

The Role of the Basal Ganglia in Beat Perception

Neuroimaging and Neuropsychological Investigations

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Perception of musical rhythms is culturally universal. Despite this special status, relatively little is known about the neurobiology of rhythm perception, particularly with respect to beat processing. Findings are presented here from a series of studies that have specifically examined the neural basis of beat perception, using functional magnetic resonance imaging (fMRI) and studying patients with Parkinson's disease. fMRI data indicate that novel beat-based sequences robustly activate the basal ganglia when compared to irregular, nonbeat sequences. Furthermore, although most healthy participants find it much easier to discriminate changes in beat-based sequences compared to irregular sequences, Parkinson's disease patients fail to show the same degree of benefit. Taken together, these data suggest that the basal ganglia are performing a crucial function in beat processing. The results of an additional fMRI study indicate that the role of the basal ganglia is strongly linked to internal generation of the beat. Basal ganglia activity is greater when participants listen to rhythms in which internal generation of the beat is required, as opposed to rhythms with strongly externally cued beats. Functional connectivity between part of the basal ganglia (the putamen) and cortical motor areas (premotor and supplementary motor areas) is also higher during perception of beat rhythms compared to nonbeat rhythms. Increased connectivity between cortical motor and auditory areas is found in those with musical training. The findings from these converging methods strongly implicate the basal ganglia in processing a regular beat, particularly when internal generation of the beat is required.

Key words: rhythm; beat perception; basal ganglia; fMRI; timing; effective connectivity; music; motor

The appreciation of musical rhythms is a universal feature of human culture. One of the most distinctive features of musical rhythm is the presence of an underlying regular beat: a perceived pulse that marks equally spaced points in time.^{1,2} The neural mechanisms of beat perception have only recently begun to be systematically investigated. In this chapter, the results of functional magnetic resonance imaging (fMRI) investigations and studies with Parkinson's disease (PD) patients are presented that provide converging evidence for the role of

the basal ganglia in beat perception. New fMRI data will also be presented, indicating that the basal ganglia are particularly activated during internal generation (as opposed to simple external perception) of the beat.

Background

Given its potential uniqueness to humans, what function does beat perception serve? Much of the temporal processing required in daily life does not require any underlying perception of a beat. However, perception of the beat enables temporal intervals to be encoded as multiples or subdivisions of the beat, rather than as unrelated intervals. As a result,

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rhythm reproduction and discrimination is improved.³⁻⁶ This mechanism may be analogous to “chunking,” a way of reducing complex patterns to simpler components.^{7,8} Although beat perception can feel automatic, and occurs without musical training even in young children, little is known about its neural mechanisms.

When we hear a musical rhythm we often move to the beat,⁹ suggesting that motor networks may be important for beat processing. Motor areas of the brain are active in many neuroimaging studies of rhythm and timing (for example, see Chen *et al.*^{9a} in this volume), in particular the premotor and supplementary motor areas (SMAs), cerebellum, and basal ganglia.¹⁰⁻¹⁹ Moreover, activity occurs in these motor areas not just during production, but during *perception* of rhythm.^{13,20-22} However, no consensus exists on the nonmotor roles these areas play.

Studies that have examined temporal processing in patients with damage to certain brain areas highlight a similar network of cortical and subcortical motor areas to that revealed by neuroimaging.²³⁻³¹ Thus, evidence from multiple methodologies highlights the connection between musical rhythm and movement, and the importance of motor areas in music processing, in particular for rhythm (for a review, see Zatorre *et al.*³²).

Interpretation of neuropsychological patient studies can sometimes be difficult because of the choice of control tasks. For example, frequency discrimination is often used as a control condition for duration discrimination,^{24,30} even though frequency discrimination can occur within a few hundred milliseconds of stimulus onset, whereas duration discrimination requires sustained attention to the entire duration. The lack of parity between frequency and duration discrimination processing requirements is supported by the fact that, in healthy volunteers, dual-task conditions do not impair frequency discrimination, but do impair duration discrimination.³³ Thus, appropriate control tasks are critical when examining temporal deficits in any neuropsychological

patients in order to be confident that observed deficits are not just due to increased difficulty.

Behavioral Studies of Rhythm Processing

In a previous study of beat processing, behavioral reproduction was compared for three different types of rhythms, termed *metric simple*, *metric complex*, and *nonmetric*.²² These stimuli were short (~ 3 s) novel rhythmic sequences, designed to be closely matched in temporal requirements, with the crucial difference between conditions being whether a beat was spontaneously perceived. The metric simple and metric complex rhythms were composed of intervals that were related by integer ratios (1:2:3:4). The metric simple rhythms also had a regular grouping of intervals, such that a regular “beat” or pulse could be perceived. The metric complex rhythms used the same intervals, but arranged such that no regular beat was likely to be perceived in the rhythm. They were both termed metric, as they both exhibited periodicity (at the level of the smallest interval: 220–270 ms). However, the metric simple condition also exhibited periodicity at rates known to be more salient^{9,34,35} for human beat perception: 440–1080 ms (two or four times the smallest interval of the metric sequences). Samples of stimuli are available to hear online (www.mrc-cbu.cam.ac.uk/personal/jessica.grahn/stimuli/ANYAS.html).

One important question is whether the presence of simple integer ratios in the rhythm is enough for participants to perceive a beat, as suggested by previous work.^{36,37} If this is the case, a beat potentially could be perceived in both the metric simple and metric complex conditions. However, if regular grouping to provide higher-level periodicities is also required, then a beat should only be perceived in the metric simple condition. As the nonmetric condition uses noninteger ratios (1:1.4:3.5:4.5), it has no periodicities, nor any regular grouping, and thus no potential for beat perception. Importantly, the rhythms are matched for all other

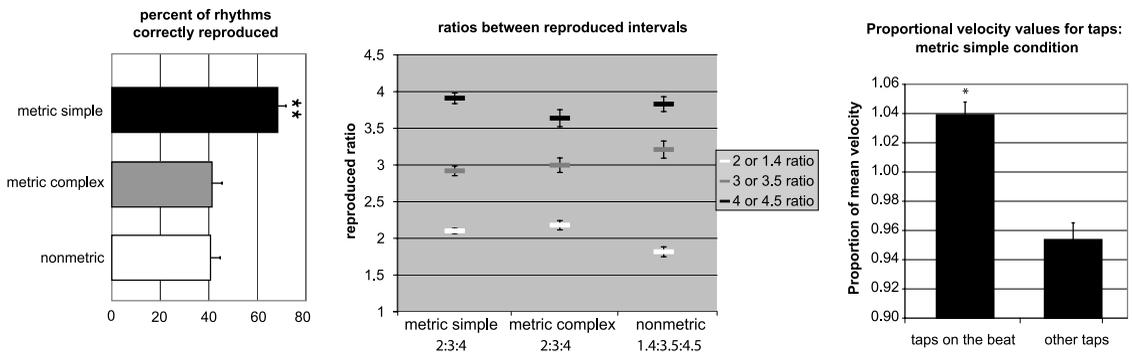


Figure 1. Results from a behavioral rhythm reproduction study, replicating findings of previous work.²² On the left, the percentage of rhythmic sequences reproduced accurately are shown; in the middle, the ratios of the reproduced intervals for each sequence type are shown (ideal performance is 2:3:4 for metric conditions, and 1.4:3.5:4.5 for the nonmetric condition); and on the right, mean velocity values are shown (depicted as proportional difference from the mean velocity for all sequences, in which the mean is normalized to 1). Taps “on the beat” have significantly higher velocity than taps “off the beat.” Error bars represent standard error.

temporal processing requirements (sequence length, number, and length of individual intervals), apart from whether or not a beat can be perceived upon initial hearing of the sequence. Participants heard each sequence three times before tapping it back as best as they could remember.

The results indicated that integer ratios are not necessarily enough to induce beat perception. Metric simple rhythms were reproduced more accurately than the metric complex or nonmetric rhythms (which did not significantly differ from each other²²). This initial experiment was then replicated, and this time tap velocity (an indicator of force) was measured. The replication experiment found again that metric simple rhythms were reproduced more accurately than metric complex or nonmetric rhythms (Fig. 1, left). In addition, in the metric simple condition, the velocity was significantly higher for taps predicted to be heard as “on the beat,”³⁸ compared to taps not on the beat, thus indicating that the predicted beat locations were consistent with participants’ representations (Fig. 1, right). In the replication, reproduction of metric complex rhythms was again similar in accuracy to nonmetric rhythms, suggesting that no beat was used in the metric complex condition. An examination of the ratios of intervals reproduced by participants indicates

that the longest intervals (3 and 4 in the metric conditions, 3.5 and 4.5) are significantly shortened in the metric complex and nonmetric conditions, but not in the metric simple condition (Fig. 1, middle). These results are the same as those found in previous work.²² Thus, integer ratios alone do not necessarily lead to beat perception, at least not strongly enough to improve performance.

fMRI Study of Metric and Nonmetric Rhythms

In order to elucidate which neural structures mediate beat perception, a discrimination paradigm was tested in fMRI. The paradigm was behaviorally piloted and adjusted until discrimination performance was equated across the different conditions, thus preventing difficulty differences from confounding interpretation of the results. The metric simple rhythms elicited increased activity (compared to the metric complex and nonmetric rhythms) in a subset of motor areas: the basal ganglia and SMA/pre-SMA.²² There were no differences in activity between the metric complex and nonmetric conditions. Activity levels in the basal ganglia for each condition are shown in Figure 2. Together, the behavioral and fMRI results suggested that simple integer ratios are

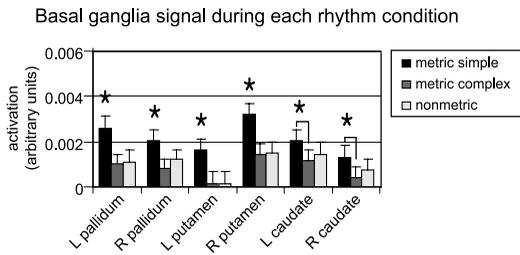


Figure 2. Average signal intensity extracted from basal ganglia nuclei for the metric simple, metric complex, and nonmetric conditions. * $P < 0.05$. Activity is greatest for the metric simple condition in the pallidum, putamen, and caudate.²²

not necessarily enough for humans to perceive a regular beat, and that the timing system engaged by beat perception may be mediated by the basal ganglia and pre-SMA/SMA, a set of neural structures connected via striato-thalamo-cortical loops.^{39–42} The lack of activation differences between the metric complex and nonmetric rhythms suggests again that integer ratios alone do not necessarily engage the beat-timing system, at least in novel (as opposed to learned) rhythms.

These results are highly suggestive of a role of the basal ganglia in beat processing; however, neuroimaging of healthy volunteers cannot tell us whether the basal ganglia system is *necessary* for this process to occur. To test whether the basal ganglia are critical for beat processing, patients were tested who had disruption of normal functioning in this system due to PD.⁴³

Rhythm Perception in Patients with Parkinson's Disease

To give some background, PD is characterized by progressive cell death in the substantia nigra that decreases dopamine release by the striatum, affecting excitatory input to the putamen.⁴⁴ Previous behavioral studies in patients with PD have shown deficits in simple timing tasks.^{25,45,46} These are likely due to the decreased dopamine levels in the striatum. For example, in PD patients, dopaminergic treatment improves motor tim-

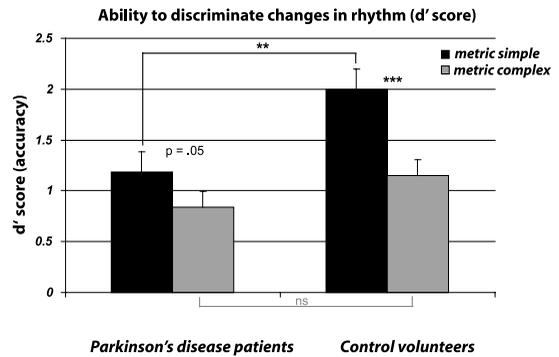


Figure 3. d' scores for patients and controls on metric simple and metric complex conditions in the deviant discrimination task. ns = not significant, ** $P < 0.01$, *** $P < 0.001$. Scores are adjusted for National Adult Reading Test performance,⁶⁴ used as an estimator of IQ.

ing^{46–48} and time perception.⁴⁹ In addition, administration of haloperidol (a dopamine receptor antagonist) to healthy adults impairs timing.⁵⁰ The exact role of the basal ganglia in temporal processing is not entirely clear, however, as some behavioral work has shown no temporal performance impairment in PD patients.^{51,52}

If the basal ganglia are necessary for successful beat processing, one would predict that PD patients should show a performance deficit when metric simple, but not metric complex or nonmetric rhythms, are used. This was recently tested, using metric simple and metric complex rhythmic stimuli.⁵³ A discrimination task was used to prevent any overt motor performance difficulties for PD patients from affecting the results. PD patients and matched control participants determined whether two auditory rhythmic sequences were the same or different (when different, two temporal intervals in the sequence had been transposed).

In controls, the condition with a beat-based structure, metric simple, was discriminated correctly significantly more often than the condition without a beat-based structure, the metric complex (results are shown in Fig. 3). In PD patients, however, the benefit for metric simple rhythms was much less, and only marginally significant. In fact, only in the metric simple

condition was PD patients' discrimination significantly worse than that of controls. In the metric complex condition, their discrimination performance did not significantly differ from that of controls. These data suggest that PD patients are either impaired at extracting the beat structure when initially listening to novel rhythms, or that they are less able to use the beat structure in these types of rhythms to improve their performance during the subsequent comparison of the rhythms.

The observed deficit for the PD patients is unlikely to be related to nonspecific effects of PD. The patients were all at early stages of PD (Hoehn and Yahr stages 1–2 at the time of testing), at which time dopamine depletion is more circumscribed and focused principally on the basal ganglia.^{54,55} In addition, unlike rhythm reproduction or beat synchronization tasks, the discrimination task did not require any motor response and therefore the results are unlikely to be explained by a motor deficit. Most importantly, the patients are significantly impaired on the condition that healthy participants find *easier*. A nonspecific timing impairment would be expected to be present across all conditions, and if anything, to a greater extent in the more difficult condition. As the PD patients are not significantly impaired in the more difficult metric complex condition, the deficit appears to be specific to sequences that involve beat processing.

PD patients did show a small benefit in discrimination of the beat-based rhythms compared to the nonbeat-based rhythms. Their capacity to process the beat appears therefore to not be completely lost (consistent with some residual preserved function in the basal ganglia in PD). However, all patients were in the early stages of PD, and on medication, which may have mitigated any underlying deficit to a certain extent. In addition, other brain areas are involved in timing processes, and may provide compensation for any deficits in timing functions normally subserved by the basal ganglia.

In the work described thus far, the beat could only be extracted from the temporal structure

of the stimuli. When a more obvious beat is present in the auditory stimulus, such as during music listening (when volume, pitch, timbre, harmony, etc. all provide cues to the beat), this deficit is likely to be obscured. Anecdotally, this is supported by the fact that none of the patients described any reduction in his or her enjoyment of music or inability to perceive its rhythmic characteristics.

fMRI Study of Different Accent Types

A new study was conducted to examine different types of cues to the beat. These cues are often termed *accents*. An accent is an increase in salience when an event differs from surrounding events.^{1,34,56} In the metric simple rhythms, the accents that cue the beat are temporal, arising from the temporal durations of the intervals.^{38,57} However, accents can also be “dynamic,” involving volume changes,⁵⁸ or even “subjective.” Subjective accents are perceived when no external accents exist (for example, in a sequence of tones identical in volume, duration, pitch, etc.), but listeners still internally emphasize certain tones in the sequence.^{59–61}

These different accent types vary in the degree to which they are externally salient. Regular volume accents can provide a very strong external beat emphasis, whereas duration accents are a weaker external beat cue. In sequences with no accents, there is no external beat emphasis, and any accents or beat cues perceived in the sequence are purely internally generated. fMRI was used to compare neural responses to internal versus external beat perception in musicians and nonmusicians for rhythms with these different accent types⁶² (see Fig. 4 for schematic depictions of stimuli).

Three sets of sequences were generated, Volume accented, Duration accented, and Unaccented. For each set there were Beat and Nonbeat versions. All stimuli were between 11 and 18 s long. The stimuli are schematically

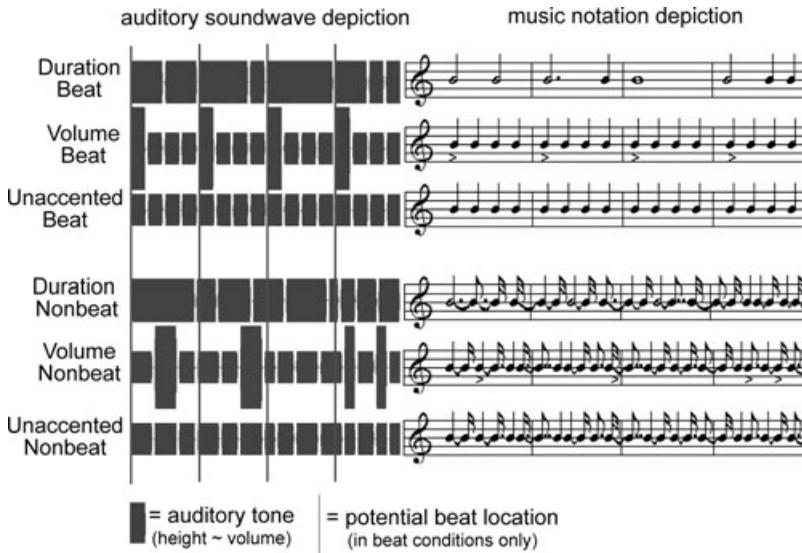


Figure 4. Schematic depictions of the auditory stimuli used in the fMRI study of different accent types.⁶² On the left is a depiction of the auditory waveform, and on the right is a depiction in standard musical notation. Long vertical lines mark the onsets coinciding with the beat (applicable to beat conditions only), and correspond to the first note of each measure in the music. Volume accents are indicated by higher relative height (in left panel) or accent symbols ("<" in the right panel). The depictions represent an excerpt of approximately 2.5 s.

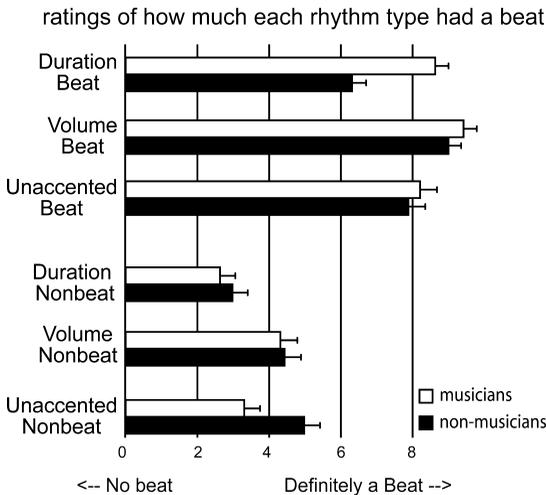


Figure 5. Ratings of beat presence for each of the conditions, as given by participants with and without formal musical training.⁶²

depicted in Figure 4, and samples can be heard at www.mrc-cbu.cam.ac.uk/personal/jessica.grahn/stimuli/ANYAS2.html.

Volume-accented beat rhythms had increases in volume on every 4th tone, giving rise to perception of a beat occurring on the volume-accented tones. In the Volume Non-

beat condition, tones were randomly jittered in length to be irregular, and the volume increases were also applied to randomly chosen tones in the sequence. For the Duration Beat condition, longer versions of metric simple rhythms from previous studies were used. For the Duration Nonbeat condition, each Duration Beat pattern was jittered such that the intervals were randomly lengthened or shortened to prevent any regular beat from occurring. Unaccented Beat and Unaccented Nonbeat stimuli were created by removing amplitude modulation from the corresponding Volume conditions. The intervals in the Unaccented conditions were therefore temporally identical to the Volume Beat and Volume Nonbeat conditions.

Behavioral ratings of how much each sequence had a beat were obtained for each of the rhythm types. As seen in Figure 5, the Beat conditions were all rated as having more of a beat than the Nonbeat conditions, confirming that the stimulus manipulations were successful. High ratings of beat perception occurred even in the absence of external

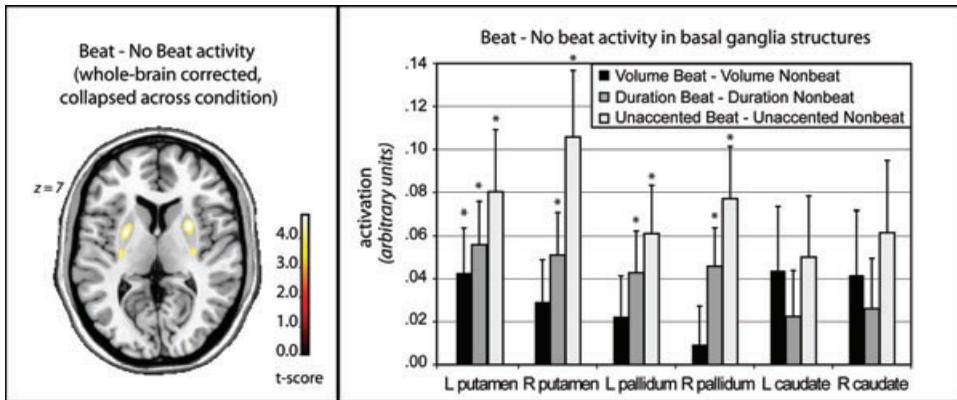


Figure 6. fMRI results for study of different accent types.⁶² The Beat versus Nonbeat contrasts overlaid on a template brain (left) and as extractions from the basal ganglia (right). Beat versus Nonbeat SPM contrasts show significant bilateral activity in the putamen for this contrast. Peak voxels are $P < 0.05$ whole-brain FDR corrected; z refers to the level of the axial slice shown in stereotaxic MNI space. The graph at the right shows mean activation (in arbitrary units) for the Volume Beat versus Volume Nonbeat, Duration Beat versus Duration Nonbeat, and Unaccented Beat versus Unaccented Nonbeat contrasts. Extractions from basal ganglia regions (as defined by Tzourio-Mazoyer *et al.*⁶³) were of *a priori* interest in this study. * $P < 0.05$ (significant difference between Beat and Nonbeat for that condition). (In color in *Annals* online.)

accents (Unaccented Beat condition), corroborating other work showing that internal subjective accents are generated when listening to unaccented isochronous rhythms.^{59,61} Moreover, the ratings indicate that these internal accents were as effective as external duration accents at inducing beat perception.

During scanning, participants completed an unrelated pitch change detection task, and thus all reported activity is elicited by perceptual processing of the rhythms (participants were instructed not to move, and visually monitored to ensure compliance). When Beat versus Nonbeat rhythms were contrasted at the whole-brain level, significantly greater activity for Beat conditions (collapsed across accent type) was found in the putamen bilaterally (Fig. 6). The activity of different basal ganglia structures (putamen, pallidum, and caudate⁶³) is shown in Figure 6. The putamen, pallidum, and caudate all responded more to the Beat conditions than the Nonbeat conditions.

Putamen activity was greatest for the Unaccented Beat–Nonbeat condition, followed by the Duration Beat–Nonbeat condition, then the Volume Beat–Nonbeat condition. Why might this be the case? A critical difference be-

tween conditions is the requirement for internal beat generation: As alluded to above, internal generation is unnecessary in the Volume Beat condition, as the accents that indicate the beat are highly externally salient. In the Unaccented Beat condition, internal generation is essential. Internal generation therefore appears to modulate the basal ganglia response to beat perception. Importantly, the putamen response was not due to temporal complexity, as complexity was matched in the Unaccented Beat and Volume Beat conditions.

Functional connectivity between brain regions was also examined, using psychophysiological interaction analyses, or PPI.⁶² During the Volume and Duration Beat conditions compared to the Volume and Duration Nonbeat conditions, the anterior putamen showed increases in functional connectivity with the premotor cortex (PMC), SMA, and right superior temporal gyrus (STG) and a similar trend in the left STG and right cerebellum. This is illustrated in Figure 7 (top). Similar functional connectivity results were observed for the Unaccented Beat–Unaccented Nonbeat condition. One interpretation of the increased coupling is that the putamen encodes information

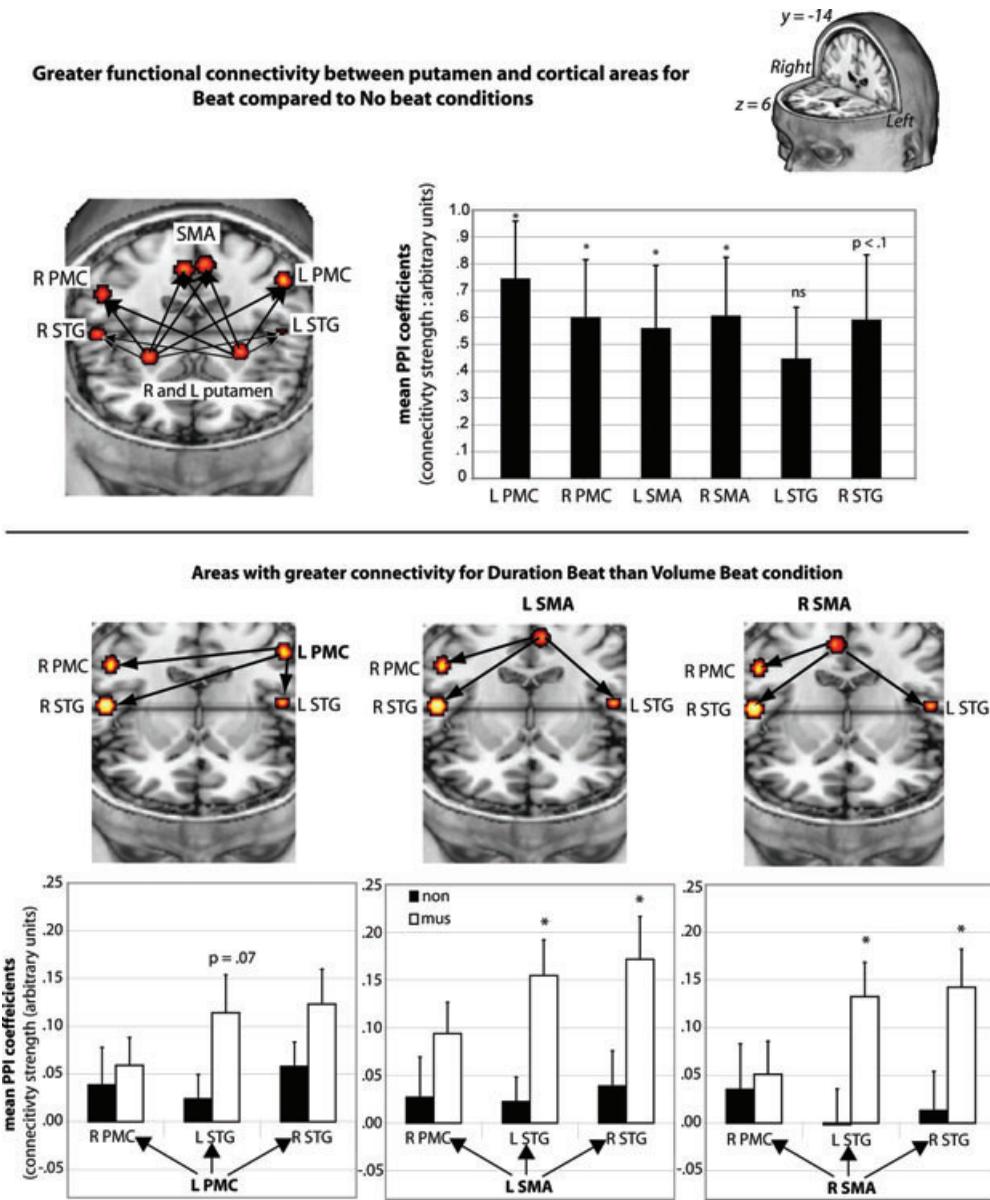


Figure 7. Connectivity analyses. Top panel displays regions showing increased coupling with the anterior putamen in Beat compared to Nonbeat conditions. The graph shows mean PPI coefficients (arbitrary units) for each of the target regions. * $P < 0.05$; small volume corrected. The bottom panel displays regions with increased coupling during the Duration Beat condition versus the Volume Beat condition. Mean PPI coefficients (arbitrary units) from the target regions for each of the significant source → target pairs are shown in the graph ($P < 0.05$; small volume corrected). Coefficients for musicians and nonmusicians are shown: * $P < 0.05$, significant difference between groups (independent samples t -test). (In color in *Annals* online.)

about beat timing that facilitates cortical motor areas in precise control of movement timing, required, for example, when movements are made in time with beats.

There were no significant differences in regional activation associated with musical training. However, there were greater increases in cortical auditory-motor functional connectivity

during the Duration Beat compared to the Volume Beat condition. Specifically, the SMA bilaterally and left PMC showed increased coupling with the bilateral STG and right PMC. In contrast, nonmusicians did not show different levels of auditory-motor coupling between the SMA and the STG in the Volume and Duration conditions (Fig. 7, bottom).

Thus, the results of this study indicate that the basal ganglia show a specific response to the beat during rhythm perception, regardless of musical training or how the beat is indicated. A cortico-subcortical network including the putamen, SMA, and PMC appears to be engaged for the analysis of temporal sequences and perhaps also prediction or generation of putative beats, especially under conditions that require internal generation of the beat. In these conditions, the coupling among cortical motor and auditory areas is facilitated for musically trained individuals.

Conclusions

Taken together, the findings presented here indicate that the basal ganglia are not just active, but required for successful beat processing. The activation is modulated by the degree of internal beat generation that is required. It remains to be seen whether the basal ganglia are responsible for the detecting/encoding stages of beat processing, or for maintaining a continuing internal representation of the beat after beat detection or encoding has occurred.

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Conflicts of Interest

The author declares no conflicts of interest.

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