

Individual Differences in Rhythm Skills: Links with Neural Consistency and Linguistic Ability

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Abstract

■ Durational patterns provide cues to linguistic structure, thus so variations in rhythm skills may have consequences for language development. Understanding individual differences in rhythm skills, therefore, could help explain variability in language abilities across the population. We investigated the neural foundations of rhythmic proficiency and its relation to language skills in young adults. We hypothesized that rhythmic abilities can be characterized by at least two constructs, which are tied to independent language abilities and neural profiles. Specifically, we hypothesized that rhythm skills that require integration of information across time rely upon the consistency of slow, low-frequency auditory processing, which we measured using the evoked cortical response. On the other hand, we hypothesized

that rhythm skills that require fine temporal precision rely upon the consistency of fast, higher-frequency auditory processing, which we measured using the frequency-following response. Performance on rhythm tests aligned with two constructs: rhythm sequencing and synchronization. Rhythm sequencing and synchronization were linked to the consistency of slow cortical and fast frequency-following responses, respectively. Furthermore, whereas rhythm sequencing ability was linked to verbal memory and reading, synchronization ability was linked only to nonverbal auditory temporal processing. Thus, rhythm perception at different time scales reflects distinct abilities, which rely on distinct auditory neural resources. In young adults, slow rhythmic processing makes the more extensive contribution to language skills. ■

INTRODUCTION

Rhythms pervade our auditory environment. Whether the steady pulse of waves on a beach, the accelerating staccato of approaching footsteps, or the characteristic tempo that distinguishes one animal's call from another, these patterns in time convey vital acoustic cues. Rhythm also plays important—and strikingly similar—roles in speech and music. In both domains, for example, rhythm cues the location of structural boundaries (Yang, Shen, Li, & Yang, 2014; Krumhansl & Jusczyk, 1990; Scott, 1982), as the ends of phrases are marked by lengthened durations and longer pauses (Penel & Drake, 2004; Wightman, Shattuck-Hufnagel, Ostendorf, & Price, 1992). Both domains also use lengthened durations to mark elements as stronger or weaker, directing attention to important points in the signal; in speech, lengthened durations indicate stressed syllables (Lieberman & Prince, 1977) and facilitate speech intelligibility (Bradlow, Kraus, & Hayes, 2003), whereas in music, lengthened durations are associated with stronger metrical positions (Lerdahl & Jackendoff, 1985).

Given the central role that rhythm plays in speech and music, one might expect rhythmic competence to be widespread. Surprisingly, however, people vary widely

in their rhythmic proficiency. Moreover, certain rhythm skills seem to be dissociable: Severe congenital disruption of synchronization ability can co-occur with preserved ability to discriminate rhythms, and vice versa (Palmer, Lidji, & Peretz, 2015; Launay, Grube, & Stewart, 2013; Sowinski & Dalla Bella, 2013). Impaired synchronization to the beat of music can also coexist with preserved synchronization to a metronome (Phillips-Silver et al., 2011). Finally, difficulty reproducing rhythmic sequences can co-occur with preserved synchronization ability, and vice versa (Tierney & Kraus, 2015a). These lines of evidence motivate a concept of rhythm as a constellation of distinct (albeit potentially intercorrelated) skills rather than a single competence.

The existence of dissociable rhythm skills suggests that the neural networks subserving certain rhythm skills may also be dissociable. Precise synchronization requires the detection and correction of small auditory-motor asynchronies and therefore relies upon temporal processing on a fast time scale (on the order of less than 10 msec). Supporting this idea, intertrial phase consistency in the fast frequency-following response (FFR), which reflects precise temporal encoding across the auditory system (Coffey, Herholz, Chepesiuk, Baillet, & Zatorre, 2016; Bidelman, 2015; Warrier, Nicol, Abrams, & Kraus, 2011; Chandrasekaran & Kraus, 2010), is linked to the variability

of synchronization (Tierney & Kraus, 2013a) and the ability to adapt to perturbations while synchronizing (Tierney & Kraus, 2016). Perception of entire rhythm sequences, on the other hand, requires the integration of rhythmic information across time and therefore relies upon temporal processing on a slow time scale (>0.5 sec). Thus, tracking of rhythmic patterns may rely upon phase-locking of slower amplitude modulations within auditory cortex and transmission of this information to frontal regions responsible for motor planning and temporal prediction (Patel & Iversen, 2014). Variability in slower, low-frequency cortical processing, therefore, may interfere with rhythm sequencing but not synchronization. Although we draw lines along a fast versus slow dichotomy, we view auditory processing as the product of a distributed, but integrated, network of cortical, subcortical, and cochlear circuits (Kraus & White-Schwoch, 2015). A hypothesis derived from this framework is that system-wide pathways specialize for faster and slower auditory processing and that, in humans, the FFR reflects faster processing whereas the cortical evoked response to sound reflects slower processing.

Because of the similar roles that rhythm plays in speech and music, deficits in the perception of nonverbal rhythms may bear on language skills. Mounting evidence suggests that rhythmic deficits are tied to language impairment: Abnormally poor reading and phonological awareness have been linked to difficulties with rhythm skills as diverse as synchronization (Flaugnacco et al., 2014; Tierney & Kraus, 2013b; Corriveau & Goswami, 2009; Thomson & Goswami, 2008; Thomson, Fryer, Maltby, & Goswami, 2006), beat extraction (David, Wade-Wolley, Kirby, & Smithrim, 2007), metrical perception (Huss, Verney, Fosker, Mead, & Goswami, 2011), rhythm memory (Flaugnacco et al., 2014; González-Trujillo, Defior, & Gutiérrez-Palma, 2014; Dellatolas, Watier, Le Normand, Lubart, & Chevrie-Muller, 2009), and rhythm discrimination (Strait, Hornickel, & Kraus, 2011; Douglas & Willatts, 1994; McGivern, Berka, Languis, & Chapman, 1991). In fact, links between synchronization ability and reading readiness skills have even been observed in preschoolers too young to have received reading instruction (Woodruff Carr, White-Schwoch, Tierney, Strait, & Kraus, 2014). It remains unclear, however, which aspects of language function track with which sorts of rhythm skills. Answering this question could suggest common neural resources on which both rhythm and language rely and motivate future attempts to identify those children whose language impairments could be remediated through targeted rhythm training.

Here, we investigated the neural foundations of rhythmic proficiency and relationships between rhythm and language skills by using statistical modeling to reduce the performance of participants on the cusp of young adulthood on a large number of rhythm tests to a few common factors. This test battery captured a diverse range of rhythm skills, including synchronization to a metronome, adaptation to timing and tempo shifts, synchro-

nization to the beat of rhythmic sequences, drumming along to sequences, and remembering sequences. Early findings from these data are consistent with our hypotheses that synchronization and sequences are distinct skills related to fast and slow auditory processing, respectively (Tierney & Kraus, 2015a, 2016); here, we focus on a more thorough analysis of this data set incorporating additional tests of rhythm skills, tests of language abilities, and two sets of neurophysiological recordings not previously reported. We predicted that the intertrial consistency of fast FFRs would track with tests that require temporal judgments on a fast time scale whereas the consistency of slow evoked responses would relate to tests that require temporal judgments on a slow time scale. Furthermore, we predicted that both clusters of rhythm skills would be linked to phonological skill and reading, as the acquisition of language skills relies on the perception of patterns of time at slow and fast time scales. However, we predicted that only slower rhythm tests would be linked to verbal working memory skills, given that perceiving and reproducing a rhythmic sequence require storing and integrating information across a longer time span than does synchronization.

METHODS

Participants

Sixty-four participants (30 women) with a mean age of 18.0 years ($SD = 1.0$ year) were recruited from the greater Chicago area and were given a battery of rhythm tests. Forty-nine participants (22 women) were given additional batteries of language and cognitive tests and neurophysiological recordings. Informed written consent was obtained for participants over the age of 18 years; for younger participants, informed written assent was obtained, and written consent was obtained from the participant's legal guardian. All participants had normal hearing (defined as pure-tone air-conduction thresholds of <20 dB normal hearing level for octaves between 250 and 8000 Hz). No participant had been diagnosed with a language, learning, or neurological disorder. All procedures were approved by the Northwestern University Institutional Review Board pursuant to the Declaration of Helsinki.

Rhythm Tests

The rhythm battery was designed to encompass a range of nonverbal rhythm skills, spanning faster and slower time scales. All stimuli were constructed using custom MATLAB (The MathWorks, Inc., Natick, MA) programs. The synchronization task used a 99-msec snare drum stimulus, whereas all other tests used a 150-msec conga drum stimulus (both stimuli were acquired from free-sound.org). Participants completed six rhythm tests in

which they listened to stimuli through headphones and drummed along on a conga drum using their dominant hand. A drum trigger, pressed against the underside of the conga drum, recorded the drum head vibrations resulting from each drum hit. The drum trigger output was combined with a copy of the stimulus track being presented to participants as the two channels of a stereo input to a computer running the sound recording program Audacity (The Audacity Team). Thus, the relationship between the timing of the sound events and the timing of the drum hits was recorded in real time.

Data from all rhythm tasks were analyzed in MATLAB. For each test, the drumming and stimulus data were converted to sequences of onset times. To convert continuous amplitude data to discrete onsets, an amplitude threshold and refractory period were set. A time point was marked as a drum hit if, at that time point, (1) the amplitude of the hit exceeded the amplitude threshold and (2) the time between the last recorded drum hit and the current time point exceeded the refractory period. Thus, the refractory period ensured that adjacent time points exceeding the amplitude threshold (e.g., from vibration of the drum head after an especially hard hit) were not interpreted as multiple drum hits. Participants varied in the exact manner in which they struck the drum, and so the amplitude thresholds and refractory periods were set manually for each participant. For example, if a hit fell below the amplitude threshold and so was not marked, the amplitude threshold would be lowered. Similarly, if two hits were separated by a length of time below the refractory period and so the second hit was

not marked, the refractory period would be shortened. Drum hit onsets as marked by the program were visually compared with the raw amplitude data to ensure that each drum hit was marked only once and to ensure that background noise was not marked. These stimulus and response drum hit sequences were then further analyzed using different methods for each test to produce summary scores, as described below.

Six drumming tasks were presented: synchronization, tempo adaptation, timing adaptation, beat synchronization, drumming to sequences, and sequence memory (see Figure 1 for a schematic displaying a typical stimulus and ideal response for each task). Each test consisted of multiple conditions, some more difficult than others, to avoid ceiling and floor effects. Performance on these conditions was averaged to limit the number of variables included in the modeling analysis, given the limitations posed by the number of participants we were able to test.

Synchronization

This test provided a measure of participants' ability to maintain a steady beat while synchronizing to an isochronous stimulus at multiple rates. Participants were asked to drum along with a snare drum sound such that their drum hits occurred at the same time as the sounds they heard. Six trials were presented. During each trial, the stimulus was presented 40 times with a constant interonset interval (IOI); the end of the trial was indicated with a beep. Two trials were presented at each of

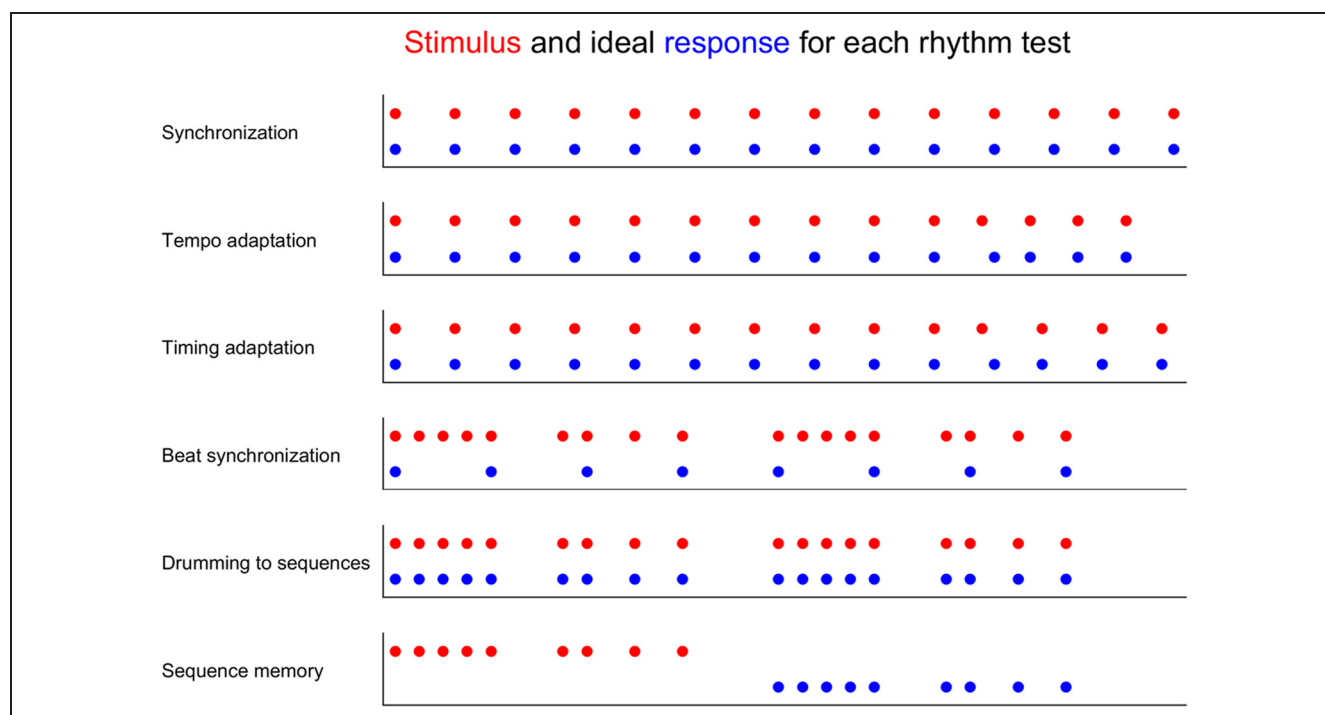


Figure 1. Schematics displaying typical stimuli and ideal responses for all six rhythm tests. For the timing adaptation and tempo adaptation tests, the size of the largest shifts has been doubled for display purposes.

three different IOIs: 333, 500, and 667 msec. Data for the first 20 sound presentations were not analyzed to give participants time to internalize the metronome tempo and begin synchronizing. For the last 20 sound presentations, synchronization variability was calculated as the standard deviation of intervals between drum hits divided by the mean interval between drum hits for that condition averaged across all six trials.

Tempo Adaptation

This test provided a measure of participants' ability to rapidly adjust to a change in tempo (speeding up or slowing down) while synchronizing. Participants drummed along with a conga drum sound that was presented at a steady rate. This rate then changed in tempo, and the participants were asked to rapidly switch the tempo of their drumming to match this change. Fifty-five trials were presented to the participants. Each trial consisted of between 11 and 15 presentations of the conga drum sound with a constant IOI of 500 msec, immediately followed by four more presentations with a new IOI. Five trials were presented at each of the 11 intervals: 450, 460, 470, 480, 490, 500, 510, 520, 530, 540, and 550 msec. Pseudorandomization of interval presentation ensured that the direction and magnitude of the tempo shift were unpredictable. Tempo adaptation was calculated as the absolute value of the difference between each of the last two intervals produced by the participant and the new stimulus IOI. These two values were then averaged to form an adaptation score for that trial. For example, if the target IOI was 520 msec and the last two intervals produced by the participant were 510 and 540 msec, the participant's adaptation score for that trial would be 15 msec. Finally, performance was averaged across the five trials for each target IOI.

Timing Adaptation

This test provided a measure of participants' ability to rapidly adjust to an occasional temporal perturbation while synchronizing. Participants drummed along with a conga sound that was presented at a steady rate. Occasionally, a single IOI was either lengthened or shortened. Participants were asked to stay on the beat as much as possible despite these occasional timing shifts such that their drum hits occurred at the same time as the stimulus onsets. Four trials were presented. During each trial, conga sounds were presented 169 times with a constant IOI of 500 msec, but occasionally, one of these intervals was shortened or lengthened. During each trial, 16 shifts occurred, each of which was separated from the next by at least eight isochronous 500-msec IOIs. Four trials were presented. During the first two trials, shifts were 50 msec in magnitude; during the last two trials, shifts were 10 msec in magnitude. Timing adaptation was calculated as the

standard deviation of the offset between drum hits and stimulus onsets for the six hits after each shift.

Beat Synchronization

This test provided a measure of participants' ability to steadily drum to the beat of a rhythmic sequence. First, participants heard nine repetitions of a conga drum sound presented at a constant IOI of 800 msec. Immediately after these sounds, they heard a four-measure sequence (Povel & Essens, 1985) with an underlying interbeat interval of 800 msec repeated eight times. Participants were asked to begin drumming to the drum sound and then continue drumming at this rate once the sequence started, matching their drumming up to the beat of the sequence. Each sequence consisted of the same set of IOIs arranged in different orders: five 200 msec, two 400 msec, one 600 msec, and one 800 msec (i.e., equivalent to quarter, half, dotted-half, and whole notes). Each sequence was four measures in duration. Four trials were presented: two that Povel and Essens (1985) characterized as "strongly metrical" and two that were deemed "weakly metrical." Weakly metrical sequences, compared with strongly metrical sequences, contained fewer drum hits on the first and third beats of each measure. Beat synchronization variability was calculated as the standard deviation of intervals between drum hits divided by the mean interval between drum hits for that trial averaged across all four trials.

Drumming to Sequences

This test provided a measure of participants' ability to rapidly perceive, reproduce, and synchronize with a rhythmic sequence. Participants were asked to drum along to conga drum sequences such that each drum hit they heard was matched by a drum hit they produced. Four trials were presented. In each trial, a four-measure sequence taken from Povel and Essens (1985) was repeated 10 times. Participants were told to listen to the sequence and begin drumming along as soon as they had a good idea of what the sequence was. Four sequences were presented, two "strongly metrical" and two "weakly metrical." Drumming to sequences accuracy was calculated by dividing each sequence into 16 segments, each of which could contain either a rest or a drum hit. For each segment, the analysis determined whether the participant correctly produced either a rest or a drum hit in a 200-msec window centered on either the sound onset of the time point or, in the case of a silence in the stimulus pattern, on the time point when a sound would have occurred. The score for each trial, therefore, consisted of the number of correctly performed hits or rests divided by the total number of analyzed segments. For example, if one measure was [0 0 0 1] and the participant's drumming was [0 0 1 1], where a zero indicates a rest and a 1 indicates a drum hit, the participant would receive a

score of 0.75 for this section. This procedure produced a measure of the ability to perceive and reproduce rhythmic sequences that was relatively insensitive to the ability to align movements precisely in time to a stimulus (i.e., to synchronize). Analysis was begun on the second repetition of the sequence and continued for the remainder of the trial; thus, the more quickly the participant was able to learn the sequence, the better they performed on the test.

Sequence Memory

This test provided a measure of participants' ability to remember metrical sequences. During each trial, a four-measure sequence (Povel & Essens, 1985) was repeated three times, followed by a pause equal in length to a full repetition of the sequence. Participants were asked to listen to the three repetitions without drumming and then drum out the sequence during the pause, producing the sequence exactly when it would have occurred had it repeated a fourth time. Thirty trials were presented, fifteen "strongly metrical" and fifteen "weakly metrical." Sequence memory accuracy was calculated analogously to the accuracy calculation for the drumming along to sequences test: The drum sequence produced during the pause was compared with the target drum sequence to calculate proportion correct.

Language and Cognitive Tests

Phonological skills measured included phonological awareness and rapid naming. Phonological awareness is the explicit knowledge of, and ability to manipulate, the speech sounds that make up one's native language. Phonological awareness was measured using tests of elision, in which participants are asked to remove a single phoneme from a word and speak the resulting word, and blending words, in which participants hear a series of isolated phonemes and are asked to put these together to form a word. Rapid naming is the ability to quickly recite an array of familiar items. Rapid naming was measured using tests of rapid letter naming and rapid digit naming, in which participants see lists of either letters or digits and are asked to speak them aloud as rapidly as possible. All tests of phonological skills were taken from the Comprehensive Test of Phonological Processing (Wagner, Torgesen, & Rashotte, 1999).

Reading skills measured included word reading and nonword reading. Nonword reading refers to the ability to read aloud a list of increasingly lengthy phonotactically legal nonsense words. Word reading consists of the ability to read aloud a list of increasingly lengthy English words. Word and nonword reading were measured using the Woodcock-Johnson III Test of Achievement (Woodcock, McGrew, & Mather, 2001) subtests Letter-Word ID and Word Attack, respectively. For display purposes (see Figure 2), a reading composite was formed by convert-

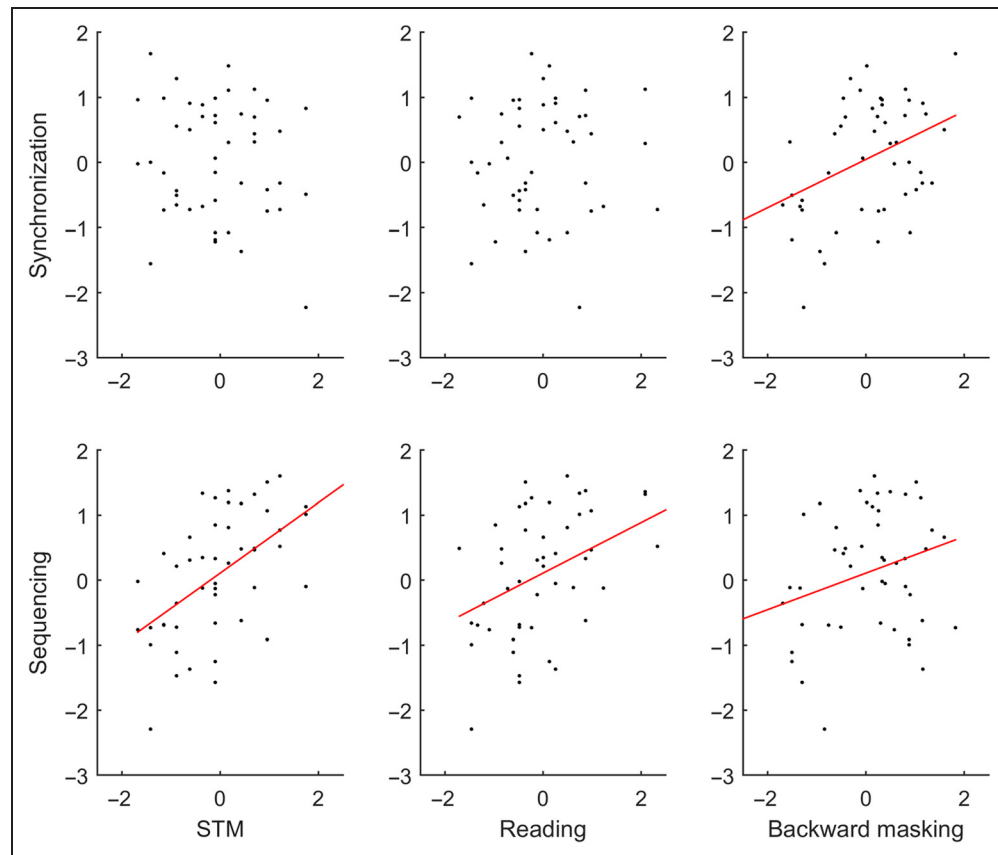
ing word and nonword reading scores to *z* scores and then averaging performance across the two tests.

Memory skills measured included short-term memory (STM) and verbal working memory. STM is the ability to keep speech sounds in a short-term store. STM was measured using tests of nonword repetition, in which participants hear phonotactically legal nonsense words spoken aloud and are asked to repeat them back, and digits forward, in which participants hear lists of numbers and are asked to repeat them back. Verbal working memory is the ability to take in auditory verbal information and mentally manipulate it before repeating the information back. Working memory was measured using tests of auditory working memory, in which participants hear a mixed sequence of numbers and objects and are asked to repeat them back by repeating first the numbers and then the objects in the order in which they were presented, and digits reversed, in which participants hear sequences of digits and are asked to repeat them in reverse order. Phonological memory was measured using the Comprehensive Test of Phonological Processing (Wagner et al., 1999), whereas working memory was measured using the Woodcock-Johnson III Test of Cognitive Ability (Woodcock et al., 2001).

Perceptual Tests

Auditory temporal resolution was measured using a backward masking test. Backward masking tests evaluate the ability to detect a faint tone despite the presence of masking noise that immediately follows the tone. Backward masking was measured using the IHR Multicentre Study of Auditory Processing battery (Barry, Ferguson, & Moore, 2010). Participants were shown, on a laptop computer, three cartoon characters. Three sounds were played in sequence, and each sound presentation was accompanied by one of the cartoon characters opening its mouth. Participants were asked to indicate which of the three sounds was different from the other two by pressing one of three buttons on a response box. The spatial layout of the buttons (left, right, and center) corresponded to the location of the characters on the screen. All three stimuli consisted of 300-msec band-pass noise bursts with 100-Hz center frequency, 800-Hz width, and a fixed spectrum level of 30 dB. One of the three stimuli also contained a target stimulus, a 20-msec 1000-Hz pure tone with a 10-msec cosine ramp. Two conditions were presented. In the no-gap condition, the noise burst was presented immediately after the tone ended. In the gap condition, a 50-msec gap was presented between the offset of the tone and the onset of the noise. The intensity of the tone relative to the noise was varied via a one-up, two-down adaptive staircase procedure to determine the signal-to-noise threshold at which participants were able to reliably detect the target tone. Lower thresholds indicate better ability to detect the tones despite the presence of the masking noise. A

Figure 2. Scatterplots displaying relationships between rhythm skills and performance on language and cognitive tests. Data are in z scores. Reading data are a composite of nonword reading and word reading scores.



composite score was created by averaging thresholds across the gap and no-gap conditions.

Electrophysiology

Participants underwent an electrophysiological testing battery to evaluate their neural coding of sound.

Stimulus

The stimulus used to evoke electrophysiological responses to sound was a Klatt-synthesized 170-msec /da/ (20,000 Hz sampling rate) consisting of a 5-msec onset burst, a 45-msec formant transition period, and a 120-msec steady-state period. The fundamental frequency stayed steady throughout the stimulus at 100 Hz. During the formant transition, the first formant increased from 400 to 720 Hz, the second formant decreased from 1700 to 1240 Hz, and the third formant decreased from 2580 to 2500 Hz. The fourth, fifth, and sixth formants stayed steady throughout the stimulus at 3300, 3750, and 4900 Hz, respectively. The stimulus was presented using Neuroscan Stim² (Compumedics, Abbotsford, Victoria, Australia) monaurally at alternating polarities to the right ear through ER-3 insert earphones (Etymotic, Elk Grove Village, IL) at 80-dB sound pressure level. To elicit FFRs, stimuli were

presented with an IOI of 251 msec, whereas to elicit cortical evoked responses, stimuli were presented with an IOI of 1006 msec. During both cortical and FFR recordings, stimuli were presented in two conditions: In a quiet condition, they were presented without any competing sound, whereas in a noise condition, they were presented simultaneously with background babble from six talkers (three men, three women) at a 10-dB signal-to-noise ratio (see Smiljanic and Bradlow [2005] for more information on the acoustics of the background babble).

Recording

During the recording of FFRs, continuous electrophysiological data were recorded using Neuroscan Acquire 4.3 (Compumedics) at 20000 Hz using a Synamp2 system (Compumedics) with a montage of three Ag–AgCl electrodes, with forehead as ground, the right earlobe as reference, and Cz as the active electrode. Electrode impedances were kept below 5 k Ω . Recordings were monitored online for artifacts (greater than ± 35 μ V), and 6000 artifact-free epochs were collected. Data were processed in MATLAB using custom scripts. Recordings were band-pass filtered from 70 to 2000 Hz (12-dB/octave roll-off) using a Butterworth filter. Next, recordings were epoched from 40 msec before to 190 msec after the

presentation of each stimulus. Epochs were baseline-corrected, and epochs with amplitudes exceeding $\pm 35 \mu\text{V}$ were rejected as artifacts.

During cortical recording, electrophysiological data were collected using Neuroscan Acquire 4.3 at 500 Hz using a Synamp2 system with a 31-channel tin cap referenced to the earlobes. Electrodes were placed above the left pupil and outer canthus of the left eye to capture eye movements. Electrode impedances were kept below 10 k Ω . Recordings were monitored online for large artifacts (greater than $\pm 100 \mu\text{V}$), and 400 artifact-free epochs were collected. Data were processed in MATLAB using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014). Recordings were band-pass filtered from 1 to 35 Hz (24-dB/octave roll-off) using a Butterworth filter. Next, recordings were epoched from 100 msec before to 500 msec after the presentation of each stimulus. Epochs were baseline-corrected, and epochs with amplitudes exceeding $\pm 100 \mu\text{V}$, eye blinks, eye movements, or other artifacts were automatically detected and rejected as artifacts.

Analysis: Consistency of the Electrophysiological Responses

Intertrial FFR consistency was calculated in the following manner. First, 3000 of the 6000 total epochs were randomly selected and averaged. The remaining 3000 epochs were then also averaged, and the two resulting sub-average waveforms were correlated. A higher correlation between waveforms indicates more similar subaverages and therefore greater intertrial response consistency. This procedure was repeated 300 times, each time with different random samplings, to ensure that the result reflected consistency across all trials. Finally, the resulting 300 response consistency scores were averaged to form a global measure of FFR consistency. Before the statistical analysis, response consistency scores were Fisher transformed. Response consistency scores for the quiet and noise presentation conditions were combined to form an FFR consistency score.

The passive cortical response to sound consists of four main components: P1, N1, P2, and N2. A cross-electrode average was computed, the latency of each peak was marked on the average by an automated algorithm within time regions appropriate for each component (P1: 40–100 msec, N1: 70–170 msec, P2: 140–180 msec, N2: 180–250 msec). The largest maximum (for P1 and P2) or minimum (for N1 and N2) found within this window was then defined as the latency of the component. These latencies were then manually checked by a trained peak-picker simultaneously viewing the average across all channels, the waveforms for each individual channel, and the global field power. Those participants without an identifiable peak were assigned a peak latency equivalent to the population mean. Because P2 in the noise response did not have an identifiable peak

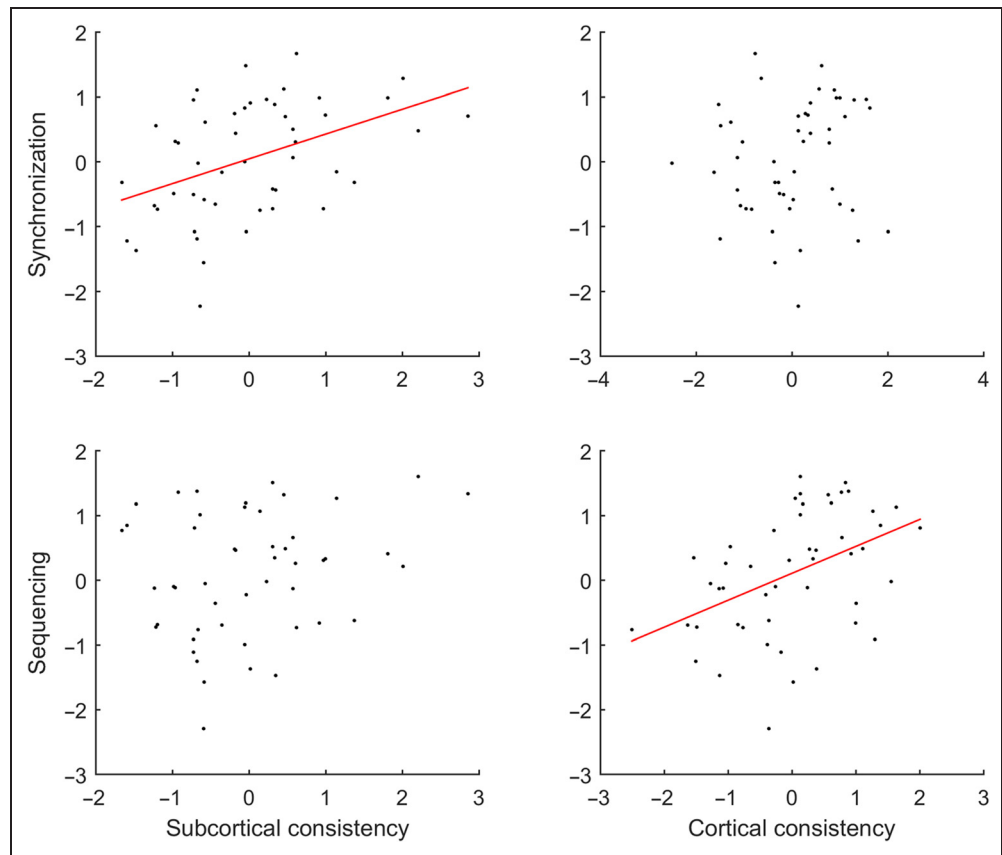
in most participants (33), this component was eliminated from the analysis.

An automated procedure was used to select the set of channels used to analyze each component. First, for each channel, the difference between the maximum and minimum values was calculated within a 40-msec window centered on the peak latency (which was defined as the mean of the manually picked latencies across all participants). A given channel was included in the channel set for a particular component if this difference was at least 40% of the greatest difference across all channels. For example, if the max–min difference was greatest with a value of 0.5 at Cz but was only 0.1 at Pz and 0.3 at Fz, only Cz and Fz would be included in the analysis. Visual inspection of waveform topographies confirmed that this algorithm successfully picked the channels where each component was most prominent.

This procedure picked the following channel sets for each component. For the quiet condition, P1 was measured across F3, Fz, F4, FC3, FCz, FC4, FT8, C3, Cz, C4, CP3, CPz, CP4, and Pz; N1 was measured across FP1, FPz, FP2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, T3, C3, Cz, F4, TP7, CP3, CPz, CP4, T5, P3, Pz, and P4; P2 was measured across FP1, FPz, FP2, F3, Fz, F4, FC3, FCz, FC4, T3, C3, Cz, C4, TP7, CP3, CPz, CP4, P3, and Pz; and N2 was measured across FP1, FPz, FP2, F7, F3, Fz, F4, F8, FC3, FCz, FC4, C3, Cz, and CPz. For the noise condition, P1 was measured across FP1, FPz, FP2, F7, F3, Fz, F4, FT7, FC3, FCz, FC4, T3, C3, Cz, C4, CP3, CPz, and CP4; N1 was measured across FP1, FPz, FP2, F3, Fz, F4, FT7, FC3, FCz, FC4, C3, Cz, C4, TP7, CP3, CPz, and T5; and N2 was measured across FP1, FPz, FP2, F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T3, C3, Cz, C4, T4, CP3, CPz, CP4, TP8, P3, and Pz.

Intertrial cortical consistency was calculated using a bootstrapping method introduced by Fitzroy, Krizman, Tierney, Agouridou, and Kraus (2015). This procedure provides a global measure of the intertrial consistency of the passive cortical response. First, continuous data were averaged across the appropriate channel set for each component (see the last paragraph). Second, 150 epochs of the pool of artifact-free epochs were randomly selected. Next, these epochs were divided into five groups of 30 epochs, each of which was averaged to form five subaverages. For each time point in a window surrounding each response component (using the component-specific windows listed above), the standard deviation of the amplitude across the five subaverages was calculated; these variability measures were then averaged across the entire time window, giving a score for each component. This procedure therefore creates a measure of how stable a given response component is across trials. This procedure was then repeated 1000 times, with each repetition using a different random sampling to create the five subaverages, and the resulting scores were averaged. Next, because we did not have a specific hypothesis about the relationship between rhythm skills and the consistency of

Figure 3. Scatterplots displaying relationships between rhythm skills and auditory neural consistency. Data are in z scores.



individual components, scores for all of the components for each condition were averaged. Finally, scores were averaged across the quiet and noise conditions to form a global composite measure of cortical consistency.

Because FFR consistency is calculated by correlating subaverages, whereas cortical consistency is calculated by examining variability across subaverages, a larger FFR score indicates a more consistent response, whereas a smaller cortical score indicates a more consistent response. To facilitate direct visual comparison of the relationship between rhythm skills and FFR and cortical consistency, therefore, the inverse of the z -transformed cortical scores is plotted in Figure 3. To increase the transparency of the

results, the sign of correlations with the cortical metric has also been flipped in Table 4 and the Results section.

Statistical Methods

Several variables were nonnormally distributed, and different transformations were employed as needed to normalize the data before analysis. Synchronization variability, timing adaptation, and beat synchronization variability were log-transformed. Drumming to sequences accuracy and sequence memory accuracy were arcsine-transformed. A cubic transformation was applied to the phonological awareness scores (i.e., x^3 to reduce leftward skew). These

Table 1. Correlations between Rhythm Measures

	<i>Synchronization</i>	<i>Tempo Adaptation</i>	<i>Timing Adaptation</i>	<i>Beat Synchronization</i>	<i>Sequence Memory</i>
Tempo adaptation	0.56 ^a (0.23, 0.79)				
Timing adaptation	0.60 ^a (0.35, 0.79)	0.48 ^a (0.16, 0.72)			
Beat synchronization	0.34 ^a (0.02, 0.60)	0.41 ^a (0.02, 0.71)	0.59 ^a (0.34, 0.77)		
Sequence memory	0.11 (−0.24, 0.45)	0.25 (−0.14, 0.57)	0.26 (−0.13, 0.58)	0.34 (−0.02, 0.64)	
Drumming to sequences	0.16 (−0.19, 0.49)	0.04 (−0.27, 0.38)	0.23 (−0.17, 0.58)	0.41 ^a (0.08, 0.67)	0.79 ^a (0.61, 0.90)

^aIndicates rejection of the null hypothesis, based on 99.75% confidence intervals (displayed inside parentheses).

transformations resulted in these variables being normally distributed ($p > .05$ according to the Jarque–Bera test). All other variables were normally distributed without transformation ($p > .05$). Variables were then transformed to z scores and inverted (where necessary) such that larger scores always indicated better performance.

Skipped Pearson’s correlations (Pernet, Wilcox, & Rousselet, 2013) were used to investigate relationships between scores across the six rhythm tests. For all correlations, the decision to reject the null hypothesis was based on 99.75% confidence intervals, which are supplied for each correlation in Tables 1 and 3–5. A generalized least squares factor analysis with varimax rotation was then used to uncover latent variables reflecting shared variance across rhythm measures, and factor scores were calculated using the least squares regression approach, as implemented in SPSS (SPSS, Inc., Chicago, IL). This procedure produced two factors (see Results). Forty-nine of the 64 participants underwent an additional battery of electrophysiological and behavioral tests; in these participants, rhythm factor scores were correlated with performance on language and cognitive tests as well as measures of auditory neural consistency.

RESULTS

Relationships among Rhythm Tests

Pearson’s correlations revealed that the synchronization, tempo adaptation, and timing adaptation tests were all correlated with one another ($r > .45$) but not with either the sequence memory or drumming to sequences tests ($r < .3$). The sequence memory and drumming to sequences tests were also correlated ($r = .79$). Performance on the beat synchronization test significantly correlated with performance on all rhythm tests except sequence memory ($r > .3$; see Table 1 for r values for correlations between all rhythm tests).

Factor Analysis

Factor analysis revealed that performance across all six rhythm tests was best captured by two factors, which accounted for 71% of the cumulative variance across the rhythm data set. The index was 0.697, and Bartlett’s test of sphericity returned a significant result ($\chi^2 = 133.9, p < .001$). All further factors had eigenvalues of less than 1, and the slope of the scree plot decreased dramatically between the second and third factors; therefore, we limited subsequent analysis and interpretation to the first two factors. Factor loadings are displayed in Table 2; here, we will highlight variables with eigenvalues greater than 0.5 for each factor. Factor 1 was primarily composed, in descending order of loading strength, timing adaptation, synchronization, beat synchronization, and tempo adaptation. This factor appears to reflect synchronization skill and will be referred to as

Table 2. Factor Loadings for All Rhythm Measures

	<i>Synchronization Factor</i>	<i>Sequencing Factor</i>
Synchronization	0.71	0.03
Tempo adaptation	0.60	0.07
Timing adaptation	0.81	0.15
Beat synchronization	0.60	0.44
Sequence memory	0.16	0.72
Drumming to sequences	0.05	0.99

Boldface indicates loadings of greater than 0.5.

the synchronization factor. Factor 2 was primarily composed of drumming to sequences and sequence memory. As this factor primarily indicates rhythm sequence perception and production, we will refer to it as the sequencing factor. For subsequent correlational analyses, the composite scores generated by the factor analysis are used rather than the individual rhythm tests that comprised them. For each factor, larger scores indicate better performance.

Rhythm Sequencing Correlates with Linguistic and Cognitive Skills

Participants with stronger rhythm sequence skills (as reflected by higher sequencing scores) performed significantly better on tests of STM ($r = .57$) and reading ($r = .47$). Participants with stronger synchronization skills, on the other hand, performed significantly better only on backward masking ($r = .42$). Follow-up analysis using the Fisher z transform confirmed that STM was significantly more correlated with rhythm sequencing than with synchronization ($z = 2.62, p = .0087$), as was reading ($z = 3.18, p = .0015$). Backward masking on the other hand was significantly more correlated with synchronization than with rhythm sequencing ($z = 3.18, p = .0015$). See Table 3 for r values for all correlations between rhythm factors and cognitive skills and Figure 2 for an illustration of relationships between the rhythm factors and reading, phonological memory, and backward masking.

Synchronization and Rhythm Sequencing Correlate with Auditory Neural Consistency

Participants who were better at synchronizing, as reflected by higher synchronization factor scores, also had FFRs that were more consistent from trial to trial ($r = .43$). However, there was no significant relationship between synchronization ability and cortical response consistency. Conversely, participants who were better at perceiving and remembering rhythms, as reflected by higher sequencing factor scores, had cortical responses that were more consistent across trials ($r = .43$). However, there

Table 3. *r* Values for Pearson's Correlations between Rhythm Factors and Performance on Language and Cognitive Tests

	<i>Sequencing Factor</i>	<i>Synchronization Factor</i>
Verbal memory		
Verbal working memory	.27 (−0.19, 0.65)	.11 (−0.31, 0.52)
STM	.57 (0.23, 0.82) ^a	.10 (−0.37, 0.49)
Reading		
Reading composite	.47 (0.11, 0.72) ^a	−.05 (−0.45, 0.33)
Phonological skills		
Rapid naming	.06 (−0.36, 0.49)	.05 (−0.38, 0.46)
Phonological awareness	.02 (−0.45, 0.51)	.10 (−0.33, 0.49)
Auditory temporal resolution		
Backward masking	−.22 (−0.58, 0.35)	.42 (0.02, 0.70) ^a

Positive values indicate that better rhythm performance was linked to better language performance.

^aIndicates rejection of the null hypothesis, based on 99.75% confidence intervals (displayed inside parentheses).

was no relationship between sequencing ability and FFR consistency. Follow-up analysis using the Fisher *z* transform revealed that cortical consistency was more correlated with rhythm sequencing than with synchronization ($z = 2.90, p = .0038$) but that there was only a trend for FFR consistency to be more strongly correlated with synchronization than with rhythm sequencing ($z = 1.78, p = .075$; see Table 4 for *r* values for all correlations between rhythm and neural consistency and Figure 3 for an illustration of relationships between the rhythm factors and neural consistency).

Auditory Neural Consistency Does Not Correlate with Linguistic and Cognitive Skills

There were no relationships between either FFR or cortical neural consistency and tests of linguistic and cognitive skills ($r < .35$; see Table 5 for *r* values for all correlations between language tests and neural measures).

DISCUSSION

Overall Summary

We presented participants with tests covering a spectrum of rhythm perception and performance and used factor analysis to derive latent variables corresponding to distinct clusters of rhythmic skills. We extracted two factors: a sequencing factor, which reflected the ability to perceive and reproduce rhythmic sequences, and a synchronization factor, which reflected the ability to consistently

tap in time to stimuli, a process that relies on auditory-motor timing integration. Sequencing performance was linked to reading ability and verbal memory. In contrast, synchronization was only linked to nonverbal auditory temporal processing. Sequencing was tied to the consistency of the slow cortical response to sound, whereas synchronization was tied to the consistency of the fast FFR to sound.

Language Correlates of Rhythm Skills

Previous work from our laboratory has shown that synchronization ability and rhythm sequencing are dissociable, such that participants can display striking difficulties with one of these skills but be unimpaired on the other (Tierney & Kraus, 2015a). It is an open question, however, whether synchronization or rhythm sequencing impairments reflect broader modality-general timing abilities with consequences for language skills. To address this question, we compared synchronization and rhythm sequencing ability with cognitive, perceptual, and literacy skills.

Participants with higher synchronization factor scores had better backward masking thresholds, indicating fine auditory temporal resolution. This is consistent with the idea that synchronization relies on the ability to precisely track the timing of auditory events (Krause, Pollok, & Schnitzler, 2010). Synchronization and backward masking abilities have been independently linked to phonological skills in preschoolers, school-aged children, and early adolescents (Woodruff Carr et al., 2014; Tierney & Kraus, 2013b; Coriveau & Goswami, 2009; Thomson & Goswami, 2008; Griffiths, Hill, Bailey, & Snowling, 2003; Wright et al., 1997). These relationships may be driven by auditory temporal acuity, which is important for perceiving word and syllable boundaries and discriminating speech sounds (Tierney & Kraus, 2014). However, unlike previous studies and contrary to our predictions, we did not find a relationship between synchronization abilities and language skills. This is despite the relationship between synchronization ability and backward masking as well as between synchronization and FFR consistency, both

Table 4. *r* Values for Pearson's Correlations between Rhythm Factors and Auditory Neural Consistency

<i>r</i> Values	<i>Sequencing Factor</i>	<i>Synchronization Factor</i>
FFR consistency	.08 (−0.30, 0.43)	.43 ^a (0.05, 0.69)
Cortical consistency	.43 ^a (0.12, 0.70)	−.16 (−0.59, 0.24)

Positive values indicate that better rhythm performance was linked to more consistent brain responses.

^aIndicates rejection of the null hypothesis, based on 99.75% confidence intervals (displayed inside parentheses).

Table 5. *r* Values for Pearson's Correlations between Auditory Neural Consistency and Performance on Language and Cognitive Tests

	<i>Cortical Consistency</i>	<i>FFR Consistency</i>
Verbal memory		
Verbal working memory	.20 (−0.33, 0.61)	−.15 (−0.55, 0.33)
STM	.33 (−0.19, 0.68)	−.14 (−0.47, 0.28)
Reading		
Reading composite	.20 (−0.25, 0.59)	.06 (−0.32, 0.41)
Phonological skills		
Rapid naming	−.09 (−0.51, 0.36)	−.07 (−0.43, 0.33)
Phonological awareness	−.10 (−0.56, 0.39)	−.14 (−0.51, 0.24)
Auditory temporal resolution		
Backward masking	−.03 (−0.43, 0.30)	−.28 (−0.64, 0.07)

Positive values indicate that more consistent neural responses were linked to better language performance.

measures that have been linked to reading in previous work (Hornickel & Kraus, 2013; Griffiths et al., 2003).

This discrepancy may be due to the age of the participants (mean = 18 years), who were on the cusp of leaving adolescence and entering adulthood. By the age of 18 years, these participants have likely mastered phonological skills, and reading ability may depend more heavily on their memory for and perception of temporal patterns. Indeed, participants with higher rhythm sequence factor scores were more proficient on a number of language and cognitive measures, including auditory working memory, word reading, and nonword reading. This finding replicates reports of a link between rhythm sequence perception and both reading (Flaugnacco et al., 2014; González-Trujillo et al., 2012; Strait et al., 2011; Dellatolas et al., 2009; Forgeard et al., 2008; Overy, 2000, 2003; Douglas & Willatts, 1994; McGivern et al., 1991; Atterbury, 1985) and verbal memory (Saito, 2001). Further research (longitudinal and cross-sectional) is needed to understand how links between rhythm and language skills change with age. A caveat is that all of our participants were normal readers; the link between synchronization and phonological skills may be preserved in young adults with reading impairment (Thomson et al., 2006).

Neural Correlates of Rhythm Skills

Error correction during synchronization requires precise, rapid integration of auditory event timing and motor output. Timing shift adaptation can take place within 100 msec of a stimulus shift (Repp, 2011) and can be initiated to subliminal shifts as small as 1.5 msec (Madison & Merker, 2004; Repp, 2000). Synchronization, therefore, may require a high degree of temporal precision in auditory neural processing. Supporting this idea, participants with variable

synchronization demonstrate greater trial-to-trial variability in the FFR to speech (Woodruff Carr, Tierney, White-Schwoch, & Kraus, 2016; Tierney & Kraus, 2013a). Prior work from our laboratory has shown that synchronization ability is related to fast high-frequency, but not slow low-frequency, intertrial phase-locking (Tierney & Kraus, 2016). However, in that study, low-frequency intertrial phase-locking was assessed in the response to a speech sound presented at a fast rate (4 Hz) with neural data collected from a single electrode, a setup that is not ideal for investigating the passive cortical response (as the later components cannot be clearly detected).

Here, by collecting cortical data with a 32-channel cap and 1-Hz stimulus presentation rate, we confirm that the synchronization factor relates to the trial-by-trial consistency of the fast FFR to speech but that the variability of the slow cortical evoked response to sound is largely unrelated to synchronization skills. This finding suggests that slow low-frequency auditory neural consistency may be less important for synchronization than fast high-frequency auditory neural consistency. However, it should be noted that, in the current study, cortical data were collected passively, with participants ignoring the sounds and watching a subtitled movie. It is possible, therefore, that the consistency of slow neural activity when a sound stream is attended may be more closely tied to synchronization ability, especially given that performing a rhythmic task such as synchronization can enhance phase-locking to rhythmic information (Nozaradan, Schönwiesner, Caron-Desrochers, & Lehmann, 2016).

In contrast, we found that the variability of the slow evoked cortical response to sound related to rhythm sequence processing, such that participants with more consistent responses performed better when drumming along to and remembering rhythms. However, the consistency of the faster FFR to sound did not relate to

rhythm sequencing. These findings suggest that both synchronization and rhythm sequence perception may rely upon temporally precise auditory neural processing but on different time scales: at ~10 msec and below for synchronization and ~100 msec and up for rhythm sequence perception. Further support for this idea comes from studies showing that the perception of metrical rhythms is linked to phase-locking of slow low-frequency cortical oscillations to rhythmic structure (Tierney & Kraus, 2015b; Nozaradan, Peretz, & Mouraux, 2012; Nozaradan, Peretz, Missal, & Mouraux, 2011) and that the ability to synchronize to the beat of metrical rhythms (which requires the integration of rhythmic information across time) is linked to the strength of slow low-frequency cortical phase-locking (Nozaradan, Peretz, & Keller, 2016).

Previous work has reported a relationship between FFR consistency and reading ability in elementary school children (Hornickel & Kraus, 2013). However, we found no significant relationship between FFR consistency and literacy skills in the adolescents tested here. As suggested above, participants in young adulthood may have already mastered phonological skills, and thus, the temporal precision of the auditory system may be a less important bottleneck for language skills at this age. However, we also find no relationship between cortical consistency and literacy skills, despite its link to rhythm sequencing ability. The neural foundations of the link between rhythm sequencing and language skills, therefore, remain an important topic for future study. One possibility is that both rely on links between auditory and motor processing (Patel & Iversen, 2014; Steinbrink, Groth, Lachmann, & Riecker, 2012).

Compared with the evoked cortical response to sound, the FFR reflects greater contribution from subcortical auditory structures (Bidelman, 2015; Warrier et al., 2011), as evidenced by the close correspondence between FFR recorded from the scalp and from the inferior colliculus in guinea pigs (White-Schwoch, Nicol, Warrier, Abrams, & Kraus, 2016). The fact that synchronization abilities are linked to FFR consistency, but not the consistency of the evoked cortical response to sound, may indicate a dependence of synchronization on subcortical auditory processing. However, given that the FFR may reflect processing in cortical areas as well (Coffey et al., 2016) and that subcortical auditory processing is shaped by top-down factors (Kraus & White-Schwoch, 2015), our findings cannot be taken as direct evidence for a unique relationship between synchronization and subcortical processing. Future work on synchronization ability and the FFR using techniques with greater spatial resolution (such as MEG) could provide more direct evidence for this hypothesis.

Translational Implications

The links reported here between rhythm sequencing and language skills join a growing body of work suggesting shared foundations for these two seemingly disparate

sets of skills. The perception of rhythmic sequences has also been linked to individual differences in grammar (Gordon et al., 2015) and phonological skills (Flaugnacco et al., 2014), and experience with multiple languages is linked to enhanced perception of musical rhythms (Roncaglia-Denissen, Roor, Chen, & Sadakata, 2016). These findings have two main translational implications. First, recent work has suggested that musical training emphasizing rhythm perception is particularly effective in boosting language skills such as phonological processing and reading (Flaugnacco et al., 2015). The close link we find between rhythm memory and verbal memory suggests that music training that incorporates the memorization of rhythms could benefit memory for verbal material as well. Moreover, our finding that synchronization skills and language skills do not relate in participants on the cusp of adulthood suggests that people with language problems in late adolescence and early adulthood may respond better to rhythm training that emphasizes rhythm sequence processing rather than training that emphasizes synchronization. Second, rhythmic priming may provide benefits for language skills such as phonological processing (Cason & Schön, 2012) and grammaticality judgments (Bedoin, Brisseau, Molinier, Roch, & Tillmann, 2016). Rhythmic priming could potentially aid the encoding of verbal material into memory as well.

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