How beat perception coopts motor neurophysiology: a proposal

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Abstract

Beat perception is central to music cognition. The motor system is involved in beat perception, even in the absence of movement, yet current frameworks for modeling beat perception do not strongly engage with the motor system's neurocomputational properties. We believe fundamental progress on modeling beat perception requires a synthesis between cognitive science and motor neuroscience, yielding predictions to guide future research. Success on this front would be a landmark in the study of how "embodied cognition" is implemented in the details of brain activity. We illustrate this approach by proposing specific roles for two key motor brain structures (the supplementary motor area and basal ganglia) in covert beat maintenance, building on current research on their role in actual movement.

Glossary

ASAP: The Action Simulation for Auditory Prediction hypothesis

Striatum: The main input structure to the basal ganglia

Putamen: The subregion of striatum most associated with motor function

Isochronous: Occurring periodically in time with a constant interval between events

SMA: Supplementary motor area (a cortical region that contributes to motor control, planning, and coordination)

fMRI: Functional magnetic resonance imaging.

Highlights

- The Action Simulation for Auditory Prediction (ASAP) hypothesis posits that covert anticipatory timing of a musical beat is performed by the motor system.
- Supplementary motor area is hypothesized to host adjustable-speed timing processes that also underlie movement and that inform the timing of sound expectations on each beat cycle.
- Dorsal striatum is hypothesized to initiate and sequence these timing processes, akin to the way it initiates and sequences movement.
- Striatal dopamine is hypothesized to serve as an index of confidence in the internally represented beat and facilitate the initiation of beat-timing processes.

Outstanding Questions

- Could a computational model based on predictive processing and active inference give suitable expression to the ideas outlined here?
- To what extent are our proposed motor mechanisms of beat maintenance shared across species?
- How does the development of the motor system parallel the development of beat perception?

What is the motor system doing during beat perception?

The widely shared experience of an **isochronous** "beat" (an underlying regularly timed pulse) in rhythmic music is a fascinating example of human perception extending beyond what is presented to our senses. When an auditory rhythm has induced the sense of a beat, the listener implicitly knows where each beat falls in time, even though some beats may not be marked by sound and some sounds can occur at non-beat times. (see Figure 1A and supplemental sound file). We will refer to this implicit anticipation and perception of beat times as "beat maintenance." (We consider it independently of the process of "beat finding" that precedes it: see [1,2] for neural research dissociating these two processes.)

In humans, the internal maintenance of a beat is closely related to movement. A perceived beat often elicits rhythmic motion (a response that emerges spontaneously in children, is seen across cultures, and is foundational to dance [3–5]), and rhythmic motion improves accuracy on beat-based perception tasks [6]. However, even in the absence of movement (i.e., in covert beat maintenance), the beat retains a link to motion, because a beat may be described as a point in a rhythm at which the listener *would* step *if* they were dancing. Actual movement to a beat reveals a key feature of beat maintenance: when synchronizing movement with beat-based patterns, adults *spontaneously predict the timing of beats with a high degree of accuracy*, tapping or stepping within a few 10s of ms of beat times and often slightly ahead of the beat. This contrasts with monkeys, who spontaneously move reactively rather than predictively when entraining movements to rhythmic sounds, and who require special training to move predictively [7].

A crucial finding linking covert beat maintenance and movement comes from neuroimaging: **fMRI** research reveals that a number of cortical and subcortical motor regions are strongly active and interacting while a beat is perceived even in the absence of movement. The most consistent of these regions are the cortical **supplementary motor area (SMA)** and the subcortical **dorsal striatum** of the basal ganglia (most often its subregion the **putamen**, but also the caudate nucleus) [8–14], which are part of the brain's "direct pathway" for motor control (Figure 1B). Another line of neural evidence linking beat perception with the motor system comes from Parkinson's disease: Parkinsonian dopamine depletion in basal ganglia is linked to

impaired beat-based timing [15–17], and beat-based rhythms show great promise in rehabilitating Parkinsonian gait [18] and other rhythmic impairments [19].

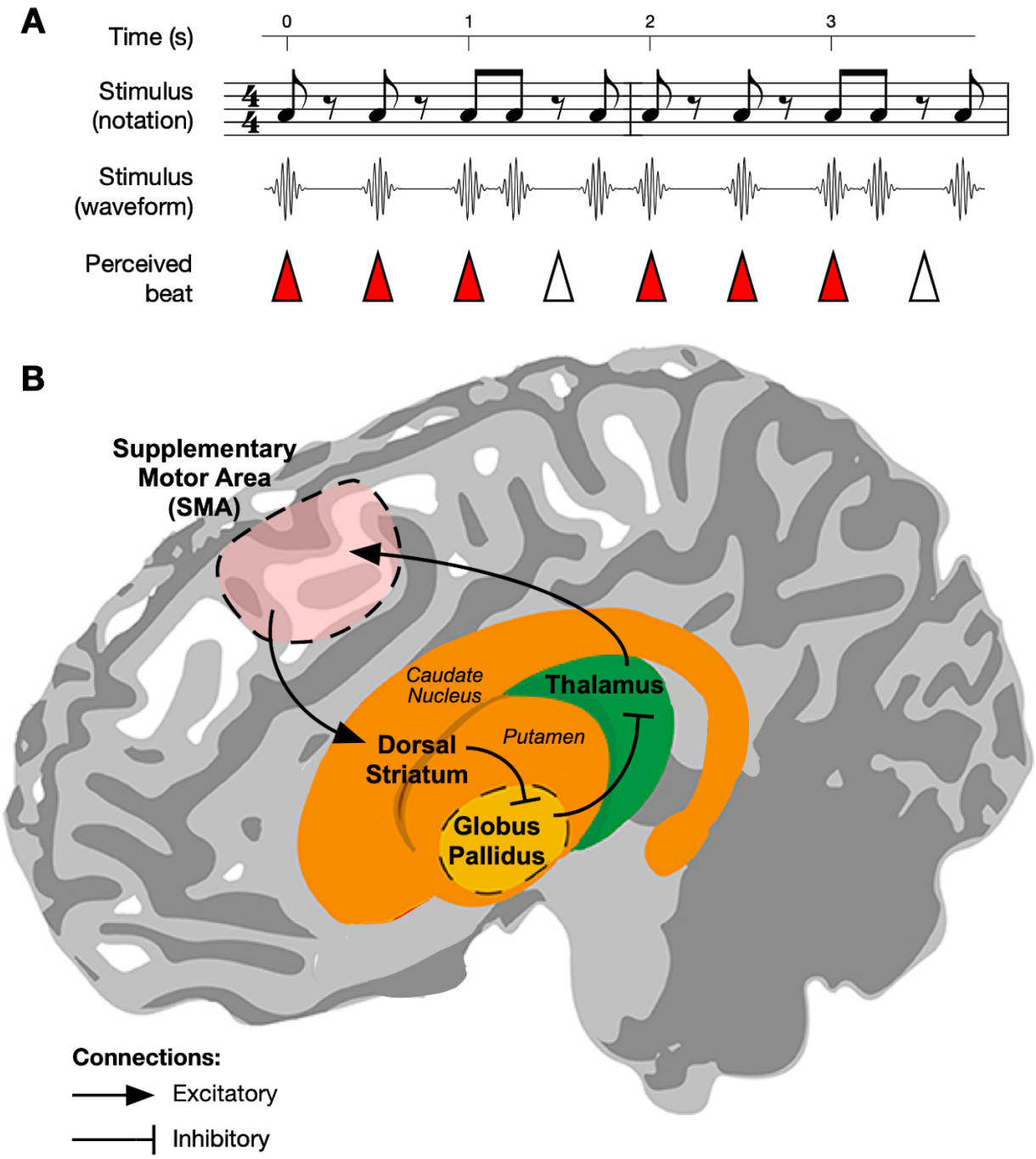

Figure 1: Beat perception and the motor system. A) A simple, repeating non-isochronous rhythm is shown in music notation and as an acoustic waveform. The rhythm induces an isochronous beat percept (beat locations shown by triangle tips). Note that some beats are not marked by sounds (hollow triangles), and some sounds occur at non-beat times. The reader is encouraged to listen to the

corresponding sound example (in which the above rhythm is looped several times) to verify the beat percept. **B)** A simplified schematic of the direct pathway loop connecting the two key areas discussed in this paper in reference to beat perception. The supplementary motor area (SMA) projects to the dorsal striatum (consisting of the putamen and caudate nucleus). Dorsal striatum inhibits the internal segment of globus pallidus (shown here hidden behind the striatum), which inhibits thalamus. Closing the loop, thalamus excites SMA. During physical movement, this pathway is thought to selectively disinhibit populations in SMA necessary for the next sub-movement in a sequence. Here, we propose that the same process is used to disinhibit populations that generate the temporal dynamics necessary to covertly anticipate the next beat in a rhythm. Figure adapted from [20]. CC BY 3.0 https://creativecommons.org/licenses/by/3.0/

It is possible that the motor system's activation by covert beat maintenance is a passive byproduct of the frequent association of beat perception and movement. However, a number of authors over the past two decades have argued that the motor system plays a causal role in beat perception even when no movement is involved, e.g., in temporal prediction of beats [12,21–23]. Some have specifically suggested that beat-based temporal predictions arise from "simulated rhythmic actions" in the motor system [24–28]. For example, the "Action Simulation for Auditory Prediction" (**ASAP**) hypothesis [26] posits that simulated actions in motor planning regions provide temporal predictions about beat times which influence activity in auditory regions via two-way connections in a cortical dorsal auditory stream (see [29] for one recent test of this hypothesis).

In this opinion piece, we argue that the idea of temporal computations via internal actions can be mapped on to a specific proposal about the roles of the SMA and dorsal striatum in beat maintenance. Crucially, this proposal draws heavily on known aspects of motor system physiology (and the roles of the SMA and dorsal striatum in actual movement), thus integrating cognitive science and motor neuroscience. This integration allows us to hypothesize and explore how "embodied cognition" works in terms of specific regions and pathways in the brain.

Our paper focuses on the roles SMA and the dorsal striatum because we find that an understanding of the motor functions of these brain structures can be generalized to account for the maintenance of an internal pulse underlying a rhythm. We emphasize that our intent in this paper is not to construct a full model of beat perception. In particular, our proposal does not account for the process by which one first recognizes that a rhythm supports a beat and identifies the beat's tempo and phase ("beat finding") [1,2]. However, by focusing on the regenerative process of temporal prediction once a beat is found ("beat maintenance"), we hope that our limited proposal can catalyze a more thorough program of identifying and modeling the neurophysiological mechanisms responsible for our sense of beat in rhythmic patterns.

SMA: "proto-action" for timing and prediction

In humans, the supplementary motor area (SMA)[1] is activated by a range of beat-based tasks, including self-paced finger tapping, tapping entrained to music, and (most importantly for this discussion) tasks involving the covert generation of a beat [8,9,14,30]. Differences in SMA activation account for individual differences in performance on covert beat-based timing tasks [31,32], indicating that SMA plays an important functional role in covert beat generation. A covert repetitive timing task in monkeys has demonstrated that neural activity in SMA can maintain an ongoing "metronome," tracking task-relevant periodic time intervals even in the absence of sensory cues [33].

As we attempt to formulate hypotheses of the mechanistic roles played by SMA in beat-based predictive timing, the ASAP hypothesis suggests that we look to its role in movement. To fully appreciate this role, it is important to look at motor control through the increasingly influential "dynamical systems" lens [34,35]. While the classical "tuning/decoding" perspective on brain activity asks how the activity of specific neurons may represent different aspects of movement (such as direction, velocity, etc.), the "dynamical systems" perspective asks how dynamic interactions between neurons can give rise to reliable, flexible time series of motor commands. For example, monkey electrophysiology and computational modeling have shown that arm reaching actions are orchestrated by temporal fluctuations in firing rates of neurons in motor cortex, and that over the course of one reach, these fluctuations are likely attributable largely to interactions between these neurons via recurrent connections [35]. These fluctuations can be viewed as tracing out reliable paths ("trajectories") in an underlying space of possible firing rates, with each position in space corresponding to a set of signals being relayed to the muscles controlling the action (see Figure 2 for illustration).

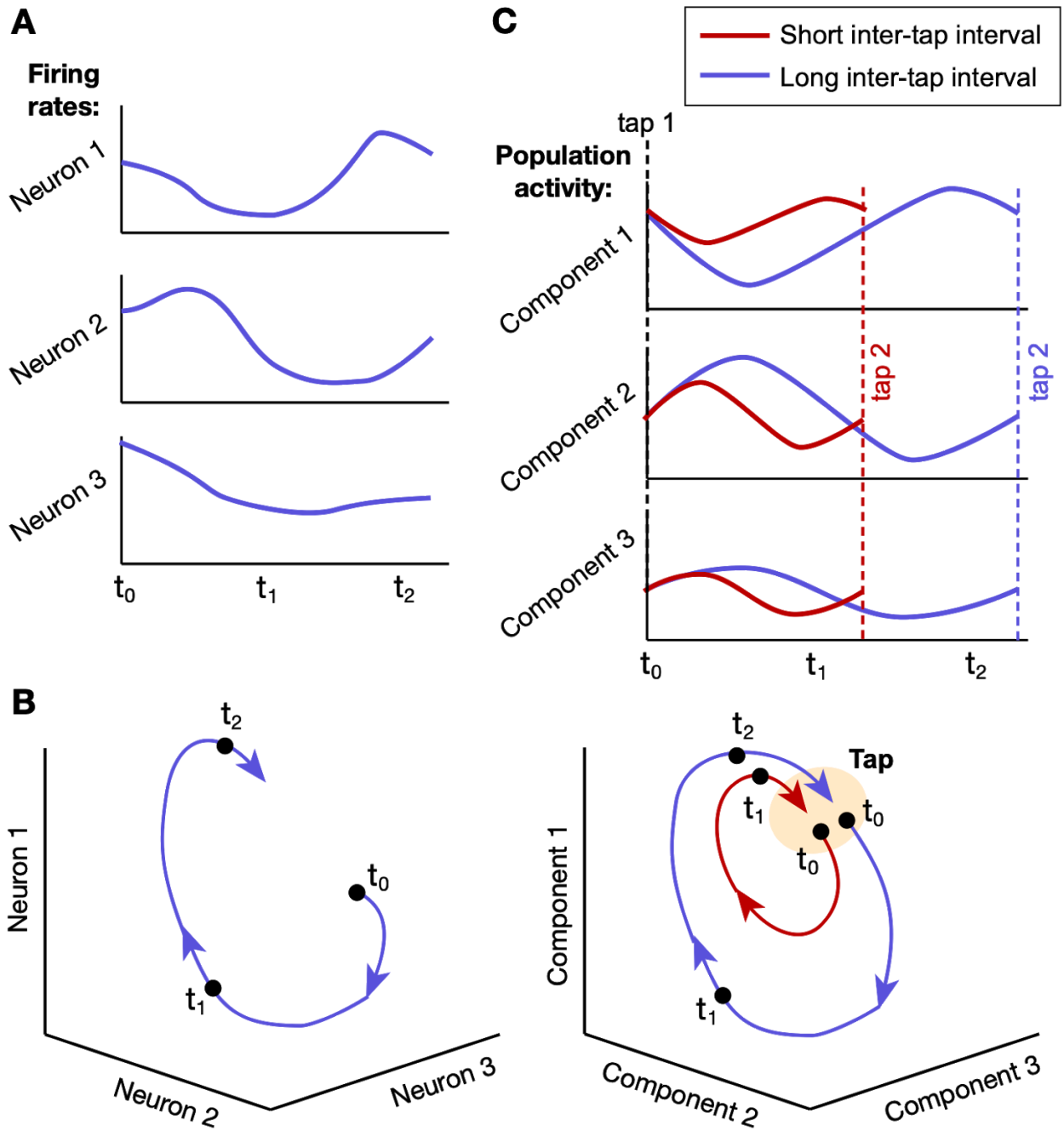

Figure 2: Illustration of time-keeping by neural firing rate trajectory. In monkey SMA, reliably patterned fluctuations in the collective firing rates of neural populations keep time during deliberately timed behaviors like rhythmic tapping. These fluctuations can be visualized as tracing out paths ("trajectories") in a high-dimensional space of firing rates, with the shape and time course of the path dependent on the time course of the behavior. A) Fluctuations in the firing rates of three neurons graphed over time

during a timed behavior. B) The same fluctuations visualized as a trajectory in a three-dimensional space, where each axis represents the firing rate of one neuron and each point on the trajectory represents the three firing rates at one point in time (three example time points are marked). C) Trajectories traced by firing rates in large neural populations (i.e., hundreds, rather than just three) are easier to visually understand in “principal component” space [36], where each axis is a “component” corresponding to the correlated activation of many neurons, and where components accounting for the most combined variance in population firing rates are displayed. Empirical research on periodic tapping in monkeys shows that the firing-rate fluctuations in SMA between consecutive taps trace out circular trajectories in principal component space. For shorter inter-tap intervals, firing rates fluctuate faster but with lower amplitudes, creating smaller loops that repeat with a shorter period [37]. (Image adapted from the results of [37] and simplified for illustration.)

Research shows that during movement execution, dynamics in SMA resemble those in motor cortex: neural firing rates during a specific movement pattern follow reliable, repeatable trajectories. But recent results indicate that firing rates in SMA give a more abstract representation of progress through a given action, continuing to change over time through periods of motionlessness (e.g., between consecutive finger taps [38]) and occupying distinct states on consecutive repetitions of the same movement [39–41]. Importantly, when motionless behavioral intervals are deliberately lengthened or shortened (i.e., a wait time or the time between repeated actions is extended to meet task demands), some combination of the speed and amplitude of these trajectories and the number of neurons involved adjusts accordingly, *tuning the system to arrive at a similar end state associated with a behavioral response (e.g., a tap) in a different amount of time* [37,38,42] (see Figure 2C).

Following ASAP's analogy of covert inter-beat interval timing to action, we hypothesize that SMA behaves in covert beat-based timing like it behaves during overt cyclic movement (such as repetitive reaching or tapping) , but without the accompanying motor cortex activation directing physical action. In other words, **we propose that SMA tracks progress through each beat interval by generating firing rate dynamics that are tuned to arrive at a characteristic state at the next beat time**, whether or not there is a behavioral response attached to that beat.

How is SMA tuned to create dynamics that anticipate the appropriate interval? Analysis of brain dynamics in regions upstream and downstream from SMA in monkeys (and supporting models) indicate that interval-specific adjustments to these trajectories seem to be made through modulation of tonic inputs to and/or initial state of an SMA network, with the resulting dynamics generated through local interactions within SMA [42–44]. (As noted previously, the question of how the beat interval is initially measured, internalized, and updated such that it can be used to inform SMA falls outside the scope of this paper, which focuses on internal maintenance of a beat once it is identified.)

The beat-anticipatory trajectory in SMA plays the role of the timing component of the "simulated action" posited by the ASAP hypothesis. Note, however, that it need not correspond

to a specific action. We will refer to a beat-anticipatory trajectory in SMA as a “proto-action” because this type of brain activity appears to underlie and temporally structure action without necessitating any specific movement.

It is important to note that monkeys do not spontaneously engage in predictive audio-motor synchronization, and therefore monkey recordings must be applied cautiously to understanding human rhythmic timing [7]. However, the movement-tracking activity observed in monkey SMA is observed across a range of tasks, and may represent a timing mechanism widely shared across primates. Human-monkey differences in audio-motor timing may be attributable to differences in communication between auditory and motor brain areas rather than differences in motor-system based timing mechanisms [7,26].

Anticipating sound and correcting timing

The proposal that neural trajectories in SMA keep time between beats is much enriched by incorporating another line of SMA research attributing it a role in predicting and canceling the sensory consequences of one’s own actions, particularly in the auditory domain [45–47]. This allows an animal to focus on unexpected, i.e., informative, acoustic events. In the language of motor control, SMA is thought to provide an “efference copy” of motor commands that can be used by a “forward output model” [48] to predict the sensory feedback that will be produced by those commands. The function of a forward output model has traditionally been ascribed to cerebellum [49–51] (which is indeed involved in beat perception [9,52]); however, collected evidence, especially from speech research, suggests that SMA may be driving auditory predictions using the more flexible forward models in premotor and parietal cortex, via the dorsal auditory pathway [26,53–55].

Given this role of SMA, the cyclic dynamic state of SMA during rhythmic movement can be understood as providing an efference copy of cyclic motor commands to a forward predictive model. However, it has been proposed that forward models can also be used for prediction in the absence of movement-generating motor commands [22,56,57]. In this case, the dynamic state of SMA might better be interpreted as providing a sound-predictive model with an estimate of progress through the time course of a temporally structured stimulus[2].

Thus, we can flesh out our previous hypothesis by positing that **as SMA tracks progress through each beat interval, it informs a selected auditory forward model that dynamically anticipates auditory input over the course of the interval.**[3] The predictions of the forward model could be used to attenuate the perception of uninformative sounds or to increase gain on informative sounds as needed [57,58]. In addition to anticipating a sound that often (but not always) marks the position of the beat, a forward auditory model might also learn to predict intervening sounds between beats, e.g., subdivisions of the beat.

The combination of a "proto-action" timing progress in SMA and a forward model predicting auditory input at specific points in time constitutes a "simulated action for auditory prediction" as proposed by ASAP. We propose that cyclic dynamics in SMA informing premotor forward models are the source of the delta-frequency oscillations originating in the motor system that have been proposed to scaffold temporal prediction and particularly active audition [6,28,57,59,60], though we apply the word "oscillation" cautiously, as we discuss below.

A forward model of expected sound also provides a mechanism for aligning trajectories in SMA to the cycle of sound. During actual movement, the timing of real sounds and sounds predicted by a forward model could be directly compared, and timing errors could be used to adjust SMA's representation of progress through the movement. This same process could be used during covert beat maintenance to align the perceived beat cycle with auditory cues. Such processes of comparison and adjustment are at the heart of the predictive processing / active inference modeling framework we discuss below.

Dorsal striatum: initiating and sequencing "simulated actions"

Like SMA, dorsal striatum (especially the putamen) is consistently found to be activated by tasks requiring the covert maintenance of a beat [14,30,61]. It appears to be especially important to top-down (rather than stimulus-driven) aspects of beat perception: it is more activated by beat maintenance than by beat finding [1], and putamenal lesions specifically impair neural tracking of difficult rhythms requiring internal maintenance of a beat [52].

Motivated by the ASAP hypothesis, we look to the role of dorsal striatum in movement to begin to unravel its role in beat-based timing. In the canonical model of the basal ganglia's role in motor control [62,63], the dorsal striatum serves as the first link in the motor "direct pathway" (Figure 1B). In the leadup to action initiation, motor areas and other cortical and thalamic areas representing sensory and cognitive context send inputs to dorsal striatum, activating populations representing possible actions. These populations compete with each other through mutual inhibition such that only one self-consistent action plan can ultimately survive. It is not yet clear how the right time for initiation is selected, but it is widely hypothesized that a short pulse of dopamine delivered to striatum from dopaminergic neurons in substantia nigra pars compacta provides the impetus to initiate action [64,65]. This pulse is thought to cause a burst of activity in dorsal striatum that propagates through the direct pathway (from dorsal striatum to globus pallidus to thalamus back to cortex, see Figure 1B) leading to the disinhibition of populations corresponding to the selected action in motor and supplementary motor area [62].

Motor neuroscience literature draws an important distinction between "externally triggered" actions, where action timing is determined by a sensory cue, and "self-initiated" / "internally cued" actions, where action timing is determined by an internal process. Early studies indicated [66–69] (and more recent work has confirmed [70–72]) that SMA is essential for establishing the timing of self-initiated actions, and that the interaction of SMA and dorsal striatum plays a key role in self-initiated (but not externally-triggered) movements. It seems that when there is no external cue, the input from SMA to dorsal striatum is essential for activating the direct pathway and disinhibiting action.

Building on these findings, we hypothesize that in covert beat maintenance, **the direct pathway is using input from SMA to striatum as an internal cue to initialize the next "proto-action" in SMA**, just as it draws on SMA input as a cue to initialize self-generated action during actual movement. It does so by disinhibiting the appropriate sub-population in SMA to generate the neural dynamics that will unfold over the course of the next beat cycle. (See [73], which similarly proposes that the basal ganglia disinhibits selected "emulations" of action for prediction). The role of striatum in detecting and responding to the state of a cortical timer

hearkens back to the influential “striatal beat frequency” model, which proposed that striatum detects a specific state of an ensemble of cortical oscillators as a cue that a specific duration has elapsed [74]. However, our proposal differs in two respects: first, that the cortical input is already tuned to represent a specific time course, and second, that the striatum serves not just to detect a cortical state but to initiate a new process in response.

The importance of striatal dopamine in initiating self-generated actions suggests that dopamine may also play an important role in sustaining an internal representation of a beat. See Box 1 for discussion.

From action sequencing to metrical anticipation

To anticipate auditory input in a uniformly repeating cycle (such as the one in Figure 1), the basal ganglia could select the exact same pattern of activity in SMA over and over again. Yet why should such a complex subcortical brain structure be necessary to play such a role -- surely the flexible cortical dynamics of SMA could sustain a repeating cycle on its own? Crucially, cyclic movement and musical rhythm both have repeating temporal structure not only within sub-second (beat-like) cycles but also across multiple cycles. In cyclic movement, multiple actions are sequenced into longer cycles (such as the left-right cycle of stepping), and in music, metrical structure contains repeating temporal patterns at multiple scales (beats, groups of a few beats, etc.). For a brain structure like SMA that seems to specialize in generating dynamics over short time scales, flexibly structuring “chunks” of dynamic activity into longer repeating patterns may not be trivial.

Thus, the motor function of dorsal striatum most relevant to our sense of the beat may be its role in sequencing movements. Striatum activity is important for making transitions between sequential motor “chunks” in learned motor sequences, both in mice [75,76] and in humans [77]. During rhythmic action, striatal activity (in monkeys) varies predictably from one action repetition to the next [78], suggesting that even repetitions of superficially similar movements are being represented as a sequence of distinct actions in striatum. Similar sequential activity in striatum during covert timing tasks (in mice) suggests that even undifferentiated wait time is

represented as a sequence of distinct states [79]. Models suggest that sequential transitions in striatum may be orchestrated by patterns of inhibitory connectivity among striatal neurons trained by sequential motor cortical input [80], or else by a “competitive queuing” process among cortical representations [81,82] (a mechanism recently used to model rhythmic sequencing [83]).

Following this thread of evidence, **we hypothesize that striatum sequences the short “proto-actions” of SMA into longer repeating patterns**[4]. Each beat in, for example, group of 4 (a common repeating unit in Western music) would have its own characteristic identity in SMA as a proto-action with identical duration but different signatures in neural dynamics. As one reached its end, the dorsal striatum would prepare the next in the sequence (see Figure 3). Thus, activity in both regions should show patterns that repeat with the metrical cycle as well as with the beat; this is indeed observed in a recent EEG-fMRI study [84].

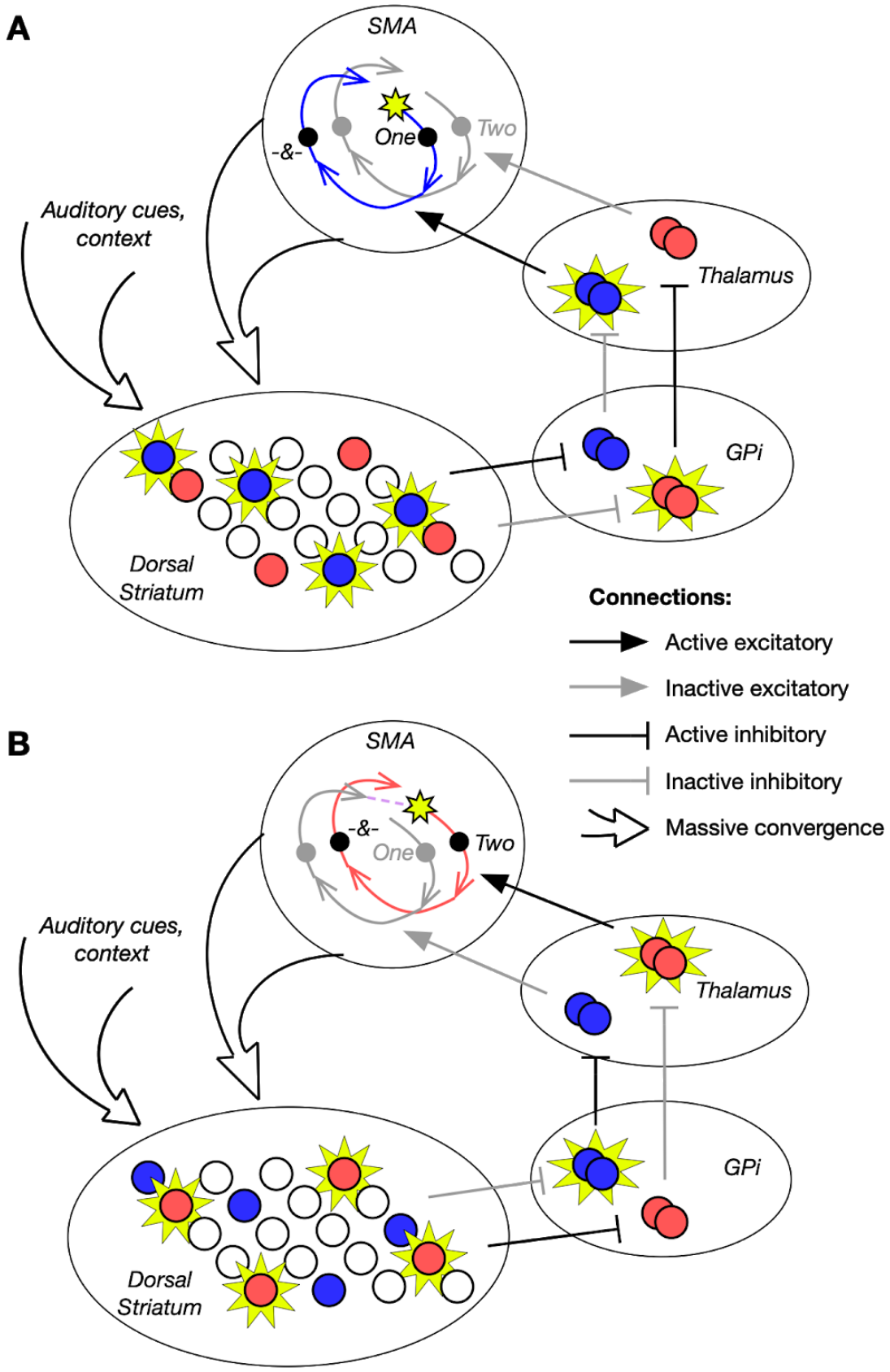
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Figure 3: Basal ganglia sequences the beat-tracking trajectories in SMA. A) Once a beat has been identified in an auditory rhythm, neural firing rates in SMA follow a trajectory which tracks progress through a beat cycle, informing the anticipation of the beat and possibly other sounds locked to the beat cycle. The activity of the neurons generating this trajectory is initiated and reinforced by selective disinhibition by the basal ganglia: a population specific to the first beat cycle is active in dorsal striatum (blue), which disinhibits a thalamic population that provides SMA with excitation specific to that trajectory. B) As the first beat cycle ends and the second beat arrives, some combination of SMA's evolving input to dorsal striatum and inhibitory interactions within dorsal striatum activates a new striatal subpopulation (red). This population disinhibits a new subpopulation in SMA that allows SMA activity to continue to evolve along a trajectory similar to but distinct from the previous one. It spans the same time interval, but may inform different auditory expectations specific to the next beat cycle.

A major advantage of a framework that separates the timing and sequencing activity into separate brain regions is that it allows for metrical structures that include non-isochronous durations as "beats" [85] (as in various traditional musics like Balkan music, where such musical structures inspire tightly coordinated rhythmic movement in enculturated performers and dancers). For example, each grouping in a "2/2/3" Balkan pattern (in which every third inter-beat-interval is 1.5 the duration of the previous two intervals) would be represented by its own distinct proto-action in SMA and sequenced by dorsal striatum, with the third proto-action being longer in duration than the other two.

Implications for beat perception modeling

How does our framework relate to current models of beat perception? The covert beat-maintenance process we hypothesize based on the neurophysiology of motor processing can be loosely summed up as follows:

- An adjustable-speed proto-action in SMA aligns to perceptual intervals, informing auditory anticipation over the course of the interval and on the next beat, and correcting its alignment based on new auditory cues.
- On each beat cycle, output from SMA signals dorsal striatum to select and disinhibit a new cycle-specific neural subpopulation in SMA to generate the next proto-action.

In combination, when the proto-actions sequenced by striatum and executed by SMA are of a consistent duration, this creates a self-sustaining cycle of internal activity that creates a beat-based pattern of auditory anticipation. Thus, this system can be understood as a neurophysiological implementation of dynamic attending theory [86,87], which posits that such attention is directed in time by self-sustaining cycles called “attending rhythms.”

However, our neurophysiological hypotheses are only partially consistent with the oscillator-based modeling that has been put forward to explain the origins of attending rhythms and beat perception more generally [88–90]. Since our hypothesized brain dynamics do not account for initial phase and tempo inference, they are not *inconsistent* with a model in which a bank of oscillators collectively identify phase and tempo [89]. And once phase and tempo is established, aspects of the brain dynamics we describe could indeed be described as a limit-cycle oscillation. However, such a description suggests that the process is a continuous, homogeneous cycle (like a pendulum), whereas we hypothesize that discrete re-initiation events are necessary on each cycle to keep it going (like a combustion event in the cycle of an engine). Our account of proto-action sequencing by striatum allows for the generation of non-isochronous beat patterns (discussed above) that could not be easily generated by homogeneous oscillators (though oscillator banks are capable of recognizing and discriminating such patterns [91]). We also believe our account may generalize more easily than an oscillator account to describe the related phenomenon of non-isochronous rhythmic anticipation in speech [92–94]. The sequential nature of our neurophysiological account of the beat would be better described by the model of concatenated diffusion processes proposed and evidenced by Merchant & Averbeck (2017) [95] than by an oscillator-based framework.

While our idea that trajectories in SMA are aligned to sound could be described in terms of the “information-processing” models that characterize corrective responses to timing errors, the core idea of using a forward model to correct an underlying state is more closely related to the “predictive processing” / ”active inference” school of brain modeling. According to this perspective (recently invoked in describing and modeling musical rhythm [96,97]), the brain is constantly predicting its inputs and adjusting underlying representations of states in the world based on its errors in prediction. In our picture of SMA, a dynamic neural state represents

either physical progress through a cyclic action or progress through an externally-generated cycle of auditory events. In either case, predictions of auditory input based on this dynamic state are compared to actual auditory input, and errors are used to correct the state. A valuable direction for future research will be identifying an appropriate modeling framework that expresses this process in the language of predictive processing (see Outstanding Questions). This could help connect this neurophysiological picture to Bayesian models of timing (reviewed in [98]; see also [99], which connects Bayesian timing inference with SMA dynamics).

Concluding remarks

Beat perception offers cognitive science an exciting opportunity to explore how cognition and action are intertwined in the brain *even in the absence of movement* (during covert beat maintenance). Based on the idea that simulated actions support the precise temporal predictions involved in covert beat maintenance, we have drawn on the motor neuroscience literature to propose specific roles for two key motor structures engaged by beat perception, SMA and the dorsal striatum. This leads to testable predictions, listed below, and illustrates how cognitive science, by engaging with the details of motor neuroscience, can move toward biologically-detailed models of "embodied cognition."

Our hypotheses about the roles of SMA and dorsal striatum in beat maintenance lead to several testable predictions in humans.

- If the beat is covertly tracked by a firing rate trajectory in SMA, then firing rate trajectories of ECoG recordings in human SMA should align to the beat cycle during complex rhythms and account for variations in performance of covert beat-based timing tasks.
- If dorsal striatum is sequencing and initiating a series of proto-actions to maintain the beat, there should be a burst of basal ganglia activity at a characteristic phase of the beat cycle during passive listening to any (syncopated or unsyncopated) rhythm that induces a beat percept. This activity should be detectable by recordings in human striatum and globus pallidus, and possibly in neighboring structures like the subthalamic nucleus (such recordings can be made during deep-brain stimulation (DBS) surgery)

- If internal beat maintenance is essentially a process of sequencing action-like processes, then trajectories in SMA and activity in striatum should align to and anticipate non-isochronous beats in listeners enculturated to non-isochronous meters.
- If tonic and phasic striatal dopamine are important for initiating beat-tracking proto-actions in SMA, then time-sensitive measures of dopamine (such as fast-scan cyclic voltammetry [100]) should show phasic dopamine pulses on every beat cycle and elevated tonic dopamine in conditions of a strong internal beat (see Box 1).

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BOX 1: Dopamine as an index of internal beat strength

The neurotransmitter dopamine is widely associated with reward anticipation and motivation. However, these associations are most appropriate to dopamine in the cortex and ventral striatum, provided by dopaminergic neurons in the midbrain's ventral tegmental area. By contrast, dopamine in dorsal striatum, delivered by dopaminergic cells in the nearby substantia nigra pars compacta ("nigrostriatal dopamine"), is more closely associated with (and capable of triggering) the initiation of action [101]. It is possible that nigrostriatal dopamine is similarly involved in initiating the time-keeping proto-actions in SMA that we have discussed above.

A current line of research suggests that dopamine (and nigrostriatal dopamine in particular) may encode certainty in cognitive constructs. Friston et al. 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" [102]. One such "sensorimotor construct" could be an internal representation of the period and phase of a temporal cycle underlying an ongoing sound. In this case, dopamine would also serve as an index of confidence in temporal predictions based on that cycle. Recent experimental evidence has offered support for this interpretation [103–105]. In particular, striatal dopamine level has been found to index temporal expectation of perceptual cues [106] and certainty about timing [107].

Combining these ideas with our current framework, we hypothesize that when SMA accurately anticipates rhythmic timing, dopamine levels rise, making it easier for the striatum to initiate the proto-actions that serve as an internal representation of the beat cycle and strengthening the internally generated component of the beat percept.

BOX 2: Insight into dance and Parkinson's

The role of the basal ganglia in selecting, sequencing, and disinhibiting movement combined with their proposed role in doing the same for anticipatory dynamic forward models suggests that this may be the key point of intersection for musical anticipation and movement. Several processes in the basal ganglia have global motor-modulatory effects that are not limited to specific movements, and that therefore may be responsible for our inclination to move (and our facility at moving any body part) along with music. The pulses of dopamine that are thought to time the output from dorsal striatum could have the effect of encouraging motor output at the same moments as the output disinhibiting the next forward auditory model in SMA. Action initiation also appears to involve a drop in the globally inhibitory effect of the "hyperdirect" pathway through basal ganglia [108]. If hyperdirect pathway drive is suppressed to allow for striatal output initiating the next forward model, this may have the additional effect of broadly facilitating the initiation of movement.

Both of these mechanisms -- dopaminergic and hyperdirect -- are plausible links to the remarkable gait-facilitating effects of rhythmic cueing in Parkinson's [18]. An extra dopamine pulse could help overcome the dopamine deficiency thought to make action initiation so difficult in Parkinsons; alternatively (or additionally), a drop in hyperdirect pathway drive could make it easier for weak dopaminergic signals to successfully initiate action. And both mechanisms offer a possible mechanism for the modulation of beta (~20Hz) oscillation power that has been repeatedly observed to synchronize with a beat [109,110]: activation of the hyperdirect pathway is linked to beta [111,112], and phasic dopamine pulses are thought to attenuate beta [113].

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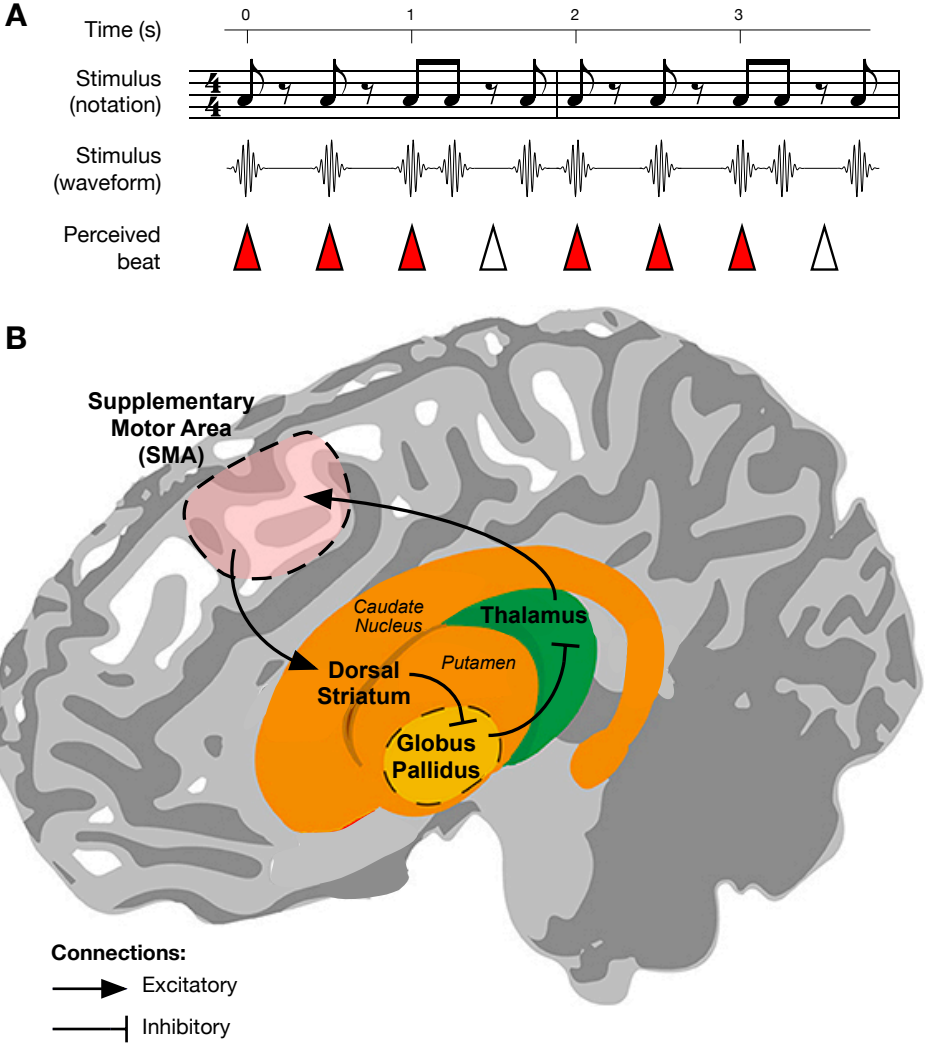
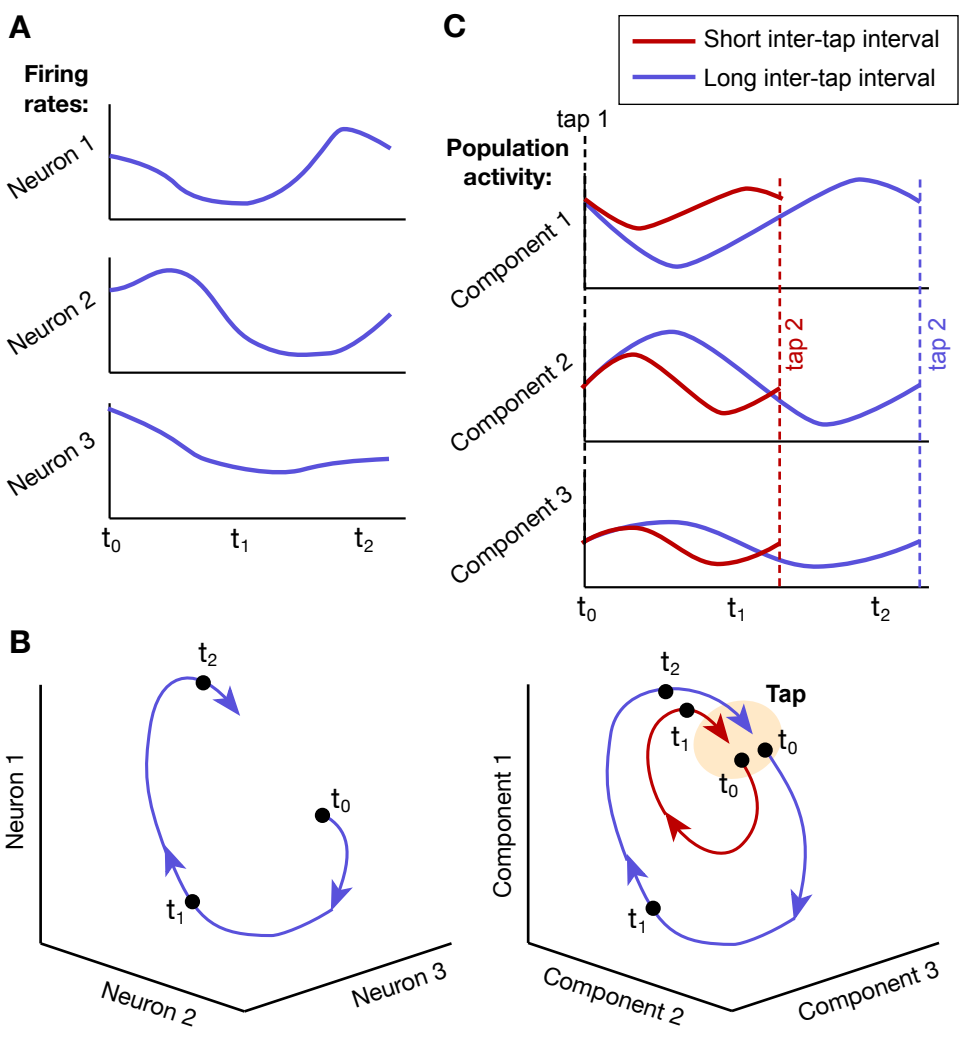
Endnotes

1. Here and throughout we refer primarily to “SMA proper,” the caudal subregion of the medial premotor cortex which also includes the more rostral subregion “pre-SMA,” though some of the results cited here do not differentiate between the two.
2. The hypothesized framework of “active inference” for movement generation [114] suggests that this may also be a better framework than the “efference copy” for understanding the role of SMA in motor control [115].
3. If the models used to predict auditory timing are indeed the same as the forward models used to anticipate sensory consequences of action, then learning timing patterns is inseparable from motor learning, as discussed in [116].
4. Of course, the metric structure of music is not only sequential, but also hierarchical: in a 4/4 meter, the first beat in each group of two, four, eight, etc. occupies a position of greater perceptual prominence than the beats that follow [117]. Interestingly, recent results indicate hierarchical sequencing may be native to dorsal striatum: in a sequential behavioral paradigm in mice, different striatal populations controlled transitions between sequential actions and transitions between groups of actions [118].


A
Time (s)
0
1
2
3
Stimulus (notation)
Stimulus (waveform)
Perceived beat
B
Supplementary Motor Area (SMA)
Caudate Nucleus
Thalamus
Putamen
Dorsal Striatum
Globus Pallidus
Connections:
Excitatory
Inhibitory


A
Firing rates:
Neuron 1
Neuron 2
Neuron 3
t0
t1
t2
C
Short inter-tap interval
Long inter-tap interval
tap 1
Population activity:
Component 1
Component 2
Component 3
tap 2
tap 2
t0
t1
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B
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Neuron 1
Neuron 2
Neuron 3
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Tap
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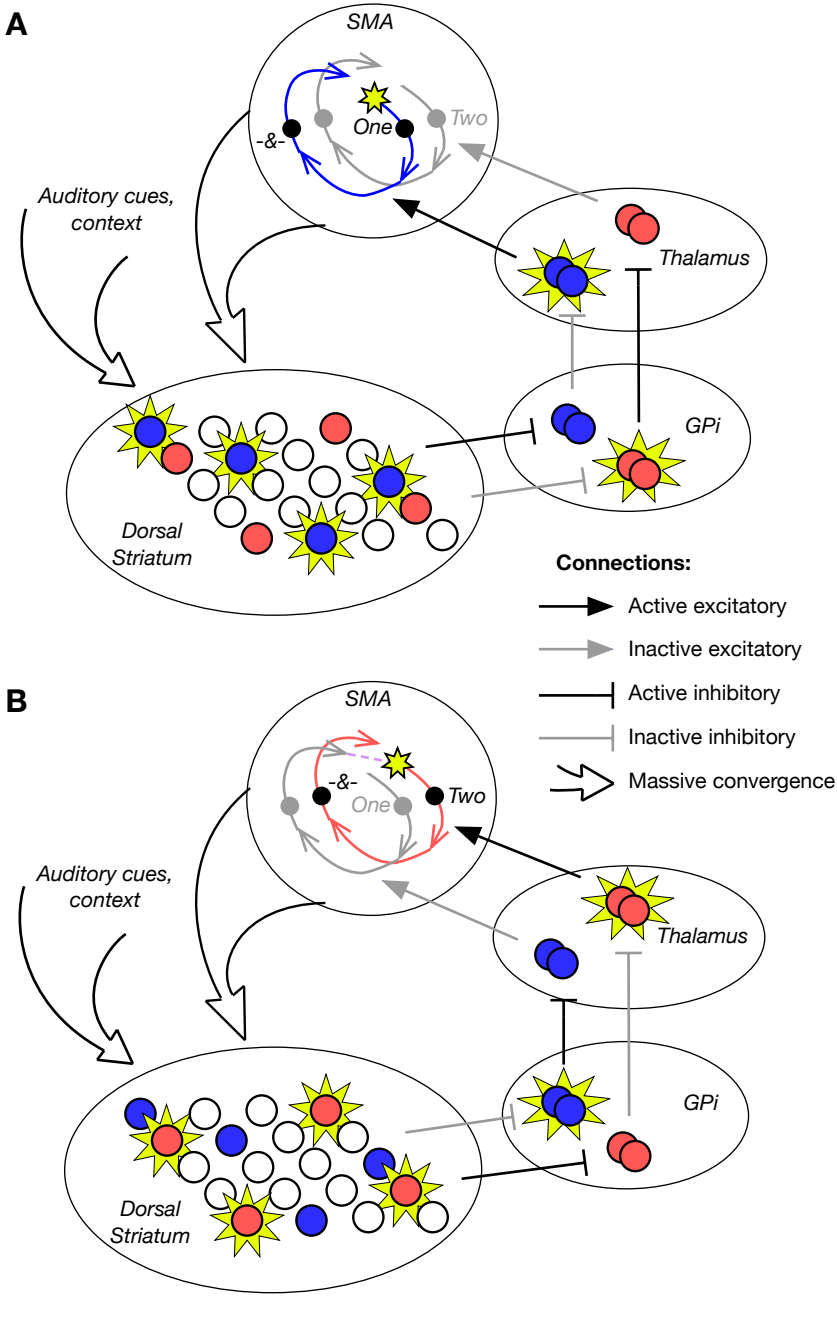
Component 1
Component 2
Component 3


A
SMA
-&-
One
Two
Auditory cues,
context
Thalamus
GPi
Dorsal
Striatum
Connections:
Active excitatory
Inactive excitatory
Active inhibitory
Inactive inhibitory
Massive convergence
B
SMA
-&-
One
Two
Auditory cues,
context
Thalamus
GPi
Dorsal
Striatum