

Rhythm and Beat Perception in Motor Areas of the Brain

Jessica A. Grahn and Matthew Brett

Abstract

■ When we listen to rhythm, we often move spontaneously to the beat. This movement may result from processing of the beat by motor areas. Previous studies have shown that several motor areas respond when attending to rhythms. Here we investigate whether specific motor regions respond to *beat* in rhythm. We predicted that the basal ganglia and supplementary motor area (SMA) would respond in the presence of a regular beat. To establish what rhythm properties induce a beat, we asked subjects to reproduce different types of rhythmic sequences. Improved reproduction was observed for one

rhythm type, which had integer ratio relationships between its intervals and regular perceptual accents. A subsequent functional magnetic resonance imaging study found that these rhythms also elicited higher activity in the basal ganglia and SMA. This finding was consistent across different levels of musical training, although musicians showed activation increases unrelated to rhythm type in the premotor cortex, cerebellum, and SMAs (pre-SMA and SMA). We conclude that, in addition to their role in movement production, the basal ganglia and SMAs may mediate beat perception. ■

INTRODUCTION

In most Western music, people perceive a regular, underlying pulse called the “beat” or “tactus” (Drake, Penel, & Bigand, 2000). Perception of the beat often causes spontaneous synchronized movement, such as toe tapping or head nodding. The presence of a beat also affects the ability to remember and perform a rhythm. For example, when a rhythm is presented with a beat (the beat occurring as a series of external metronome clicks), reproduction accuracy of the rhythm improves (Patel, Iversen, Chen, & Repp, 2005; Essens & Povel, 1985). The beat is emphasized in musical contexts by nontemporal cues such as pitch, volume, and timbre, yet even rhythms without these cues can induce listeners to “feel” a beat internally (Brochard, Abecasis, Potter, Ragot, & Drake, 2003). The beat is somehow conveyed solely by the temporal properties of the rhythm itself. It is still unclear, however, exactly what temporal properties are critical for beat perception to spontaneously occur. One property that may be important for beat perception in rhythm is the presence of simple integer ratio relationships between intervals in a sequence (Sakai et al., 1999; Essens, 1986). For example, a sequence containing intervals of 250, 500, and 1000 msec has a 1:2:4 relationship between its intervals. By using a beat that is the length of the smallest interval, the sequence can be encoded in terms of beats, instead

of encoding each individual interval length. In non-integer ratio sequences (e.g., 1:2.4:3.6) beats cannot be used, and thus, sequence reproduction is worse. Subjects may even “regularize” noninteger ratio sequences, reproducing them as integer ratios (Collier & Wright, 1995; Essens, 1986).

Others propose that integer ratios are insufficient to induce a beat and that regularly occurring “perceptual accents” may also be necessary (Essens & Povel, 1985). Accents cause a particular note to feel more prominent than surrounding notes, and previous work shows that our attention is attracted to accented events (Drake, Jones, & Baruch, 2000; Jones & Pfordresher, 1997; Jones & Boltz, 1989). One common type of accent occurs in music, where louder notes are perceived as more prominent. However, humans perceive a beat in rhythmic patterns even when no volume changes occur. In this case, any perceptual accents that occur are due to the temporal pattern. This is the type of accent investigated in the current experiments: the type of accent that arises solely from the temporal context when all other factors (such as pitch or volume) are held constant. For example, onsets not closely followed by other onsets in time are perceived as accented (Parncutt, 1994), as is the final onset of two or three onsets in a row (Povel & Okkerman, 1981). The latter type of accent is present in the Overture to William Tell (da da dum, da da dum, da da dum dum dum ...) on the “dum” of each “da da dum.” If perceptual accents occurring at regular temporal intervals are necessary to feel the beat, then

MRC Cognition and Brain Sciences Unit, Cambridge, UK

sequences with this property should be reproduced more accurately (Essens, 1995).

Perceptual accents have not always been considered in previous research (Sakai et al., 1999). Thus, enhancement in integer ratio sequence performance may be due to some sequences in that condition that also had regular perceptual accents. The role of perceptual accents and integer ratios in rhythm reproduction is examined in our first experiment. Subjects listened to and then reproduced rhythms that contained either integer ratios or noninteger ratios and regular or irregular perceptual accents. A follow-up functional magnetic resonance imaging (fMRI) study used the same rhythms to investigate neural activity during rhythm perception. Perception and production are likely to rely on similar neural mechanisms, as previous behavioral work demonstrates comparable difference thresholds between timing during perception and production tasks (Ivry & Hazeltine, 1995). This behavioral similarity is supported by neuroimaging experiments. Timing, duration perception, and rhythm perception and production tasks consistently activate the same brain areas, including the premotor and supplementary motor areas (SMAs), cerebellum, and basal ganglia (Coull, Vidal, Nazarian, & Macar, 2004; Lewis, Wing, Pope, Praamstra, & Miall, 2004; Pastor, Day, Macaluso, Friston, & Frackowiak, 2004; Dhamala et al., 2003; Ferrandez et al., 2003; Nenadic et al., 2003; Ramnani & Passingham, 2001; Rao, Mayer, & Harrington, 2001; Schubotz & von Cramon, 2001; Penhune, Zatorre, & Evans, 1998). Damage to these areas also impairs timing abilities (Molinari, Leggio, De Martin, Cerasa, & Thaut, 2003; Mangels, Ivry, & Shimizu, 1998; Halsband, Ito, Tanji, & Freund, 1993; Artieda, Pastor, Lacruz, & Obeso, 1992). It is thus reasonably clear that the timing processes that underlie both perception and production involve these areas.

However, these brain regions are unlikely to subserve identical timing functions. It has been suggested that one distinction between commonly activated neural structures may be their respective roles in “automatic” timing, defined as “the continuous measurement of predictable subsecond intervals defined by movement,” and “cognitively controlled” timing, defined as the “measurement of suprasedond intervals not defined by movement and occurring as discrete epochs” (Lewis & Miall, 2003). Beat perception has characteristics of both automatic and cognitively controlled timing, as the length of the beat humans perceive can span from approximately 200 to 2000 msec (Parncutt, 1994; Warren, 1993), and the beat may or may not be marked by movement. Accordingly, a different distinction may be that certain motor areas are involved in extracting a regular beat from incoming temporal stimuli. The role for motor areas in beat processing is supported by findings of a direct link between movement and beat perception in infants (Phillips-Silver & Trainor, 2005). Thus, the current studies were conducted to determine

if certain brain areas responded to perception of a beat (induced by the temporal structure of the rhythms).

Beat perception may require a temporal representation or level of processing that is more complex than that required for the more basic timing of individual intervals. Given that the basal ganglia and SMA are not only involved in attention to time (Coull et al., 2004), but are critical to temporal sequencing (Shima & Tanji, 2000; Brotchie, Iansek, & Horne, 1991) and predictable, internally generated movements (Cunnington, Windischberger, Deecke, & Moser, 2002; Freeman, Cody, & Schady, 1993), we hypothesize that they are the most likely candidate areas for the detection or generation of an internal beat.

METHODS

Reproduction Experiment

Subjects and Stimuli

Twenty subjects (9 men, 11 women) took part in the reproduction experiment. Subjects ranged in age from 24 to 40 years, with an average age of 30 years. For each condition, 30 rhythmic sequences were constructed from sets of five, six, or seven intervals. The intervals in the metric rhythms were related by ratios of 1:2:3:4, and the intervals in the nonmetric rhythms were related by ratios of 1:1.4:3.5:4.5. The metric rhythms were of two types: simple and complex.

In the metric simple condition the intervals were arranged to induce a perceptual accent at the beginning of each group of four units (see Figure 1). Nothing was added to the sequence to produce the perceptual accents: they arise spontaneously from the temporal

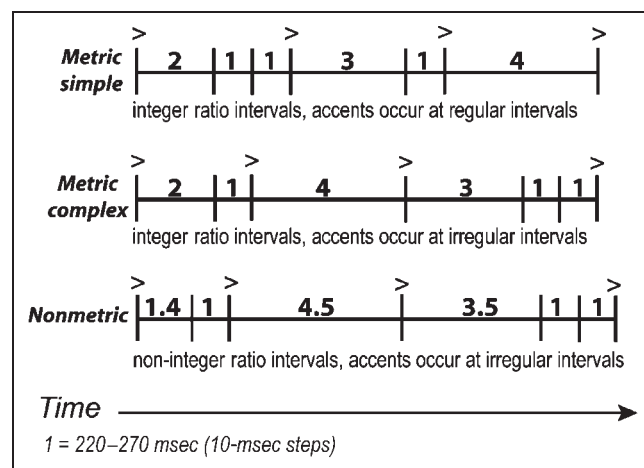


Figure 1. Schematic of sample stimuli. Vertical bars indicate interval onset; “>” indicates where perceptual accents should be heard (Povel & Okkerman, 1981). Perceptual accents can occur on final interval onsets of consecutive runs of two or three short intervals and on onsets either preceded or followed by a relatively long period of no onsets (such as the first and last onsets of a sequence).

context, in accordance with the model of Povel and Essens (Essens & Povel, 1985). The perceptual accents were there to induce subjects to hear a regular beat coinciding with the onset of each group of four units. Other work in our laboratory suggests that participants' representation of the beat agree with the model's accent predictions. Pilot data reveal that when participants are asked to listen to rhythmic sequences and decide if a beat is present, a beat is felt 90% of the time for metric simple sequences. Increased finger tap velocity or force on particular taps during reproduction can also indicate where participants feel the beat. When tap velocity was measured during a reproduction task similar to the one outlined here, the velocity was significantly higher for taps coinciding with the perceptual accents at the onset of each group of four units than for the other taps in each sequence (Grahn & Brett, 2005, 2006).

In the metric complex condition, the intervals were identical to those in the metric simple condition, but rearranged so as not to be regularly grouped, and therefore had irregular perceptual accents. The nonmetric rhythms had the same interval arrangements as the metric complex rhythms but used the noninteger ratio interval lengths: 1.4 replaced 2, 3.5 replaced 3, and 4.5 replaced 4. For a complete list of sequences, see Table 1.

The length of the "1" interval was chosen randomly from 220 to 270 msec (in 10-msec steps) on each trial to prevent subjects from using a beat perceived in the previous trial. The rest of the intervals in each sequence were multiples of the 1 interval. For example, with a 1 interval of 250 msec, the sequence 321411 has intervals of length 750 500 250 1000 250 250 (msec). Sine tones (rise/fall times of 8 msec) sounded for the duration of each interval, ending 40 msec before the specified interval length to create a silent gap that demarcated the intervals. The sequences used filled intervals, as piloting indicated performance was similar for empty and filled interval sequences, and filled intervals provide the benefit of attenuation of environmental noise (e.g., that experienced during MRI). In addition, differences in the average psychophysical discrimination threshold between empty and filled auditory intervals are a few milliseconds and thus unlikely to affect perception of sequences composed of the interval lengths used here (Grondin, 1993). One of six pitches (varying from 294 to 587 Hz) was picked at random for each trial and held constant for that trial. The pitch differences between trials helped cue subjects to each new trial.

In the first experiment, the task was to reproduce the sequence as accurately as possible. During reproduction, the onset of each reproduced interval is indicated by the subject's tap, and the reproduced lengths of each interval were measured by the intertap time. We therefore added an additional tone, the length of the 1 interval, to the end of each sequence. Otherwise, without this final onset for subjects to tap, the last reproduced interval's length would not have been measured.

Experimental Design

Rhythms were presented diotically over headphones. On each trial a rhythm was presented three times, with 1100 msec between presentations. After the third presentation, subjects tapped the rhythm from memory on one key of a computer keyboard. Subjects had 4.5 sec to tap the rhythm before the next one was presented. Subjects practiced four trials, then completed three blocks of 30 trials each. There were 30 trials of each rhythm type (metric simple, metric complex, nonmetric) presented in random order.

Data Analysis

Performance was evaluated based on the keypresses the subjects reproduced. Trials with the incorrect number of keypresses or incorrect order of intervals were considered errors. Incorrect ordering was defined as any reproduced interval exceeding the length of another reproduced interval that was supposed to be shorter (e.g., a 2 interval exceeding the length of a 3 interval) and vice versa (e.g., a 4 interval shorter than a 1 interval). More stringent criteria (e.g., rejecting any sequence with a reproduced interval that deviated by more than 10% or 20% of the specified interval length) were also used, but led to the same pattern of results between conditions and thus are not presented here. On correct trials, the reproduced ratios were calculated from the mean duration of each reproduced interval length on each trial. Perfect reproduction results in ratios of 2, 3, and 4 for both metric conditions, and 1.4, 3.5, and 4.5 for the nonmetric condition. In order to compare accuracy between conditions, each reproduced ratio was divided by its ideal ratio (the ratio actually presented in the stimulus), so reproduction across the different ratios was normalized to 1 (perfect reproduction). The absolute value of the deviation from 1 was then tested to see if accuracy differed across ratios and conditions.

Functional Imaging Experiment

Subjects

Twenty-seven right-handed subjects participated (19 men, 8 women). Fourteen had musical training (over 5 years of formal musical training and current regular musical activity) and 13 had no musical training (reported no formal musical training or musical activities). They ranged in age from 19 to 38 years, and the average age was 24.5 years. The fMRI participants had not taken part in the previous reproduction experiment.

Experimental Design

Rhythms were presented diotically over electrostatic headphones (Palmer, Bullock, & Chambers, 1998) inserted into

Table 1. Rhythmic Sequences for Each Condition

	<i>Interval Set</i>	<i>Metric Simple</i>	<i>Metric Complex</i>	<i>Nonmetric</i>	
5 Intervals	11334	31413	11343	1 1 3.5 4.5 3.5	
		41331	33141	3.5 3.5 1 4.5 1	
		43113	41133	4.5 1 1 3.5 3.5	
	12234	22413	13242	1 3.5 1.4 4.5 1.4	
		31422	21324	1.4 1 3.5 1.4 4.5	
		43122	41232	4.5 1 1.4 3.5 1.4	
6 Intervals	111234	112314	124113	1 1.4 4.5 1 1 3.5	
		211134	214311	1.4 1 4.5 3.5 1 1	
		211413	321411	3.5 1.4 1 4.5 1 1	
		411231	421311	4.5 1.4 1 3.5 1 1	
	112224	112422	122142	1 1.4 1.4 1 4.5 1.4	
		211224	214221	1.4 1 4.5 1.4 1.4 1	
		222114	221241	1.4 1.4 1 1.4 4.5 1	
		422112	412212	4.5 1 1.4 1.4 1 1.4	
	112233	221331	121233	1 1.4 1 1.4 3.5 3.5	
		223113	132321	1 3.5 1.4 3.5 1.4 1	
		311322	231123	1.4 3.5 1 1 1.4 3.5	
		312213	323211	3.5 1.4 3.5 1.4 1 1	
	7 Intervals	1111134	1111431	1314111	1 3.5 1 4.5 1 1 1
			3141111	1411311	1 4.5 1 1 3.5 1 1
			4111131	3114111	3.5 1 1 4.5 1 1 1
1111224		1122114	1112412	1 1 1 1.4 4.5 1 1.4	
		2211114	2141211	1.4 1 4.5 1 1.4 1 1	
		4221111	4111221	4.5 1 1 1 1.4 1.4 1	
1111233		1123113	1132131	1 1 3.5 1.4 1 3.5 1	
		2113113	2331111	1.4 3.5 3.5 1 1 1 1	
		3121113	3113121	3.5 1 1 3.5 1 1.4 1	
1112223		1123122	1132212	1 1 3.5 1.4 1.4 1 1.4	
		2112231	2123211	1.4 1 1.4 3.5 1.4 1 1	
		3122112	3221112	3.5 1.4 1.4 1 1 1 1.4	

1 = 220–270 msec (in steps of 10 msec), chosen at random for each trial. All other intervals in that sequence are multiplied by length chosen for the 1 interval.

sound-attenuating ear defenders. Further attenuation of scanner noise was achieved with insert earplugs rated to attenuate by ~30 dB (3M 1100 earplugs, 3M United Kingdom PLC, Bracknell, UK). When wearing earplugs and ear defenders, participants reported no difficulty in hearing the rhythms or focusing on the task. The discrimination task used the same sequences as the reproduction task but required participants to listen to two identical

presentations of a rhythm, to which they compared a subsequent third presentation. The third presentation could be the same rhythm or a different rhythm. To indicate whether the third rhythm was same or different, participants pressed one of two buttons with either the right index or middle finger. On 39% of trials the third presentation was different. Each rhythm presentation was separated by 1100 msec. The deviant sequences contained

two temporal changes (as piloting indicated that the presence of two deviants allowed behavioral performance between conditions to be equal, but not at ceiling or floor). One interval in the sequence was divided into two intervals, and two separate intervals were combined into one (e.g., 211314 becomes 223113, 11 → 2, and 4 → 13). Thus, the number of intervals and overall sequence length was identical between standard and deviant sequences. Before scanning, participants completed eight practice trials. During scanning, participants completed four consecutive sessions of 38 trials each, approximately 40 min in total. Trials were equally distributed between four types: rest (no sound presented), metric simple, metric complex, or nonmetric rhythms, presented in a pseudo-random order. Participants were instructed not to move any part of their body during the scan (other than to respond).

Image Acquisition

Participants were scanned on a Bruker MEDSPEC 3-T scanner at the Wolfson Brain Imaging Centre in Cambridge, using a head coil gradient set. Echo-planar imaging (EPI) data were collected with the following parameters: 21 slices, matrix size of 64×64 , TE = 37.5 msec, TR = 1.1 sec, FOV = 20×20 cm, flip angle = 65.5° . The resulting EPIs had a slice thickness of 4 mm, interslice distance of 1 mm, and in-plane resolution of 3.125×3.125 mm. The EPI acquisition was continuous to prevent periodic silent gaps between TRs from disrupting participants' encoding of the rhythms. Although some studies of auditory cortex have used "sparse" imaging in order to reduce the effects of scanner noise on detecting subtle differences in auditory activity, we chose to use standard continuous imaging, as this offered considerably greater power (number of scans) and the stimuli were easily heard over the scanner noise. In addition, motor areas, not auditory areas, were of primary interest. A map of the magnetic field was acquired to correct for distortion to the EPIs resulting from inhomogeneities in the field. High-resolution three-dimensional spoiled gradient recalled (SPGR) at steady-state anatomical images were collected for anatomic localization and coregistration.

Image Processing and Statistical Analysis

SPM2 was used for preprocessing of the fMRI data and SPM99 for statistical analysis (SPM99, SPM2; Wellcome Department of Cognitive Neurology, London, UK). SPM99 was used to take advantage of previously adapted routines to remove time series artifacts from the data (www.mrc-cbu.cam.ac.uk/Imaging/Common/missing_time.shtml). Images were slice-timing corrected, with the first slice in each scan used as a reference. They were then realigned spatially (to correct for subject

motion) with respect to the first image in the series by using trilinear interpolation. Magnetic field maps were used to undistort the EPI images (Cusack & Papadakis, 2002). The SPGR image was skull-stripped by using the Brain Extraction Tool (BET) (Smith, 2002), then normalized (using affine and smoothly nonlinear transformations) to a brain template in Montreal Neurological Institute (MNI) space. The resulting normalization parameters were then applied to the EPIs and all normalized EPI images were spatially smoothed with an 8-mm full width half maximum Gaussian kernel.

For each participant, each session, and each condition (metric simple, metric complex, and nonmetric) the following event types were modeled separately: first presentation; second presentation; third presentation for same trials; third presentation for different trials; button press response. Each event was modeled by using a regressor made from an on-off boxcar convolved with a canonical hemodynamic response function. Six estimated parameters of movement between scans (translation and rotation along x , y , and z axes) were entered as covariates of no interest. Before running the model, the time course of the average brain signal was screened for spikes of high variance. Short periods of high variance are usually associated with brief subject movements as shown in the spatial realignment parameters. The high-variance scans were removed from the model by using a modified version of the SPM99 modeling routines (www.mrc-cbu.cam.ac.uk/Imaging/Common/missing_time.shtml). Low-frequency noise was removed with a standard high-pass filter of 120 sec. The results estimated from single subject models were entered into second-level random effects analyses for standard SPM group inference (Penny & Holmes, 2003). All reported peaks passed a whole-brain false detection rate (FDR) threshold (Genovese, Lazar, & Nichols, 2002; Benjamini & Hochberg, 1995) of $p < .05$.

A region-of-interest (ROI) analysis was conducted to test the prediction that the basal ganglia and SMA are more active to rhythms that induce a beat, and to elucidate the pattern of activation between conditions in other ROIs. For the basal ganglia, where structure is easily defined by anatomy and relatively invariant across individuals, structural ROIs were used for the pallidum, putamen, and caudate (Tzourio-Mazoyer et al., 2002). For the SMA, dorsal premotor areas (PMds), superior temporal gyri, and cerebellum, functional ROIs were defined from the all rhythms–rest contrast. The SMA activation was predominantly anterior to the anterior commissure, so the SMA ROI should be considered to be largely pre-SMA with some component of SMA proper (Picard & Strick, 1996; Rizzolatti, Luppino, & Matelli, 1996). The ROI analysis was conducted with the software package MarsBar (marsbar.sourceforge.net). For each ROI, a t test was carried out to compare the mean voxel value during trials of each rhythm type, and between each group.

RESULTS

Reproduction Results

After hearing a rhythm three times, participants tapped the rhythm back on one key of a computer keyboard. As shown in Figure 2, participants correctly performed metric simple rhythms significantly more often than the metric complex and nonmetric rhythms (metric simple, 74% correct; metric complex, 53% correct; nonmetric, 58% correct). Metric complex and nonmetric rhythms were not significantly different in percent correct performance, as confirmed by a one-way analysis of variance (ANOVA) with Rhythm type (metric simple, metric complex, nonmetric): $F(2,38) = 20.67, p < .001$, with Bonferroni-corrected post hoc tests: metric simple versus metric complex: $t(1,19) = 5.47, p < .001$; metric simple versus nonmetric: $t(1,19) = 5.24, p < .001$; metric complex versus nonmetric: $t(1,19) = 1.38, p = .19$. The error types varied widely and could be due to the taxing nature of the reproduction task on working memory. Usually just part of the sequence was reproduced incorrectly. For example, in sequences with several short intervals in a row, participants sometimes reproduced the wrong number of short intervals, but the rest of the intervals were correct. Sometimes just the beginning or the end of a sequence was reproduced incorrectly. Other time intervals were transposed. Occasionally participants only reproduced the beginning or the end of a sequence without attempting the rest of the sequence.

Analyses of how accurately participants reproduced the timing of the intervals were conducted on sequences where the overall order of the intervals was correct (see Methods for details). Perfect reproduction would result in ratios of 2:3:4 for the metric conditions, and 1.4:3.5:4.5 for the nonmetric condition. The ratios reproduced by the participants were, in the metric simple condition, 2.08:3.01:3.83 ($SE = .04, .06, .10$); in the metric complex condition, 2.05:2.84:3.34 ($SE = .04, .08, .11$); and in the nonmetric condition, 1.41:2.95:3.51 ($SE = .04, .09, .12$). Overall, in all conditions, participants

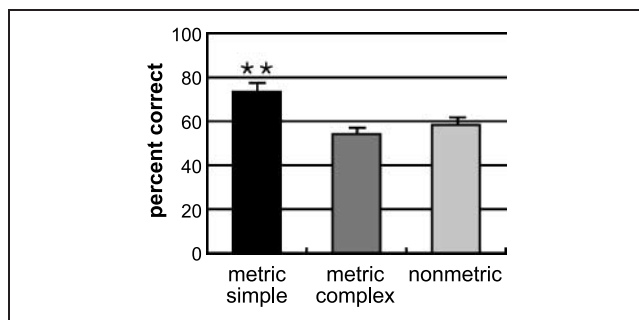


Figure 2. Reproduction results. Graph demonstrating the percentage of sequences performed correctly for each of the rhythm conditions. $**p < .001$.

tended to shorten the longest intervals in a sequence. To determine if the timing accuracy significantly differed between conditions, the absolute value of the deviation of these ratios from perfect performance was tested. Differences between conditions were confirmed by a significant interaction between Rhythm type and Ratio on timing accuracy: $F(4,76) = 4.41, p = .003$. Further analyses revealed that accuracy of the longest ratios (the 4 ratio in the metric conditions and the 4.5 ratio in the nonmetric condition) did significantly differ between conditions. The accuracy of the longest ratio in the metric simple condition was significantly better than in the metric complex and nonmetric conditions, which did not significantly differ: metric simple versus metric complex, $t(1,19) = 6.52, p < .001$; metric simple versus nonmetric, $t(1,19) = 5.00, p < .001$; metric complex versus nonmetric, $t(1,19) = 1.42, p = .17$ (Bonferroni-corrected post hoc tests). In addition, the 3 ratio was significantly more accurate in the metric simple than the nonmetric condition: metric simple versus nonmetric $t(1,19) = 2.88, p = .029$ (Bonferroni-corrected post hoc tests). No other significant differences in ratio accuracy were found. Examination of histograms and rasters of the reproduced ratios for each participant in each condition showed no evidence that participants were “regularizing” the nonmetric rhythms, that is, reproducing them using integer ratios instead of noninteger ratios.

Overall, in the metric simple condition, participants did not truncate the longer ratios as much as they did in the other conditions. Thus, the metric simple condition had not only the greatest number of correctly reproduced sequences, but also more accurate timing of the longest intervals within those sequences.

Discrimination Results

Based on extensive pilot testing, a discrimination task that equalized behavioral performance was created (see Methods), thus removing confounds of difficulty between conditions. In fMRI, difficulty confounds might have led to activation differences between rhythm conditions that were unrelated to beat processing. Behavioral performance across groups and conditions was similar. Mean d' and percent correct scores for each condition were as follows: metric simple, $d' = 2.5$, percent correct = 87%; metric complex, $d' = 2.2$, percent correct = 84%; nonmetric, $d' = 2.4$, percent correct = 84%. For each group, musicians: $d' = 2.6$, percent correct = 87%; nonmusicians: $d' = 2.2$, percent correct = 82%. There were no main effects or interactions between conditions or groups on percent correct or d' scores, as shown by a 3×2 repeated measures ANOVA with Rhythm type as the within-subjects factor and Musical training (musician, nonmusician) as the between-subjects factor: Rhythm type: d' : $F(2,50) = 1.44, p = .25$, percent correct: $F(2,50) = 1.86, p = .17$;

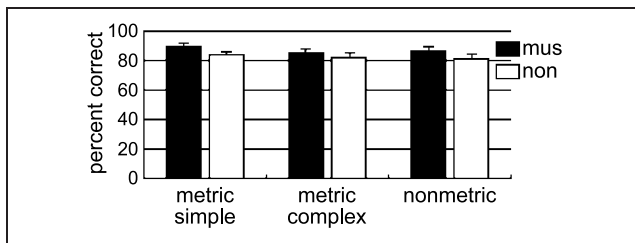


Figure 3. Behavioral data collected during fMRI experiment. The graph demonstrates the percentage of trials discriminated correctly by musicians (mus) and nonmusicians (non) for each of the rhythm conditions. There are no significant differences between groups or conditions.

Musical training: d' : $F(1,25) = 2.41$, $p = .13$, percent correct: $F(1,25) = 1.85$, $p = .19$. Figure 3 shows the percent correct scores for musicians and nonmusicians across the different rhythm conditions. Reaction times were not analyzed because participants were not asked to make a speeded response. Although behavioral performance was equal across conditions, the data indicate this is not due to floor or ceiling effects.

Functional Imaging Results

All analyses presented here were conducted on the first two presentations of the rhythms to exclude activation due to deviant detection, decision making, and response preparation during the third rhythm presentation, and motor activation during the subsequent response. The activity therefore likely reflects listening to and maintaining in memory two identical presentations of a

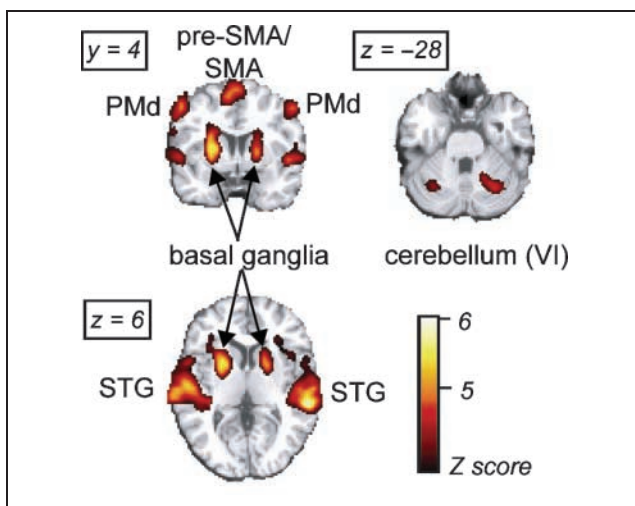


Figure 4. Brain activation during all rhythm conditions–rest. The cortical and cerebellar activations from this contrast defined functional ROIs for further analysis. Z score of 3.3 = $p < .01$, whole-brain corrected (FDR). PMd = dorsal premotor area; SMA = supplementary motor area; STG = superior temporal gyrus; VI = cerebellar crus VI. x , y , and z refer to axes in stereotaxic space.

Table 2. Stereotaxic Locations of Peak Voxels in All Rhythms–Rest Contrast

Brain Region	Z Score	p	x	y	z
L pre-SMA/SMA	5.03	<.001	-9	6	60
R pre-SMA/SMA	4.97	<.001	3	6	66
L putamen	5.67	<.001	-24	6	9
R putamen	5.08	<.001	21	6	6
L premotor	5.3	<.001	-54	0	51
R premotor	5.24	<.001	54	0	45
R cerebellum	4.68	<.001	30	-66	-27
L cerebellum	4.41	<.001	-30	-66	-24
R superior temporal gyrus	6.02	<.001	60	-33	6
L superior temporal gyrus	5.8	<.001	-57	-15	9
L superior temporal pole	4.68	<.001	-57	6	3
R inferior frontal	4.52	<.001	27	30	15

This table shows the brain region, p and Z values, and stereotaxic coordinates (in millimeters) of peak voxels in MNI space. Thresholded at $p < .001$, whole-brain corrected (FDR). R = right; L = left; SMA = supplementary motor area.

rhythm. Figure 4 shows the results of the random effects analysis of all rhythms–rest, collapsed across group and condition. Activation was observed in the pre-SMA/SMA, PMd, basal ganglia, cerebellum, superior temporal gyrus (STG), and ventrolateral prefrontal cortex/insula, all bilaterally (see Table 2 for Z scores of local maxima).

For these experiments, we created one set of sequences (the metric simple condition) that were predicted to induce a beat through the presence of regular perceptual accents (Essens, 1995; Essens & Povel, 1985; Povel & Essens, 1985). These sequences were reproduced more accurately than sequences composed of identical intervals, but ordered in such a way as to not induce a beat. Because the sequences were so closely matched, we provisionally concluded that the differences in performance were due to the predicted differences in beat induction. As the behavioral data showed

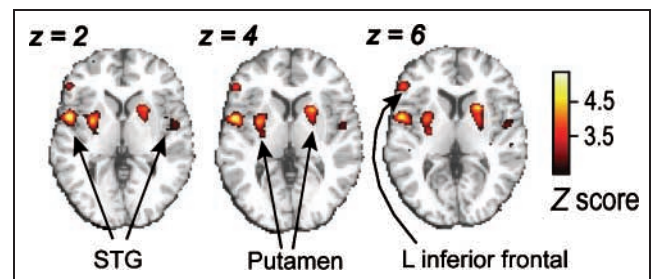


Figure 5. Brain regions more active for metric simple than metric complex or nonmetric rhythms. Z score of 3.43 = $p < .05$, whole-brain corrected (FDR).

Table 3. Stereotaxic Locations of Peak Voxels in Metric Simple–Metric Complex and Nonmetric Contrast

Brain Region	Z Score	p	x	y	z
L superior temporal gyrus	4.60	.039	-51	3	3
	3.87	.040	-51	-9	-3
R superior temporal gyrus/insula	3.78	.045	42	-36	18
	3.92	.040	45	6	-6
R insula	3.87	.040	30	-21	12
	4.47	.039	-27	0	-9
L putamen	4.19	.039	-27	0	0
	3.77	.045	-27	-12	6
	4.31	.039	24	0	-9
R putamen	4.31	.039	24	12	6
	4.24	.039	24	-3	9
	4.03	.040	-51	33	6
L inferior frontal gyrus	4.01	.040	-12	69	18
L superior frontal gyrus	3.88	.040	21	9	-15

This table shows the brain region, *p* and *Z* values, and stereotaxic coordinates (in mm) of peak voxels in MNI space. Thresholded at *p* < .05, whole-brain corrected (FDR). R = Right, L = Left.

that the metric simple condition was performed significantly better than the other two conditions, we compared activation in the metric simple condition to that in the metric complex and nonmetric conditions. We suggest that this comparison is between beat-inducing and non-beat-inducing rhythms. Increased activation for metric simple rhythms was observed bilaterally in the putamen and superior temporal gyri, as well as left inferior frontal gyrus, shown in Figure 5. See Table 3 for *Z* scores of local maxima.

The ROI analysis (shown in Figure 6) found that the metric simple condition compared to the metric com-

Table 4. *t* Values for Metric Simple–Metric Complex, and Metric Simple–Nonmetric Contrasts, for Each ROI

ROI	<i>t</i> Value	
	Metric Simple–Metric Complex	Metric Simple–Nonmetric
L superior temporal gyrus	4.13***	2.08*
R superior temporal gyrus	3.91***	1.72*
Pre-SMA/SMA	2.36*	2.12*
L caudate	1.83*	1.1 (<i>ns</i>)
R caudate	2.06*	1.19*
L pallidum	2.66**	1.74**
R pallidum	3.45***	2.78***
L putamen	4.05***	3.4***
R putamen	3.65***	2.97***
R premotor cortex	1.25 (<i>ns</i>)	0.46 (<i>ns</i>)
L premotor cortex	1.49 (<i>ns</i>)	0.58 (<i>ns</i>)
R cerebellum	0.48 (<i>ns</i>)	-0.22 (<i>ns</i>)
L cerebellum	0.71 (<i>ns</i>)	-0.22 (<i>ns</i>)

ns = not significant; R = right; L = left; SMA = supplementary motor area.

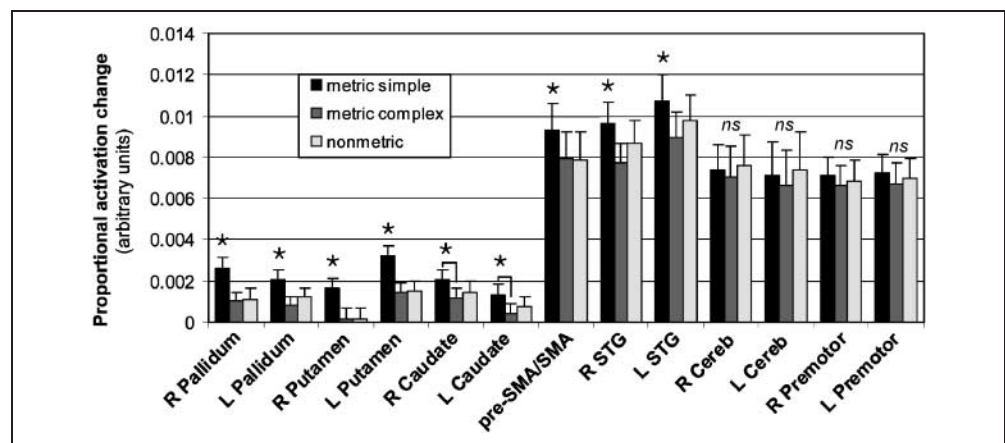
**p* < .05.

***p* < .01.

****p* < .001.

plex condition significantly activated the pallidum, putamen, caudate, pre-SMA/SMA, and STG bilaterally. The same pattern was observed when the metric simple condition was compared to the nonmetric condition, although the caudate no longer reached significance (*t* values for both contrasts shown in Table 4). No significant differences in activation were seen between the metric complex and nonmetric rhythms. In addition,

Figure 6. Graph of activation during each rhythm condition—rest in each ROI. Metric complex and nonmetric activations in all areas were not significantly different from each other. **p* < .05 for both metric simple versus metric complex and metric simple versus nonmetric (except in the caudate, where only the metric simple versus metric complex difference reaches significance). R = right; L = left; SMA = supplementary motor area.



none of the areas were activated significantly more by the metric complex or nonmetric rhythms than the metric simple rhythms. This finding confirms that removal of difficulty confounds was successful: If the metric complex and nonmetric conditions were more difficult or required greater attentional or working memory demands, increased, not decreased, activity would be expected in the dorsolateral prefrontal and anterior cingulate cortices (Duncan & Owen, 2000). To verify this had not occurred, a whole-brain, random effects analysis was conducted, contrasting metric complex and nonmetric rhythms to metric simple rhythms (i.e., all non-beat-inducing–beat-inducing rhythms). Even at a much reduced statistical threshold ($p < .5$, FDR corrected), no significant activation was observed.

The ROI analysis found that musicians showed several areas of greater activation compared to nonmusicians (see Figure 7). Musicians activated the pre-SMA/SMA, bilateral cerebellum, and right PMd significantly more than did nonmusicians in all rhythm conditions compared to rest (see Table 5 for t values). Further analysis showed no significant interactions between group and rhythm type. In addition, a correlation analysis was performed to determine if a relationship between activation in any of the ROIs correlated with behavioral discrimination performance. No significant results were found, probably due to the low variability in behavioral performance.

DISCUSSION

Previous work indicates that rhythms encoded in relationship to a beat are reproduced more accurately than rhythms that are not (Patel et al., 2005; Essens & Povel, 1985). In this experiment, we compared the performance of metric simple rhythms (which had regular perceptual accents) to that of metric complex rhythms (which did not). If regular perceptual accents induce a

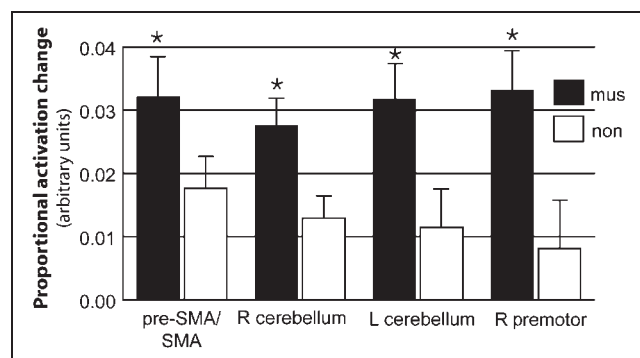


Figure 7. Activation during all rhythms–rest for musicians and nonmusicians. Graph of activation collapsed across conditions, for pre-SMA/SMA, right and left cerebellum, and right premotor area. $*p < .05$. mus = musician; non = nonmusicians.

Table 5. t Values for Activation Differences between Musicians and Nonmusicians in Selected ROIs

ROI	t Value
Pre-SMA/SMA	1.99*
R premotor cortex	2.99**
L premotor cortex	0.75 (<i>ns</i>)
R cerebellum	2.77**
L cerebellum	2.91**
L superior temporal gyrus	0.30 (<i>ns</i>)
R superior temporal gyrus	1.1 (<i>ns</i>)
L caudate	0.32 (<i>ns</i>)
R caudate	0.98 (<i>ns</i>)
L pallidum	1.26 (<i>ns</i>)
R pallidum	0.47 (<i>ns</i>)
L putamen	0.76 (<i>ns</i>)
R putamen	−0.21 (<i>ns</i>)

$ns = p > .05$. R = right; L = left; SMA = supplementary motor area.

* $p < .05$.

** $p < .01$.

beat (as predicted by the Povel and Essens model [Essens, 1995; Essens & Povel, 1985]), then metric simple rhythms should be more accurately reproduced. This is indeed what we found. Significantly more metric simple rhythms were reproduced accurately. In addition, shortening of the longest intervals was observed during reproduction in all rhythm types, but this shortening was significantly less in the metric simple condition. Given that the metric simple and metric complex conditions were identical apart from whether the arrangement of the intervals produced regular or irregular perceptual accents, we feel that the most plausible explanation for these effects is that, as predicted, a regular beat was induced in the metric simple condition.

The reproduction results suggest that integer ratios and regular perceptual accents are required for beat induction. However, as we did not succeed in creating a condition with regular perceptual accents and noninteger ratios, it is possible that regular perceptual accents alone could induce a beat. This remains an interesting avenue for future research. In contrast to previous research (Sakai et al., 1999), we find that integer ratios alone appear to be insufficient for beat induction, as the number of correctly reproduced metric complex (integer ratios) and nonmetric (noninteger ratios) rhythms was not significantly different in this experiment. The difference between previous work and the current experiments likely arises because the previous study did not assess accent structure. Therefore, the integer ratios

condition in that study contained sequences with varying levels of regularity in the accent structure; the sequences with greater accent regularity may be responsible for the better performance. In the current study, accent structure was manipulated to be regular or irregular, allowing us to assess the role of accents separately from that of integer ratios. When accent structure is accounted for, then the presence of integer ratios is not enough to improve behavioral rhythm performance.

Another interesting phenomenon reported in temporal reproduction studies is that some participants “regularize” noninteger ratio sequences during performance, such that the noninteger ratios are distorted into integer ratios. We find no evidence of regularization in our study, although this is likely due to the stimuli we used. In most previous studies that find regularization (Collier & Wright, 1995; Essens, 1986; Essens & Povel, 1985) only one ratio (e.g., 1:2.5 or 1:3.3) is present in any given sequence or block of stimuli. Therefore, the perception of the unit level (1) and the level that is the noninteger multiple of that unit (2.5 or 3.3), and the resulting relationship between the levels is quite easy to discern. The perception of this relationship may then allow participants to stretch or shrink the noninteger ratio in order to make it into an integer multiple of the unit level. This regularization presumably decreases the timing difficulty of the task. Other work (Sakai et al., 1999) has used more than one noninteger ratio (1:2.5:3.5), but in this case, only three (of 6) participants showed regularization, and only for some sequences. Another contributing factor to whether regularization occurs may be the use of block presentations of the noninteger ratio sequences (Sakai et al., 1999) or high numbers of sequence repetitions (Collier & Wright, 1995; Essens, 1986; Essens & Povel, 1985), giving participants a greater number of exposures to perceive the relationships between the intervals. Again, this perception of the relationship may lead subjects to regularize in order to simplify the task. When many ratios are present, such as 1:1.4:3.5:4.5 in the current study, it is presumably less clear what the relationships between the unit level (1) and the other levels (1.4, 3.5, and 4.5) are. The relationships are further clouded by the presence of other ratios between intervals in the sequence (1.4:3.5, 1.4:4.5, and 3.5:4.5). These sequences may be too complex for participants to determine *how* to go about regularizing them, especially in the current study, where there are only a small number of presentations of each rhythm and no blocked presentation of the rhythm types. Finally, other work has used noninteger ratios rhythms and does not report regularization, although perhaps this specific issue was not assessed in detail (Lewis et al., 2004; Ullén, Forssberg, & Ehrsson, 2003). It should be noted that our account for lack of regularization, is speculative and requires evidence from further investigations in which the number of noninteger ratios present in a sequence, or the number of sequence

presentations, is systematically manipulated and the effects on reproduction performance are assessed.

Moving on to the fMRI data collected in the second experiment, we find that a bilateral network of motor areas is activated when rhythms are perceived, even when no movement is made. When listening to all the rhythms compared to rest, bilateral activation was observed in the pre-SMA/SMA, PMd, basal ganglia, cerebellum, superior temporal gyri, and ventrolateral prefrontal cortex/anterior insula. The lack of activation in primary motor cortex suggests that participants complied with instructions not to move any part of their body during presentation of the rhythms, and thus the activation observed is likely due only to perception of rhythm. These findings are consistent with other studies (Lewis et al., 2004; Schubotz, Friederici, & von Cramon, 2000; Penhune et al., 1998) confirming that a bilateral network of motor areas mediate perception of rhythm in addition to rhythm production. These data may also suggest that rhythm perception may lie more within the “automatic” timing system proposed by Lewis and Miall (2003), as this system is composed mainly of motor areas and is most involved in timing of subsecond intervals. However, the automatic system is thought to operate mainly for predictable or overlearned stimuli, and without “attentional modulation.” The stimuli here were not learned and in many cases were unpredictable. It also seems unlikely that perception of such complicated rhythms would occur without attention, therefore it may be that the automatic system is responsible for perception of the individual intervals that compose the sequences, but does not mediate cohesive perception of the rhythm as a whole.

The fMRI data provide additional confirmation of the importance of regular perceptual accents in rhythm perception. Listening to metric simple rhythms significantly increased activity bilaterally in the basal ganglia, anterior superior temporal gyri, left inferior frontal gyrus, and the pre-SMA/SMA (although the latter activation only reached significance in the ROI analysis), compared to the metric complex and nonmetric conditions. A role for the basal ganglia and SMAs in beat induction is consistent with their involvement in motor prediction (the spontaneous response to hearing a beat is often to move at the time when the next beat is predicted). The anatomy supports their mutual contribution, as the basal ganglia and pre-SMA/SMA are richly connected through striato–thalamo–cortical loops (Inase & Tanji, 1994; Alexander, DeLong, & Crutcher, 1992) and are involved in timing (Macar, Anton, Bonnet, & Vidal, 2004; Ferrandez et al., 2003), including timing of future movements (Sardo, Ravel, Legallet, & Apicella, 2000; Rao et al., 1997). Patients with lesions in SMAs are impaired at reproducing temporal sequences from memory (Halsband et al., 1993). However, further research is needed to clarify whether increased activity in basal ganglia and pre-SMA/SMA underlies the spon-

taneous movement that often spontaneously occurs to the beat.

The bilateral anterior superior temporal gyri were also more active during metric simple rhythms compared with metric complex and nonmetric rhythms. The peak of this activation is ~ 3 cm anterior to the peak of the auditory cortex activation observed in the all rhythms minus rest contrast, placing it in the anterior secondary auditory cortex. Activity here has been observed for auditory imagery (Zatorre, Halpern, Perry, Meyer, & Evans, 1996). Accordingly, our participants may have been able to form a better auditory image of the beat-based rhythms, consistent with the better performance of these rhythms in the reproduction experiment. Alternatively, the anterior auditory areas may be important for perceiving the beat in the first place. This is consistent with neuropsychological work (Liegeois-Chauvel, Peretz, Babai, Laguitton, & Chauvel, 1998) that shows that the anterior STG is necessary for normal musical meter perception (determining if beat groupings are in a “waltz” or “march” meter). Beat perception itself was not directly tested in the patients, but musical meter perception depends fundamentally on perceiving the underlying beat (London, 2001). Intriguingly, resection in either hemisphere produced impairment, consistent with the bilateral nature of the activation in the current study. A visual rhythm condition in future experiments may help determine whether the auditory cortex makes a supramodal contribution to rhythm processing, or if its role is restricted to the auditory modality.

Difficulty can be a major confound in fMRI experiments. Increased difficulty in a wide range of paradigms cause greater activation in the dorsolateral prefrontal and anterior cingulate cortices, suggesting a specific network for effortful processing across domains (Duncan & Owen, 2000). To avoid difficulty confounds in the fMRI experiment, we used a task that had similar levels of performance across conditions. Reassuringly, although the metric complex and nonmetric conditions were the most difficult in the reproduction task, they produced less, not more activity in the fMRI study. In addition, the timing requirements of the individual intervals across the conditions were very well matched. Taken together, these findings indicate that it is unlikely that the increased activation in the metric simple condition can be explained by difficulty. Nevertheless, it was initially surprising that no brain areas were significantly more active in the metric complex or nonmetric conditions than in the metric simple condition, given that the reproduction study indicates the metric complex and nonmetric conditions are more difficult. Working memory studies, however, indicate that prefrontal areas can show increased activity when encoding easier stimuli compared with harder stimuli if the easier stimuli contain structure (Bor, Cumming, Scott, & Owen, 2004; Bor, Duncan, Wiseman, & Owen, 2003). The prefrontal area activated in those studies is very near the left inferior frontal gyrus activation found in this study. This

suggests that the beat in the metric simple condition may be providing a regular structure (sometimes called a “temporal grid”; Povel, 1984) that aids working memory performance for the rhythms.

We also found that activation to the metric complex and nonmetric conditions did not significantly differ. Thus, the fMRI results are in contrast to a previous study (Sakai et al., 1999), which reported different patterns of activation for sequences with integer- and noninteger ratio intervals (although the two conditions were not statistically compared, so it is unclear if the differences are reliable). However, as mentioned before, the integer ratio sequences in that study likely contained varying levels of regularity in the accent structure, as the authors did not consider perceptual accents in their stimuli; thus, any differences may not be due to the presence of integer ratios versus noninteger ratios per se.

These data may illuminate a controversy about the existence of a “beat-based” (or entrainment) timer (Pashler, 2001). A beat-based timer is hypothesized to encode intervals in reference to an underlying isochronous beat (using a beat to measure if an interval is one beat long, two beats long, etc.). Several studies have examined whether a beat-based timer exists, and if so, whether it can improve timing. Generally, these studies test how accurately humans time a single time interval, under conditions that are or are not conducive to using beat-based timing. The results are conflicting (McAuley & Jones, 2003; McAuley & Kidd, 1998; Vos, van Assen, & Franek, 1997; Schulze, 1978; cf. Pashler, 2001; Ivry & Hazeltine, 1995; Keele, Nicoletti, Ivry, & Pokorny, 1989) perhaps because timing of a single interval is most frequently tested. The reproduction data here, acquired on a more complicated temporal rhythm task, show a substantial performance benefit for rhythms that are designed to induce a beat. These data suggest that a beat-based mechanism does exist, and improves timing performance when more difficult temporal tasks are tested. In addition, a specific network of areas was more active during perception of beat-inducing rhythms compared with other rhythms, even when no significant behavioral performance differences were observed. This suggests that the beat-based system can be active even when no behavioral performance benefit is observed. Thus, the fact that some previous work does not find a behavioral beat-based timing benefit does not necessarily mean that such a mechanism was not active or used.

Interestingly, the observed cerebellum and premotor cortex activations were not significantly different across the three rhythm types. Many other studies show involvement of these areas in temporal processing (Penhune & Doyon, 2002; Ramnani & Passingham, 2001), but they appear not to have a specific role in beat-based timing. Musically trained participants recruit these areas more than untrained participants do, although behavioral discrimination performance is the same between these

groups. Premotor areas have been implicated in rehearsal during working memory tasks (Smith & Jonides, 1999) and general working memory operations that are not task or material specific (Cabeza & Nyberg, 2000); accordingly, musicians may have used rehearsal strategies to a greater degree than did nonmusicians. Alternatively, the cerebellum and/or premotor areas may be responsible for more basic timing processes that are required to encode the time intervals in the first place. The basal ganglia and pre-SMA/SMA (perhaps also with the anterior STG) may then be responsible for detecting or relating that information to an isochronous beat interval. If this relationship can be established, a more stable and accurate representation of the sequence can occur, which would result in improved reproduction performance. The fact that musicians do not activate these areas more than the nonmusicians do supports the theory that forming a temporal representation in relation to a beat is a universal process; nearly all humans can perceive a beat in music, without special training or practice, but merely through exposure to beat-based patterns (Drake, 1998).

One theory on the roles of the basal ganglia and cerebellum suggests that the latter subserves timing in the milliseconds to seconds range, and the former subserves timing in the seconds to minutes range (Ivry, 1996). Although our experiment did not directly test this theory, the results suggest that both areas are involved in timing in the milliseconds to seconds range, but the basal ganglia are more involved when the structure of a rhythm allows beat-based timing to be used. This suggests that the types of deficits found on timing tasks when testing neuropsychological patients will be dependent on the type of timing that can be used to accomplish the task. As the majority of neuropsychological studies test timing of isochronous intervals, which do not reliably show beat-based timing advantages, future studies using complex sequences will be important to clarify the roles of the basal ganglia and cerebellum in timing. For example, the current results suggest that patients with basal ganglia dysfunction would be impaired at using beat-based timing. If so, deficits may be reliably observed only for performance of more complicated rhythmic stimuli, not performance of isochronous intervals.

In conclusion, regular accent structure appears to be critical for hearing a beat in rhythm. When regular perceptual accents are present, reproduction performance is improved. Although several brain areas are activated during rhythm perception, the basal ganglia, pre-SMA/SMA, and anterior superior temporal gyri show increased activity specifically to beat-based rhythms, in both musicians and nonmusicians.

Reprint requests should be sent to Jessica A. Grahn, MRC Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge CB2 2EF, UK, or via e-mail: Jessica.grahn@mrc-cbu.cam.ac.uk.

REFERENCES

- Alexander, G. E., DeLong, M. R., & Crutcher, M. D. (1992). Do cortical and basal ganglionic motor areas use "motor programs" to control movement? *Behavioral and Brain Sciences*, *15*, 656–665.
- Artieda, J., Pastor, M. A., Lacruz, F., & Obeso, J. A. (1992). Temporal discrimination is abnormal in Parkinson's disease. *Brain*, *115*, 199–210.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B*, *57*, 289–300.
- Bor, D., Cumming, N., Scott, C. E. L., & Owen, A. M. (2004). Prefrontal cortical involvement in verbal encoding strategies. *European Journal of Neuroscience*, *19*, 3365–3370.
- Bor, D., Duncan, J., Wiseman, R. J., & Owen, A. M. (2003). Encoding strategies dissociate prefrontal activity from working memory demand. *Neuron*, *37*, 361–367.
- Brochard, R., Abecasis, D., Potter, D., Ragot, R., & Drake, C. (2003). The "ticktock" of our internal clock: Direct brain evidence of subjective accents in isochronous sequences. *Psychological Science*, *14*, 362–366.
- Brotchie, P., Ianssek, R., & Horne, M. K. (1991). Motor function of the monkey globus pallidus. 2. Cognitive aspects of movement and phasic neuronal activity. *Brain*, *114*, 1685–1702.
- Cabeza, R. C., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, *12*, 1–47.
- Collier, G. L., & Wright, C. E. (1995). Temporal rescaling of simple and complex ratios in rhythmic tapping. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 602–627.
- Coull, J. T., Vidal, F., Nazarian, B., & Macar, F. (2004). Functional anatomy of the attentional modulation of time estimation. *Science*, *303*, 1506–1508.
- Cunnington, R., Windischberger, C., Deecke, L., & Moser, E. (2002). The preparation and execution of self-initiated and externally-triggered movement: A study of event-related fMRI. *Neuroimage*, *15*, 373–385.
- Cusack, R., & Papadakis, N. (2002). New robust 3-D phase unwrapping algorithms: Application to magnetic field mapping and undistorting echoplanar images. *Neuroimage*, *16*, 754–764.
- Dhamala, M., Pagnoni, G., Wiesenfeld, K., Zink, C. F., Martin, M., & Berns, G. S. (2003). Neural correlates of the complexity of rhythmic finger tapping. *Neuroimage*, *20*, 918–926.
- Drake, C. (1998). Psychological processes involved in the temporal organization of complex auditory sequences: Universal and acquired processes. *Music Perception*, *16*, 11–26.
- Drake, C., Jones, M. R., & Baruch, C. (2000). The development of rhythmic attending in auditory sequences: Attunement, referent period, focal attending. *Cognition*, *77*, 251–288.
- Drake, C., Penel, A., & Bigand, E. (2000). Tapping in time with mechanically and expressively performed music. *Music Perception*, *18*, 1–24.
- Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences*, *23*, 475–483.
- Essens, P. J. (1986). Hierarchical organization of temporal patterns. *Perception & Psychophysics*, *40*, 69–73.
- Essens, P. J. (1995). Structuring temporal sequences: Comparison of models and factors of complexity. *Perception & Psychophysics*, *57*, 519–532.
- Essens, P. J., & Povel, D. J. (1985). Metrical and nonmetrical

- representations of temporal patterns. *Perception & Psychophysics*, *37*, 1–7.
- Ferrandez, A. M., Hugueville, L., Lehericy, S., Poline, J. B., Marsault, C., & Pouthas, V. (2003). Basal ganglia and supplementary motor area subattend duration perception: An fMRI study. *Neuroimage*, *19*, 1532–1544.
- Freeman, J. S., Cody, F. W., & Schady, W. (1993). The influence of external timing cues upon the rhythm of voluntary movements in Parkinson's disease. *Journal of Neurology, Neurosurgery, and Psychiatry*, *56*, 1078–1084.
- Genovese, C. R., Lazar, N. A., & Nichols, T. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage*, *15*, 870–878.
- Grahn, J. A., & Brett, M. (2005). *Rhythm processing in patients with basal ganglia dysfunction*. Paper presented at the Neurosciences and Music II: From perception to performance, Leipzig, Germany. New York: New York Academy of Sciences, Vol. 1060.
- Grahn, J. A., & Brett, M. (2006). Rhythm reproduction and discrimination: The role of integer ratios and perceptual accents. *Manuscript submitted for publication*.
- Grondin, S. (1993). Duration discrimination of empty and filled intervals marked by auditory and visual signals. *Perception & Psychophysics*, *54*, 383–394.
- Halsband, U., Ito, N., Tanji, J., & Freund, H. J. (1993). The role of premotor cortex and the supplementary motor area in the temporal control of movement in man. *Brain*, *116*, 243–266.
- Inase, M., & Tanji, J. (1994). Projections from the globus pallidus to the thalamic areas projecting to the dorsal area 6 of the macaque monkey: A multiple tracing study. *Neuroscience Letters*, *180*, 135–137.
- Ivry, R. B. (1996). The representation of temporal information in perception and motor control. *Current Opinion in Neurobiology*, *6*, 851–857.
- Ivry, R. B., & Hazeltine, E. (1995). Perception and production of temporal intervals across a range of durations: Evidence for a common timing mechanism. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 1–12.
- Jones, M. R., & Boltz, M. (1989). Dynamic attending and responses to time. *Psychological Review*, *96*, 459–491.
- Jones, M. R., & Pfordresher, P. Q. (1997). Tracking musical patterns using joint accent structure. *Canadian Journal of Experimental Psychology*, *51*, 271–290.
- Keele, S. W., Nicoletti, R., Ivry, R., & Pokorny, R. (1989). Mechanisms of perceptual timing: Beat-based or interval-based judgments? *Psychological Research*, *50*, 251–256.
- Lewis, P. A., & Miall, R. C. (2003). Distinct systems for automatic and cognitively controlled time measurement: Evidence from neuroimaging. *Current Opinion in Neurobiology*, *13*, 250–255.
- Lewis, P. A., Wing, A. M., Pope, P. A., Praamstra, P., & Miall, R. C. (2004). Brain activity correlates differentially with increasing temporal complexity of rhythms during initialisation, synchronisation, and continuation phases of paced finger tapping. *Neuropsychologia*, *42*, 1301–1312.
- Liegeois-Chauvel, C., Peretz, I., Babai, M., Laguitton, V., & Chauvel, P. (1998). Contribution of different cortical areas in the temporal lobes to music processing. *Brain*, *121*, 1853–1867.
- London, J. (2001, 13 July 2006). Metre. *Grove music online*. Retrieved July 13, 2006, from www.grovemusic.com.
- Macar, F., Anton, J.-L., Bonnet, M., & Vidal, F. (2004). Timing functions of the supplementary motor area: An event-related fMRI study. *Cognitive Brain Research*, *21*, 206–215.
- Mangels, J. A., Ivry, R. B., & Shimizu, N. (1998). Dissociable contributions of the prefrontal and neocerebellar cortex to time perception. *Cognitive Brain Research*, *7*, 15–39.
- McAuley, J. D., & Jones, M. R. (2003). Modeling effects of rhythmic context on perceived duration: A comparison of interval and entrainment approaches to short-interval timing. *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 1102–1125.
- McAuley, J. D., & Kidd, G. R. (1998). Effect of deviations from temporal expectations on tempo discrimination of isochronous tone sequences. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 1786–1800.
- Molinari, M., Leggio, M. G., De Martin, M., Cerasa, A., & Thaut, M. (2003). Neurobiology of rhythmic motor entrainment. *Annals of the New York Academy of Sciences*, *999*, 313–321.
- Nenadic, I., Gaser, C., Volz, H.-P., Rammsayer, T., Hager, F., & Sauer, H. (2003). Processing of temporal information and the basal ganglia: New evidence from fMRI. *Experimental Brain Research*, *148*, 238–246.
- Palmer, A. R., Bullock, D. C., & Chambers, J. D. (1998). A high-output, high-quality sound system for use in function magnetic resonance imaging. *Neuroimage*, *7*, S539.
- Parncutt, R. (1994). A perceptual model of pulse salience and metrical accent in musical rhythms. *Music Perception*, *11*, 409–464.
- Pashler, H. (2001). Perception and production of brief durations: Beat-based versus interval-based timing. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 485–493.
- Pastor, M. A., Day, B. L., Macaluso, E., Friston, K. J., & Frackowiak, R. S. J. (2004). The functional neuroanatomy of temporal discrimination. *Journal of Neuroscience*, *24*, 2585–2591.
- Patel, A. D., Iversen, J. R., Chen, Y., & Repp, B. H. (2005). The influence of metricality and modality on synchronization with a beat. *Experimental Brain Research*, *163*, 226–238.
- Penhune, V. B., & Doyon, J. (2002). Dynamic cortical and subcortical networks in learning and delayed recall of timed motor sequences. *Journal of Neuroscience*, *22*, 1397–1406.
- Penhune, V. B., Zatorre, R. J., & Evans, A. C. (1998). Cerebellar contributions to motor timing: A PET study of auditory and visual rhythm reproduction. *Journal of Cognitive Neuroscience*, *10*, 752–765.
- Penny, W., & Holmes, A. P. (2003). Random effects analysis. In R. S. J. Frackowiack, K. J. Friston, C. D. Frith, R. Dolan, C. J. Price, J. Ashburner, W. Penny, & S. Zeki (Eds.), *Human brain function II* (2nd ed.). San Diego, CA: Elsevier.
- Phillips-Silver, J., & Trainor, L. J. (2005). Feeling the beat: Movement influences infant rhythm perception. *Science*, *308*, 1430.
- Picard, N., & Strick, P. (1996). Motor areas of the medial wall: A review of their location and functional activation. *Cerebral Cortex*, *6*, 342–353.
- Povel, D.-J. (1984). A theoretical framework for rhythm perception. *Psychological Research*, *45*, 315–337.
- Povel, D. J., & Essens, P. J. (1985). Perception of temporal patterns. *Music Perception*, *2*, 411–440.
- Povel, D.-J., & Okkerman, H. (1981). Accents in equitone sequences. *Perception & Psychophysics*, *30*, 565–572.
- Ramnani, N., & Passingham, R. E. (2001). Changes in the human brain during rhythm learning. *Journal of Cognitive Neuroscience*, *13*, 952–966.
- Rao, S. M., Harrington, D. L., Haaland, K. Y., Bobholz, J. A., Cox, R. W., & Binder, J. R. (1997). Distributed neural systems underlying the timing of movements. *Journal of Neuroscience*, *17*, 5528–5535.
- Rao, S. M., Mayer, A. R., & Harrington, D. L. (2001). The

- evolution of brain activation during temporal processing. *Nature Neuroscience*, *4*, 317–323.
- Rizzolatti, G., Luppino, G., & Matelli, M. (1996). The classic supplementary motor area is formed by two independent areas. *Advances in Neurology*, *70*, 45–56.
- Sakai, K., Hikosaka, O., Miyauchi, S., Takino, R., Tamada, T., Iwata, N. K., et al. (1999). Neural representation of a rhythm depends on its interval ratio. *Journal of Neuroscience*, *19*, 10074–10081.
- Sardo, P., Ravel, S., Legallet, E., & Apicella, P. (2000). Influence of the predicted time of stimuli eliciting movements on responses of tonically active neurons in the monkey striatum. *European Journal of Neuroscience*, *12*, 1801–1816.
- Schubotz, R. I., Friederici, A. D., & von Cramon, D. Y. (2000). Time perception and motor timing: A common cortical and subcortical basis revealed by fMRI. *Neuroimage*, *11*, 1–12.
- Schubotz, R. I., & von Cramon, D. Y. (2001). Interval and ordinal properties of sequences are associated with distinct premotor areas. *Cerebral Cortex*, *11*, 210–222.
- Schulze, H.-H. (1978). The detectability of local and global displacements in regular rhythmic patterns. *Psychological Research*, *40*, 172–181.
- Shima, K., & Tanji, J. (2000). Neuronal activity in the supplementary and presupplementary motor area for temporal organization of multiple movements. *Journal of Neurophysiology*, *84*, 2148–2160.
- Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, *283*, 1657–1661.
- Smith, S. M. (2002). Robust automated brain extraction. *Human Brain Mapping*, *17*, 143–155.
- Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., et al. (2002). Automated anatomical labelling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single subject brain. *Neuroimage*, *15*, 273–289.
- Ullén, F., Forssberg, H., & Ehrsson, H. H. (2003). Neural networks for the coordination of the hands in time. *Journal of Neurophysiology*, *89*, 1126–1135.
- Vos, P. G., van Assen, M., & Franek, M. (1997). Perceived tempo change is dependent on base tempo and direction of change: Evidence for a generalized version of Schulze's (1978) internal beat model. *Psychological Research*, *59*, 240–247.
- Warren, R. M. (1993). Perception of acoustic sequences: Global integration versus temporal resolution. In S. McAdams & E. Bigand (Eds.), *Thinking in sound: The cognitive psychology of human audition* (pp. 37–68). Oxford: Oxford University Press.
- Zatorre, R. J., Halpern, A. R., Perry, D. W., Meyer, E., & Evans, A. C. (1996). Hearing in the mind's ear: A PET investigation of musical imagery and perception. *Journal of Cognitive Neuroscience*, *8*, 29–46.