A neurocomputational model of beat-based temporal processing

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Keywords: Rhythm, music, timing, prediction, premotor, basal ganglia, cerebellum

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Abstract

A fundamental aspect of music cognition is the perception of an underlying metronome-like pulse ("the beat") in complex rhythmic patterns. A key finding from neuroimaging is that *even in the absence of movement,* beat perception strongly engages the motor system. Existing efforts to create conceptual and computational models of beat perception do not strongly engage with known neurocomputational properties of the motor system. Here we construct a mechanistic model of beat perception grounded in neurophysiology. The model uses two distinct timing signals in medial frontal cortex to infer tempo and to produce intervals that anticipate beats. Signals are sent along the direct pathway through basal ganglia to initiate the covert production of intervals. In the absence of direct pathway activation, medial frontal cortex is driving the hyperdirect pathway, creating a periodic cycle of global inhibition and facilitation of movement initiation. Striatal dopamine reinforces a top-down beat percept when anticipation is accurate and a bottom-up percept when it is not. We highlight the experimental results and lines of reasoning that support these hypotheses; we implement the model in silico and note important aspects of human beat-based timing that it reproduces; and we explore the model's predictive and explanatory power, especially regarding the therapeutic effect of the beat in Parkinson's disease.

Highlights Box

- The Action Simulation for Auditory Prediction (ASAP) hypothesis posits that covert anticipatory timing of a musical beat is performed by the motor system.
- Current discussion of beat-based timing does not address the balance between external responsiveness and internal maintenance necessary to adapt to beat timing changes but maintain a beat through syncopated or ambiguous rhythms.
- Beats may be anticipated by an adjustable-speed ("relative") timer in the supplementary motor area, initiated and reset like a movement via the basal ganglia direct pathway.
- The beta oscillation that fluctuates with the beat may be an anti-kinetic "hold" signal that would scaffold entrainment of non-specific movements.

- Striatal dopamine may serve as an index of confidence in the beat tempo and phase, allowing the motor system to transition between a synchronization and beat-continuation.

Abbreviations
BBT = beat-based timing
MFC = medial frontal cortex
PMC = premotor cortex
IBS = "internal beat strength"
SCT = synchronization/continuation task

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Introduction

"The last and ultimate challenge is to provide a mapping between psychological operations and neural circuits. This mapping need not be in a one-to-one correspondence. While some operations may be localized to particular neural structures, it is possible that the operations we describe at a computational level of explanation are implemented in a distributed manner within the brain. Exploring this mapping not only provides a first step towards developing a mechanistic explanation at the neural level, but also can help shape our understanding of the psychological operations."

Diedrichsen, Ivry & Pressing (2003)[1]

Much of the world's music is built upon the scaffolding of an isochronous pulse with an inter-pulse interval somewhere between 300ms and 1.5s (cite). For some reason, humans seem to enjoy identifying this underlying pulse ("the beat") and moving their bodies in time with it. Physical synchronization with a pulse is a temporal predictive mechanism: though physical or covert synchronization, we develop strong expectations about where the next pulse will occur. Even in the absence of a beat-based auditory stimulus, most humans can keep a covert steady pulse, as is evident from our tendency to measure time by covertly counting the passage of isochronous intervals that fall comfortably within our preferred pulse range -- namely, seconds. This example alone illustrates the importance of beat-based timing as one of our primary timing faculties.

In this paper, we draw on existing literature to inform a series of hypotheses about the neurological underpinnings of beat-based timing (BBT). We collect these hypotheses into a single coherent model and computationally demonstrate the capacity of this model to reproduce some key characteristics of human BBT.

A few defining features of human beat-based timing are:

- Humans recognize beats underlying beat-based stimuli over a range of tempi
- Humans often spontaneously entrain a broad repertoire of body movement patterns to the cycle of the beat (i.e., dance)
- If tapping to a beat, listeners can smoothly transition from stimulus-based synchronization to continuation when the stimulus is discontinued

To this list we add a few more features that help us focus our modeling effort:

- Not all beats are marked by sound
- Not all salient sound onsets represent beats
- The beat percept shows hysteresis: once inferred from a more rhythmically straightforward stimulus, it can be maintained as the stimulus is made more rhythmically complex[2].

As a jumping-off point, we use the hypothesis that **beat-based auditory stimuli entrain dynamics within the motor system, which produces a signal that returns to auditory cortex marking the anticipated times of beats**[3]. This hypothesis has received ample support in recent years (cite). If this is the case, it is reasonable to construct a model of beat-based timing that excludes auditory areas, treating the processed output of the auditory cortex as an input to a beat-anticipation system.

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[1] Diedrichsen, J. D., Ivry, R. B., & Pressing, J. (2003). Cerebellar and basal ganglia contributions to interval timing. In W. H. Meck (Ed.), *Functional and neural mechanisms of interval timing*.

[2] Lenc, T., Keller, P.E., Varlet, M., Nozaradan, S. (2019). Hysteresis in the selective synchronization of brain activity to musical rhythm. BiorXiv. **doi:** https://doi.org/10.1101/696914

[3] Rimmele, J. M., Morillon, B., Poeppel, D., & Arnal, L. H. (2018). Proactive Sensing of Periodic and Aperiodic Auditory Patterns. *Trends in Cognitive Sciences*, *22*(10), 870–882. https://doi.org/10.1016/j.tics.2018.08.003

In this article, we follow neurophysiological observations as well as known properties of BBT to guide the construction of a systems-level model of beat-based timing within the motor system (with an accompanying computational model as a proof-of-concept). We start by considering simple metronomic stimuli, and find that the neurological processes implicated by the experimental literature naturally generalize to some syncopated and subdivided click-based stimuli.

Most research in beat-based timing has approached beat-based timing guided largely by the questions:

- How do humans correct their errors in motor synchronization? (cite)
- How do humans entrain to a range of different tempi embedded within complex auditory signals? (cite)
- How do humans measure precise intervals? (cite)
- How do humans produce precise intervals? (cite)

As we develop our model along the lines described above, we find that the discussion leaves some ambiguity around these questions, but offers specific answers to a different but overlapping set of questions:

1. How and where are measurements of interval timing converted into durations of interval production?
2. What physiological process provides the medium for physical entrainment to a beat with any effector?
3. How do humans moderate between the influence of a (bottom-up) external stimulus and a (top-down) internally generated beat?

We find that the excellent experimental literature on beat-based timing offers us ample clues with which to begin to construct concrete answers to these questions. In response to the first, we use the literature on timing-related activity in medial frontal cortex and subcortical structures to inform a systems-level framework for interval measurement, memory, and production consistent with ASAP. To address the second, we explore evidence that suggests that well-established motor pathways leading through basal ganglia are activated by covert beat-based timing, and argue that they provide a natural substrate for coordinating multi-effector rhythmic motion. In response to the third, we look to the striatal dopaminergic system as a possible mediator between external stimulus and internal representation of the beat, drawing a connection between this role of dopamine and its hypothesized broader function as an index of confidence and expectation.

The picture that emerges from this investigation is expansive but certainly not complete. It addresses certain key points in detail, but leaves room for a wide range of possiblities in other important areas. Our hope is that this paper will point the way toward a number of hypotheses with some degree of independence from one another that can be explored individually but also viewed in the context of a hypothesized whole.

Timing signals in MFC

We begin this section with some important notes on terminology that may help us navigate the ambiguous language of timing. Most timing tasks can be usefully split into up to three components:

1. **Time measurement**, where external signals mark behaviorally relevant durations and the brain produces some internal representation of those durations.
2. **Time memory**, where the internal representations of durations are sustained over time.
3. **Time production**, where a duration in time memory is used to produce motor or covert activity with duration related to the remembered duration.

The first and third component of timing tasks each require the generation of dynamic neural activity. We will refer to the neural system or subsystem in which this temporally-evolving activity is generated as a **central timing mechanism**. The state or some substate of a central timing mechanism can serve as an input to downstream neural or motor systems; we will refer to such an input as a **timing signal**. In time measurement, a downstream neural mechanism must combine incoming sensory information and the state of a timing signal in order to create a lasting internal representation of elapsed time; we will call such a mechanism a **time reader**.

Central timing mechanisms may be best viewed as dynamical systems [cite] in multi-dimensional state space. Initial conditions and parameters can determine the trajectory followed by the state of the system through this space. A timing signal is perhaps best considered as a single- or multi-variate measurement of this state. Two types of timing signals that may play an especially important role in BBT are signals we will call absolute and relative timing signals. We define an **absolute timing signal** as a signal that passes through a sequence or continuum of states at a reliably stereotyped rate. Dynamical systems that produce absolute timing signals include the pacemaker in pacemaker-accumulator mechanisms, in which "ticks" of a steady clock are counted and used to increment the state of a counter [cite]; ramping activity mechanisms, in which the state would be represented by the level of neuronal activity in some population [cite]; and the Striatal Beat Frequency Model, in which the elapsed time is represented by the collective state of many neural oscillators at a range of frequencies [cite]. Such signals are well suited to time measurement: the state at any point in time is a unique representation of the total elapsed time since the pattern was initiated.

An absolute timing signal could drive a motor output and thus also serve the function of time production. However, we argue that the production of an output consisting of a continuous movement would not be well-served by an absolute timing signal. A more natural signal to drive such an output would be a **relative timing signal**, a signal that can pass through a series or continuum of states at a flexible rate and which may have a specific end-state that can be reached in a flexible amount of time. Most physical movements can be performed at many different speeds, making the movement itself function as a relative timing signal; parsimony suggest that the neural input driving the movement should also be a relative timing signal that can play out at multiple speeds. A relative timing signal could also underly relative measurements of time (i.e., what fraction of a specified interval has elapsed).

In principle, the timing signal underlying the production of a motor output after a covertly timed interval could be either absolute or relative. However, relative timing signals have been observed in multiple brain areas during covert time production, whereas absolute timing signals have been observed

during covert time measurement. In monkeys, Jazaryeri and Shadlen[4] observed that neurons in monkey area LIP ramp up activity along a stereotyped trajectory as they measured an interval they indended to reproduce, and then ramped up at a rate that scaled with the measured interval as they behaviorally produced the same interval. Their results suggest that simple tasks combining measurement and production make use of an absolute timer for measurement and a relative timer for covert production.

Physical or covert entrainment to a beat is another task that combines measurement and production. In the classic SCT, the synchronization phase requires the measurement of a repeated interval, followed quickly by the motor reproduction of the same interval. Merchant et al. (2011)[5] recorded neurons in MFC (consisting of SMA and preSMA) during an SCT and categorized their activity patterns. Some showed ramping activity with a constant slope after each button press, thus functioning as an absolute timing signal, and others showed activity patterns that temporally scaled with the interval being reproduced, thus representing relative timing signals[6]. Thus, it is clear that both absolute *and* relative timing signals are available in MFC during a SCT. Merchant et al[7] then identified a specific population of MFC cells that activate sequentially at a rate depending on the interval duration such that the sequence stretches to the length of the interval, directly demonstrating the presence of a relative timing signal in MFC.

From these results, it is not clear whether the central timing mechanism underlying these signals is upstream from or within MFC. But recent results in monkeys from Wang et al[8] show that during interval production, areas downstream from MFC show dynamics that stretch to the length of the interval, but areas projecting to MFC do not. This suggests that at least the activity generating the relative timing signal originates in MFC. They also show that variability in interval production was largely accounted for by variability in the component of the dynamics that scaled with interval length, directly linking the relative timing signal in MFC to covert interval production. Finally, they provide an elegant model of how the speed of recurrent neural net dynamics can be adjusted by modulating a tonic input parameter, demonstrating the feasibility of generating a relative timing signal in MFC.

These results, taken together, point toward a the beginning of an answer to our first essential question above. **We hypothesize that during metronomic BBT, a dynamical system in MFC produces neural trajectories that simultaneously contain both absolute and relative timing signals after each beat, that the absolute timing signal is used for the "time measurement" task of**

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[4] Rimmele, J. M., Morillon, B., Poeppel, D., & Arnal, L. H. (2018). Proactive Sensing of Periodic and Aperiodic Auditory Patterns. *Trends in Cognitive Sciences*, *22*(10), 870–882. https://doi.org/10.1016/j.tics.2018.08.003

[5] Merchant, H., Zarco, W., Pérez, O., Prado, L., & Bartolo, R. (2011). Measuring time with different neural chronometers during a synchronization-continuation task. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(49), 19784–19789. https://doi.org/10.1073/pnas.1112933108

[6] Note that their absolute/relative terminology does not align with ours: we [unfortunately] categorize their "relative timing cells" and "absolute timing cells" both as "relative timing signals."

[7] Merchant, H., Pérez, O., Bartolo, R., Méndez, J. C., Mendoza, G., Gámez, J., … Prado, L. (2015). Sensorimotor neural dynamics during isochronous tapping in the medial premotor cortex of the macaque. *European Journal of Neuroscience*, *41*(5), 586–602. https://doi.org/10.1111/ejn.12811

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estimating tempo, and that the relative timing signal is used for the "time production" task of waiting the appropriate time for the next response.

Data on monkey timing and sychronization must be taken with a grain of salt when used to inform human beat-keeping. Human behavior in a SCT differs from monkey behavior in at least one important respect: during synchronization, monkeys adopt an essentially reactive strategy [cite], whereas humans show "negative mean asynchrony," anticipating the beat by around 10ms [cite]. However, fMRI data from human BBT tasks shows MFC active during all parts of a SCT [cite a bunch].

Tempo inference.

In humans, Shwartze et al[9] found that preSMA (the rostral end of the MFC) is specifically involved in perceptual timing, making this area a prime candidate for the timing activity necessary for tempo inference (see also [10]). In monkeys, Merchant et al[7] found that of the MFC cells active during a SCT, more cells in preSMA were driven by sensory stimuli (making them better suited to time measurement) whereas more cells in SMA-proper were activated by motor output (making them better suited to time production). Thus, preSMA seems likely to produce the timing signal used for the measurements that determine tempo.

For a timing signal to be used to set a tempo for a metronomic stimulus, the time signal initiated by one auditory event must be observed by a time reader at the next auditory event. The cerebellum appears to serve as such a reader of absolute elapsed time during the timing of non-beat intervals [[[cite]]], but its role in beat-based timing is more controversial. Cerebellar degeneration and TMS do interfere with motor synchronization and the detection and correction of tempo changes[11] [12] [13]and cerebellar volume correlates with strong tempo discrimination[14] as we would expect if the cerebellum was

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[9] Schwartze, M., Rothermich, K., & Kotz, S. A. (2012). Functional dissociation of pre-SMA and SMA-proper in temporal processing. *NeuroImage*, *60*(1), 290–298. https://doi.org/10.1016/j.neuroimage.2011.11.089

[10] Macar, F., Coull, J., & Vidal, F. (2006). The supplementary motor area in motor and perceptual time processing: fMRI studies. *Cognitive Processing*, *7*(2), 89–94. https://doi.org/10.1007/s10339-005-0025-7

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[12] Théoret H, Haque J, Pascual-Leone A. Increased variability of paced finger tapping accuracy following repetitive magnetic stimulation of the cerebellum in humans. Neurosci Lett. 2001 Jun 22;306(1-2):29-32.

[13] Del Olmo, M. F., Cheeran, B., Koch, G., & Rothwell, J. C. (2007). Role of the Cerebellum in Externally Paced Rhythmic Finger Movements. *Journal of Neurophysiology*, *98*(1), 145–152. https://doi.org/10.1152/jn.01088.2006

[14] Paquette, S., Fujii, S., Li, H. C., & Schlaug, G. (2017). The cerebellum's contribution to beat interval discrimination. *NeuroImage*, *163*(August), 177–182. https://doi.org/10.1016/j.neuroimage.2017.09.017

important in extracting tempo, but they do not seem to interfere with perceptual judgments about a beat-based stimulus[15] [16].

Some of this ambiguity is resolved by separating the process of tempo inference from the process of error detection and tempo correction, as suggested by differing fMRI results between the two processes [17]. The olivocerebellar system is not active during synchronization, making it a poor candidate for initial tempo inference, but it shows activity in response to deviations from rhythmic timing, suggesting that it could be used to correct for tempo changes after entrainment[18]. This is consistent with the general picture of the cerebellum as the site of error-based learning (cite), and with results showing increased SMA-to-cerebellum influence during periods of high beat salience[19], when errors are easily detected.

An alternative candidate for observer of elapsed time during tempo inference is dorsal putamen, which receives significant converging sensory and motor input[20] [cite motor input]. Grahn and Rowe[21] found that putamen was not strongly activated during beat finding, but finer-grained fMRI study by Cameron[17] showed dorsal putamen activation during beat finding that shifted to ventral putamen during continuation. Tempo inference by dorsal putamen is consistent with high dorsal putamen firing rates observed just after clicks during synchronization vs. lower rates during continuation[22]. **We (cautiously) hypothesize that absolute timing information in preSMA is ready by dorsal putamen at the time of auditory stimuli, creating a signal that codes tempo.** This proposal turns out to appealing in the context of the larger model because because it gives striatal dopamine direct influence over tempo inference (see section on dopamine below).

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[15] Grube, M., Lee, K. H., Griffiths, T. D., Barker, A. T., & Woodruff, P. W. (2010). Transcranial magnetic theta-burst stimulation of the human cerebellum distinguishes absolute, duration-based from relative, beat-based perception of subsecond time intervals. *Frontiers in Psychology*, *1*(OCT), 1–8. https://doi.org/10.3389/fpsyg.2010.00171

[16] Grube, M., Cooper, F. E., Chinnery, P. F., & Griffiths, T. D. (2010). Dissociation of duration-based and beat-based auditory timing in cerebellar degeneration. *Proceedings of the National Academy of Sciences*, *107*(25), 11597–11601. https://doi.org/10.1073/pnas.0910473107

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[22] Bartolo, R., Prado, L., & Merchant, H. (2014). Information Processing in the Primate Basal Ganglia during Sensory-Guided and Internally Driven Rhythmic Tapping, *34*(11), 3910–3923. https://doi.org/10.1523/JNEUROSCI.2679-13.2014

A tempo established in a SCT can be maintained well beyond the end of the beat-based stimulus. We therefore seek a mechanism for the third timing sub-task, time memory. Our range of rapid tempo flexibility suggests a working memory mechanism rather than a plasticity mechanism. A brain region that emerges as a possible substrate for this memory is the lateral prefrontal cortex. Teki et al.[23] suggest this role for the DLPFC, which they observe to be active along with MFC and putamen during beat-based listening; Thaut et al[24] find this area to be especially active in tasks requiring tempo monitoring. Kung et al. (2013) find that the functional connectivity between ventrolateral PFC and putamen increases during synchronization, suggesting that VLPFC may be the source of a tempo-specific signal that sets the pace for a relative timer to anticipate beats. Covering our bases, **we hypothesize that lateral PFC receives tempo measurements from dorsal putamen and retains a representation of the tempo in working memory.**

Measurement to production via the direct pathway

If it is indeed a relative timing signal that drives interval production, information about the tempo must return to MFC to set the pace of timing. **We propose that when a beat is heard or anticipated, tempo information is conveyed from lateral PFC to MFC via the direct pathway through basal ganglia, re-initiating the central timing mechanism and setting it to the appropriate speed. [[See box -- does not exist yet]]** This hypothesis is motivated by the ASAP hypothesis, which posits that the timing processes used for beat-based timing are repeated "simulated" actions. The direct pathway conveys a signal from prefrontal cortex that initiates the temporal activity in premotor and motor cortex that drives physical movements; we propose that the same pathway conveys an analogous signal from prefrontal cortex that initiates a covert timing process in premotor areas. If a command initiating and setting the speed of a relative timer is carried by the direct pathway, then thalamus should carry duration information during motor production but should not carry a relative timing signal; this was observed in monkeys by Wang et al[8]. The idea of a single brief input setting the speed of the subsequent relative timing signal has been supported in the same lab: Remington et al. (unpublished) find evidence that the initial conditions of the central timing mechanism are sufficient to set the speed of a relative timing signal.

Note that this hypothesis makes syncopation possible: if a beat is anticipated but not heard, this can reset the beat-timing mechanism, causing another beat to be anticipated on the next round. However, in the face of auditory cues that consistently fail to corroborate the internal anticipation of the beat, something clearly has to change; see Internal Beat Strength / Dopamine section below.

Reinforcement of the internal beat by the hyperdirect pathway

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[23] Teki, S., Grube, M., Kumar, S., & Griffiths, T. D. (2011). Distinct Neural Substrates of Duration-Based and Beat-Based Auditory Timing. *Journal of Neuroscience*, *31*(10), 3805–3812. https://doi.org/10.1523/JNEUROSCI.5561-10.2011

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Further clues to the role of the motor system dynamics in beat anticipation comes from the observation of beta (20 Hz) oscillations in auditory and motor areas during BBT tasks that ramp up slowly and then fall abruptly in amplitude with the cycle of the beat[25]. When they report this finding, Fujioka et al. are not especially clear about the timing of the beta drop in motor areas, which could serve as an important clue about the timing of events during the beat cycle. But Te Woerd et al[26] observe similar oscillations in motor areas during a visual periodic timing task that drop in amplitude in immediate anticipation of the arrival of a stimulus. Similar oscillations appear in monkey MFC performing a SCT, where they seem be most prominent during the continuation phase[27].

We hypothesize that the beat-aligned drops in motor beta amplitude are related to the commonly observed drop in motor beta amplitude just before the initiation of movements and restoration of beta just after termination. This beta oscillation is thought to signify the continuation of a "set" state that "promotes the existing motor set whilst compromising neuronal processing of new movements"[28] and during which new motor plans can be formulated[29]. A drop in beta seems to be an important part of motor initiation -- movements initiated in response to unexpected cues show less high beta suppression and longer reaction and movement times, at least in the Parkinsonian brain[30] (more citations?).

Importantly, this motor-related high beta also coheres with a similar oscillation in STN[31] which is closely associated with activity along the "hyperdirect" pathway through BG. The hyperdirect pathway begins with direct cortico-subthalamic projections arising in MFC whose activation is generally understood to carry a global "hold" or "no-go" signal that can prevent the execution of commands carried

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[25] Fujioka, T., Trainor, L. J., Large, E. W., & Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic β oscillations. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *32*(5), 1791–1802. https://doi.org/10.1523/JNEUROSCI.4107-11.2012

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by the direct pathway[32 33 34]). Evidence linking the STN beta signal and cortico-subthalamic projections comes from Litvack et al[35], Tan et al[36], and Sharott et al[37], who note that high-beta activity in Parkinsonian STN seems to be directly driven by similar high-beta activity in MFC (and that this pattern is unaffected by medication, suggesting that one might observe the same in healthy subjects if one could record from healthy human STN). In a credible series of models, STN beta is generated by the negative feedback loop to and from cortex formed by the hyperdirect path, and this activity is suppressed by sufficiently strong activation of the direct pathway[38 39]. It is difficult to overlook the similarity between the antikinetic "set state" associated with cortical beta and the "hold" state associated with the hyperdirect pathway and the STN beta associated with it.

Thus, the beta oscillations modulated by the cycle of the beat **lead us to hypothesize that the periodic wax and wane of a global "hold" signal in BBT is controlled by relative timer state in MFC via drive along the hyperdirect pathway.** The drop in beta may represent this signal being interrupted by the transmission of the relative timer "reset" signal along the direct pathway; alternatively, it may indicate a preparatory drop in order to facilitate transmission along the direct pathway. In either case, the periodic modulation of this hold signal provides a periodic window of low beta amplitude which favor the initiation of movements, and periodic windows of high beta amplitude which could serve as opportunities

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[37] Sharott, A., Gulberti, A., Hamel, W., Köppen, J. A., Münchau, A., Buhmann, C., … Engel, A. K. (2018). Spatio-temporal dynamics of cortical drive to human subthalamic nucleus neurons in Parkinson's disease. *Neurobiology of Disease*, *112*(November 2017), 49–62. https://doi.org/10.1016/j.nbd.2018.01.001

[38] Leblois, A., Boraud, T., Meissner, W., Bergman, H., & Hansel, D. (2006). Competition between Feedback Loops Underlies Normal and Pathological Dynamics in the Basal Ganglia. *Journal of Neuroscience*, *26*(13), 3567–3583. https://doi.org/10.1523/JNEUROSCI.5050-05.2006

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to formulate new motor plans. See Figure 1 for illustration. **We hypothesize that this cycle provides the natural substrate for periodic movement by any effector, i.e., for beat-based dance.**

In the same way that unexpected cues fail to modulate beta and prevent the transmission of fluent motor plans via the direct pathway, auditory cues that arrive between beats while beta is high may be prevented from resetting the central timing system in MFC. This system is ideal for producing some of the recognizable components of beat-based timing. If the timing mechanism is protected from reset between beats, then auditory stimuli that are not near an anticipated beat would not restart the timer, and thus would not be perceived as beats; but stimuli sufficiently close to anticipated beats could reset the timer, allowing for the correction of small timing errors, whether due to neural noise, stimulus phase shift, or incremental tempo change. Phase shifts, in particular, could be completely corrected by this system: as long as the tempo setting does not change, a reset of the central timing system by a slightly early or late stimulus will lead to anticipating the beat exactly one period after the shifted stimulus. This does not correspond perfectly to human tapping data, in which phase shifts are either over- or under-corrected, depending on tempo[40]. However, our model is specifically designed to describe *covert* beat-based timing. The presence of auditory and proprioceptive feedback from slightly inaccurate taps could influence the relative timer too, complicating the correction process.

We note that the combination of the direct go/reset signal and the hyperdirect hold/no-go signal forms a biophysical implementation of the BG-based "gating" process proposed by Ivry and Richardson[41] to explain why tapping with two hands improved temporal consistency over one-handed tapping. In place of their tapping motor programs, we consider a covert relative timer; however, these two pictures are quite consistent with each other. The motor plans themselves coordinated by the relative timer (e.g., foot-tapping) could themselves function as relative timers, issuing the same hyperdirect feedback to basal ganglia that would coordinate their moment of initiation with other motor plans and reinforce the accurate anticipation of the beat. This could explain why physical entrainment improves beat-based timing (cite), and why entrainment of multiple effectors is even more effective[41].

Internal Beat Strength: the dopamine hypothesis

The beat-anticipation system described above can generate a steady beat percept once a tempo is established in working memory. This beat percept can be continued beyond the end of the auditory stimulus so long as the tempo remains in working memory, and can persist in spite of beat-like stimuli that might occur between anticipated beats. If a stimulus indicating a beat occurs in the immediate vicinity of the anticipated beat (while the hold signal is not active), the relative timer resets, which can correct a phase shift in the stimulus.

However, this internally-generated beat percept must be malleable. The system should be able to respond to an incremental or drastic change in tempo by updating the tempo in working memory. In both of these situations, the most apparent signal that the beat has been "lost" and the tempo needs to be

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[40] Repp, B. H., Keller, P. E., & Jacoby, N. (2012). Quantifying phase correction in sensorimotor synchronization: Empirical comparison of three paradigms. *Acta Psychologica*, *139*(2), 281–290. https://doi.org/10.1016/j.actpsy.2011.11.002

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updated would be that the anticipated beats were not corroborated by the acoustic structure of the stimulus. Here we run into a tricky situation: the beat percept must be able to persist through beats without sound (syncopation), sounds without beats (subdivision), and silence (continuation); however, it must yield when the sounds and silences indicate that the stimulus has an underlying pulse that is no longer being accurately anticipated. This problem can be cast as a tension between top-down and bottom-up processing, incorporating it into the much larger discussion of the neural mechanisms moderating between these two modes of processing that together form our perceptual experience (cite).

One useful perspective on this problem is a Bayesian one. We may consider the state of the anticipation system as a hypothesis about the stimulus and its underlying pulse. This state consists of the stored tempo and the instantaneous "phase" represented by the instantaneous position of the relative timer. Following Bayesian reasoning, the likelihood of the "beat-hypothesis" can be evaluated based on the statistical structure of the musical data that the subject has been exposed to. Similar ideas about Bayesian inference of musical structure have been explored in several recent publications, particularly for inference of musical meter[42] [43].

Here we are concerned with physiological implementation, so we will not dive too far down this intriguing rabbit-hole. If we limit ourselves to click-based rhythms and make some reasonable assumptions about the statistics of rhythms heard over the course of development, the problem becomes much more concrete. The event that best supports a beat-hypothesis should be a click corresponding perfectly with the anticipated beat. The evidence that should refute a beat-hypothesis is less obvious, but such evidence will likely include (1) many clicks, none of which correspond with the anticipated beat, indicating a total failure of the hypothesis; and (2) a click slightly but noticably before or after the anticipated beat, indicating that the tempo may have increased or decreased.

Given these constraints, is there a physiological mechanism that could provide a running estimate of the likelihood of (or level of confidence in) a beat-hypothesis? We argue that dopamine in the striatum naturally plays this role. Although dopamine has long been understood to encode reward prediction error (cite), a running line of evidence suggests that its function may be better characterized as encoding perceptual uncertainty. Friston et al[44] argue that "dopamine reports the precision or salience of sensorimotor constructs (representations) encoded by the activity of the synapses they modulate," and therefore that "changing the levels of dopamine changes the level of uncertainty about different representations." Recent experimental evidence has offered support for this interpretation[45] [46] [47]. Sarno et

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[42] van der Weij, B., Pearce, M. T., & Honing, H. (2017). A probabilistic model of meter perception: Simulating enculturation. *Frontiers in Psychology*, *8*(MAY), 1–18. https://doi.org/10.3389/fpsyg.2017.00824

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[44] Friston, K. J., Shiner, T., FitzGerald, T., Galea, J. M., Adams, R., Brown, H., … Bestmann, S. (2012). Dopamine, affordance and active inference. PLoS Computational Biology, 8(1). https://doi.org/10.1371/journal.pcbi.1002327

[45] Lak, A., Nomoto, K., Keramati, M., Sakagami, M., Harbor, C. S., States, U., … Unit, C. N. (2018). Midbrain dopamine neurons signal belief in choice accuracy during a perceptual decision, *27*(6), 821–832. https://doi.org/10.1016/j.cub.2017.02.026.Midbrain

al.[48] find that the striatal dopamine signal codes for both temporal expectation of perceptual cues and for certainty about the presence of a stimulus. Tomassini et al.[49] find that antagonists for dopamine in the nigrostriatal system increase "temporal uncertainty" in an interval-production task with motor output. This is consistent with our hypothesis that low dopamine causes a lack of confidence in their anticipation system (and, in the case of beat-based timing, a resulting reliance in sensory input to establish a beat percept). And Koshimori et al.[50] find that the presence of rhythmic auditory stimulation (RAS) during a tapping task modulates dopaminergic responses in ventral striatum of healthy adults, indicating that successful entrainment does have dopaminergic modulatory effect in basal ganglia. In light of these data points, **we hypothesize that striatal dopamine acts as a measure of "internal beat strength" (IBS) that determines how staunchly the internal beat percept should persist in the face of possible contrary evidence.** In order to moderate between the internal (top-down) interpretation and the external (bottom-up) evidence, striatal dopamine must have influence over the pathways by which new tempo measurements are internalized and by which the internal beat percept persists. We have posited above that both these pathways indeed pass through striatum, with the former in dorsal and the latter in ventral putamen; thus, **we further hypothesize that striatal dopamine levels at relevant synapses respond to accurate beat anticipation by reinforcing transmission in ventral putamen, and respond to errors indicating inaccurate beat anticipation by reinforcing transmission in dorsal putamen.** See Figure 2 for illustration.

The IBS concept offers a specific explanation for why listeners do not respond to a phase shift in a periodic stimulus by immediately changing the tempo of their tap[51]: at the moment of their first inaccurate tap, IBS is still high, preventing the tempo from being updated. Their inaccuracy lowers IBS, and if their next tap is also inaccurate, tempo is measured and updated (Figure 3). It also offers an explanation for the hysteresis of beat-tracking reported by Lenc et al[2], where subjects can track the beat of

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[46] Kwon Starkweather C, Babayan BM, Uchida N, Gershman SJ. 2017 Dopamine reward prediction errors reflect hidden-state inference across time. Nat. Neurosci. 20, 581–589. (doi:10.1038/nn.4520)

[47] Takahashi YK, Langdon AJ, Niv Y, Schoenbaum G. 2016 Temporal specificity of reward prediction errors signaled by putative dopamine neurons in rat vta depends on ventral striatum. Neuron 91, 182–193. (doi:10.1016/j.neuron.2016.05.015)

[48] Sarno, S., De Lafuente, V., Romo, R., & Parga, N. (2017). Dopamine reward prediction error signal codes the temporal evaluation of a perceptual decision report. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(48), E10494–E10503. https://doi.org/10.1073/pnas.1712479114

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[50] Koshimori, Y., Strafella, A. P., Valli, M., Sharma, V., Cho, S., Houle, S., & Thaut, M. H. (2019). Motor Synchronization to Rhythmic Auditory Stimulation (RAS) Attenuates Dopaminergic Responses in Ventral Striatum in Young Healthy Adults: [11C]-(+)-PHNO PET Study. *Frontiers in Neuroscience*, *13*(February), 1–10. https://doi.org/10.3389/fnins.2019.00106

[51] Repp, B. H., & Keller, P. E. (2004). Adaptation to tempo changes in sensorimotor synchronization: Effects of intention, attention, and awareness. *Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, *57*(3), 499–521. https://doi.org/10.1080/02724980343000369

a complex rhythm only if it starts as a simple rhythm and becomes progressively more complex: before IBS is high, it is difficult to find a beat in a complex stimulus, but once the subject has listened to and correctly parsed the beat in a simple rhythm, IBS increases, allowing the internally driven beat percept to persist as the rhythm grows more complex.

Note that the idea of tracking confidence in an interpretation of a temporal auditory signal evolving on a subsecond time scale and using this confidence to balance between bottom-up and top-down influence has already been suggested in the domain of language. Brothers et al.[52] write, "we propose that listeners track the degree to which their predictions are accurate, andadjust the strength of their predictions based on these calculations. We propose …. that when prediction error is high and the comprehension system has been unsuccessful in anticipating upcoming words, the system will ignore or inhibit top-down pre-activation, and instead devote more resources to bottom-up stimulus evaluation."

The role of dopamine proposed above requires a system for measuring small timing errors between anticipation and stimulus. We are agnostic about how this timing comparison takes place, but a similar role has been proposed for the olivocerebellar system[53]. The inferior olive has been shown to produce an absolute timing signal initiated by sensory input (cite) that is available to the cerebellum, and appears to activate in response to deviations from rhythmic timing[18]. Coupled with the recently established existence of extensive connections from cerebellum to substantia nigra[54], the olivocerebellar system is well suited to error-based dopaminergic modulation of the striatum.

Model implementation in silico

We have incorporated our main hypotheses into a proof-of-concept computational model. A detailed characterization of the model (will be added to later drafts). The most important modeling decisions included designing a profile for hyperdirect drive (signified by beta amplitude) between beats; choosing how this beta amplitude would increase with internal beat strength; choosing what level of hyperdirect drive would be sufficient to keep and auditory event from resetting the timer; and choosing a threshold for dopaminergic internal beat strength below which tempo could be changed and above which the relative timer could reset without an auditory event. See Figure 3 for results.

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[52] Brothers, T., Swaab, T. Y., & Traxler, M. J. (2017). Goals and strategies influence lexical prediction during sentence comprehension. *Journal of Memory and Language*, *93*(January), 203–216. https://doi.org/10.1016/j.jml.2016.10.002

[53] Teki, S., Grube, M., & Griffiths, T. D. (2012). A Unified Model of Time Perception Accounts for Duration-Based and Beat-Based Timing Mechanisms. *Frontiers in Integrative Neuroscience*, *5*(January), 1–7. https://doi.org/10.3389/fnint.2011.00090

[54] Milardi, D., Arrigo, A., Anastasi, G., Cacciola, A., Marino, S., Mormina, E., … Quartarone, A. (2016). Extensive direct subcortical cerebellum-basal ganglia connections in human brain as revealed by constrained spherical deconvolution tractography. *Frontiers in Neuroanatomy*, *10*(MAR), 1–10. https://doi.org/10.3389/fnana.2016.00029

Compatibility with other models

Several existing timing models can be examined in light of the ideas developed here. The Striatal Beat Frequency (SBF) model[55] posits a bank of oscillators in MFC running at a range of frequencies and reset by salient input such that the time since the input can be read from the combined state of the oscillators. This is simply one type of absolute timing signal for purpose of measurement. SBF also posits that the state of the timer is "read" by the striatum. As discussed above, we hypothesize that the absolute timer used to infer tempo is indeed read by striatum (specifically, dorsal putamen), making the tempo inference system in our model effectively equivalent to an SBF model.

One way to circumvent the need for an absolute timer in tempo inference would be for the relative timer to be initiated at some default speed, making it function as an absolute timer between the first two beats. Such a system is proposed and modeled by the Jazayeri lab (unpublished), and provides a satisfying interpretation of certain behavioral data. However, since both a relative and an absolute timing signal is available in MFC throughout synchronization, we do not find it necessary to assume that measurement and production rely on the same signals from the MFC activity.

Large and colleagues[56] propose that tempo is inferred by a bank of resonating oscillators in MFC. Finding common ground between our ideas and resonance-based models requires some conceptual stretching, but since these models show impressive ability to identify beats in complex stimuli, this attempt is worthwhile. Projecting our framework onto these models, the "reading" of an absolute time signal from this bank occurs over several beats, as the oscillator with the greatest amplitude indicates the absolute time interval that lends the most plausible isochronous structure to the stimulus. These readings could be used as we propose above: a tempo-specific signal could pass to tempo memory, and a direct pathway signal could pass from tempo memory back to MFC at beats. This signal would reinforce the appropriate one of the many oscillators such that the state of the dominant oscillator could be read as a relative timing signal.

Importantly, each of these models make claims about dynamics in motor areas, but none directly address the physiological underpinning of beat-based dance or the physiological medium for transitioning between a bottom-up and top-down beat percept. **Thus, these models leave significant space for the hypotheses about a dopaminergic index of internal beat strength and the engagement of specific motor loops that we have posited above.**

Implications for Parkinson's Disease

The implications of the integrated model for Parkinson's Disease are exciting. Parkinsons patients show impairment in rhythmic timing (cite), which is linked to the primary symptom of "freezing of gait" (FOG) (cite). Several lines of evidence suggest that this deficit is directly linked to a reduction of striatal dopaminergic signaling, suggesting a central role for striatal dopamine in rhythmic timing (cite). Our proposed role of dopamine as a measure of "internal beat strength" offers a concrete mechanism by which

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[55] Matell, M. S., & Meck, W. H. (2004). Cortico-striatal circuits and interval timing: Coincidence detection of oscillatory processes. *Cognitive Brain Research*, *21*(2), 139–170. https://doi.org/10.1016/j.cogbrainres.2004.06.012

[56] Large, E. W., Herrera, J. A., & Velasco, M. J. (2015). Neural networks for beat perception in musical rhythm. *Frontiers in Systems Neuroscience*, (November), 1–14. https://doi.org/10.3389/fnsys.2015.00159

reduced striatal dopamine could impair rhythmic timing. The hypothesis posits that certain dopamine levels represent internal beat strength, and that high dopamine strengthens the signal initiating the relative timer (via the direct pathway) and protects the tempo representation in working memory. In this case, reduced dopamine would make it difficult to initialize the relative timer essential for beat anticipation and would prevent working memory from maintaining a steady tempo.

One effective treatment for FOG is rhythmic auditory stimulation (RAS) by metronome or beat-based music (cite). RAS has recently been shown to effectively treat Parkinsonian rhythmic impairments beyond FOG (cite), suggesting that it is not just rhythmic footfall but the mechanism underlying rhythmic motion that is being addressed. A common explanation for the efficacy of RAS is that it recruits cerebellar "implicit" timing circuits to compensate for impaired "explicit" timing in basal ganglia circuits[57]. However, Fischer et al[58] found that during walking in place, STN beta peaked when the contralateral foot was on the ground and dropped rapidly as the foot was lifted, and that this pattern that was enhanced by RAS. This result strongly suggests that RAS acts directly on the basal ganglia and on the central beat-keeping system. (See also Hell 2018[59]).

In our integrated motor model of beat based timing, the relative timer underlying covert beat-keeping can be re-initialized by its own termination, but the go signal must first make its way through striatum, which is less excitable in Parkinson's due to the lack of dopaminergic modulation. A pulse of auditory input arriving at striatum at the same moment as this go signal could provide sufficient additional excitation for the signal to pass through the impaired striatum and reset the timer. The strong cycle of the beta-oscillatory hold signal induced by the relative timer could provide clear windows for planning and executing motor programs. However, the covert relative timer may only be part of the picture: *a step itself* and the motor program operating it could act as a partially-external relative timer, issuing its own hold signal during execution, and its own go signal, presumably initiating motor programs associated with the next step, at heel strike. The arrival of an auditory pulse at the time of a go signal from this overt timer would help the signal through striatum in the same way it helps the covert timer's signal.

Testable predictions.

We will explore testable predictions of each component of our model separately.

Hypothesis: An absolute timing signal is read from MFC by dorsal putamen to set a tempo representation in DLPFC.

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[57] Sen, S., Kawaguchi, A., Truong, Y., Lewis, M. M., & Huang, X. (2010). Dynamic changes in cerebello-thalamo-cortical motor circuitry during progression of Parkinson's disease. *Neuroscience*, *166*(2), 712–719. https://doi.org/10.1016/j.neuroscience.2009.12.036.Dynamic

[58] Fischer, P., Chen, C. C., Chang, Y.-J., Yeh, C.-H., Pogosyan, A., Herz, D. M., … Tan, H. (2018). Alternating Modulation of Subthalamic Nucleus Beta Oscillations during Stepping. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *38*(22), 5111–5121. https://doi.org/10.1523/JNEUROSCI.3596-17.2018

[59] Hell, F., Plate, A., Mehrkens, J. H., & Bötzel, K. (2018). Subthalamic oscillatory activity and connectivity during gait in Parkinson's disease. *NeuroImage: Clinical*, *19*(February), 396–405. https://doi.org/10.1016/j.nicl.2018.05.001

Prediction (in monkeys): Population activity in dorsal putamen at salient auditory events could be used to decode elapsed time since one or more previous events. Population activity in DLPFC at any point during music listening could be used to decode tempo.

Hypothesis: A relative timer in MFC is reinitialized by its own termination and (sometimes) by salient auditory events via the direct pathway, and this signal carries information from DLPFC setting its speed.
Prediction (in monkeys): At beats, but not necessarily at other times, there should be a pulse of activity along the direct pathway, and population activity in ventral putamen and motor thalamus could be used to decode the most recent estimate of the inter-beat interval.

Hypothesis: Indirect pathway activity rises and falls with the beat, leaving periodic windows that globally facilitate movement initiation and windows that globally inhibit movement initiation as a new motor plan is formulated.
Prediction (in humans): Firing rates or beta oscillations in STN are modulated by the beat, and drop in immediate anticipation of beats.

Hypothesis: Dopamine levels at relevant synapses in striatum determine whether the beat percept is more driven by top-down internal anticipation or bottom-up auditory input.
Prediction (in monkeys): In PET scans, dopamine levels in dorsal and ventral putamen should change in opposite directions as the beat is identified and then continued in a SCT.

Hypothesis: These same dopamine levels respond to the accuracy of temporal anticipation, tilting the table toward bottom-up when anticipation is inaccurate and toward top-down when it is accurate.
Prediction: Sequences that elicit high or low beat prediction accuracy produce different dopamine levels in PET scans. There should be a drop in dopamine as a rhythm with a steady beat dramatically changes in tempo or is replaced by a rhythm with a different beat (see Cameron (2016)[17]).

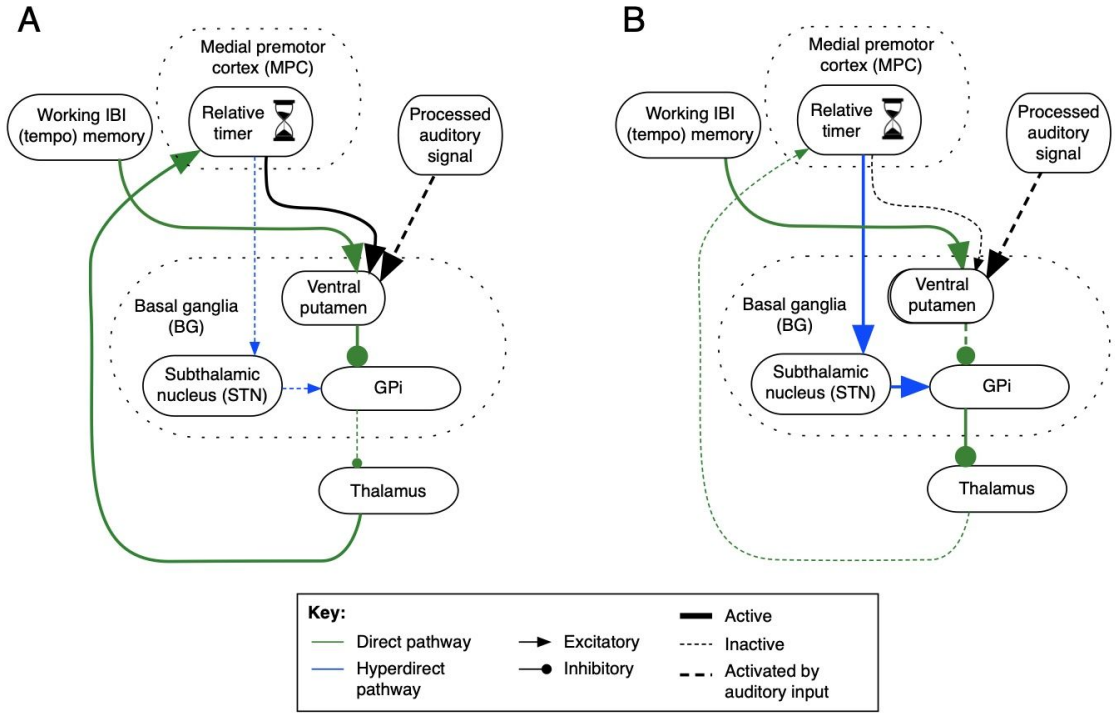

Figure 1: **Schematic diagram of beat anticipation.** Working memory sends a persistent signal to start the relative timer at a specific speed; however, this signal does not always make it through basal ganglia. Note that this signal, sent along the direct pathway, is the only signal in the diagram carrying labeled-line information. The rest are simply timed pulses of activity. **(A)** The hyperdirect pathway is not active just before or after an anticipated beat. At each perceived beat, the relative timer sends a strong signal to ventral putamen. Bolstered by this signal and/or by an auditory pulse, the command from working memory makes it through the direct pathway and re-initiates the relative timer. Thus, a beat can be anticipated without auditory input, and an auditory pulse in the neighborhood of an anticipated beat can correct the phase of the perceived beat. **(B)** Between beats, the relative timer activates the hyperdirect pathway. Even if an auditory pulse arrives, the hyperdirect signal prevents the command from passing through basal ganglia by exciting GPi. Thus, auditory input that is not near an anticipated beat is not interpreted as a beat and does not change the phase of the beat percept.

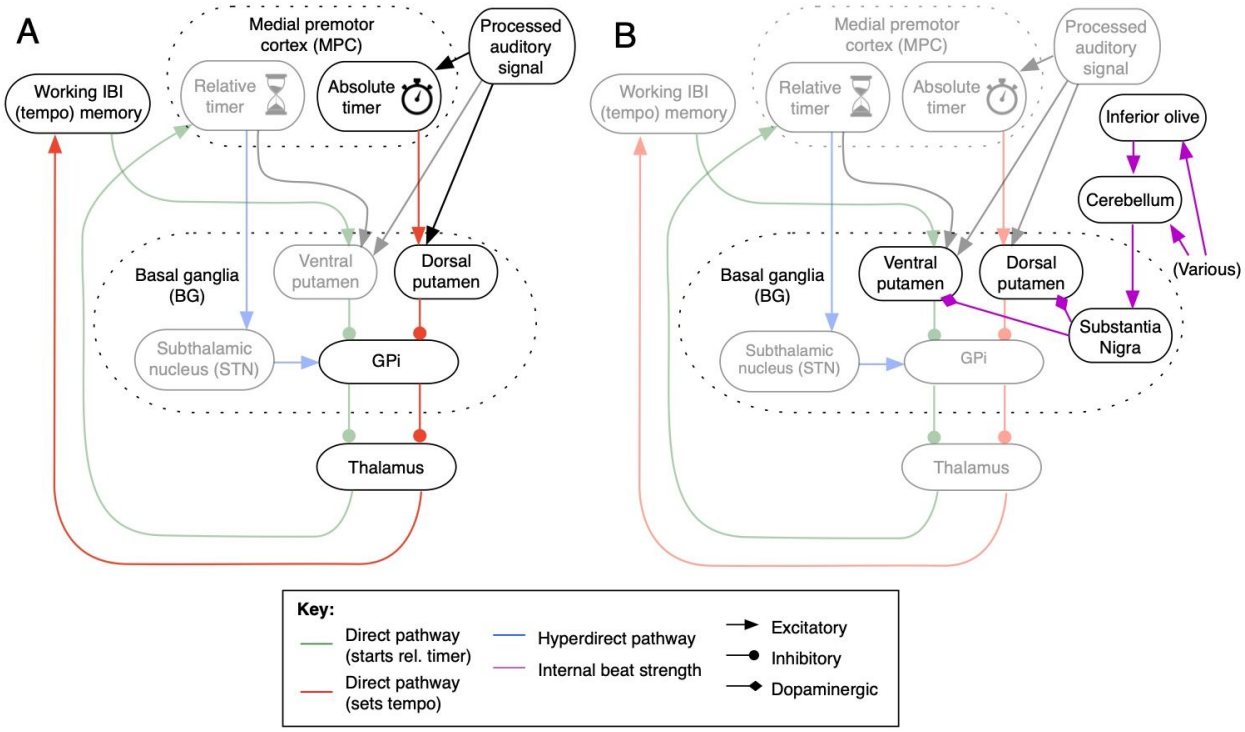

Figure 2: **The integrated motor model of beat-based timing includes a system that measures tempo and a dopaminergic mechanism representing "internal beat strength." (A)** An absolute timer in medial premotor cortex is initialized at auditory pulses. When another pulse arrives, dorsal putamen passes a measurement of the elapsed time through the direct pathway to working memory, where it is preserved as an estimate of the tempo. **(B)** The inferior olive and cerebellum perform a similar absolute timing operation to detect small errors in beat anticipation. Accurate anticipation raises the "internal beat strength" by bolstering the ventral putamen with dopamine, thus weighting the beat anticipation system over the tempo extraction system. Inaccurate anticipation lowers the "internal beat strength" by giving dopaminergic weight to the dorsal putamen instead and thus favoring the tempo extraction system over the beat anticipation system.

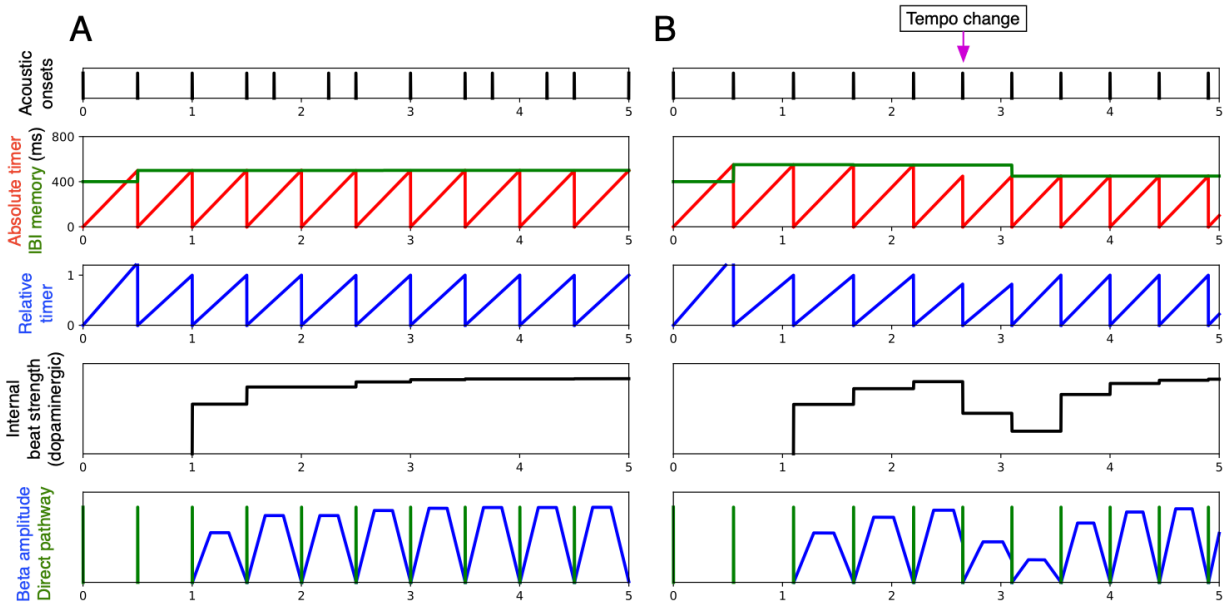

Figure 3: **The integrated model can track beat through complex rhythms and adjust to tempo changes. (A)** The model maintains a steady beat throughout a rhythm in which not all beats are marked by onsets, and not all onsets mark beats. The absolute timing system times the first interval and then sets the tempo memory that determines the speed of the relative timer thereafter. Accurate anticipation by the relative timer raises internal beat strength. While internal beat strength is high, the relative timer resets on termination even without an auditory cue. The hyperdirect drive between beats (as measured by beta amplitude) prevents the reset of the relative timer by auditory cues that are sufficiently far from anticipated beats. **(B)** The model adjusts the internal period (tempo) of perceived beats in response to a tempo increase in the auditory rhythm. Onsets arriving slightly earlier than anticipated lower internal beat strength, allowing the absolute timer reading to reset the tempo memory. This speeds up the relative timer so that it accurately anticipates the faster beat, and internal beat strength is restored.