants were instructed to click the mouse when they saw or heard a “1”; the test proceeded with a 20-trial warm-up during which only the number “1” was spoken or presented visually, 10 times each. Next, participants completed a practice session during which they were reminded of the same instructions but were also asked not to click the mouse when they saw or heard a “2”; further practice trials were presented (10 auditory and 10 visual targets). During the main portion of the test, five sets of 100 trials were presented for a total of 500 trials. Each set consisted of two blocks of 50 trials. The first block of each set measures impulsivity by creating a target to foil ratio of 5.25:1.0, resulting in targets in 84% of trials (i.e., 42 targets intermixed with eight foils per 50 trial block). The second block collects a measure of inattention by reversing the ratio and presenting many foils and few targets (i.e., 42 foils intermixed with eight targets per 50 trial block). Each trial lasts 1.5 sec, and stimuli were presented in a pseudorandom order of visual and auditory stimuli. The visual stimuli were presented for 167 msec and were 4 cm high, whereas the auditory stimuli lasted 500 msec and were spoken by a female participant.

RT was recorded for participants’ responses to the target (“1”) and foil (“2”) stimuli. The duration of the main portion of the test is 13 min, although the entire assessment including the introduction, practice, test, and cool down lasts for 20 min. The assessment generates age-normed scores in both auditory and visual modalities for the “full-scale attention quotient” as well as the “full-scale response control quotient,” a measure of inhibitory control. The full-scale attention quotient combines sub-measures of vigilance (a measure of inattention based

on errors of omission), focus (variability in processing speed for correct responses), and speed (the average RT across all correct responses). The full-scale response control quotient combines prudence (a measure of impulsivity and response inhibition based on errors of commission), consistency (a measure of the ability to stay on task, based on variability of RTs) and stamina, which compares mean RTs in the first 200 trials of the session with the last 200 trials. The full-scale attention and response control scores are combined across modalities to create composite scores (www.braintrain.com).

Self-paced, Paced, and Continuation Drumming

These tests assessed participants’ ability to drum consistently. Stimuli were stored and presented on an iPod nano (Apple), and participants were asked to drum with one hand on a conga drum. In the self-paced condition, the participants were instructed to choose a comfortable tempo and drum at that tempo as consistently as possible for 3 min. In the paced condition, participants were asked to synchronize their drumming to an isochronously presented auditory stimulus, presented through headphones. Each trial consisted of 40 repetitions of a snare drum stimulus (duration 99 msec, acquired at freesound.org) with a constant interonset interval (IOI). In two of these trials, the IOI was 667 msec (1.5 Hz presentation rate), and in two, the IOI was 500 msec (2 Hz), as in Tierney and Kraus (2013a). The trials were always presented in this order. Only the last 20 beats of each trial were analyzed to give the participant ample time to begin synchronizing to the beat. In the continuation condition, 20 repetitions of the stimuli were presented, followed by a period of silence equivalent to 20 stimulus presentations. The participant was asked to continue drumming at the same pace after the stimulus presentations stopped.

The participant’s drum hits were picked up using a vibration-sensitive drum trigger pressed against the underside of the head of the drum. The participant’s drumming and the stimulus to which the participant was listening were simultaneously recorded as separate channels of a stereo input and combined into a single sound file using version 2.0.5 of Audacity recording and

editing software (audacity.sourceforge.net), ensuring that the stimuli and response were correctly aligned in time. Continuous stimulus and drum data were converted to a list of onset times by a custom-written MATLAB program. This program used two parameters to identify onsets within the stimulus and drum signals: (1) a preset amplitude threshold and (2) a “refractory period,” during which points exceeding the amplitude threshold were ignored to ensure that multiple adjacent high-amplitude time points resulting from a single drum hit are not marked as independent onsets. Because participants vary in how they hit the drum, the marked onsets were visually compared with the raw continuous data, and any errors were manually corrected by adjusting the time and amplitude thresholds. Amplitude thresholds were set to be as small as possible, without resulting in false alarms, that is, background noise being marked as drum onsets. This ensured that individual differences in the amplitude of drum hits did not affect the reliability with which drum hit onset times could be marked.

The consistency of each participant’s drumming was assessed for each condition by calculating the coefficient of variability: The standard deviation of the IOI of the drum hits within each trial was averaged across trials to obtain a variability measure in each condition and then divided by the IOI. A composite score was generated for each of the paced and continuation conditions by averaging performance across presentation rates.

Neural Index of Beat Alignment

Stimulus presentation was as described in Tierney and Kraus (2013b), using an electrophysiological paradigm adapted from a tapping test developed by Iversen and Patel (2008). The target stimulus was a 200-msec synthesized bassoon tone with a 100 Hz pitch. The sound was presented at a +11-dB signal-to-noise ratio over the background music, which consisted of the musical piece “Pills” by Bo Diddley (171 sec). The onset time of each musical beat was determined by having a professional drummer tap to the song on a nanoPAD2 (Korg) tapping pad. The resulting mean interval between beats was 416 msec (standard deviation of intertap intervals was 13.89 msec). During the on-the-beat condition, the bassoon sound was presented such that its onset coincided with the time of each musical beat. In the off-the-beat condition, the target stimulus onset times were shifted later by one fourth of the average interval between every musical beat, rendering the stimuli “out of phase” with the beat. The song was presented once in each condition, resulting in over 1000 stimulus presentations per condition.

Electrophysiological Recording

Electrophysiological data were collected from Cz using Scan 4.3 Acquire (Compumedics, Charlotte, NC) with Ag-AgCl scalp electrodes at a sampling rate of 20 kHz and with open filters (0.1–3000 Hz). Four electrodes

were applied in a vertical, linked-earlobe reference montage. Contact impedance was 5 k or less across all electrodes. Stimuli were presented binaurally via insert earphones at 70 dB (ER-3; Etymotic Research, Elk Grove Village, IL). During recording, participants watched subtitled, muted videos of their choice to ensure that they remained alert.

Data Analysis and Statistical Methods

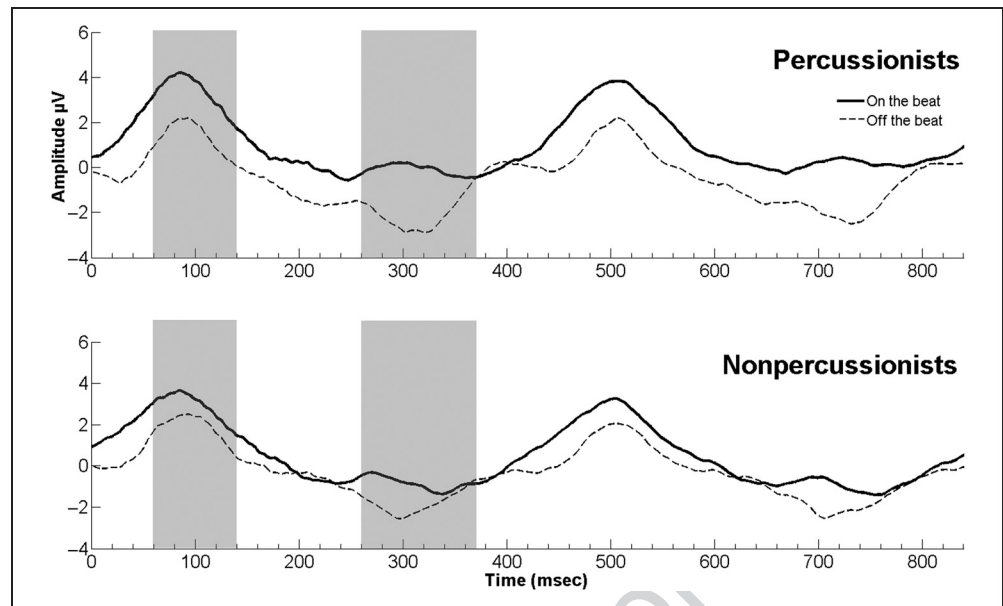
Electrophysiological response averages were created offline. The responses were epoched from 50 msec before each bassoon stimulus presentation to 834 msec after. This epoch spans two full beat cycles and, therefore, two stimulus presentations. To isolate the contribution of the cortex, responses were bandpass filtered from 0.1 to 20 Hz (12 dB/octave roll-off.) Responses were baselined to the prestimulus period of the response. Responses with activity $\geq \pm 75$ μV were rejected as artifacts, and the remaining sweeps per condition were averaged. Grand averages were created for each group in each condition (see Figure 1). Based on visual inspection and previously published differences between on-beat versus off-the-beat conditions using the same methodology (Tierney & Kraus, 2013b, 2015b), we calculated the difference between the on-beat and off-the-beat responses in the following time regions: 60–140 msec (P100) and 260–370 msec (N300).

Behavioral performance and neural measures were compared between the two groups using independent samples *t* tests. All results reported reflect two-tailed values, and an adjusted alpha level of .005 was used for correlational analyses to allow for multiple comparisons. Pearson correlations were performed between variables, and a hierarchical three-step linear regression was used to determine how well rhythm measures predicted variance in inhibitory control above and beyond demographic factors and group membership. Dependent variables conformed to the expectations of the linear model (normality and sphericity). Statistics were computed using SPSS (SPSS, Inc.).

RESULTS

Percussionists outperformed the nonpercussionists on inhibitory control, $t(34) = -3.336$, $p = .002$, $d = 1.137$ (percussionists: $M = 113.13$, $SD = 14.01$; nonpercussionists: $M = 94.45$, $SD = 18.54$), consistent with our previous findings in an overlapping data set (Slater et al., 2017). The percussionists were also less variable in their drumming than the nonpercussionists: self-paced: $t(34) = 2.762$, $p = .009$, $d = 0.832$ (percussionists: $M = 0.034$, $SD = 0.016$; nonpercussionists: $M = 0.050$, $SD = 0.022$); paced: $t(34) = 5.985$, $p < .001$, $d = 1.841$ (percussionists: $M = 0.028$, $SD = 0.006$; nonpercussionists: $M = 0.040$, $SD = 0.007$); continuation: $t(34) = 5.114$, $p < .001$, $d = 1.658$ (percussionists: $M = 0.023$, $SD = 0.005$; nonpercussionists: $M = 0.03$, $SD = 0.007$). Given that the drumming

Figure 1. Group average waveforms showing the neural index of beat alignment at 60–140 msec (P100) and 260–370 msec (N300), following Tierney et al. (2014). Positive components plotted upwards. Two epochs are shown, and the areas of interest are highlighted in the first epoch. The P100 component shows larger positive amplitudes when the stimuli are aligned with the musical beat, whereas the N300 shows large negative amplitudes when the stimuli are presented off the beat (Tierney et al., 2014). Percussionists had a significantly greater effect of condition on response amplitude in the later N300 time region, and the extent of this effect was correlated with inhibitory control score across all participants.



measures were significantly correlated with each other, these measures were combined together into a drumming variability composite score for correlational analyses (the composite was calculated as the mean value of coefficient scores across drumming conditions: self-paced, paced, and continuation). Across all participants, less variable drumming was significantly correlated with better inhibitory control and attention scores (inhibitory control: $R = -.641, p < .001$; attention quotient: $R = -.556, p < .001$).

Neural Index of Beat Alignment

Percussionists showed a greater effect of beat alignment on their neural response compared with nonmusicians in

the later N300 time region, $t(34) = -2.148, p = .039, d = 0.720$ (percussionists: $M = 2.075, SD = 1.536$; nonpercussionists: $M = 0.986, SD = 1.490$), but not for the earlier time region, $t(34) = -1.524, p = .137, d = 0.513$ (percussionists: $M = 1.980, SD = 1.824$; nonpercussionists: $M = 1.008, SD = 1.959$).

Correlations between Behavioral and Neural Measures

The P100 beat alignment effect was not significantly correlated with either inhibitory control or attention scores (inhibitory control: $R = .315, p = .061$; attention: $R = .192, p = .261$). The effect of beat alignment on the N300 component was correlated with inhibitory control

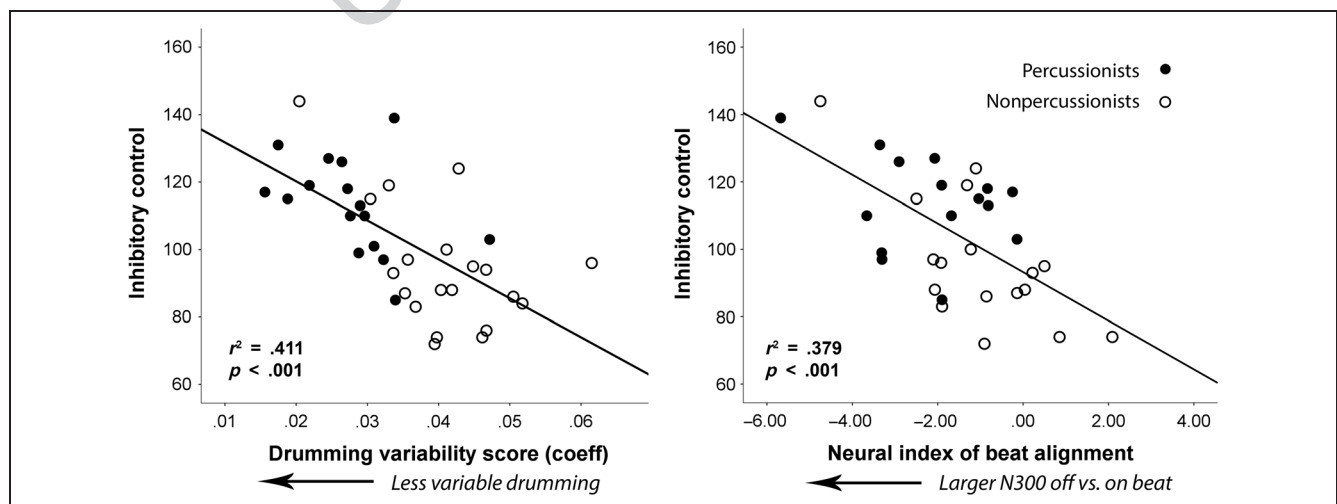


Figure 2. Better inhibitory control is linked with less variable drumming and greater neural sensitivity to the musical beat, such that the cortical evoked response to an auditory stimulus shows an increased N300 component when stimuli are not aligned with the beat of a musical excerpt.

($R = -.581, p < .001$), with better inhibitory control linked with a more negative component in the off-the-beat condition. There was no such relationship with attention ($R = -.203, p = .234$). See Figure 2 for correlations between inhibitory control and the rhythm measures.

To determine whether the drumming variability score and the N300 beat alignment effect explain unique variance in inhibitory control, above and beyond group membership and demographic factors, we performed a three-step hierarchical linear regression with inhibitory control as the dependent variable. In the first step, the independent variables age, sex, and IQ did not significantly predict variance in inhibitory control ($R^2 = .072$), $F(3, 32) = .834, p = .485$. Next we added group (percussionists and nonpercussionists), which significantly improved the model ($\Delta R^2 = .270, p = .001$; overall model: $R^2 = .342$), $F(4, 31) = 4.028, p = .010$. Finally, we added

the drumming variability score and neural index, which further improved the model ($\Delta R^2 = .232, p = .002$; overall model: $R^2 = .574$), $F(6, 29) = 6.523, p < .001$. The overall model accounts for 57% of variance in inhibitory control, with both drumming variability and neural index of beat alignment contributing unique predictive power to the model. Once drumming variability and the neural index were added, group membership no longer contributed unique predictive power to the model. For comparison, the same hierarchical regression was performed with attention as the independent variable. Consistent with our correlational findings, drumming variability was a significant predictor of attention above and beyond group membership and demographics, but the N300 beat alignment measure did not significantly contribute to the model. Overall, this model predicted 38% of variance in attention (see Table 2 for a full presentation of both regression analyses).

Table 2. Regression Analyses Using Rhythm Measures to Predict Inhibitory Control and Attention

Regression Model	Inhibitory Control	Attention Quotient
	Standardized β (p)	Standardized β (p)
<i>Step 1</i>		
Age	-.044 (.798)	.056 (.742)
Sex	-.108 (.608)	.002 (.991)
Nonverbal IQ	.192 (.367)	.323 (.126)
	$R^2 = .072, F(3, 32) = 0.834, p = .485$	$R^2 = .111, F(3, 32) = 1.329, p = .282$
<i>Step 2</i>		
Age	-.146 (.336)	-.020 (.899)
Sex	-.159 (.381)	-.036 (.853)
Nonverbal IQ	.163 (.373)	.301 (.124)
Group	.531 (.001)	.397 (.018)
	$\Delta R^2 = .270, \Delta F = 12.697, p = .001$	$\Delta R^2 = .150, \Delta F = 6.301, p = .018$
	$R^2 = .342, F(4, 31) = 4.028, p = .010$	$R^2 = .261, F(4, 31) = 2.737, p = .046$
<i>Step 3</i>		
Age	-.093 (.483)	-.073 (.648)
Sex	-.036 (.816)	-.089 (.638)
Nonverbal IQ	.114 (.453)	.295 (.115)
Group	.130 (.437)	.115 (.571)
Drumming variability	-.418 (.022)	-.481 (.029)
Neural index of beat (N300)	-.352 (.016)	-.052 (.756)
	$\Delta R^2 = .233, \Delta F = 7.953, p = .002$	$\Delta R^2 = .115, \Delta F = 2.677, p = .086$
Overall model:	$R^2 = .575, F(6, 29) = 6.541, p < .001$	$R^2 = .376, F(6, 29) = 2.914, p = .024$

DISCUSSION

We set out to investigate inhibitory control through the lens of rhythmic expertise, building from our recent discovery of a percussionist advantage for inhibitory control (Slater et al., 2017). We found that more consistent performance on simple drumming tasks is associated with better scores in both inhibitory control and selective attention, across a range of rhythmic expertise. Furthermore, we found that greater neural sensitivity to alignment with the musical beat (as indexed by an increased negative deflection around 300 msec following stimuli presented off the beat) was correlated with inhibitory control but not with attention. These outcomes suggest that there may be an overlap between brain networks involved in musical rhythm and cognitive control and provide a basis for further investigation of the potential for rhythm-based training to strengthen cognitive function.

Although correlational studies cannot establish a causal relationship between music training and inhibitory control, converging evidence has demonstrated enhanced cognitive and perceptual function in musicians (see Benz, Sellaro, Hommel, & Colzato, 2015, for a recent review). Percussionists outperformed nonpercussionists in all of our measures of interest; however, our regression analyses suggest the results are not solely driven by group differences, because drumming consistency and the neural index of beat alignment each explain unique variance in inhibitory control, above and beyond group membership and demographic factors (age, sex, and IQ).

The absence of a relationship between the P100 beat alignment effect and inhibitory control is consistent with an interpretation of the P100 as reflecting a “cost of attention,” as described by Luck and colleagues in the context of spatial attention (Luck et al., 1994). Under this interpretation, the amplitude of the P100 is greater when the stimuli fall within the focus of attention, whereas the amplitude is reduced when the stimulus occurs at an unattended location or, in this case, an unexpected point in time. The increased P100 when the stimulus is aligned with the beat is also consistent with Tierney and Kraus’ proposed neural entrainment to the frequency and harmonics of the beat tempo, which would contribute to the positive amplitude in both time regions in the on-beat condition (Tierney & Kraus, 2015b). However, here we suggest that there is an additional conflict-monitoring effect on the later component that results in a larger negative deflection when the stimulus presentation conflicts with the structure of the music. The P100 could also reflect a more basic difference in neural resource allocation rather than the cost of attentional shift, such that resources are divided between the musical beat and the stimulus when they are not aligned. However, the increased negative amplitude of the N300 for off-the-beat stimuli suggests that the P100 effect is not fully explained by an overall reduction in response amplitude in this condition. It should also be noted that the N300

beat alignment advantage for percussionists was not strongly significant and that the P100 neural index was trending in the same direction, such that percussionists also had a larger mean effect of condition on the P100. The lack of strong effects in these group comparisons may be due to the relatively small group sizes and variability within our groups, and the neural measures may warrant further investigation with more tightly constrained group inclusion criteria.

It seems that percussionists’ activities may occupy a “sweet spot” in terms of engaging motor and reward systems both through the coordination of complex movement and through the interaction with temporal structure. The specific advantage for percussionists compared with vocalists from our previous study suggests that engagement with music alone may not be sufficient (Slater et al., 2017); however, this effect could still be due to the relative emphasis on rhythmic structure versus pitch or harmonic elements in a percussionists’ practice. It therefore remains unknown whether it is engagement with rhythmic structure or the specific motor activities involved in drumming that may engender these effects. Although our correlational outcomes do not allow direct assessment of underlying mechanisms, the unique predictive contributions of the drumming variability score and the neural measure in explaining variance in inhibitory control suggest there may be multiple mechanisms at play. This is supported by the fact that our neural index of beat alignment is correlated with inhibitory control but not attention, and in our earlier study, the percussionists outperformed vocalists in inhibitory control but not attention (Slater et al., 2017). It is also interesting to note that, in a recent investigation of timing skills in percussionists, researchers found greater precision in tasks accompanied by movement, but not in a listening only condition, suggesting a percussionist benefit in temporal processing may be tightly linked with motor skills (Manning & Schutz, 2016). However, longitudinal studies are needed to determine whether motor and cognitive control can be influenced by training over time and whether both production and perception of rhythm are necessary to confer benefits.

Expertise in other domains such as sports may also provide useful insight, for example, enhanced inhibitory control has been observed in expert fencers (Di Russo, Taddei, Apnile, & Spinelli, 2006). Although fencers must coordinate precise movements and inhibit their actions according to rapidly changing demands, their coordination of movement does not occur within a temporal framework, such as provided by music. A recent study found that long-term inhibitory control advantages in fencers were associated with strengthened structural connectivity within frontal–BG networks (Chavan et al., 2017). However, these same structural networks (especially involving the BG) subserve multiple functions with regard to motor control and reward-based predictive processing. It would therefore be informative to determine how these

distinct functions relate to inhibitory control and whether they are modified in tandem by expertise. For example, our neural index of beat alignment could be assessed in fencers to determine whether they show the same increased neural sensitivity to the musical beat as percussionists. Although the absence of an inhibitory control advantage in vocalists compared with nonmusicians suggests that their expertise may not have been sufficient to elicit benefits (Slater et al., 2017), it is possible that more extensive perceptual exposure to musical rhythm could still strengthen these same networks, perhaps just at a slower rate than when motor systems are more directly involved. This represents an interesting area for future investigation.

The potential importance of rhythmic expertise may help to explain mixed outcomes across previous studies with regard to inhibitory control or other executive function advantages. If these studies included musician groups that were heterogeneous with regard to the kinds of motor activities involved in the music-making (e.g., vocalizing, using fingers and mouth with wind instruments, bimanual coordination, etc.), as well as varying degrees of emphasis on rhythmic elements, this could lead to divergent outcomes. Further research could address these discrepancies by considering both format and scale of physical activity and level of rhythmic skill within the musician cohorts.

Previous work has highlighted dissociable rhythm skills (Tierney & Kraus, 2015a), with multiple neural circuits involved in different components of rhythmic processing (Merchant et al., 2015; Schwartze & Kotz, 2013; Grahn, 2012). Here, we focused on tasks involving a simple isochronous beat, but with varying degrees of integration between internal and external timing: from self-paced drumming (in which the participant drums at a pace of their own choosing), to paced drumming (where the participant must align with an external pacing stimulus), to continuation drumming (where the participant aligns with a pacing stimulus and then continues drumming on their own at the same pace). The strong relationships across these three drumming measures could suggest that it is not simply the ability to perform consistently in one or other of these tasks that reflects important mechanisms of control but also the ability to integrate internal and external timing cues as needed for a given task. The interplay between internally generated timing (within the brain) and external timing (e.g., a pacing stimulus) reflects an ongoing balance between prediction and flexibility that is fundamental to how the brain interacts with a dynamic environment (Raichle, 2010; Engel et al., 2001).

Conclusions

These findings highlight rhythm and rhythmic expertise as an informative context for the investigation of cognitive control. The combination of precise coordination of motor activities within a complex temporal framework provides insight into the deep-rooted connections between movement, timing, and cognition. Outcomes are

consistent with a theoretical framework in which cognitive, motor, and temporal processing rely upon overlapping neural circuitry to coordinate neural activity and control behavior.

From a clinical perspective, the nonmotor symptoms of disorders, such as Parkinson's disease (Dubois & Pillon, 1996; Owen et al., 1992), and the motor deficits associated with attention-related disorders, such as ADHD (Toplak & Tannock, 2005; Ben-Pazi, Gross-Tsur, Bergman, & Shalev, 2003), highlight the need for a unified understanding of neural coordination and control across motor and cognitive domains that can more effectively describe both typical and disordered function. We hope these findings will inform further investigation into the potential use of rhythmic activities in the treatment and remediation of attention-related disorders and inspire further research embracing an integrated approach to how the brain organizes its activities in time.

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