Neural Mechanisms of Rhythm Perception: Present Findings and Future Directions

Li-Ann Leow and Jessica A. Grahn

Abstract

The capacity to synchronize movements to the beat in music is a complex, and apparently uniquely human characteristic. Synchronizing movements to the beat requires beat perception, which entails prediction of future beats in rhythmic sequences of temporal intervals. *Absolute timing mechanisms*, where patterns of temporal intervals are encoded as a series of absolute durations, cannot fully explain beat perception. Beat perception seems better accounted for by *relative timing mechanisms*, where temporal intervals of a pattern are coded relative to a periodic beat interval. Evidence from behavioral, neuroimaging, brain stimulation and neuronal cell recording studies suggests a functional dissociation between the neural substrates of absolute and relative timing. This chapter reviews current findings on relative timing in the context of rhythm and beat perception.

Keywords

Rhythm • fMRI • Music • Timing • Neuroscience

Of many uniquely human behaviours, the capacity to move to the beat in music is one of the most fascinating. To synchronize movements to the beat, we must rapidly predict the timing of future beats in rhythmic sequences of temporal intervals. Despite its complexity, this ability appears spontaneously in humans, without training. Sensitivity to the beat in temporal sequences cannot be easily accounted for by most theories of timing, as they generally focus on 'absolute' timing (also termed duration-based timing), in which patterns of temporal intervals must be encoded as a series of absolute durations. Instead, some human predictive timing behaviors, such as beat perception, seem better accounted for by relative timing mechanisms, in which the temporal intervals of a pattern are coded relative to each other. This relative timing is sometimes called 'beat-based' timing, because the intervals can be encoded relative to a regular, periodic beat interval. Converging evidence from behavioral, neuroimaging, brain stimulation and neuronal cell recording studies suggests

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a functional dissociation between the neural substrates of absolute and relative timing. Absolute timing research has been described in depth elsewhere [1, 2], and will only be briefly reviewed here. Relative timing, particularly in the context of rhythm, will be the focus of this chapter. To orient the reader, we will first provide some definitions of key terms.

Rhythm is defined as the pattern of time intervals demarcating a sequence of stimulus events. In rhythms, the onsets of stimulus events (such as tones or light flashes) tend to be the most important markers of the intervals in a rhythm, and the time between onsets (inter-onset-intervals) generally defines the lengths of the temporal intervals in the rhythmic sequence. This reliance on onsets, not offsets, to indicate intervals in a rhythm is the reason that we can recognize a rhythm whether it is played with long, connected notes (as bowed on a violin) or with short, disconnected notes (as plucked on a guitar). Listening to a musical rhythm gives rise to a sense of *pulse*, sometimes termed the *beat*. The pulse or beat is a series of regularly recurring psychological events that arise in response to a musical rhythm [3, 4]. The time interval between beats is called the *beat period* or *beat interval*, and relates to *tempo,* the rate of the beat: a shorter beat period leads to a faster tempo. Although a sense of beat arises in response to a rhythmic stimulus, it is not purely a stimulus property: beat perception is a psychological response to rhythm [5–8]. For example, beats do not always have to coincide with stimulus onsets (as evidenced by our ability to mentally continue the beat through gaps or breaks in music). Although perception of the beat can be enhanced by volume or timbral accents, such perceptual accents are not necessary for beat perception, suggesting that beat perception can arise purely from particular temporal characteristics of a rhythm. The specific temporal characteristics that induce beat perception, and thus trigger beat-based timing mechanisms, are not entirely clear, but some common heuristics have been used.

Beat-inducing rhythms (sometimes termed *metric simple* rhythms) can be formed by creating rhythmic sequences from intervals whose lengths are related by integer ratios (e.g., 1:2:4), particularly if the interval onsets systematically occur at rates known to be salient for human beat perception (440–1,080 ms) [9, 10]. The opposite of beat-inducing or metric simple rhythms are *nonmetric rhythms*, which have no beat. These can be formed by creating sequences from intervals whose lengths are related by complex or noninteger ratios (e.g., 1:2.3:3.7), or even intervals of randomly selected lengths. In these rhythms, no beat can be felt, because no regularity of onsets is present. Between metric simple and nonmetric rhythms are rhythms that are less likely to induce a sense of beat, but in which it would be possible to sense a beat (i.e., the structure is not so irregular as to preclude a beat 'fitting' to the rhythm). These are often termed metric complex rhythms. Metric complex rhythms are generally closely matched to metric simple rhythms in terms of sequence length, number of intervals in a sequence, and the lengths of individual intervals that comprise the sequence. Unlike metric simple rhythms, the intervals are arranged in such a way that a beat is not readily perceived, generally by not having onsets consistently occur at rates salient for beat perception. Different researchers use somewhat different heuristics for determining the 'complexity' of a metric rhythm, but the underlying idea is similar: simple rhythms induce clear beat perception, complex rhythms less so, and nonmetric rhythms not at all.

Behavioral Evidence of Beat-Based Timing Mechanisms

Without beat perception, the durations of each interval in the rhythm must be measured and stored in memory separately as they occur, and our capacity to remember a series of separate, unrelated time intervals is limited. Perception of the beat enables temporal intervals to be encoded as multiples or subdivisions of the beat, rather than as a series of individual and unrelated intervals. Therefore, the percept of a beat has repeatedly been shown to improve performance

on temporal processing tasks (e.g., [9, 11–13]). In general, behavioural temporal processing tasks can be categorized as either belonging to the perceptual paradigm, or the production paradigm. *Perceptual paradigms* require subjects to make perceptual judgments about sets of temporal stimuli. One commonly used perceptual task is the rhythmic discrimination task, which requires subjects to listen to a "standard" temporal sequence of rhythmic stimuli, followed by a second "test" sequence. Subjects are then asked to compare the standard and the test sequences and make judgments about the sequences (e.g., are the rhythms same or different?) When asked to discriminate if rhythms are same or different, subjects are typically better at discrimination of metric simple rhythms than with metric complex rhythms [14]. Furthermore, beat-inducing rhythms elicit better performance even when the task is not temporal: discrimination of intensity differences is better with beat rhythms than non-beat rhythms [15]. *Production paradigms* require subjects to produce a specified temporal pattern. For example, in rhythm reproduction tasks, subjects listen to rhythms and then reproduce them from memory [9]. Another commonly used production task is the synchronization-continuation task. In the synchronization phase, subjects synchronize movements (typically finger taps) to the onset of each tone of a rhythm, or to each beat in the rhythm. In the continuation phase, the sound is removed, and subjects continue to reproduce the rhythm, or only the beat, from memory. As with perceptual paradigms, performance in production paradigms is more accurate and precise with beat-inducing rhythms than with non-beat rhythms [9, 12, 13, 16, 17]. The individual intervals in beat and non-beat rhythms are the same (only the interval order differs), and the rhythms are equal in all other temporal processing requirements (such as length and number of intervals), therefore the performance advantage for beat-inducing rhythms does not result from any differences in timing of individual intervals. Instead, in beat rhythms, temporal processing performance is improved by the use of relative timing mechanisms: the intervals are perceived and organized relative to the beat interval [1]. Even though the use of relative timing can lead to better performance, its use is limited: only sequences that are structured relative to a beat can be timed this way, so absolute timing mechanisms are still required for timing of non-beat sequences.

Functional Neuroimaging Evidence

Non-invasive neuroimaging methods have contributed to our understanding of how timing and rhythm are processed in the human brain. Unlike in other areas of timing research, non-human primates do not appear to spontaneously perceive and respond to the beat. Thus, we cannot fully extrapolate mechanisms derived from invasive neural recordings in non-human primates to humans, as non-human primates may not have the same relative timing mechanisms as humans. For example, primates do not appear to match tapping movements to metronome tones in the same way as humans. Unlike humans, whose finger taps anticipate tone onset by ~50 ms, primate finger taps lag behind by approximately 250 ms [18] (for a review, see [19]). Non-invasive neuroimaging techniques can therefore provide a much needed bridge between data acquired between human and non-human primates, such that neural bases for behavioral differences between these groups can be determined. Currently, some techniques used in non-human primates, such as intracranial recordings, are too invasive for human use, making cross-species comparisons difficult. By using non-invasive methods, researchers can collect the same type of data, using the same paradigms, across species, enabling them to see which differences are the result of genuine processing differences, and which differences were simply the result of trying to compare across different methodologies.

Broadly, non-invasive neuroimaging techniques fall into two categories. The first category measures the electrical potentials or concomitant magnetic fields generated by neuronal activity using electroencephalography (EEG) or

magnetoencephalography (MEG) respectively. The second category measures the metabolic or hemodynamic consequences of neuronal activity using positron emission tomography (PET) or functional magnetic resonance imaging (fMRI). These two categories of techniques are complementary: EEG and MEG have high temporal resolution, which shows the time-course of neural activity, whereas fMRI and PET have high spatial resolution, which shows the spatial location of activity in the brain. Here, we focus on findings obtained with fMRI techniques, as EEG and MEG findings have been reviewed elsewhere (Vuust et al., final chapter of this book).

Absolute Timing

Absolute timing mechanisms are necessary for the encoding of non-beat rhythms, as the intervals have no relationship to each other. This differs from beat rhythms, in which all intervals can be encoded relative to the beat interval. Converging evidence shows that the **cerebellum** plays a key role in absolute timing. Several studies have shown that such rhythms activate cerebellar structures [17, 20–22]. For example, memorizing non-beat rhythms evokes greater cerebellar activity than memorizing beat rhythms [23]. Greater cerebellar activity is also evident for non-beat rhythms compared to beat rhythms when subjects are reproducing them [9], or make perceptual judgments about them [20, 22], or synchronize finger taps to them [17]. The ability to encode single durations is impaired when cerebellar function is disrupted through disease [24] or through transcranial magnetic brain stimulation [25]. Importantly, the deficits in encoding single durations that occur with cerebellar disruption are not accompanied by deficits in encoding beat sequences [24, 25], supporting the idea that the cerebellum is involved in absolute but not relative timing mechanisms.

Relative Timing

Beat perception necessarily requires relative timing, as all intervals are encoded relative to the beat interval. Relative encoding confers flexibility in the representation of a sequence. One can recognize the iconic 'William Tell' rhythm whether it is played very quickly or very slowly: the rhythm can be accurately rescaled. Absolute representations are not as flexible, and even trained musicians cannot rescale them [26]. This behavioral dissociation between absolute and relative representations is supported by neuroimaging work. There is reasonable consensus that the cerebellum is involved in absolute timing mechanisms (as mentioned above), and basal **ganglia-thalamo-cortical circuits** are involved in relative timing mechanisms [1]. This view arises from mounting evidence showing activation of the basal ganglia, supplementary motor area, and premotor cortex in beat perception tasks that engage relative timing mechanisms [9, 16, 20, 27–30]. In particular, perceiving a beat appears to selectively activate the basal ganglia and SMA, as beat rhythms consistently elicit greater basal ganglia and SMA activity across studies employing different perception and production paradigms [9, 15, 20–22]. Importantly, increases in basal ganglia and SMA activity during beat-inducing rhythms compared to non-beat rhythms do not arise from greater difficulty performing tasks with non-beat rhythms: even when the task difficulty is systematically manipulated to equate performance for beat and non-beat rhythms, greater basal ganglia and SMA activity is still evident for beat rhythms [9]. Furthermore, beat-inducing rhythms evoke greater activity of the basal ganglia than non-beat rhythms even when subjects are not specifically instructed to attend to any part of the rhythms [29], or when subjects attend to non-rhythmic aspects of the stimuli such as loudness [15] and pitch [21]. This suggests that greater basal ganglia activity does not arise from beat rhythms engaging more attention to temporal aspects of the rhythms than non-beat rhythms.

One question that arises is whether the neural substrates that are attributed to beat perception are specific to the auditory modality. Although beat perception certainly seems to occur more readily with auditory stimuli, it appears that the role of the basal ganglia networks in beat

perception might not be specific to the auditory modality. Visual rhythms do not usually evoke a sense of the beat the way auditory rhythms do, however, a sense of beat *can* be induced for a visual rhythm if it is preceded by an auditory version. When visual rhythms are perceived after auditory counterparts, the basal ganglia response increases during the visual rhythm presentation, and the amount of that increase predicts whether a beat is perceived in that visual rhythm [31]. This suggests that an internal representation of the beat formed during an auditory presentation may influence beat perception in subsequently presented visual rhythms, and that the basal ganglia mediate beat perception that occurs this way.

In addition to neuroimaging findings, basal ganglia involvement in beat perception is also evident from neuropsychological work showing that impaired basal ganglia function leads to worse performance on tasks assessing beat perception [14]. For example, patients with Parkinson's disease are worse than controls at discriminating changes in beat rhythms, but are similar to controls at discriminating changes in non-beat rhythms [14]. Unlike rhythm reproduction or beat synchronization tasks, discrimination tasks do not require any motor responding and therefore the results are unlikely to be explained by a motor deficit. More importantly, the patients are impaired only in the condition that is generally found by subjects to be easier. This rules out the possibility that nonspecific impairments, such as greater fatigue or poorer working memory function, caused the deficit. Any nonspecific impairment would be expected to be present across all conditions, and if anything, to a greater extent in the non-beat condition, as it is usually more difficult for healthy subjects. The selective deficit in beat rhythms and not non-beat rhythms supports the proposal that the basal ganglia are primarily involved in relative timing mechanisms. There is also preliminary evidence suggesting that Parkinson's disease patients have difficulty perceiving and synchronizing movements to the beat in music [32]. Other forms of basal ganglia dysfunction, such as in Huntington's disease patients, also show deficits in tasks assessing relative timing [33]. However, unlike the Parkinson's disease patients in the previous study [14], the Huntington's disease patients also showed deficits in tasks assessing absolute timing mechanisms. This apparent discrepancy in results might be because the pattern of basal ganglia degeneration differs substantially between Parkinson's disease and Huntington's disease: degeneration in Huntington's disease starts in the caudate nucleus, whereas degeneration in Parkinson's disease starts in the putamen [34]. Future studies comparing the same temporal processing tasks in both patient groups can help determine if striatal networks impaired in Huntington's disease but spared in Parkinson's disease are important to absolute timing mechanisms.

Basal ganglia deficits appear to selectively affect temporal processing performance around a rate that humans find ideal for beat-perception (500–700 ms). For example, patients with focal basal ganglia lesions are less able to detect tempo changes or adjust finger taps to rate changes at rates close to the ideal beat rate [35]. Parkinson's disease patients also show selective deficits in tapping at the ideal beat rate of 500 ms, but not at 1,000 or 1,500 ms [36]. This appears consistent with neuroimaging findings which show basal ganglia activity does not correlate with the speed of the beat, but shows maximal activity around the ideal beat rate and then decreases as rates are too slow (McAuley et al. 2012) or too fast for a beat to be felt [37]. Therefore, the basal ganglia are not simply responding to perceived temporal regularity at any rate in auditory stimuli, but are most sensitive to regularity at the rate that best induces a sense of beat.

Although poor beat perception has been observed in patients with impaired basal ganglia function, it is not limited to neurological patients. Healthy individuals have been diagnosed as "beat-deaf". These individuals have no other form of musical impairment, yet beat perception deficits are evident across a number of behavioral paradigms: perceiving the beat, synchronizing movements to the beat, detecting when metronome cues are off the beat in music, and detecting when a dancer's movements are off

the beat [38]. Even apart from the most severe beat impairments, there is a wide range of ability to perceive the beat in healthy individuals [39–41]. Several studies have recently attempted to examine the neural correlates of individual differences in beat perception. One study showed that good beat-perceivers more readily engage supplementary and premotor areas when making temporal judgments than poor beat-perceivers [39]. Another study found that better beat perception was positively correlated with activation of the supplementary motor area and premotor cortex during a rhythm discrimination task [41]. Better synchronization performance to rhythms has also been associated with larger ventral premotor cortices [42]. Overall, the fMRI evidence points to a key role for motor areas, rather than auditory areas, in beat perception ability. Why do healthy, neurologically intact individuals show poor beat perception? One possible explanation is that such individuals possess dopamine genetic polymorphisms which selectively impair temporal perception at intervals that are most salient for beat perception (500–700 ms). For example, individuals with the DRD2/ANKK1-Taq1a genetic polymorphism have a reduced density of D2 receptors in the basal ganglia. These individuals also show significantly greater variability in temporal discrimination of single intervals of 500 ms (at the ideal beat rate) but not 2,000 ms [43]. These commonly found genetic polymorphisms appear likely to influence individual differences in ability to perceive the beat, although this possibility has yet to be systematically examined.

Coupling Between the Auditory and Motor Areas in Beat Perception

Although many studies have shown involvement of several motor regions in rhythm processing, it is still unclear *how* these motor regions interact with each other, as well as with auditory regions, to give rise to a beat percept. The analyses that characterize the communication and interactions between brain areas are called functional connectivity analyses. Greater functional connectivity between two or more areas is thought to denote greater communication between those areas. Recent studies exploring the communication between motor areas in beat perception showed that during beat perception, greater connectivity was observed between the putamen and the supplementary motor area, as well as between the putamen and the premotor cortex (see Fig. 1) [21]. The increases in connectivity were evident regardless of whether the beat was induced by the temporal pattern of interval durations in the rhythm, or by regularly occurring volume accents (see Fig. 1) [21]. Another study showed greater connectivity between the putamen and the ventrolateral prefrontal cortex (VLPFC) when synchronizing finger taps to the beat of non-beat rhythms than to beat rhythms [17]. The VLPFC is thought to be involved in monitoring performance by comparing internal and external sensory representations [44]. Synchronization requires subjects to continuously monitor performance by comparing the output of their motor responses with internal representations of the beat intervals. Synchronizing to non-beat rhythms has more performance monitoring demands than synchronizing to beat rhythms, because unlike beat rhythms, non-beat rhythms cannot be encoded automatically through relative timing mechanisms. The VLPFC is therefore thought to interact with the basal ganglia so that beat intervals could be compared, selected and maintained for production during synchronization [17].

Individual differences in connectivity between cortical motor and auditory areas might be a useful marker of rhythmic ability. In musicians, superior performance on a synchronization task was associated with greater connectivity between the auditory and premotor cortex [12]. Furthermore, a different study found greater connectivity between the premotor and auditory cortex in musicians, even when activity of these areas was similar (see Fig. 1) [21]. That is, increased connectivity between two regions can exist in the absence of increased activity in either region. Exactly how coupling between the auditory areas and the premotor cortex improves rhythmic performance remains unclear, although it has been suggested that increased functional

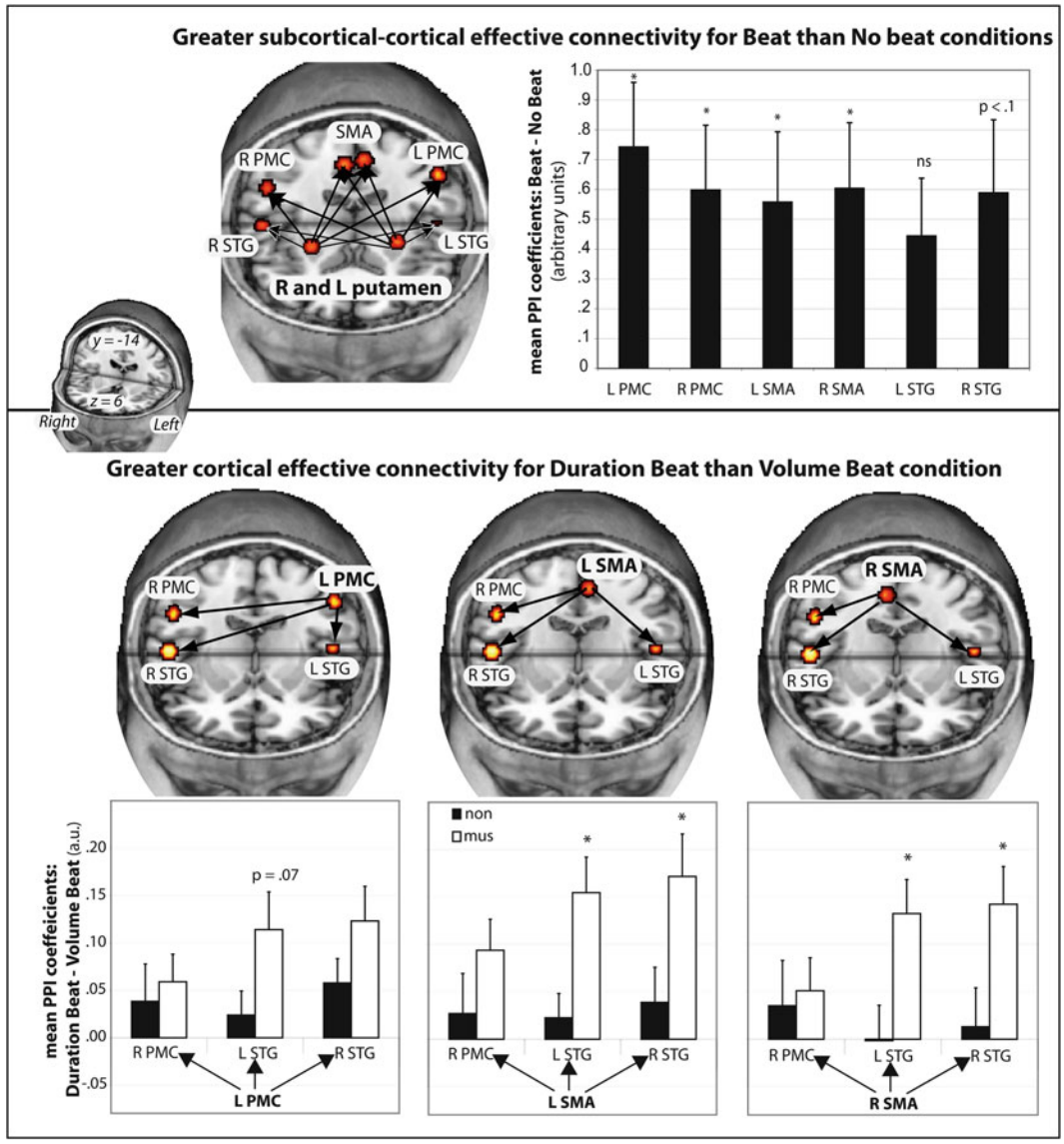

Fig. 1 *Top panel* shows functional connectivity between the putamen and the SMA and premotor cortices in Grahn and Rowe [21]. Greater subcortical-cortical connectivity was evident with beat rhythms than with non-beat rhythms. Mean PPI coefficients (arbitrary units) from the target regions for each of the significant source to target pairs are shown in the *top right* graph ($p < 0.05$; small volume corrected). *Middle panel* shows regions with increased coupling in condition where the beat was indicated by relative interval durations (duration beat condition) compared to conditions where the beat was indicated by strong external volume accents (volume beat condition). *Bottom panel* shows coefficients for musicians and nonmusicians: *$p < 0.05$, significant difference between groups (independent samples t test). *R* right, *L* left, *mus* musician, *non* nonmusician

connectivity between the premotor cortex and superior temporal gyrus might be important for integrating auditory perception with a motor response [12]. Kung et al. [17] also showed that beat perception and synchronization performance was correlated with activity in STG and VLPFC; they suggest that the connectivity between the STG and VLPFC could be important for retrieving, selecting, and maintaining the musical beat.

The Role of the Basal Ganglia in Beat Perception

Although many studies demonstrate the involvement of the basal ganglia in beat perception, its specific role in beat perception remains unclear. Recent studies have started to address this question by examining the basal ganglia's role in the component processes of beat perception. Beat perception has been proposed to require at least three processes: *beat finding*, during which the regular beat interval is detected, *beat continuation*, during which predictions of beat intervals are created and maintained, and *beat adjustment*, during which predictions of future beat intervals are updated based on accumulating evidence resulting from sensory feedback [22]. In a recent study, these processes were distinguished by having participants listen to sequentially presented beat and non-beat rhythmic sequences. For each sequence, the preceding sequence provided a temporal beat context for the following sequence. Beat sequences preceded by non-beat sequences were proposed to elicit *beat finding,* as subjects must detect the beat in the beat sequence without any previous beat information. Beat sequences preceded by beat sequences at the same beat rate elicited *beat continuation* as subjects would ostensibly maintain their internal representation of the beat intervals from the preceding sequence, and simply continue them on to the subsequent sequence. However, if the beat rate changed from one beat sequence to the subsequent beat sequence, then the internal representation of the beat would require adjustment. FMRI was used to measure brain activation during each process. Putamen activation was greatest when listening to rhythms at the same beat rate (beat continuation), was lower when the rhythms changed rated (beat adjustment), and was lowest when rhythms were preceded by non-beat rhythms (beat finding) (see Fig. 2). The finding of highest putamen activation during beat continuation suggested a role for the putamen in maintaining the internal representation of the beat interval. The suggestion that basal ganglia and SMA are involved in maintaining an internal representation of beat intervals is supported by findings of greater basal ganglia and SMA activation during the continuation phase, and not the synchronization phase, during the synchronization-continuation task [30, 45]. Similarly, patients with SMA lesions also show a selective deficit in the continuation phase but not the synchronization phase of the synchronization-continuation task [46]. Taken together, these findings strongly implicate a role of the basal ganglia and SMA networks in maintaining forward predictions of the beat. That is, when a detectable beat is present in a rhythm, human spontaneously generate predictions about the timing of future beats in the pattern. Successful predictions enhance the speed of perceptual organization of the sequence, reduce working memory load, and thus improve temporal processing performance. Accurate prediction improves performance in many domains, and beat perception may simply be one example of how humans' exploit regular structure to reduce processing load.

Recent cell recording findings in macaque monkeys have also furthered our understanding of the SMA-BG networks' role in beat perception and in rhythmic timing behavior. A first study indicated that distinct SMA cells encoded either the time left for movement (i.e., "relative timing cells"); or the time elapsed after movement (i.e., "absolute timing cells") in a synchronization-continuation task, as evidenced by distinct patterns of ramping behavior pre and post-movement [47]. Crucially, these absolute and relative timing cells interacted during selective phases of the synchronization-continuation task, revealing that rhythmic timing behavior requires the interaction of both absolute and relative timing mechanisms [47]. A subsequent study showed that many SMA cells were selectively tuned to different intervals ranging from 450 to 1,000 ms, and these cells showed the same preferred intervals across different behavioral paradigms (the synchronization-continuation task and a single interval reproduction task) [48]. These SMA cells also showed selectivity for the different task phases during the synchronization-continuation task: some cells

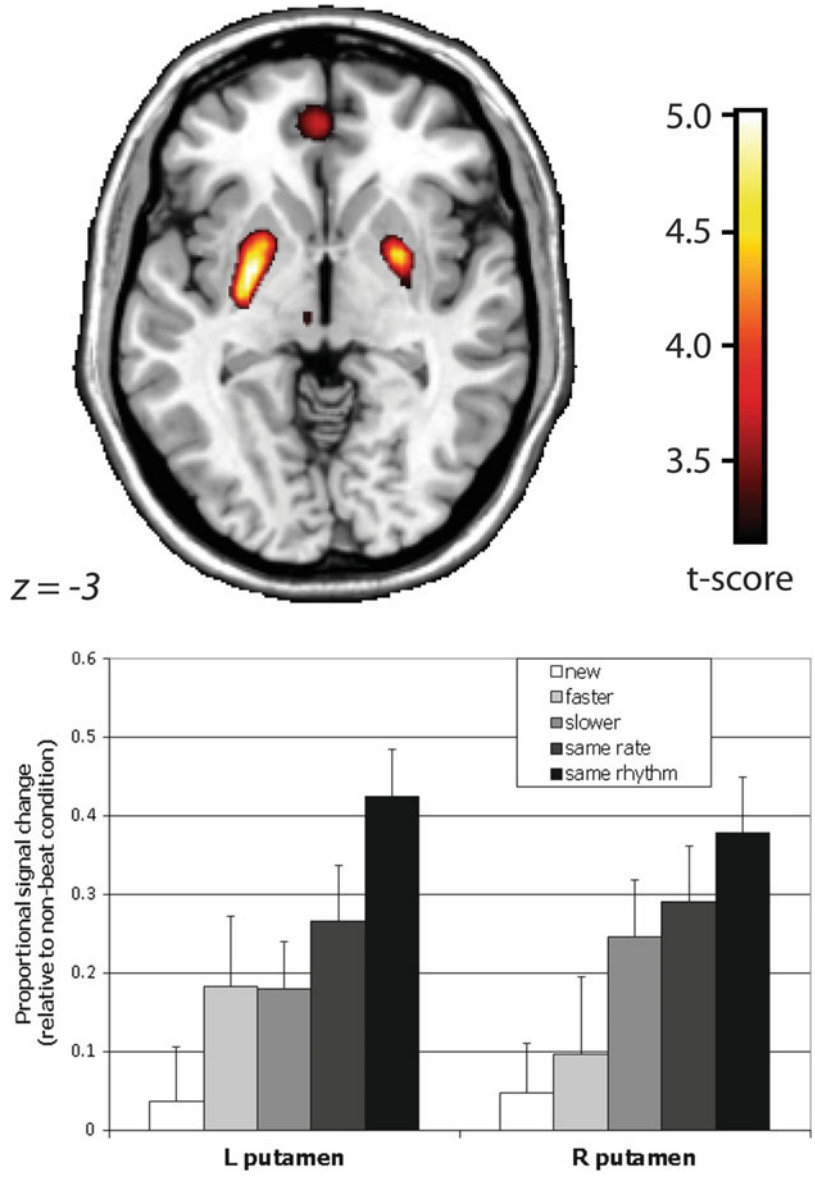

Fig. 2 *Top panel* shows the activation contrast for beat versus non-beat rhythms in Grahn and Rowe [22]. Contrasts were overlaid on a template brain, thresholded at $PFDR < 0.05$. Z refers to the level of the axial slice shown in stereotaxic Montreal Neurological Institute space. *Bottom panel* shows mean activation graphs from left and right putamen regions of interest for each beat condition relative to the nonbeat control condition. A positive value means greater activity for that particular beat condition compared with the nonbeat condition. Putamen activation was greater in conditions where the rhythms increased in similarity: greatest putamen activation was evident in beat continuation (same rhythm)

were biased to respond during synchronization phase, whereas other cells were biased to respond during the continuation phase. These findings are consistent with subsequent work showing differential beta and gamma activity in local field potentials recorded from the putamen: greater beta band activity was evident in the continuation phase, whereas greater gamma band activity was evident in the synchronization phase, in certain local field potentials [49]. Together, these findings support the proposal of distinct processes in rhythmic timing behavior: a process that underlies synchronization of rhythmic behavior, and another process that underlies continuation of rhythmic behavior. The existence of cells in both SMA and basal ganglia which are

preferentially activated by the continuation of rhythmic behavior suggests that SMA and basal ganglia networks maintain forward temporal predictions [22].

Challenges in the Study of Rhythm Processing

Localizing the neural substrates of rhythm has proven challenging, partly because rhythm is supported by processes common to temporal processing, and temporal processing unavoidably engages many distributed brain areas. One view proposes that sub and supra-second timing engage partially distinct neural mechanisms [50, 51]. Sub-second timing appears to preferentially engage the cerebellum, while supra-second timing tasks appear to preferentially engage the supplementary motor area and prefrontal cortex (for a review, see [52]). The basal ganglia is thought to be engaged by both sub and supra-second timing [50]. How this dissociation affects our current understanding of beat perception is unclear. Beat perception requires both sub-second and supra-second timing, as individual sub-second beat intervals must first be perceived, and then an internal representation of these intervals must be maintained across supra-second timescales. The component processes in beat perception (such as beat finding, beat continuation, beat adjustment) might differentially rely on sub and supra-second timing mechanisms, and this remains to be systematically examined.

An additional challenge to the study of rhythm processing is the fact that even the simplest rhythm processing task might have multiple cognitive and motor demands. Patterns of neural activation that are attributed to experimental manipulations in rhythm processing tasks can sometimes result from task demands. For example, working memory is required to compare standard rhythms with test rhythms, as subjects must remember the standard rhythm to compare with the test rhythm. It is unclear whether the memory benefits resulting from beat perception underpin the performance advantages for beat-inducing rhythms. The synchronization-continuation paradigm also relies on several cognitive and motor processes beyond just timing. During synchronization, subjects must encode and maintain the beat interval, produce a synchronized motor response, evaluate the accuracy of that response after each tap, and correct the timing of the next tap, if necessary. Better synchronization to beat rhythms might result from better encoding and maintenance of the beat interval, or from better evaluation and error correction. Hence, although temporal performance is thought to be improved by using relative timing, exactly how this mechanism improves specific aspects of performance is unclear.

Another challenge is that while many studies employ rhythms that are manipulated in terms of perceived beat strength, it remains unclear *what* factors lead to a beat percept. It has been proposed that integer-ratio relationships between intervals in a sequence induce beat perception, whereas noninteger-ratios do not [30, 53]. However, to the best of our knowledge, no studies have shown statistically reliable differences in brain activation between integer ratio and noninteger ratio rhythms. A previous study by Sakai et al. [53] did not directly compare brain activation between integer-ratio and noninteger-ratio rhythms [53]. Another study showed that integer-ratio and noninteger-ratio rhythms could result in statistically indistinguishable brain activation [9]. The integer/noninteger-ratio distinction therefore appears insufficient to fully account for what features induce beat perception, especially in rhythms composed of more than only one or two interval lengths.

Beat perception in musical rhythms typically occurs in an ongoing fashion: we spend only a very small portion of time perceiving the beginning of a rhythmic sequence. Knowledge acquired from prior context is therefore likely to drive internal predictions about the beat, optimizing estimations of beat intervals and beat onsets. Some studies have examined the role of context in the perception of individual intervals (e.g., [54]), but debate remains on its role [55]. One view suggests that time perception occurs through

interactions of a core timing network with cortical areas that are activated in a context-dependent fashion [2]. Computational studies suggest that prior contextual knowledge about temporal uncertainty is used to optimally adapt internal interval timing mechanisms to the temporal statistics of the environment [56, 57] (for a review, see [58]). Although context appears intuitively important to beat perception, little is known about how to integrate contextual information into mechanistic accounts of relative timing.

Finally, beat perception is also affected by other aspects of musical structure, such as melody, harmony, and timbre. The influence of musical structure on beat perception have been examined [59–67], but these findings have yet to be integrated into a single unifying model. Additional basic research that tests the influences of these non-temporal musical factors on beat perception will need to be done to extrapolate modes of beat perception to apply in real music, rather than monotone rhythmic sequences.

Future Directions

As we move towards more complete understanding of the neural mechanisms underlying relative timing and rhythm processing, converging evidence from complementary techniques becomes increasingly important in overcoming the limitations of individual techniques. For example, the use of Parkinson's disease patients as models of impaired basal ganglia function is limited by the fact that areas connected to the basal ganglia are also affected in Parkinson's disease. Furthermore, neurodegenerative diseases like Parkinson's disease result in heterogenous degeneration of striatal pathways, and the different patterns of degeneration are associated with different behavioral impairments on timing tasks [36, 68]. An exciting new complementary approach involves testing individuals with particular genetic variants that alter function of the basal ganglia. For example, one could examine how beat perception is affected by selective reductions in dopamine receptor function in healthy adults, such as carriers of specific genetic polymorphisms which reduce dopamine neurotransmission within the basal ganglia, but do not affect dopamine neurotransmission outside the basal ganglia. Studies that combine neuroimaging and genetic approaches have already shown promising results. For example, individuals with genetic polymorphisms that reduce striatal dopamine receptor function showed worse performance on a temporal discrimination task [69]. Interestingly, in these individuals, better temporal discrimination performance was associated with greater activation in the basal ganglia and right dorsolateral prefrontal cortex, as well as greater cerebellar volume [69]. One possible interpretation is that these findings indicate functional and structural compensatory mechanisms for poor temporal discrimination.

There is also increasing interest in why non-human primates differ from humans in rhythmic timing behavior. It has recently been proposed that non-human primates lack connectivity between the auditory and motor regions which enable rhythmic timing behavior in humans [19]. Comparative studies using non-invasive neuroimaging techniques may help bridge the gap in understanding the inter-species differences in rhythmic timing behavior (e.g., [70]). FMRI and EEG studies can be conducted with both humans and macaques, often with identical equipment and using identical paradigms. In addition, the increasing availability of intracranial recordings in patients may make it possible to make compare invasive neural recordings in humans and in primates [18, 19].

Overall, advances in analysis methods for existing techniques, adaptation of these techniques to different species, and adoption of new techniques are leading to better understanding of the characteristics of human rhythm processing. In coming years, greater integration of data acquired across different methodologies will be important to progress our understanding of how the complexities of rhythmic behaviour arise.

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