

Individual Differences in Rhythmic Ability: Behavioral and Neuroimaging Investigations

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Rhythmic abilities vary widely in the general population, but little is known about the factors that give rise to this variability. One factor may be musical training. Another may be differences in auditory short-term memory (STM) capacity (the amount of auditory information that can be remembered over a few seconds). Finally, as rhythms with temporal regularity (e.g., a beat) are more easily remembered and reproduced, individual differences in sensitivity to regularity may contribute to rhythmic ability differences. To investigate the contribution of each of these factors to rhythm reproduction ability, we assessed auditory STM capacity (using digit and pseudoword span tasks), beat sensitivity (using the Beat Alignment Test [BAT]), and levels of musical training. Rhythmic ability was measured using a rhythm reproduction test. We found that STM capacity, beat sensitivity, and musical training predicted unique variance in rhythm reproduction performance. Using functional magnetic resonance imaging (MRI), we assessed individual differences in brain activity related to the previously measured auditory STM capacity, BAT score, musical training, and rhythmic ability, while participants performed a rhythm discrimination task. Activity in posterior superior temporal gyrus and middle temporal gyrus negatively correlated with auditory STM capacity. Positive correlations with BAT score were found in left angular gyrus, supplementary motor area, and premotor cortex. Positive correlations with musical training were observed in left posterior middle temporal gyrus, and negative correlations were observed in left supplementary motor area. The findings implicate both auditory and motor areas in factors that underlie individual differences in rhythmic ability.

Keywords: music, rhythm, timing, auditory perception

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Anecdotally, rhythmic ability is thought to vary widely across healthy individuals. Several individuals report having “no sense of rhythm,” and previous work has investigated individuals with specific rhythmic impairments or “beat deafness” (Foxton, Nandy, & Griffiths, 2006; Phillips-Silver et al., 2011). However, little work has specifically investigated and reported on the range of rhythmic ability in the general population, and the underlying causes of individual differences in rhythmic ability have yet to be fully elucidated. Three factors seem like promising candidates and form the focus of the current study. The first is auditory short-term memory (STM) capacity, as this has been shown to relate to

rhythm reproduction, discrimination, and synchronization ability in previous work (Bailey & Penhune, 2010; Saito, 2001; Wallentin, Nielsen, Friis-Olivarius, Vuust, & Vuust, 2010). The second is sensitivity to the presence of regular temporal structure (e.g., beat structure). Rhythms that have a regular temporal structure are discriminated and reproduced better than irregular rhythms (Grahn & Brett, 2007; Patel, Iversen, Chen, & Repp, 2005); therefore, it is likely that individuals with better ability to detect this regularity (when it exists) should do better on rhythm tasks. The third factor is musical training. However, musical training may exert an indirect effect by influencing the aforementioned factors: musical training is associated with better auditory STM span (Bailey & Penhune, 2010; Saito, 2001; Wallentin et al., 2010), and seems likely to improve beat detection, although this has not been tested directly. Music also may have direct effects on rhythmic ability, such as providing a range of strategies for accurate rhythmic encoding and reproduction. The potential role of each of these factors will now be described and considered in more detail.

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Auditory STM

Most models of auditory STM posit two components: one involved in representing the to-be-remembered items and the other involved in maintaining those representations (Baddeley & Hitch, 1974; Cowan, 1999). In Baddeley's influential model of STM, the first component is the “phonological short-term store,” a storage

buffer for auditory memory traces, but the traces are subject to rapid decay. The second component, called the "articulatory loop," is therefore required to maintain items in auditory memory by refreshing the representations in STM through active rehearsal (Baddeley, 2003). Rhythmic sequences enter automatically into the phonological store, which acts as an "inner ear," remembering the sounds in the correct order. The articulatory process then acts as an "inner voice" and repeats the auditory information to prevent it from decaying. A third component, called a timing signal, was recently proposed to mark the serial order of different items in the store (Baddeley, 2000; Henson, Hartley, Burgess, Hitch, & Flude, 2003). However, this component only signals the order of items in memory and does not specify how timing between the items is coded, which is the key element in representing a rhythm.

Auditory STM capacity is generally measured using span tasks, such as digit span. To measure digit span, participants listen to a list of spoken digits and then repeat the list in the order it was presented. The maximum number of correctly recalled items represents the capacity of the short-term auditory memory store. The usual score for healthy individuals is between five and nine items (Miller, 1956). Instead of digits, pseudowords can also be used, and the participant's pseudoword span is calculated. Pseudowords are nonsense words, which are composed using the same phonological rules as English words, yet have no meaning whatsoever in English (Gathercole, Frankish, Pickering, & Peaker, 1999; Rauschecker, Pringle, & Watkins, 2008). This means that cognitive processing of pseudowords cannot be influenced by semantic or episodic memory; therefore, pseudoword span may demonstrate a purer or more sensitive index of phonological STM than digit span.

Previous work suggests that the articulatory loop is important for performance in rhythm tasks (Hall & Gathercole, 2011; Saito, 2001). For example, Saito (1998) tested participants on a rhythm reproduction task that involved listening to a short rhythm and reproducing it after a 5-s delay. During encoding and delay, participants did one of two concurrent tasks: articulatory suppression (silently mouthing the vowels A E I O U) or drawing of squares. Articulatory suppression occupies the articulatory loop, whereas square drawing does not. Concurrent articulatory suppression interfered with rhythm performance much more than drawing of squares, suggesting that accurate rhythm encoding and maintenance rely on the articulatory loop. A further relationship between phonological STM and rhythmic ability is suggested by the fact that digit span scores are positively correlated with rhythm synchronization (Bailey & Penhune, 2010), reproduction (Saito, 2001), and discrimination (Wallentin et al., 2010) performance.

Other studies have demonstrated that the correlation between rhythmic and phonological processing extends to populations with impaired phonological processing. British children with dyslexia show reduced sensitivity to temporal cues to the rhythm in auditory signals (Corriveau, Pasquini, & Goswami, 2007; Goswami et al., 2002; Huss, Verney, Fosker, Mead, & Goswami, 2011; Richardson, Thomson, Scott, & Goswami, 2004), and score worse compared with age-matched and language-matched control children when tapping along to a metronome (Corriveau & Goswami, 2009). French dyslexic children display similar results, suggesting the connection between phonological and rhythmic processing extends to languages besides English (Muneaux, Ziegler, Truc, Thomson, & Goswami, 2004).

Beat Perception

A second factor in rhythm performance may be the capacity to detect temporal structure in rhythms. In auditory rhythms, we often spontaneously perceive an underlying beat, or a perceived pulse that marks equally spaced points in time (Large & Palmer, 2002; Nettl, 2000). Perception of a beat occurs without effort in auditory sequences that have a regular temporal structure, such as periodically regular events occurring at particular points in time. Music or rhythm that has regular periodicities in the range of ~300 to 900 ms (Parncutt, 1994; van Noorden & Moelants, 1999) will generally induce beat perception. Beat perception, in turn, leads to better representation of the rhythm itself, as evidenced by higher accuracy in rhythm discrimination or reproduction (Grahn, 2012; Grahn & Brett, 2007; Patel et al., 2005).

Previous work has not assessed individual differences in the capacity to detect or use beat structure and how this may relate to rhythmic ability. Here we use the perceptual subtest of the Beat Alignment Test (BAT; Iversen & Patel) to assess participants' sensitivity to the beat. In the BAT, participants hear excerpts from pop, orchestral, jazz, and rock songs, with a series of regular beeps superimposed. The beeps may coincide with the beat (aligned condition), may be at the wrong rate (period error condition), or may consistently occur just before or just after the actual beat (phase error condition). Participants judge whether the superimposed beeps are on or off the beat. One advantage of this task is that it measures perceptual ability without the confound of motor production.

Musical Training

The third factor that may influence rhythmic ability is musical training. Musical training is known to affect performance on rhythm tasks (Bailey & Penhune, 2010; Chen, Penhune, & Zatorre, 2008), although not always (Grahn & Brett, 2007). There are multiple ways in which musical training may improve performance. First, musical training is associated with higher auditory STM capacity (Bailey & Penhune, 2010; Chan, Yim-Chi, & Cheung, 1998; Wallentin et al., 2010; Williamson, Baddeley, & Hitch, 2010), so may have an influence on rhythmic ability by simply increasing STM capacity. However, partial correlation analyses have found that musical training predicts rhythm synchronization accuracy (Bailey & Penhune, 2010) even when individual differences in STM are accounted for. Therefore, musical training appears to contribute to rhythmic ability independently of increases in STM capacity. Bailey and Penhune (2010) suggest that formal lessons may emphasize explicit learning of many complex rhythmic structures, giving musicians a better ability to parse the rhythms. Another possibility, however, is that musical training enhances sensitivity to underlying temporal structure: nearly all previous research has used regular rhythms that have a beat structure, and do not account for individual differences in beat sensitivity. By assessing STM, beat sensitivity, and musical training in the same participants, the contribution of musical training to rhythmic ability can be tested for specific contributions apart from its effects on STM or beat sensitivity.

In the current study, we assessed STM capacity using digit span and pseudoword span tasks, averaging the scores to produce a single composite span measure. We assessed beat sensitivity using

the BAT, using the proportion of trials in which beat alignment was judged correctly. We assessed musical training through self-report, relying on years of formal musical training to group subjects into three categories: no musical training, <5 years of musical training, and ≥ 5 years of musical training. Finally, we measured rhythmic ability using a rhythm reproduction task in which participants heard a rhythm and then tapped the rhythm back. Unlike previous studies, we included both regular (beat) and irregular (nonbeat) rhythms in our stimuli. We also varied rhythm length (short, medium, and long) to ensure that individuals at all ability levels were challenged. Having beat and nonbeat rhythms of different lengths enabled us to test hypotheses about the contribution of each factor to different aspects of rhythm reproduction. We predicted that STM capacity would play a greater role in the accurate reproduction of longer rhythms compared with shorter rhythms, as longer rhythms tax STM to a greater degree. STM capacity was predicted to benefit beat and nonbeat rhythm performance equally. Beat sensitivity, however, was predicted to benefit performance of beat rhythms, as nonbeat rhythms have no beat structure, so greater beat sensitivity is not necessarily useful. We also tested whether musical training contributed to rhythmic ability only through concomitant increases in span and/or beat sensitivity or through an independent route.

Along with behavioral measures, we had functional magnetic resonance imaging (fMRI) data that had been acquired on a similar task (discrimination rather than reproduction) for a subset of the participants. The fMRI data were originally collected for a separate study that was designed to compare the neural mechanisms underlying rhythmic and verbal STM, and thus was not directly related to the behavioral reproduction study (full details of the fMRI study will be reported elsewhere). However, as many of the same processes would be required for rhythm reproduction and discrimination, particularly during the encoding stages of each task, we believed it would be relevant to analyze neural activation that correlated with the individual difference measures from the behavioral study (span, BAT, and musical training) as well as with rhythm reproduction ability (proportion of rhythms correctly reproduced in the behavioral study, collapsed across all rhythm conditions). Each fMRI trial consisted of a stimulus presentation, silent delay, and then a discrimination phase, after which participants judged whether the second stimulus was the same as or different from the first. The full fMRI design involved discrimination of rhythmic sequences (comparing two rhythms to determine whether the timing was same or different) and letter sequences (comparing two strings of several different letters to determine whether letter order was the same or different). As all sequences were presented with regularly and irregularly timed versions, all trials involved processing of timing information. We therefore collapsed data across trial types to obtain task-related activity in each participant, and analyzed the brain responses related to the individual difference factors outlined earlier in the text. Separate correlations were conducted for stimulus presentation, delay, and discrimination phases. We believed that, particularly for the presentation phase, activation that correlated with the different capacities during rhythm discrimination would be comparable with that observed if the scanning task had been rhythm reproduction.

Behavioral Methods

Participants

Sixty-two subjects participated (30 female and 32 male), with an age range between 15 and 75 years ($M = 29.02$ years, $SD = 10.8$ years; only one participant was aged >55 years). The Cambridge University Psychological Research Ethics Committee approved this study (CPREC 2009.17). The average level of musical training was 4.2 years ($SD = 5.0$ years). Twenty-four subjects reported no formal musical training, 17 reported <5 years of formal training, and 21 reported ≥ 5 years of formal training.

Tasks

Forward digit span. The digits 1 through 9 were recorded by a native female speaker of Southern British English. These recordings were used to create random digit strings of different lengths. The random digit strings consisted of two to nine digits, and a digit was never repeated within a single string. For all eight string lengths, two strings were created. The task began with an auditory presentation of a two-digit string. The participant had to recall at least one of the two strings correctly to proceed to the next length. When the participant could not correctly reproduce both strings of the same length, or finished both nine-digit strings, the task ended.

Pseudoword span. Pseudowords were recorded by a native female speaker of Southern British English. Twenty-seven high-probability nonwords from Gathercole (Gathercole et al., 1999) were used. This task was similar to the digit span task except that participants verbally reproduced strings of one-syllable pseudowords (e.g., nars, garm, chack). Pseudoword strings were two to four pseudowords long. Participants completed four trials of each string length, and no pseudoword was repeated within a single string. Participants were required to accurately reproduce at least two of the four trials of each string length to proceed to the next length, and the task ended when a participant failed to do so.

Beat alignment task. We used part 3 of a test developed by Iversen and Patel (2008). Participants were required to decide whether beeps superimposed over a musical excerpt were in time with the perceptual beat of the excerpt. The beeps were of three different types: aligned (in time with the beat of the music), period (or tempo) error (a rate 10% faster or slower than the true beat rate), or phase error (consistently early or late by 25%). The task consisted of 36 trials in which three different versions of 12 excerpts were used. There were 12 aligned, 12 tempo error, and 12 phase error versions, and the tempo error and phase error versions were counterbalanced to provide equal numbers of the too slow/too fast, or too early/too late versions, respectively. After listening to the whole excerpt, participants were asked to judge whether the beeps were in time with the beat by pressing the "y" key to indicate yes and the "n" key to indicate no. For further information regarding the musical excerpts or procedure, please see Iversen and Patel (2008).

Rhythm reproduction task. The stimuli for the rhythm reproduction task were created using GarageBand (Apple, Inc., v4.1.2 [248.7]) using a sampled rim shot on a snare drum sound. Beat rhythms were constructed using the following six core patterns: 1111, 112, 211, 22, 31, and 4, similar to previous work (Grahn & Brett, 2007; Grahn & Rowe, 2009). Short, medium, and long rhythms consisted of two, three, and four core patterns, respectively. One final

note was added to the end of each sequence to mark the end of the last interval. None of the six core patterns were repeated within a rhythm. The shortest interval (i.e., 1) ranged from 220 to 280 ms, in 10-ms steps, creating seven potential tempi. The other intervals in the rhythm were multiples of the shortest interval. On each trial, one of the seven different tempi was used. The trial-to-trial tempo changes prevented carryover of the beat from one trial to the next trial. Beat rhythms were modified to create nonbeat versions. One third of the intervals in each rhythm kept their original length, one third were increased in length by 1/3 of 1 unit, and one-third decreased in length by 1/3 of 1 unit. Thus, the nonbeat rhythms were the same as the beat rhythms in overall duration and number of intervals, but had irregular timing.

Participants were presented with the rhythms through headphones and had to reproduce the presented rhythm by tapping the "0" key on a computer keyboard. To familiarize participants with the different rhythms, they first practiced nine trials, with rhythmic patterns not used during the experimental session. The nine practice trials consisted of three short-rhythm trials, three medium-rhythm trials, and three long-rhythm trials. Participants could repeat the practice trials if they desired. The experimental session comprised 72 trials—12 short, 12 medium, and 12 long beat rhythms, in addition to their nonbeat counterparts. The trials were presented in a random order. A trial started with the auditory presentation of a rhythm, during which the screen was black. After a 500-ms delay, the screen turned red, signaling to the participant to reproduce the rhythm. The response window was equal to the duration of the rhythm plus four additional seconds to accommodate a delayed response.

Behavioral Analysis

Digit span was calculated as the longest digit string length for which the participant was able to accurately reproduce at least one of the two strings of that length. Pseudoword span was calculated as the longest word string for which the participant was able to accurately reproduce at least two of the four strings of that length. As pseudoword span and digit span were highly correlated ($r = .53, p < .001$), the two span scores were averaged to give a single span score for each participant. The BAT score was the proportion of correct responses across the three different conditions (beeps correctly aligned, phase error, tempo error).

For rhythm reproduction, any trial with too many or too few taps was deemed incorrect. For trials with the correct number of taps, timing accuracy was calculated using the same technique as Saito (2001), with an absolute and a relative criterion. For the absolute criterion, if any interval differed from that present in the original rhythm by 20% or more, the trial was considered incorrect. This measure, therefore, assessed whether participants had reproduced the original rhythm with accurate absolute timing. The relative criterion assessed the timing accuracy of the interval lengths relative to other intervals in the same rhythm, and therefore did not penalize participants for correctly reproducing the relative time intervals but perhaps at a different overall rate. That is, the entire rhythm could be sped up or slowed down and still be judged correct if the relative relationship between the time intervals in the rhythm was maintained. The average length of the shortest interval in the trial was used to determine the relative structural unit for that trial. If the shortest interval in the stimulus was 250 ms, but the participant reproduced it as 230 ms, the timings of all other intervals in the trial were recalibrated to be relative to 230 ms, and

the accuracy was assessed relative to this recalibrated rhythm. However, if any interval differed from the relative structure by $>20\%$, the trial was judged incorrect.

fMRI Methods

Participants

Eighteen volunteers (four female; mean age = 28.3, $SD = 8.65$) participated in the brain-imaging study. All had previously participated in the behavioral study. All participants completed the experiment and received financial compensation for participation. The Cambridge University Psychological Research Ethics Committee provided clearance for the study (CPREC 2009.17).

Materials

As stated in the introduction, the full fMRI study was originally designed to investigate comparisons between rhythmic and verbal working memory, and hence there were alterations in the stimuli and task between the behavioral and fMRI studies. For the rhythm sequences, beat and nonbeat rhythms were created using the same core patterns and tempi as in the behavioral study, but with the sound of a single letter (e.g., "B") repeated, rather than a percussion sound. Only short- and medium-length rhythms were used, as the behavioral data indicated that the long rhythms were very difficult. For the letter sequences, strings of four (short-length) or eight (medium-length) different letters were created (e.g., "Q L D C U M J P"). Half the sequences had regular timing, and half had irregular timing. For the regular sequences, the strings were divided in half (two groups of two letters or two groups of four letters). The letter onsets within a group were separated by 400 ms, and each group was separated by 800 ms. The irregular strings were separated by unequal time intervals. The four-letter strings used 233-, 533-, and 833-ms intervals (in random order). The eight-letter strings used 257-, 307-, 357-, 457-, 557-, and 657-ms intervals (again, in random order).

Design

A 2×2 within-subject design was used, with experimental factors *stimulus type* (rhythm, letter) and *temporal regularity* (beat/nonbeat for the rhythms, regular/irregular for the letters). The experiment featured three trial types: full trials, stimulus-response-only trials, and null trials. Full trials consisted of a stimulus period, delay period, discrimination period, and response period. Each period was accompanied by a differently colored display to aid the participant in distinguishing different parts of the trial. At the beginning of the trial, the first stimulus was presented (*stimulus period*), and the display turned blue. A *delay period* followed. The delay period could be of three different lengths: no delay, delay of $1 \times$ the length of the preceding stimulus, or a delay of $2 \times$ the length of the preceding stimulus. The delay period had a black display. Then, a discrimination stimulus was played that was either the same as or different from the first stimulus (*discrimination period*). During this period, the display was green. For different rhythms, another rhythm of the same type as the stimulus (beat/regular or nonbeat/irregular) was used. After the discrimination stimulus, the screen turned red, and the participant had 2 s to

Table 1
Accuracy in Each Rhythm Condition for Relative and Absolute Criteria

Rhythm condition	Beat (relative, absolute)	Nonbeat (relative, absolute)
Short	68%, 61%	13%, 10%
Medium	47%, 42%	3%, 3%
Long	19%, 16%	0.5%, 0.3%

respond, by button-press, indicating whether the stimuli were same or different (*response period*). Stimulus-response-only trials started with the stimulus period. After that, the screen immediately turned red and prompted the participant to press the left or right button by on-screen text. Null trials consisted of a 9-s blank screen. The variable length delay, stimulus-response-only trials, and null trials were necessary to allow the hemodynamic response to the different trial stages to be decorrelated and therefore estimable. The variable delay decouples the stimulus presentation stage from the delay stage and also the delay stage from the discrimination stage. The stimulus-response-only trials decouple the stimulus stage from the discrimination stage and the discrimination stage from the response. One block comprised eight stimulus trials (2 with no delay, 4 with $1 \times$ rhythm length delay, 2 with $2 \times$ rhythm length delay), two stimulus-response-only trials, and two null trials. The total experiment lasted 16 blocks, and each block contained only the rhythm or only the letter condition. The condition alternated (rhythm, letter condition) with each block.

Procedure

Participants gave written informed consent and practiced the experiment in a separate room before entering the scanner. Participants read the task instructions and practiced one rhythm and one letter condition block. One practice block consisted of four full trials and one stimulus-response-only trial. All stimuli were unique to the practice session. After the practice trials, the participant could ask questions about the task.

MR Scanning Specifications

A 3-T Siemens Tim Trio MRI scanner was used to collect two runs with 540 echoplanar imaging (EPI) volumes in each. All EPI data had 36 slices, matrix size of 64×64 , TE (echo time) of 30 ms, TR (repetition time) of 2.19 s, FOV (field of view) of 19.2×19.2 cm, flip angle of 78° , slice thickness of 3 mm, interslice distance of 0.75 mm, and in-plane resolution of 3×3 mm. High-resolution magnetization prepared rapid acquisition gradient echo (MPRAGE) anatomical images (TR = 2250 ms, TE = 2.99 ms, flip angle = 9° , IT (inversion time) = 900 ms, $256 \times 256 \times 192$ isotropic 1-mm voxels) were collected for anatomic localization and coregistration.

Data Preprocessing and Analysis

SPM5 was used for data analysis (SPM5; Wellcome Department of Imaging Neuroscience, London, United Kingdom). The first five EPI volumes of each run were discarded to allow for T1 equilibration. Images were sinc-interpolated in time to correct for acquisition time differences within each volume and realigned spatially with respect to the first image of the first run using trilinear interpolation. The coregistered MPRAGE image was segmented and normalized using affine and smoothly nonlinear transformations to the T1 template in Montreal Neurological Institute space. The normalization parameters were then applied to the EPIs, and all normalized EPI images were spatially smoothed using a Gaussian kernel of full-width half-maximum 8 mm. For each participant, stimulus, delay, discrimination, and response were modeled separately for each condition. These were modeled using a regressor made from an on-off boxcar convolved with a canonical hemodynamic response function (apart from response, which was modeled using a delta function convolved with the canonical hemodynamic response function). EPI volumes associated with discrete artifacts were included as covariates of no interest (nulling regressors). This included volume displacements >4 mm or spikes of high variance in which scaled volume-to-volume variance was 4 times greater than the mean variance of the run. Autocorrelations were modeled using a first-order autoregressive model, and low-frequency noise was removed using a standard high-pass filter of 128 s.

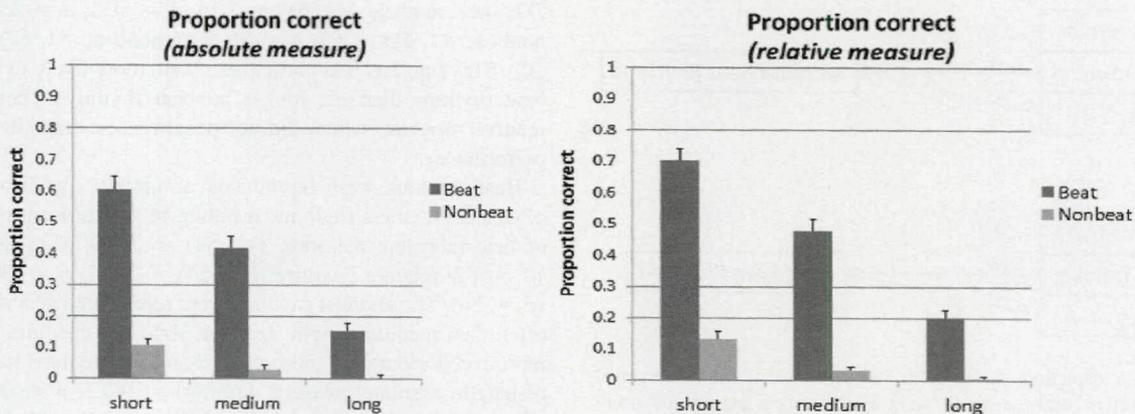


Figure 1. Proportion of correctly reproduced beat (left column) and nonbeat (right column) rhythms, using the absolute (left) and relative (right) measures of accuracy.

Table 2

Summary of the Multiple Regressions Between Beat Rhythm Reproduction Accuracy (Absolute and Relative Criteria) and Individual Differences on BAT, Span, and Musical Training

Rhythm condition	Absolute criterion					Relative criterion				
	B	SE B	beta	t	Sig.	B	SE B	beta	t	Sig.
Short rhythms										
BAT score	.501	.256	.233	1.953	.056	.497	.245	.242	2.032	.047
Span	.047	.039	.143	1.210	.231	.090	.041	.271	2.192	.032
Musical training	.113	.043	.325	2.630	.011	.066	.037	.211	1.784	.080
Medium rhythms										
BAT score	.654	.201	.323	3.247	.002	.610	.211	.295	2.889	.005
Span	.089	.031	.289	2.930	.005	.112	.035	.335	3.164	.002
Musical training	.127	.034	.387	3.751	.000	.111	.032	.350	3.458	.001
Long rhythms										
BAT score	.282	.146	.210	1.936	.058	.365	.159	.234	2.291	.026
Span	.086	.022	.417	3.883	.000	.057	.027	.224	2.120	.038
Musical training	.056	.024	.256	2.275	.027	.119	.024	.497	4.910	.000

Note. Beta (B), standard error (SE), and standardized beta (beta) scores are shown. Values in bold are statistically significant ($p < .05$). Sig. = p value.

The contrast images estimated from single participant models were entered into second-level random-effects analyses for group inference (Penny & Holmes, 2003). This resulted in a 2×2 analysis of covariance (ANCOVA) design, with the factors *temporal regularity* and *stimulus type*, and four covariates: span, BAT score, musical training, and rhythm score (absolute measure, the total proportion of correct performance from the behavioral study, collapsed across beat/nonbeat and short/medium/long). All effects were estimated using t -contrasts. Using false discovery rate correction (Genovese, Lazar, & Nichols, 2002), significance level was $\alpha = .05$, and only the analyses of the covariates are reported here. As the activation levels that correlated with the individual difference covariates did not significantly differ between the rhythm

stimuli and the letter stimuli, the reported correlations with individual differences are collapsed across stimulus type.

Results

Behavioral Results

A 2×3 repeated-measures ANCOVA was conducted on the absolute and relative accuracy scores, with beat (beat or nonbeat) and length (short, medium, long) as within-subject factors, and span, BAT score, and musical training (<1 year, <5 years, 5+ years) as covariates. Analyses that used years of musical training as a continuous covariate were also conducted, but produced very similar results, so are not included here.

In general, accuracy was higher in the relative measure than the absolute measure, particularly for beat rhythms (see Table 1 and Figure 1). Paired t tests comparing the relative and absolute accuracy measures showed significant differences for short, medium, and long beat rhythms, as well as the short nonbeat rhythms (short beat: $t(1, 61) = 3.06, p = .003, d = .39$; medium beat: $t(1, 61) = 2.62, p = .01, d = .33$; long beat: $t(1, 61) = 2.89, p = .005, d = .37$; short nonbeat: $t(1, 61) = 2.16, p = .035, d = .27$; medium nonbeat: $t(1, 61) = .07, p = .95$; long nonbeat: $t(1, 61) = 1, p = .32$). This suggests that participants were more likely to rescale the beat rhythms than the longer nonbeat rhythms. Therefore, the relative measure, which did not penalize rescaling, shows better performance.

Beat rhythms were reproduced accurately significantly more often than nonbeat rhythms, resulting in a significant main effect of beat (absolute measure: $F(1, 54) = 237.9, p < .001$, partial $\eta^2 = .82$; relative measure: $F(1, 54) = 293.2, p < .001$, partial $\eta^2 = .84$). The shortest rhythms were reproduced accurately more often than medium-length rhythms; short and medium were both reproduced accurately more often than long rhythms (main effect of length: absolute measure: $F(1, 54) = 140.3, p < .001$, partial $\eta^2 = .72$; relative measure: $F(1, 54) = 191.1, p < .001$, partial $\eta^2 = .78$; post hoc t tests, absolute measure: short vs. medium: $t(1, 61) = 8.7, p < .001, d = 1.11$; short vs. long: $t(1, 61) = 15, p < .001, d = 1.91$).

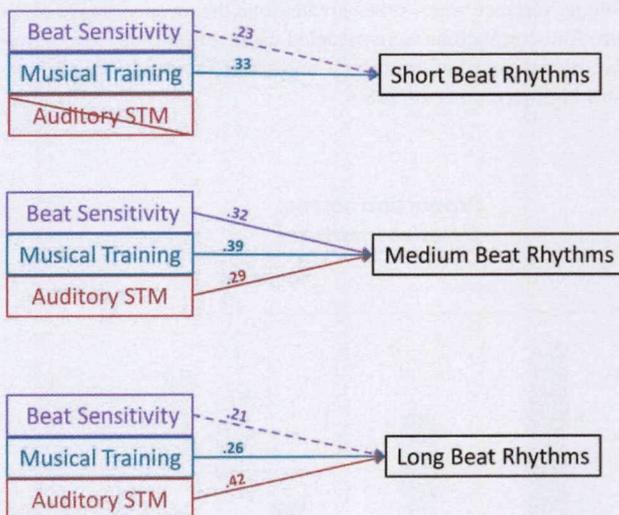


Figure 2. A depiction of the contribution of each of the individual difference factors (beat sensitivity, auditory STM span, and musical training) to performance accuracy for beat rhythms (absolute criterion). Values of β are taken from Table 2. Solid lines = significant ($p < .05$) contribution, Dashed lines = marginally significant ($p < .06$) contribution.

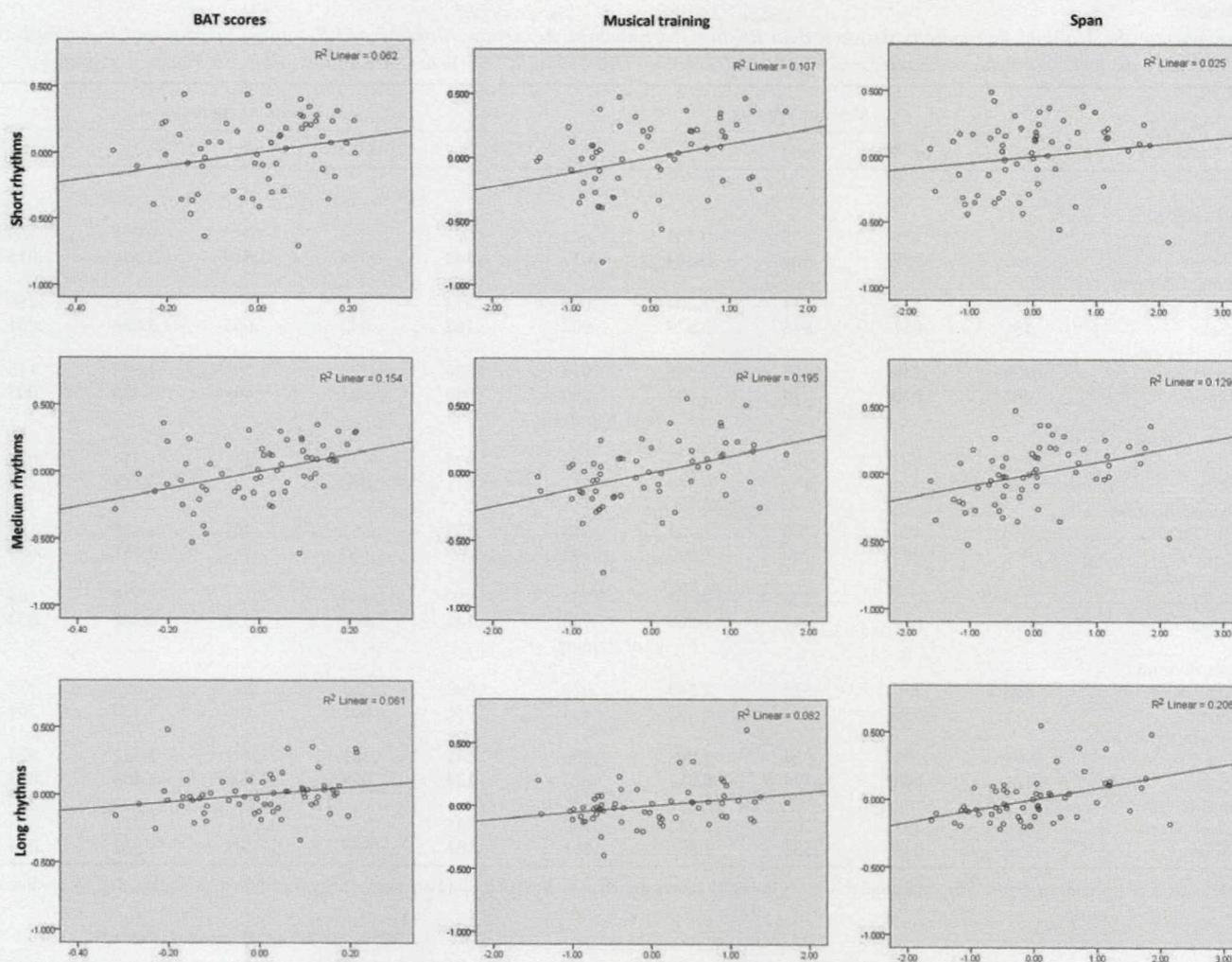


Figure 3. Regression of BAT scores, musical training, and span on rhythm reproduction accuracy (relative measure) for beat rhythms. The effect of each regressor is shown after controlling for the other two regressors.

.001, $d = 1.9$; medium vs. long: $t(1, 61) = 10.5$, $p < .001$, $d = 1.33$; relative measure: short vs. medium: $t(1, 61) = 11.6$, $p < .001$, $d = 1.47$; short vs. long: $t(1, 61) = 17.4$, $p < .001$, $d = 2.21$; medium vs. long: $t(1, 61) = 11.1$, $p < .001$, $d = 1.41$). The effect of length on reproduction was more pronounced for beat rhythms than nonbeat rhythms, as confirmed by a significant interaction between beat and length (absolute measure: $F(2, 108) = 93.5$, $p < .001$, partial $\eta^2 = .63$; relative measure: $F(2, 108) = 102.7$, $p < .001$, partial $\eta^2 = .66$). The interaction can be explained by a substantial floor effect in the nonbeat rhythms. Performance was poor in all nonbeat conditions, reducing the effect of length on nonbeat performance accuracy. See Table 1 and Figure 1 for reproduction accuracy in all conditions. Significantly more nonbeat than beat rhythms were judged incorrect owing to the incorrect number of taps (42% vs. 33%, $t(1, 37) = 4.04$, $p < .001$; owing to a data corruption issue, the number of taps was only calculated for 38 subjects, but they had a representative range of overall performance and so likely give an accurate picture of the full data set).

Turning to the covariates, musical training correlated with BAT score ($r = .29$, $p = .02$) and span ($r = .27$, $p = .037$). There were no correlations between BAT and span ($r = .036$, $p = .78$).

Greater musical training was associated with better rhythm performance, as indicated by a significant main effect of musical training (absolute measure: $F(1, 54) = 11.8$, $p = .001$, partial $\eta^2 = .18$; relative measure: $F(1, 54) = 9.5$, $p = .003$, partial $\eta^2 = .15$), although this effect was greater for the beat rhythms than the nonbeat rhythms, as confirmed by a significant Beat \times Musical training interaction (absolute measure: $F(1, 54) = 11.6$, $p = .001$, partial $\eta^2 = .17$; relative measure: $F(1, 54) = 6.7$, $p = .013$, partial $\eta^2 = .11$). Higher span and BAT scores also were associated with better rhythm performance, as confirmed by significant main effects of each (span absolute measure: $F(1, 54) = 5.27$, $p = .026$, partial $\eta^2 = .09$; span relative measure: $F(1, 54) = 8.7$, $p = .005$, partial $\eta^2 = .14$; BAT absolute measure: $F(1, 54) = 6.4$, $p = .014$, partial $\eta^2 = .11$; BAT relative measure: $F(1, 54) = 6.3$, $p = .015$, partial $\eta^2 = .11$). Again, both these effects were more pronounced for the beat rhythms than the nonbeat rhythms, as confirmed by interactions

Table 3

Summary of the Multiple Regressions Between Beat Rhythm Reproduction Accuracy (Absolute and Relative Criteria) and Individual Differences on BAT and Span for Each Level of Musical Training (No Training, <5 Years of Training, and ≥5 Years of Training)

Rhythm condition	Absolute criterion					Relative criterion				
	B	SE B	beta	t	Sig.	B	SE B	beta	t	Sig.
No training										
Short rhythms										
BAT score	.330	.421	.153	0.785	.441	-.021	.398	-.010	-0.052	.959
Span	.147	.057	.506	2.594	.017	.142	.054	.510	2.650	.015
Medium rhythms										
BAT score	.612	.278	.379	2.204	.039	.373	.319	.200	1.168	.256
Span	.134	.037	.615	3.575	.002	.167	.043	.665	3.886	.001
Long rhythms										
BAT score	.378	.148	.395	2.565	.018	.284	.173	.291	1.638	.116
Span	.092	.020	.710	4.607	.000	.080	.023	.608	3.428	.003
<5 yr of training										
Short rhythms										
BAT score	.627	.564	.294	1.113	.286	.975	.532	.455	1.834	.090
Span	.059	.102	.152	0.577	.574	.011	.096	.028	0.113	.912
Medium rhythms										
BAT score	.548	.484	.290	1.131	.278	.779	.552	.364	1.411	.182
Span	.096	.087	.280	1.092	.295	.045	.100	.117	0.451	.659
Long rhythms										
BAT score	.246	.272	.226	0.902	.384	.459	.344	.301	1.336	.204
Span	.077	.049	.391	1.560	.143	.147	.062	.532	2.367	.034
5+ yr of training										
Short rhythms										
BAT score	.893	.350	.514	2.549	.020	.692	.366	.397	1.888	.075
Span	.015	.058	.051	0.252	.804	.056	.061	.196	0.930	.364
Medium rhythms										
BAT score	.905	.292	.524	3.098	.006	.741	.301	.442	2.462	.024
Span	.121	.048	.424	2.511	.022	.124	.050	.446	2.483	.023
Long rhythms										
BAT score	.422	.295	.267	1.432	.169	.335	.331	.183	1.011	.325
Span	.139	.049	.532	2.851	.011	.182	.055	.603	3.332	.004

Note. Beta (B), standard error (SE), and standardized beta (beta) scores are shown. Values in bold are statistically significant ($p < .05$). Sig. = p value.

between beat and span (absolute measure: $F(1, 54) = 8.7, p = .005$, partial $\eta^2 = .14$; relative measure: $F(1, 54) = 15, p < .001$, partial $\eta^2 = .22$) and beat and BAT score (absolute measure: $F(1, 54) = 6.5, p = .014$, partial $\eta^2 = .11$; relative: $F(1, 54) = 6.7, p = .012$, partial $\eta^2 = .11$).

To illustrate the degree of contribution made by each factor to the different rhythm conditions, when controlling for the remain-

ing factors, multiple regression analyses were conducted for each covariate at each rhythm length (short, medium, and long). The β coefficients for all beat conditions are given in Table 2, and summary diagram is shown in Figure 2. The partial regression plots are shown for beat rhythms in Figure 3 and Supplementary Figure 1 and for nonbeat rhythms in Supplementary Figures 2 and 3. The β coefficients and partial regression plots indicate the



Figure 4. A depiction of the contribution of beat sensitivity and auditory STM capacity at each level of musical training to performance accuracy for beat rhythms (absolute criterion). Values of β are taken from Table 3. Solid lines = significant ($p < .05$) contribution. † = β for relative criterion, absolute criterion nonsignificant.

unique portion of variance accounted for by each covariate at each length of each rhythm type, when controlling for the other covariates. When controlling for musical training and BAT score, span significantly predicts performance only in the medium and long beat rhythms, although this effect interacts with levels of musical training (as described later in the text) and hence must be interpreted with care. When controlling for span and BAT score, musical training significantly predicts performance in the short, medium, and long beat rhythms. When controlling for musical training and span, BAT score significantly predicts performance in the medium and long beat rhythms (Table 2, Figure 3, and Supplementary Figure 3).

In addition, there was a significant four-way interaction between beat, length, musical training, and span (absolute measure: $F(2, 108) = 4.79, p = .01$, partial $\eta^2 = .08$; relative measure: $F(2, 108) = 4.47, p = .014$, partial $\eta^2 = .08$). However, as nonbeat rhythm performance was extremely low, the interaction with beat was likely due to compression of performance to floor in the nonbeat condition. To test whether this was the case, a one-way

repeated-measures ANCOVA with length (short, medium, long) and the same covariates (span, BAT, and musical training) was run separately for beat and nonbeat conditions. No significant interactions were observed for the nonbeat rhythms; however, the interaction between length, musical training, and span remained significant for the beat rhythms (absolute measure: $F(2, 108) = 4.43, p = .014$, partial $\eta^2 = .08$; relative measure: $F(2, 108) = 4.85, p = .01$, partial $\eta^2 = .08$). To determine the nature of the interaction in the beat rhythms, a series of multiple regressions were calculated for each of the musical training levels, at each length, for absolute and relative measures. The multiple regressions controlled for BAT score, and tested the correlation between rhythm accuracy and span for short, medium, and long beat rhythms, for each musical training group. On visual inspection of scatterplots, there was an outlier in the group with <5 years of musical training (one individual with very poor rhythm performance and a very high span), so analyses were conducted without this individual. The β coefficients are shown in Table 3, and the partial correlation plots are shown in Figures 4 and 5, and Supplementary Figure 4. The

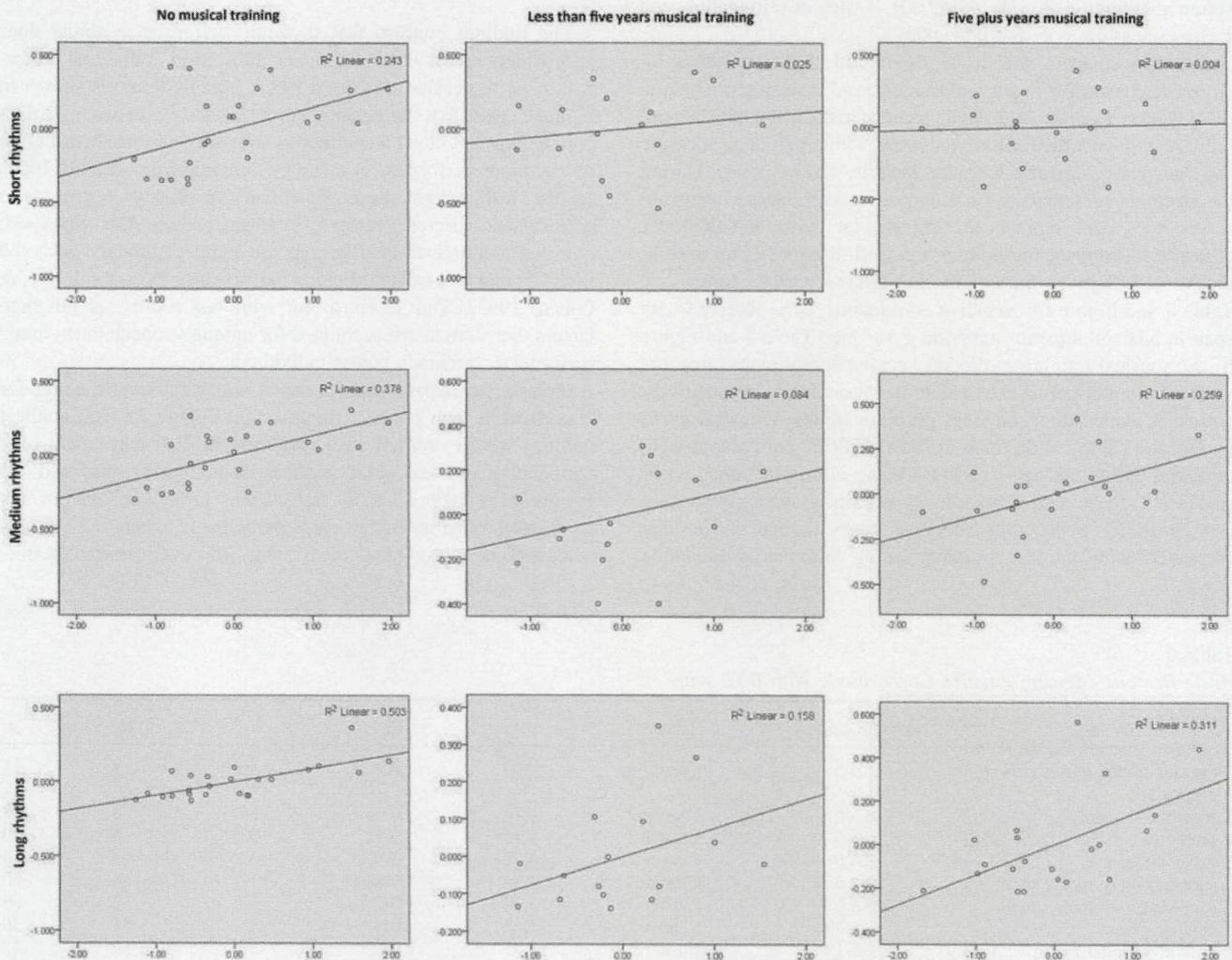


Figure 5. Regression of span on rhythm reproduction accuracy (absolute measure) for beat rhythms, at each level of musical training. BAT scores are controlled for.

regression analysis indicated that for nonmusicians, when controlling for BAT score, span significantly correlated with nonmusician performance for short, medium, and long beat rhythms. However, for both groups of musicians (<5 years and ≥ 5 years), span did not significantly correlate with performance of short beat rhythms. For the musicians with < 5 years of training, span performance significantly correlated with long beat rhythms (relative measure) only. For the musicians with ≥ 5 years of training, span performance correlated with both medium and long beat rhythms, in both absolute and relative measures. Thus, without musical training, span predicted performance for all rhythm lengths, whereas with musical training, span no longer predicted performance of shorter rhythms.

fMRI Results

Behavioral performance in the fMRI rhythm discrimination task (collapsed across beat/nonbeat) correlated significantly with both the absolute and relative measures of overall rhythm accuracy (collapsed across beat/nonbeat and short/medium/long) in the behavioral rhythm reproduction task (fMRI discrimination and absolute measure: $r = .71$, $p < .001$; fMRI discrimination and relative measure: $r = .64$, $p = .005$).

Significance level was $\alpha = .05$ for all fMRI analyses. All covariates (span, BAT, musical training, and rhythm reproduction overall score) were tested in the same statistical model; thus, all brain regions in which activity covaries with a particular measure show unique covariation with that measure and no others. During the stimulus presentation period, positive correlations were observed with BAT score in the left angular gyrus, left premotor cortex, left supplementary motor area, left inferior frontal operculum/ventral premotor cortex, and left inferior parietal cortex (see Table 4 and Figure 6). Negative correlations were observed with span in bilateral superior temporal gyrus (see Table 5 and Figure 6) and musical training in the left supplementary motor area and ventral premotor cortex (see Table 7). Musical training positively correlated with activity in right posterior middle temporal gyrus (MTG; see Table 7 and Figure 6). No significant correlations were observed during the delay period. During discrimination, significant positive correlations with musical training were observed in right posterior MTG, with identical peaks to one cluster that correlated with musical training during stimulus presentation

(Cluster 1 of Table 7). No other correlations during the discrimination period reached significance. No significant correlations with rhythm reproduction were observed at any stage. Performance on beat rhythms only (collapsed across short, medium, and long beat rhythms) was also used as a regressor, but there was still no significant correlation.

Both the letter and rhythm conditions contained regular and irregular timing, and the activation levels that correlated with the individual difference covariates did not significantly differ between the rhythm stimuli and the letter stimuli, so the reported activation correlations with individual differences are collapsed across stimulus type. However, to double-check that the letter condition could not be driving observed effects, all brain areas showing significant correlations were analyzed using data from the rhythm condition only. All areas still showed significant correlations (small-volume-corrected $p < .05$, volumes defined by clusters reported in Tables 4, 5, 6, and 7), indicating that the effects are significant in the rhythm condition, and are not being driven solely by differences in the letter condition.

Discussion

The findings confirm that rhythmic performance ability does vary widely across individuals. For illustration, individual performance on the easiest condition (short beat rhythms) is shown in Figure 7. Note that there is not a clear separation between distinct populations, but rather a continuous and fairly uniform distribution of rhythmic performance accuracy ranging from 0% to 100% correct (with a slight skew). When very few factors contribute to performance, discrete classes of performance are often observed; however, continuous distributions are more commonly observed when several factors contribute to performance (Khoury, Beaty, & Cohen, 1993). This is consistent with our results, as all three factors that were tested accounted for unique variance in rhythmic performance accuracy across individuals.

Overall, participants' performance was significantly better for beat rhythms than nonbeat rhythms (see Figure 1). The nonbeat rhythms were extremely difficult, with the best participant only reproducing 50% of short nonbeat rhythms correctly, and the average was 10% to 13%. Subsequent pilot work in our lab modified the rhythm task to allow participants to hear the rhythms twice before reproducing them. This improved overall perfor-

Table 4
Brain Regions Showing Positive Correlations With BAT Score

Brain area	Brodman area	Cluster ^a	<i>t</i>	<i>p</i> FDR	<i>x</i>	<i>y</i>	<i>z</i>
L inferior frontal gyrus, pars opercularis	BA 6	Cluster 4	4.57	.028	-60	9	18
L premotor cortex	BA 6	Cluster 2	4.18	.033	-39	6	48
L premotor cortex	BA 6	Cluster 2	4.15	.035	-33	6	60
L premotor cortex	BA 6	Cluster 2	4.78	.024	-30	3	48
L supplementary motor area	BA 6	Cluster 3	4.69	.026	-12	6	60
L supplementary motor area	BA 6	Cluster 3	3.74	.047	-6	12	69
L angular gyrus	BA 39	Cluster 1	5.62	.011	-45	-51	36
L middle occipital gyrus	BA 19	Cluster 5	4.37	.032	-30	-69	42

This table shows the brain region, *t* values, and stereotaxic coordinates (in mm) of peak voxels ($p < .05$ whole-brain FDR corrected) in MNI space.

^a Cluster volumes: 1 = 50 voxels, 2 = 53 voxels, 3 = 46 voxels, 4 = 15 voxels, 5 = 39 voxels.

R = right; L = left.

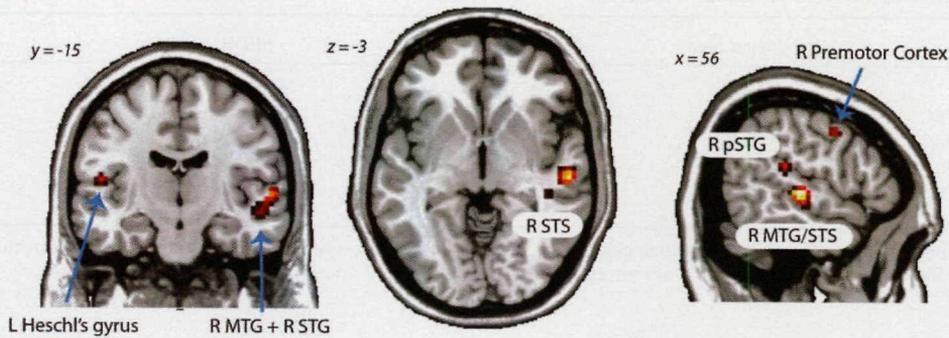
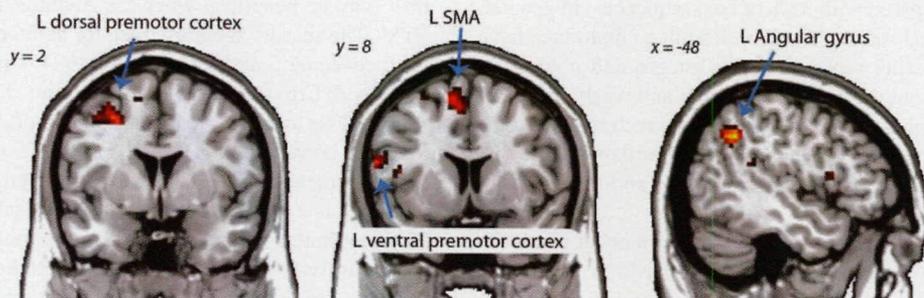
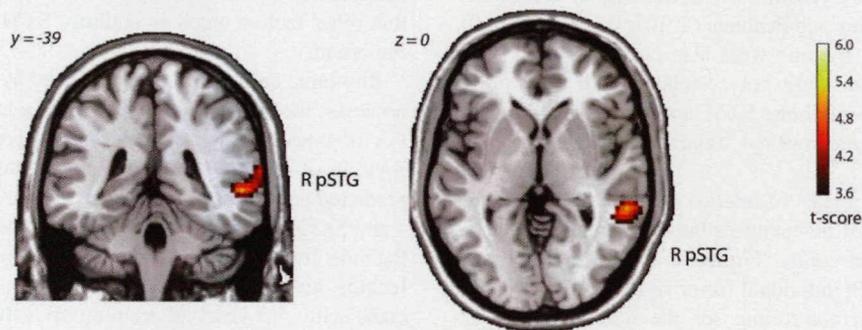
Negative correlations with span**Positive correlations with Beat Alignment Test score****Negative correlations with musical training**

Figure 6. Brain areas showing significant correlations in activity with span, BAT score, and musical training.

mance slightly (e.g., the short nonbeat average increased to 18%), but not enough to remove the substantial floor effect for nonbeat rhythms.

Previous work has measured reproduction accuracy for other types of nonbeat sequences (Grahn & Brett, 2007), particularly those comprising noninteger ratios of intervals. The noninteger-ratio rhythms were about the same length as the medium-length rhythms in the current study, but each rhythm was repeated three times before reproduction instead of once. In that study, performance was 58% correct, compared with 3% in the current study. However, pilot work with the current rhythms, repeated twice before reproduction, found that nonbeat performance was still very low (9% correct), so a third presentation is unlikely to have

boosted accuracy up to the 58% observed for noninteger-ratio rhythms. We suspect that the current nonbeat rhythms are more difficult to reproduce than noninteger-ratio rhythms. The exact reason for this discrepancy is unclear. The current nonbeat rhythms were constructed by “jittering” a beat rhythm: onsets from a beat rhythm were manipulated so that a third of onsets were early, a third were late, and the remaining third remained as they were. It may be that this jittering allows some perception of the beat structure from the original sequence to remain, and that participants systematically distorted their nonbeat production to conform to the original beat sequence. However, if that were the case, the number of sequences that had the wrong number of taps would be similar for beat and nonbeat conditions, as participants would have

Table 5
Brain Regions Showing Negative Correlations With Span

Brain area	Brodmann area	Cluster ^a	<i>t</i>	<i>p</i> FDR	x	y	z
R premotor cortex	BA 6	Cluster 5	4.21	.037	60	0	39
R superior temporal gyrus	BA 42	Cluster 2	4.40	.026	60	-30	15
R superior temporal sulcus	BA 22	Cluster 1	6.36	.001	57	-21	0
R middle temporal gyrus	BA 22	Cluster 2	5.44	.004	69	-39	21
L middle temporal gyrus	BA 21	Cluster 3	4.88	.010	-60	-30	6
L Heschl's gyrus	BA 41	Cluster 4	4.64	.017	-51	-12	12

This table shows the brain region, *t* values, and stereotaxic coordinates (in mm) of peak voxels ($p < .05$ whole-brain FDR corrected) in MNI space.

^a Cluster volumes: 1 = 50 voxels, 2 = 53 voxels, 3 = 46 voxels, 4 = 15 voxels, 5 = 39 voxels.

R = right; L = left.

an accurate representation of the number of taps, but simply a distorted representation of the timing between taps. This was not the case: overall, 42% of nonbeat sequences had the incorrect number of taps, compared with 33% of beat sequences. In general, only some factors that make a rhythm difficult to reproduce have been studied (comparing sequences with integer and noninteger ratios or sequences that are metrically strong and weak, or examining effects of grouping and repetition). Thus, much remains to be explored about the relevant parameters that contribute to the difficulty in different types of nonbeat sequences, and this is a rich avenue for future research.

Whatever the cause, the floor effects in the nonbeat condition necessitate that the interpretation of the behavioral results be restricted to effects on the accuracy of beat rhythm reproduction only, and how that accuracy was predicted by the various covariates.

Span correlated positively with musical training, in accordance with previous work (Bailey and Penhune (2010); Wallentin, 2010). BAT score and musical training were also positively correlated. However, BAT and span were not correlated with each other, indicating that although auditory STM and beat sensitivity are higher in those with more musical training, they appear to be distinct capacities.

Moreover, all the covariates of interest (i.e., span, BAT score, and musical training) had independent but interacting influences on rhythmic reproduction ability (Figures 2 and 3). Partial correlations indicated that each individual factor significantly predicted performance even when controlling for the remaining factors. Using the absolute criterion, BAT score significantly predicted performance only for medium beat rhythms ($\beta = .29$), although prediction of short and long beat performance was marginally significant (β values = .23 and .21). Using the relative criterion,

BAT score significantly predicted performance for all rhythm lengths (β values ranging from .24 to .30). The weaker effect for shorter rhythms (β values of .23-.24) indicates that beat sensitivity may only be beneficial when the rhythms are long enough to tax STM. The sensory memory trace for auditory stimuli is thought to last between 1.5 and 4 s (Cowan, 1984; Crowder, 1982; Darwin, Turvey, & Crowder, 1972), and the short rhythms were ~2 to 2.5 s long, close to the hypothetical lower limit. The medium and long rhythms, however, ranged from 2.9 to 4.75 s, a length at which the sensory trace would likely have decayed somewhat, requiring more reliance on beat structure and rehearsal strategies to maintain a representation of the rhythm. At the longer lengths, therefore, beat sensitivity becomes a significant predictor of performance of rhythms that have beat structure. The relative reduction in the importance of beat sensitivity for the longest rhythms ($\beta = .21-.23$) compared with the medium rhythms ($\beta = .30-.32$) may indicate that beat sensitivity is of limited use for long rhythms and that other factors (such as auditory STM capacity) become more important.

Rhythmic ability was also predicted by auditory STM capacity; however, the effects were dependent on levels of musical training. For nonmusicians, span significantly predicted performance for rhythms of all lengths. For those with musical training, span only predicted performance for longer rhythms (see Table 3 and Figures 4 and 5). Counterintuitively, however, span predicted performance the most for nonmusicians (β values from .51 to .71 for all rhythm lengths, absolute and relative measures), the next most for musicians with >5 years of training (β values from .42 to .60 for medium and long rhythms, absolute and relative measures), and the least for musicians with <5 years of training (long rhythms' $\beta = .53$, relative measure only). If musical training was linearly associated with a reduced reliance on auditory STM for rhythm

Table 6
Brain Regions Showing Negative Correlations With Musical Training

Brain area	Brodmann area	Cluster ^a	<i>t</i>	<i>p</i> FDR	x	y	z
L supplementary motor area	BA 6	Cluster 1	5.29	.040	-6	12	63
L inferior frontal gyrus, pars opercularis	BA 44	Cluster 2	4.73	.048	-60	12	18
L inferior frontal gyrus, pars triangularis	BA 47	Cluster 3	4.64	.048	-48	30	0

This table shows the brain region, *t* values, and stereotaxic coordinates (in mm) of peak voxels ($p < .05$ whole-brain FDR corrected) in MNI space.

^a Cluster volumes: 1 = 10 voxels, 2 = 2 voxels, 3 = 3 voxels.

L = left.

Table 7
Brain Regions Showing Positive Correlations With Musical Training

Brain area	Brodman area	Cluster ^a	<i>t</i>	<i>p</i> FDR	<i>x</i>	<i>y</i>	<i>z</i>
R middle temporal gyrus	BA 21	Cluster 1	5.10	.042	57	-39	0
R middle temporal gyrus	BA 22	Cluster 1	4.83	.042	66	-42	9
R middle temporal gyrus	BA 37	Cluster 2	4.31	.044	57	-57	6

This table shows the brain region, *t* values, and stereotaxic coordinates (in mm) of peak voxels ($p < .05$ whole-brain FDR corrected) in MNI space.

^a Cluster volumes: 1 = 37 voxels, 2 = 3 voxels.

R = right.

performance, musicians with the most training should have span score predicting the least variance. We do not have a clear interpretation of the middle musical training group showing the smallest effect of span. It may arise from sample variability (see Figure 5) or may be a true effect, and a replication is necessary to distinguish these interpretations. In general, it seems reasonable that musical training may reduce the importance of auditory STM in rhythm reproduction ability, through use of alternate strategies or "chunking" (considered in more detail later in the text).

It was not possible to test whether span, BAT, and musical training made different contributions to beat and nonbeat rhythms because of the difficulty with nonbeat rhythms, but future work with easier nonbeat rhythms may be able to address these questions.

Musical training predicted performance for all rhythm lengths, and did so independently of span and BAT score (although it did correlate with both factors). This indicates that musical training does not enhance rhythmic ability solely through changes to auditory STM capacity or beat sensitivity. This is consistent with previous work (Bailey & Penhune, 2010) that finds better rhythm synchronization ability in musicians, which is not explained by changes in auditory STM capacity. It is possible musicians have greater exposure to rhythm structures, giving them a better ability to parse and remember them. Musicians' representation may be compressed, or make greater use of "chunking" (Glenberg & Jona, 1991; Gobet et al., 2001), which would reduce musicians' need to rely on auditory STM, consistent with the effects described earlier. Of course, it is possible that the musical training itself is not the cause of the better rhythmic ability, but rather that a genetic predisposition or environmental inducement to engage in musical training is the root cause. People with innately good rhythm perception might be more attracted to musical training and, because of their better skills, get more out of their training and stay with it longer. In addition, perhaps those who have musical training are inclined to do so because of environmental influences, higher motivation levels, or other factors that were not evaluated in this study. Disentangling these influences remains an issue for future work.

Pitch is the natural counterpart to rhythm in music, and some work implies that pitch and rhythm are processed by the same system (Boltz, 1989; Jones, Boltz, & Kidd, 1982). However, more recent studies suggest that rhythm and pitch ability are dissociable, starting in early childhood (Anvari, Trainor, Woodside, & Levy, 2002), and that poor pitch discrimination ability does not affect performance on rhythm tasks when the rhythms are monotone (i.e., have no pitch changes), like the rhythms used here (Foxton et al., 2006; Hyde & Peretz, 2004). For these reasons, pitch discrimination ability was not assessed.

We also did not measure general intelligence, which has been shown to relate to performance on very basic timing tasks (Helmbold,

Troche, & Rammsayer, 2006; Helmbold, Troche, & Rammsayer, 2007; Rammsayer & Brandler, 2007). However, auditory STM capacity and general intelligence are highly correlated (Colom, Abad, Rebollo, & Shih, 2005; Colom, Flores-Mendoza, Quiroga, & Privado, 2005; Engle, 2002; Kyllonen & Christal, 1990), so general intelligence may not have uniquely predicted variance beyond that accounted for by span. Moreover, most of the timing tests involve very low-level tasks involving duration discrimination, temporal order judgments, synchronization to isochronous stimuli, and so forth. In Rammsayer's study (2007), there was a "rhythm" test, although much simpler than the current rhythm test—it involved detecting small temporal deviations in a stream of five otherwise isochronous tones. Interestingly, performance on the rhythm task did not significantly correlate with performance on the other temporal tasks, suggesting that the correlation between intelligence and timing may not extend to rhythm performance.

In addition to analyzing the contributions of STM capacity, beat sensitivity, and musical training to behavioral measures of rhythmic ability, individual differences in brain responses to rhythm stimuli were analyzed. Significant correlations were observed between neural activity and span, beat sensitivity, and musical training during stimulus presentation, and with musical training during discrimination. We found no significant correlations of activation with rhythmic ability, as measured by accuracy on the rhythm reproduction test. However, by including the other covariates that the behavioral data indicate are associated with rhythmic ability, it may be that rhythmic ability did not account for any additional variance in neural responses. Alternatively, with only 18 subjects, it may be that power was insufficient to detect differences associated with rhythmic ability.

During stimulus presentation, there was a negative correlation with span in the posterior superior temporal gyrus and MTG; participants with low STM capacity activated this area more than participants with high STM capacity. This is consistent with neuropsychological studies indicating that lesions of posterior superior temporal gyrus (STG) are associated with auditory-verbal STM deficits (Leff et al., 2009; Markowitsch et al., 1999; Takayama, Kinomoto, & Nakamura, 2004), and neuroimaging data showing that gray matter density in this area correlates with digit span (Richardson et al., 2011). In addition, activation of this area occurs during auditory-verbal maintenance (Buchsbaum, Olsen, Koch, & Berman, 2005). However, most previous studies have implicated the left posterior STG, not the right posterior STG as we observed. Although we found a correlation in left posterior STG, there was a rightward asymmetry in the extent of activation. One possibility is that both hemispheres play a role in auditory STM, but that contralateral recruitment of the right hemisphere supports performance more for those with lower capacity

Reproduction accuracy for short, medium, and long beat rhythms across all participants

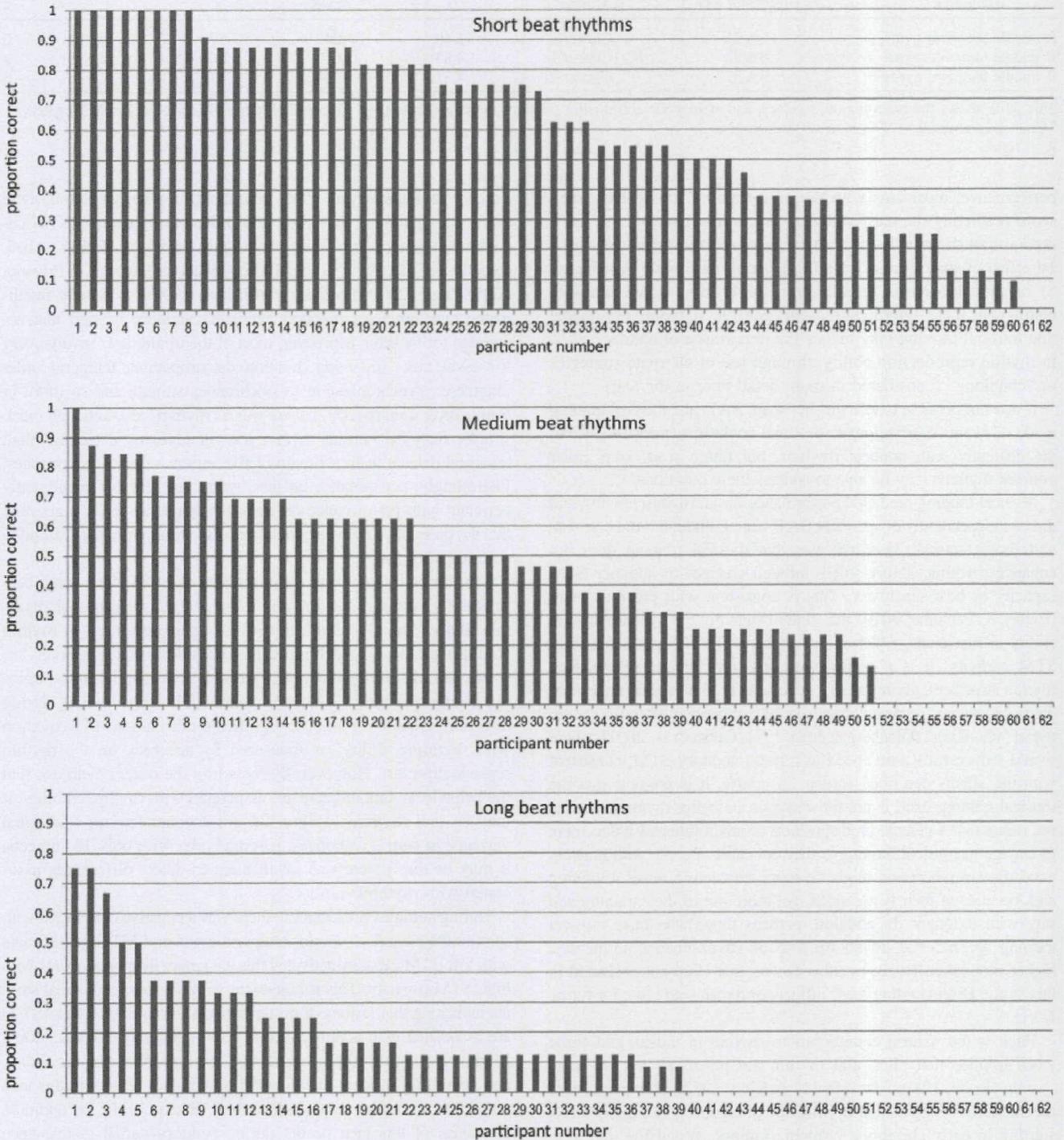


Figure 7. Individual participants' rhythm reproduction accuracy scores for short, medium, and long beat rhythms.

owing to the greater difficulty of the task for them (Cabeza, 2002; Hester, Murphy, & Garavan, 2004).

In addition, we found correlations with beat sensitivity during stimulus presentation in the left angular gyrus, left supplementary

motor area, left dorsal and ventral premotor cortex, and inferior frontal operculum. This network of parietal and motor areas overlaps highly with areas implicated in the posterodorsal auditory stream, which performs auditory to motor transformations in

speech (Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Hickok, Okada, & Serences, 2009; Rauschecker & Scott, 2009). Auditory-motor transformations in rhythm also occur (Brown, Martinez, & Parsons, 2006; Chen et al., 2008; Grahn & Brett, 2007), and it may be that those with high beat sensitivity are engaging the auditory-motor representational system rather than relying more on a purely auditory code to remember the rhythmic sequences.

Finally, we found positive correlations with musical training during stimulus presentation and discrimination in the posterior MTG. Negative correlations were found in the left supplementary motor area and ventral premotor cortex. The posterior MTG has been shown to be more active in pianists than nonmusicians listening to melodies (Bangert et al., 2006) and in musicians compared with nonmusicians listening to piano pieces (Seung, Kyong, Woo, Lee, & Lee, 2005). Posterior MTG is most strongly associated with accessing of semantic meaning, potentially acting as a sound-to-meaning interface (Hickok & Poeppel, 2000, 2004). None of the rhythms, however, were taken from known identifiable pieces of music, and no musicians reported attempting to associate the rhythms with meaningful music as a strategy. Therefore, the functional significance of this greater response remains to be fully elucidated. The increased supplementary and premotor activation in those with less musical training may indicate a greater reliance on strategies to remember the stimuli like subvocalizing (covert rehearsal), which activates these motor areas (Awh et al., 1996; Grasby et al., 1993; Gruber, Kleinschmidt, Binkofski, Steinmetz, & von Cramon, 2000). Alternatively, it may reflect a more efficient processing of rhythm in these areas for those with greater musical training.

Taken together, the neuroimaging data suggest that differential activation of auditory and motor areas is associated with the factors that contribute to individual differences in rhythmic ability. In some cases, however, activity in the same general area is associated with low scores on one factor and, counterintuitively, high scores on another. For example, different parts of the supplementary motor area are associated with low musical training levels and with high beat sensitivity. This highlights the problem of reverse inference (Poldrack, 2006): single brain areas are rarely activated by only one cognitive process. In this case, we cannot distinguish between engagement of the motor system in what may be a beneficial way (an auditory-motor transformation of the rhythm representation) and what may be a less beneficial way (subvocalizing to maintain the auditory representation of the rhythm through rote rehearsal) by simply looking at activation in one general brain area.

In conclusion, rhythmic ability varies widely across individuals, but with a relatively continuous and uniform distribution, rather than a bimodal one, suggesting that deficits in rhythmic ability represent the tail of a continuum and not a separate specific deficit. Consistent with the observation of a continuous distribution, multiple factors were found to predict rhythmic ability. In particular, auditory STM capacity, beat sensitivity, and musical training each accounted for unique portions of variability in rhythm reproduction performance, indicating that each factor made an independent contribution to rhythmic ability. Musical training predicted performance regardless of the length of the rhythm. Auditory STM capacity and beat sensitivity were important only when rhythms were longer. Finally, each factor was associated with alterations in

auditory and motor brain activity during a rhythm discrimination task, further highlighting the importance of auditory-motor interactions for rhythm performance ability.

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