Specifying the motor system's role in beat perception

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Submitted to *Trends in Cognitive Sciences*

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April 17, 2020

Keywords

Music Cognition; Beat Perception; Basal Ganglia; Beta; Dopamine; Motor System

Abstract

A fundamental aspect of music cognition is the perception of an underlying metronome-like pulse ("the beat") in complex rhythmic patterns. Neuroimaging shows that beat perception strongly engages the motor system *even in the absence of movement*, but few efforts have been made to connect neurocomputational properties of the motor system to beat perception. Here we hypothesize three specific, interacting roles for the motor system in beat perception: predictive timing of beats by neuronal population clocks reset through the basal ganglia's direct pathway, periodic motor facilitation by entrained hyperdirect pathway drive to basal ganglia, and balancing top-down and bottom-up influences on beat perception through striatal dopaminergic modulation. This leads to testable predictions about the motor system's contribution to auditory cognition.

Highlights

The Action Simulation for Auditory Prediction (ASAP) hypothesis posits that covert anticipatory timing of a musical beat is performed by the motor system.

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.

Beta oscillations (known to fluctuate with the beat) may be an anti-kinetic "hold" signal that scaffolds motor entrainment and beat timer resetting.

Striatal dopamine may serve as an index of confidence in the beat tempo and phase, allowing the brain to balance between bottom-up and top-down influences on the beat percept.

Glossary

ASAP: The Action Simulation for Auditory Prediction hypothesis

GPi: Internal Globus Pallidus (an output region of the basal ganglia)

IOI: Inter-onset interval (time between consecutive events)

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

PFC: Pre-frontal cortex

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

STN: Sub-thalamic nucleus (a region the basal ganglia with input from cortex and other basal ganglia regions)

What is the motor system doing during beat perception?

This article concerns the role of the motor system in auditory processing, focusing on beat perception. We begin by briefly introducing beat perception's significance for cognitive science, then list the key questions addressed in this paper.

In music cognition, beat perception refers to the perception of an underlying regular pulse in rhythmic patterns. Beat perception often elicits rhythmic movement in humans and is foundational to dance (Damm et al., 2020). This motoric response emerges spontaneously in young children and is seen in every culture (Nettl, 2015; Savage et al., 2015). Beat perception seems effortless, yet involves ongoing precise temporal predictions, implying sophisticated neural processing (Bouwer et al., 2020; Merchant, Grahn, et al., 2015). This is easily demonstrated by asking a person to tap with an acoustic metronome (the simplest beat-inducing stimulus): people spontaneously align their taps closely in time with the metronome's clicks (often tapping slightly ahead of each click), indicating repeating, accurate prediction of beat timing (Patel et al., 2005).

Beat perception is of interest to cognitive science for at least three reasons. First, as illustrated in **Figure 1A**, (see supporting information for audio), the beat percept does not always have a one-to-one relationship with acoustic timing: many non-isochronous temporal patterns can readily elicit an isochronous beat percept (see glossary) (Kung et al., 2013). Second, beat perception emerges at specific timescales: we perceive beats in a range of about 250ms - 2s, and the beat percept is strongest when the interval between beats is between about 400-1200 ms (London, 2012). Third, the beat percept is constructed through a dynamic interplay of bottom-up and top-down influences. Sensitivity to bottom up (stimulus-driven) influences is apparent from tapping experiments in which a metronome changes phase or tempo (e.g., **Figures 1B,C**). The rapid adjustment of synchronized taps to such metronomes indicates that the beat percept quickly adjusts to slight misalignments of event timing and beats (Repp, 2005). Yet beat perception also has strong internally-driven (top-down) influences. Consider again Figure 1A. In this pattern, 25% of beats occur at times where there is no sound, and 40% of

sounds occur at non-beat positions, yet the internal sense of beat is not perturbed by these discrepancies between event and beat timing.

Beat perception thus appears to be in a “sweet spot” for cognitive neuroscience: it has several cognitively interesting features, yet seems simple enough to allow full elucidation of its underlying brain mechanisms. Further, beat perception is of interest for its clinical applications. For example, beat-based rhythms can facilitate the initiation and maintenance of stable, fluid walking in certain patients in Parkinson’s disease (Dalla Bella et al., 2017), and sensorimotor training with beat-based rhythms can improve aspects of language processing in developmental dyslexia (Flaugnacco et al., 2015). Understanding the mechanisms behind these and other clinical effects of beat processing could help optimize beat-based therapies for several neurological disorders.

One of the most interesting and well-replicated findings from neural research on beat perception is that it engages the motor system *even in the absence of movement*. fMRI research reveals that a number of cortical and subcortical motor regions are active during beat perception, including the supplementary motor area (SMA) and the basal ganglia (J. L. Chen et al., 2008; J. A. Grahn & Rowe, 2009; Kung et al., 2013). Furthermore, electrophysiological measures (MEG and EEG) reveal salient modulations of beta oscillations during beat perception (Fujioka et al., 2012; Iversen et al., 2009) and beta has long been associated with motor-related neural activity (Khanna & Carmena, 2015; Kilavik et al., 2013). Yet current neurally-inspired models of beat perception, such as those focusing on entrainment of cortical neural oscillations by auditory rhythms (Large et al., 2015), do not strongly engage with known neurophysiological properties of the motor system. In this opinion piece we argue that the time is right to start unifying the cognitive science of beat perception with the neuroscience of the motor system. To illustrate our point, we address three key questions about beat perception using a framework that draws connections between specific aspects of beat perception and existing neural research on the motor system. This leads to testable hypotheses, and also suggests why beat-based music can improve gait in some patients with Parkinson’s disease.

Before listing the three questions, we note that our broader theoretical framework is one in which the motor system plays a *causal* role in beat perception, and in particular, in the prediction of beat timing. In this view, motor system activity during beat perception is not simply a passive byproduct of the frequent association of beat perception and movement. Instead, it indicates that beat perception is a sensorimotor process *even when no movement is involved*. This idea has been articulated by a number of authors over the past two decades (J. A. Grahn & Rowe, 2009; Repp, 2005; Schubotz, 2007; Zatorre et al., 2007), with some specifically suggesting that beat-based temporal predictions arise from simulated rhythmic actions by the motor system (Arnal, 2012; Iversen et al., 2009; Morillon & Baillet, 2017; Patel & Iversen, 2014; Ross et al., 2016). For example, the "Action Simulation for Auditory Prediction" (ASAP) hypothesis (Patel & Iversen, 2014) 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 (Ross et al., 2018) for one recent test of this hypothesis). The current paper focuses on the "action simulation" aspect of ASAP rather on auditory-motor interactions, and seeks to relate the prediction of beat timing to specific structures and pathways within the motor system.

Turning to the three questions addressed in this paper, the first concerns how the brain maintains a pattern of periodic temporal predictions once the beat of a stimulus has been found. That is, **what neural mechanisms support a regenerating pattern of beat anticipation?** The second question relates to our ability to map beat perception onto different kinds of movements. Humans can easily mark the beat with rhythmic movements of a wide variety of body parts, including the head, torso, arms, feet, etc., and this flexibility is a key part of dance (Burger et al., 2013). **What physiological process supports a flexible mapping between beats and different types of movements?** The third question concerns one of the most cognitively interesting aspects of beat perception: **how does beat perception moderate between the influences of an external stimulus and an internally-generated beat percept (bottom up vs. top-down processing)?** The following sections address each of these three questions in turn.

Repeated temporal predictions of beats by the motor system

When a listener hears a beat-based rhythm, an early stage of "searching" for temporal regularity (beat finding) rapidly informs a regenerating pattern of beat-based temporal predictions (J. A. Grahn & Rowe, 2013; Toiviainen et al., 2019). We focus on the role of the motor system in this regenerating pattern. Since a person can move predictively to beats that span a wide range of tempi (e.g., ~250 ms – 2s IOI), some aspect of the dynamic neural activity directing this movement must be matching movements to the tempo and phase of the beat, and also be easily scalable across a continuum of speeds in this temporal range. We use the term *relative timing activity* to describe a temporal pattern of neural activity that can play out at a continuum of speeds, as opposed to *absolute timing activity*, a pattern that plays out at the same speed regardless of the duration being timed. Relative timing is useful for predicting the end points of a temporal interval in a flexible way, because the state of a relative timer indicates how far into the interval one is.

Monkey neurophysiology reveals that relative timing patterns exist in SMA proper/pre-SMA (henceforth, SMA) during processing of isochronous rhythmic sequences. **Figure 2A** shows a cell in this region recorded during a task in which monkeys synchronized their taps to a metronome: activity in this cell rises and falls across the span of the temporal interval between metronome events, and the rate of this rise and fall is scaled such that one rise-fall cycle spans the temporal interval (i.e., the cell shows relative timing activity (Merchant & Averbeck, 2017), see (Emmons et al., 2017) for a related result in rodents). This contrasts with **Figure 2B**, which shows a different cell in SMA during the same task. In this cell the firing rate increases steadily, with longer intervals corresponding to higher final firing rates (i.e., the cell shows absolute timing activity,(Merchant & Averbeck, 2017)). While Figure 2A shows relative timing activity for just one cell, measurements across many cells in monkey SMA during a similar interval production task reveal that the joint pattern of activity across a subset of cells creates a stereotyped "neural state space trajectory" that is traversed at a speed that scales to fill the temporal interval between metronome events (Merchant, Pérez, et al., 2015; Wang et al.,

2018). In other words, SMA has population-level activity that can act as a relative timer, i.e., stretching or compressing to fit different length intervals **(Figures 2C and 2D**). Subcortical recordings reveal that this population-level relative timing originates cortically (in SMA) rather than subcortically (in the thalamus) (Wang et al., 2018).

We argue that stereotyped neural state-space trajectories in SMA could provide the basis for temporal prediction of beats (Buonomano & Laje, 2010). Importantly, stereotyped neural trajectories in monkey SMA have been found in research on motor planning (e.g., (Kaufman et al., 2014; Lara et al., 2018)). This is consistent with the idea that state-space trajectories during beat perception could reflect a simulated action of a certain duration, as posited by the ASAP hypothesis. However, since a single simulated action would correspond to a single traversal of a state-space trajectory, and thus a to single temporal prediction, how would re-initiation of this simulated movement (as soon as it ends) be instantiated in the motor system, to create a regenerative pattern of beat-based temporal predictions?

According to the canonical model of basal ganglia function, the direct pathway (**Figure 3A**) carries voluntary movement-initiating signals from cortical areas (including SMA, prefrontal cortex [PFC], and high level sensory and parietal cortices) into basal ganglia (putamen and GPi), and out to thalamus, where they serve to disinhibit motor cortical areas necessary to generate movement. (This aspect of the canonical model has largely held up under recent experimental scrutiny (Calabresi et al., 2014).) Recent optogenetic work has determined that the direct pathway carries information not only on movement choice but also movement speed (Yttri & Dudman, 2016). We suggest that the same pathway conveys an analogous signal that reinitiates a *covert* timing process (neural state-space trajectory) at a specific speed in SMA.

In other words, we propose that the process of reinitiating the relative timer at a particular speed involves a cortico-basal ganglia-thalamic loop. Specifically, we propose that the neuronal activity at the end of each covert motor program in SMA sends a signal via the direct pathway to initiate a timing program (i.e., a reset signal that restarts the relative timer at a specific speed). Based on fMRI research on ongoing brain activity once a beat has been found, we suggest that this reset signal engages ventral (rather than dorsal) putamen (Cameron, 2016).

This leads to our first testable prediction: beat perception is associated with periodic direct pathway activity "on the beat". More specifically, we predict that activity occurs at times of perceived beats in ventral putamen and motor thalamus, even when a listener is not moving and even on beats occurring at points with no sound (e.g., empty red arrowheads in Figure 1A).

Of course, ongoing relative timer activity must also accept input from auditory stimuli in order to adjust its timing when necessary (e.g., during a tempo change). Thus we suggest the relative timer could also be reset by a salient auditory stimulus (possibly relayed to striatum rapidly via cerebellum and thalamus (Ponvert & Jaramillo, 2019; Schwartze & Kotz, 2013), allowing the sensory stream to initiate or reset the beat-anticipatory (relative) timer (Figure 3A). And before beats can be accurately anticipated, the brain must somehow identify the beat tempo and phase and internalize the tempo -- i.e., the speed of the relative timer -- in working memory (this internalization is what allows people to continue tapping a beat when a metronome stops (Y. Chen et al., 2002)). While we do not focus on beat finding in this paper, recent results lead to specific suggestions about the role of the motor system in this process, outlined in Box 1. We offer the dorsolateral prefrontal cortex, a region of cortex that supports persistent representations (Qi et al., 2015) and is specifically activated by tempo-based tasks (Thaut et al., 2014), as a likely site of the internal representation of tempo once it has been identified. As long as the tempo remains the same, each reset signal sent along the direct pathway would set the relative timer at the same speed, to time the same interval over and over.

Flexible mapping between beats and movements

An important feature of the link between beat perception and movement is "effector flexibility:" beat perception can be mapped onto a wide range of bodily rhythmic movements, supporting the diversity of human dance. What physiological process supports this mapping? We believe that effector flexibility is a result of a specific role that beta oscillations play in the motor system and in beat processing, as explained in this section.

Empirically, beta power in sensorimotor cortex and basal ganglia is observed to drop before and during voluntary movement and increase immediately afterwards (Brittain & Brown, 2014). Intriguingly, EEG studies of humans listening to metronomic rhythms (without moving) show that "high-beta" (~20-26 Hz) in auditory and motor areas ramps up slowly in amplitude and then falls abruptly with the cycle of the beat (Fujioka et al., 2012). (A similar cycle of high-beta modulation was observed in monkey putamen during a synchronization-continuation task, especially during the continuation phase (Bartolo & Merchant, 2015), and in human Parkinsonian subthalamic nucleus (STN), where it entrained to the subject's footsteps and was significantly enhanced by rhythmic auditory stimulation (Fischer et al., 2018).) Beta is often observed in cases of long-range coupling between cortical areas (Kopell et al., 2000) and in top-down cortical communication (Buschman & Miller, 2007), so beta modulation in auditory and motor areas could indicate auditory-motor functional coupling supporting beat perception (Fujioka et al., 2012; Iversen et al., 2009; Patel & Iversen, 2014).

In neuroscience, beta in the motor system has very specific connotations. Since beta amplitude is commonly observed to drop just before the initiation of movements (and return just after termination), elevated beta amplitude is thought to signify a "hold" state that "promotes the existing motor set while compromising neuronal processing of new movements" (Engel & Fries, 2010), and during which new motor plans can be formulated (Leventhal et al., 2012). Thus a drop in beta seems to be an important part of motor initiation. (In a rhythmic serial reaction task, reaction times were longer when motor cortical beta was less deeply modulated in anticipation of movement (te Woerd et al., 2015).)

In terms of the neuroanatomy, beta in STN is closely associated with activity along the "hyperdirect" pathway through basal ganglia (Litvak et al., 2011; Sharott et al., 2018; Tan et al., 2014) (**Figure 3B**), a path beginning with direct cortico-subthalamic projections from SMA whose activation is generally understood to carry a global "hold" or "no-go" signal that can prevent the execution of commands carried by the direct pathway (Dunovan et al., 2015; Frank, 2006; Wessel et al., 2016). (However, see (Chartove et al., 2020) for an alternative striatal pathway by which a global "hold" signal may produce beta oscillations.)

We propose that the dynamic fluctuations in beta power between beats are key to the effector-flexibility of dance. Specifically, we propose that elevated beta amplitude between beats is a hold signal antagonistic to direct pathway transmission/movement initiation, and that beta amplitude fluctuations are driven and timed by the relative timer in SMA operating at the beat period. Consequently, periodic modulation of this hold signal would provide a periodic window of low beta amplitude around the time of beats favoring the initiation of movements by *any effector* (i.e., effector flexibility), while periodic windows of elevated beta amplitude between beats could serve as opportunities to formulate new motor plans.

According to this view, the SMA not only gives rise to elevated beta amplitude between beats (via hyperdirect drive), but also times the drops in beta amplitude in a way that anticipates direct pathway activity on the beat. That is, when the relative timer is mid-stream there is strong drive to the hyperdirect pathway, and it is the timer coming to the end of each cycle that leads to the drop in beta around beat times.

These ideas lead to **our second testable prediction, namely that hyperdirect drive in STN drops in anticipation of the beat.** A first step in testing this prediction would be to examine how firing rates or beta oscillations in STN are modulated by the beat, to see if they drop right before beats. This could be examined in beat perception experiments in patients with electrodes implanted in STN for deep brain stimulation surgery.

We emphasize that the idea of high-amplitude beta serving as a “hold” signal between beats does not entail the idea that we cannot move between beats: we obviously can (e.g., in dance). Rather, it involves the idea that initiation of *new* movements is inhibited between beats, and facilitated at beat times. Interestingly, evidence for a “protective temporal window” before an event expected at a specific time (within the next few hundred ms) has recently emerged in neuroscience (van Ede et al., 2018), and the rhythmic timing of movements with any effector by a periodic relative timer bears distinct similarities to the “gating” process proposed by Ivry and Richardson (Ivry & Richardson, 2002).

We note that an interesting corollary of our proposal is that if the direct pathway is used for timer resets (as argued in the previous section), then high-amplitude beta between beats

should inhibit timer resets by incoming auditory information. Thus, events mid-way between beats (such as the fourth and ninth events in Figure 1A) should not reset the relative timer for beats. On the other hand, low beta amplitude close to beats would allow incoming auditory information near beat times to affect the relative timer.

Balancing bottom-up and top-down influences

As alluded to in the introduction (cf. Figure 1A), a beat percept can persist through beats without sound (syncopation), and sounds without beats (subdivision). However, it also yields when the ongoing pattern of sounds and silences indicates that the stimulus no longer supports the current beat percept (cf. Figures 1B,C). How does the brain moderate between the regenerative internal sense of beat and bottom-up timing information? This problem can be cast as a tension between top-down and bottom-up processing, a larger issue that is central to conscious perceptual experience.

One useful perspective on this problem is a Bayesian one. The problem of inferring metrical structure has already been considered through a Bayesian lens (Koelsch et al., 2019; van der Weij et al., 2017). Here, we note that we may consider the phase and tempo of an internally generated beat as a "beat-hypothesis" about a stimulus' underlying pulse. This state consists of the stored tempo and the instantaneous "phase" represented by the instantaneous position of the relative timer.

What physiological mechanism could provide a running estimate of the likelihood of (or level of confidence in) a beat-hypothesis? We argue that dopamine in the striatum could play this role. Although dopamine has long been understood to encode reward prediction error, a running line of evidence suggests that dopamine (and nigrostriatal dopamine in particular) may encode perceptual uncertainty. 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" (Friston et al., 2012). One such "sensorimotor construct" could be an internal model of the cause or structure of a sensory stream; for

example, an internal representation of the period and phase of an isochronous pulse underlying an ongoing sound. An internal model makes specific predictions about future sensory input, so in this picture dopamine also serves as an index of confidence in temporal predictions. Recent experimental evidence has offered support for this interpretation (Lak et al., 2017; Starkweather et al., 2017; Takahashi et al., 2016). In particular, striatal dopamine level has been found to index temporal expectation of perceptual cues (Sarno et al., 2017) and certainty about timing (Tomassini et al., 2016).

In order to moderate between external (bottom-up) evidence and internal (top-down) interpretation in beat perception, striatal dopamine must have influence over the pathways involved in beat finding and regenerative beat anticipation. Above, we suggest that the internal beat is regenerated by the direct pathway through ventral putamen, and in Box 1 we discuss the possibility that beat-finding inferences are transmitted to working memory via dorsal putamen; thus, striatal dopamine could indeed have direct modulatory access to both processes. When dopamine levels indicate high confidence in the beat-hypothesis, the beat is regenerated robustly (via ventral putamen); when dopamine levels indicate low confidence, bottom-up evidence is incorporated (via dorsal putamen) for purposes of beat-finding and beat-adjustment (Cameron, 2016).

To track the likelihood of a beat-hypothesis, dopamine would have to respond to events that indicate changes in beat tempo or phase. If we limit our scope to click-based rhythms (like Figure 1A), a beat-hypothesis should be supported by an accurately anticipated click and undermined by a click displaced in time from the anticipated beat, i.e., an error in temporal anticipation. (As noted in the previous section on beta oscillations, such displacements should impact the beat hypothesis if they occur near predicted beat times.) Detecting such errors would require a system for measuring small timing errors between anticipation and stimulus. This role has previously been proposed for the olivocerebellar system (Teki et al., 2011). In particular, the inferior olive is a good candidate for measuring such errors during beat perception as it has been shown to a) produce a precisely timed signal initiated by sensory input (Gellman et al., 1983) that is available to the cerebellum (Huang et al., 1982), b) have cells which respond to auditory input (Gellman et al., 1983), and c) activate in response to deviations

from rhythmic timing (Xu et al., 2006). Given the evidence of extensive connections from cerebellum to basal ganglia (Milardi et al., 2016) and the effects of cerebellar stimulation on striatal dopamine (Neychev et al., 2008), the olivocerebellar system seems well suited for a role in error-based dopaminergic modulation of the striatum.

We note that the hypothesized role of dopamine described above provides a specific explanation for the dynamics of physical entrainment during a metronome tempo change. Research shows the first tap after a tempo change is shifted in time only enough to account for the time shift of the early or late stimulus, but not as much as it would be if the subject believed that the underlying beat period had changed; only the second tap after the tempo change begins to correct for the change of period (Bavassi et al., 2013; Repp & Keller, 2004) (see Figure 1C). According to our hypothesis, at the moment of the first inaccurate tap, dopamine is still high (so tempo is not updated with new measurements), but the inaccuracy causes dopamine to drop. Since the internal tempo has not been updated, the next tap is also inaccurate, and at this point, the lower dopamine level allows the tempo to be measured and updated (see **Figure 4, Key Figure** for illustration).

Our hypothesized role of dopamine in representing confidence in the internal representation of an underlying beat leads to our **third testable prediction: striatal dopamine levels should rise as auditory input reinforces the listener's impression of the beat and should drop when auditory input arrives slightly early or late relative to the anticipated beat.** Ideally, these dopamine dynamics would be macroscopically observable in PET scans of the striatum. We note that an interesting question for future research concerns how this type of "confidence-related" striatal dopamine fluctuation in the putamen (dorsal striatum) relates to fluctuations in reward-related dopamine in ventral striatum regions such as the nucleus accumbens (Matthews et al., 2020; Salimpoor & Zatorre, 2013).

Concluding remarks

We have long known that the motor system is active during pure beat perception (in the absence of movement), but what is the motor system doing? We present a framework for integrating known aspects of motor system neuroscience into research on auditory beat

perception. Based on the idea that prediction of beat times involves repeated simulated actions, the framework proposes specific roles for supplementary motor area, motor-related basal ganglia pathways, beta oscillations, and striatal dopamine in constructing a perceived beat. This leads to three novel and testable predictions, and raises a number of questions for future research (see Outstanding Questions). More generally, the framework offers a physiological description of the interaction between movement initiation and beat tracking that underlies our desire to move rhythmically to music.

Outstanding Questions Box

- **Which conceptual framework better describes the neural correlates of beat perception: an entrained oscillator or a resetting timer?**
  We use the latter framework because it allows us to map onto known aspects of motor system physiology. Since both frameworks are simplifications of complex neural dynamics, the two are not necessarily incompatible, and each points toward its own set of predictions and insights.

- **Can the interplay of bottom-up and top-down influences in beat perception be aligned with predictive coding theory?**
  We believe that the ideas presented here provide the groundwork for a predictive coding model of beat perception, and we have begun work in this direction. Challenges will include adapting temporal predictive coding models to accommodate variables that are discrete events in time rather than continuous fluctuating values.

- **To what extent are our proposed mechanisms of beat perception shared across species?**
  Some, such as relative timing in population clocks in SMA, have been directly observed in monkeys. Yet spontaneous movement synchronized to the beat appears to be unique to humans among primates. Future work should aim to elucidate which aspects of motor system engagement in beat processing are human-specific.

- **How does the development of the motor system parallel the development of beat perception?**
  Babies and toddlers often respond rhythmically to music, but stable synchronization of movement to a beat does not occur until between 3-5 years of age. As the motor system develops, how do the different motor contributions to beat perception come online?

Figures

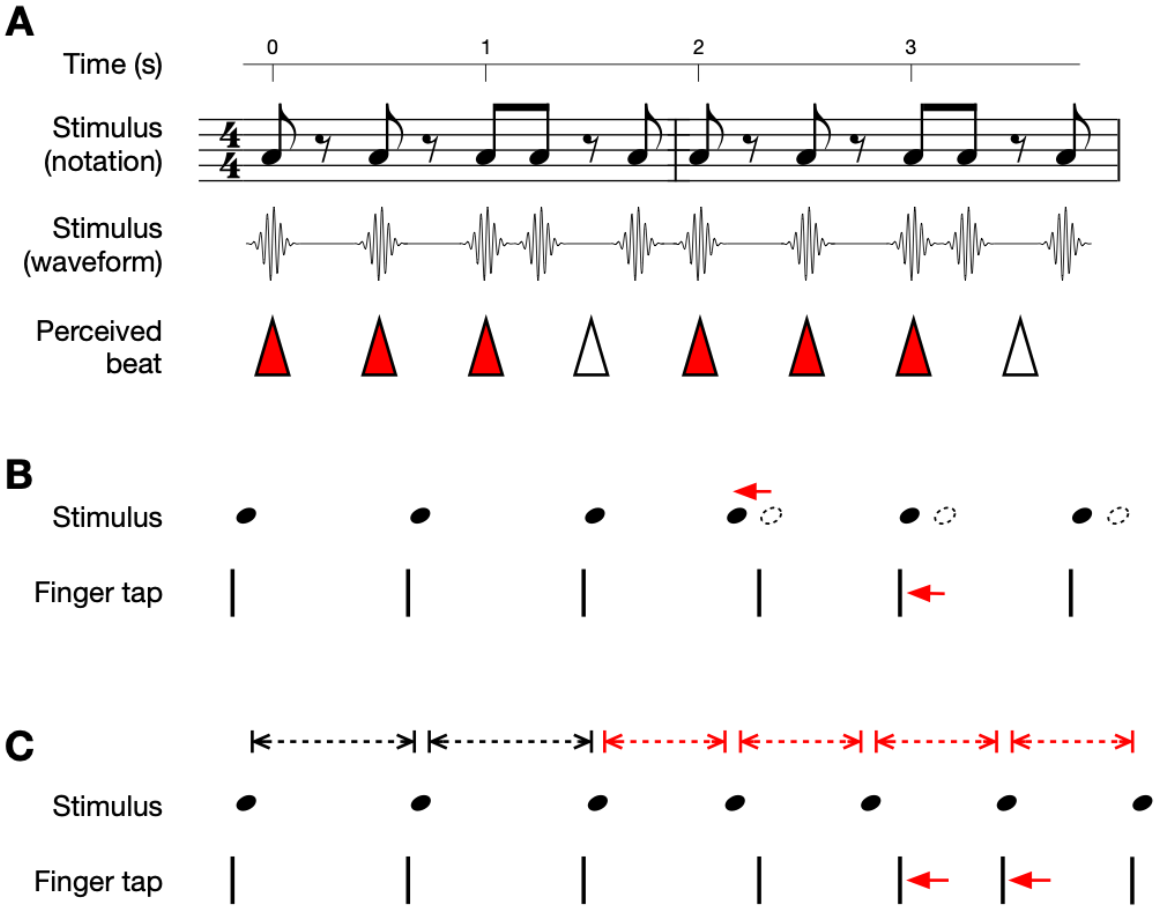

Figure 1: Examples of beat perception. A) A simple non-isochronous rhythm that induces an isochronous beat percept (triangles). Note that some beats are not marked by acoustic events (hollow triangles). B,C) Beat perception quickly adjusts to slight changes in stimulus timing. In B) a metronomic rhythm is perturbed by a "phase shift": the fourth event and all subsequent events are shifted forward in time by the same amount (hollow ovals show where the events would have occurred if there was no phase shift). When a person tapping with a metronome experiences such a phase shift, their first tap is late relative to the time-shifted event but subsequent taps are quickly adjusted in timing to come back into synchrony with the metronome. In (C) a metronomic rhythm increases in tempo after the third event (IOIs before and after the tempo change are indicated by dashed arrows). A person tapping along adjusts for the perturbation (red solid arrows) over the next few events. Timing adjustment process in (B) and (C) has been simplified for illustration.

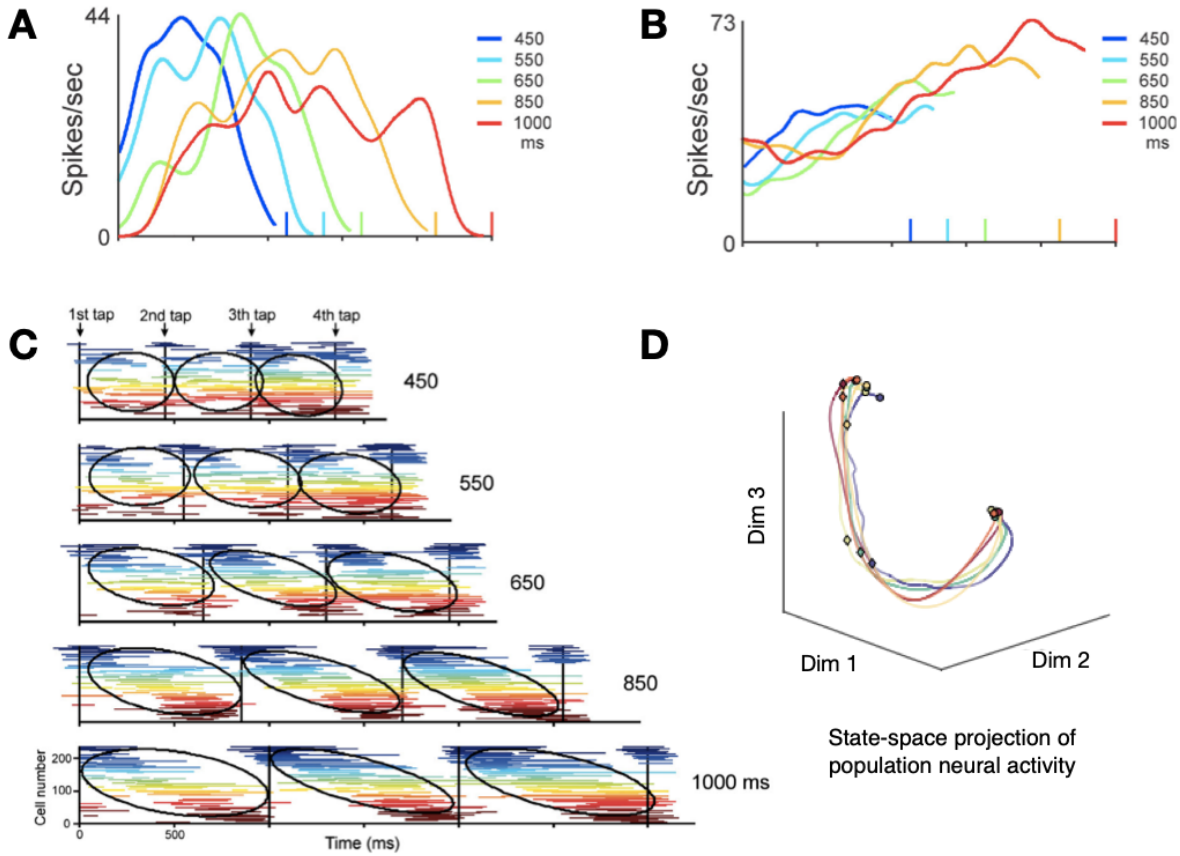

Figure 2: Relative and absolute timing activity patterns in monkey SMA during processing of isochronous rhythms. A) During a synchronization task the firing rate of this cell in SMA rises and falls from one event to the next at a rate that scales to span the time between events (from 450-1000 ms IOI) (Merchant & Averbeck, 2017). This is an example of relative timing activity. B) During the same task, the firing rate of a different cell in SMA increases steadily from one event to the next at a rate that does not change as a function of IOI, an example of absolute timing activity (Merchant & Averbeck, 2017). C) Measurements across many monkey MFC cells during a similar interval production task reveal that the joint pattern of activity across a subset of cells plays out at a rate that scales to fill the temporal interval between metronome events and thus functions as a population-level relative timer (colored lines show cell activity, ovals highlight temporal stretching of activation pattern) (Merchant, Pérez, et al., 2015). D) Population neural firing rates in monkey SMA during interval timing tasks can be understood as tracing out a trajectory in a high-dimensional space. Here, a set of neural trajectories is displayed projected down into three dimensions. The population acts as a relative timer by following a stereotyped path in this space which is traversed at a speed that scales to fill the temporal interval between metronome events (Wang et al., 2018).

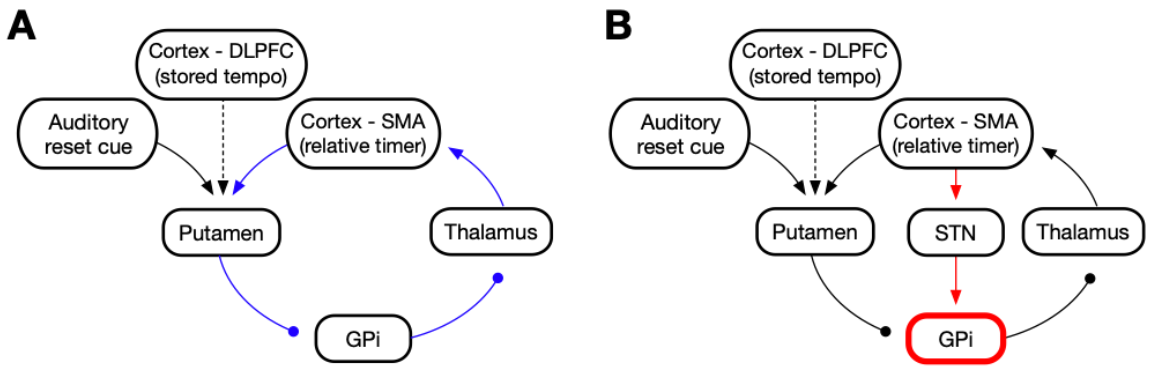

Figure 3: Motor pathways that may support the beat percept. A) The "direct pathway" (blue), which carries signals from cortex through basal ganglia (putamen and GPi) and thalamus back to cortex to activate motor programs, could also carry the signal necessary to reinitiate a relative timer. This reset signal could be initiated by the termination of the cortical timer (or by a salient auditory cue), allowing both the internal beat cycle and the sensory stream to reinitiate the relative (beat-anticipatory) timer, individually or in combination. This signal could carry tempo information from cortex (possibly DLPFC) to inform the relative timer of an appropriate speed. B) The "hyperdirect" pathway through basal ganglia (red) is generally understood to carry a global "hold" or "no-go" signal that can prevent the execution of commands carried by the direct pathway by exciting GPi and is associated with beta-rhythmic activity. Activation of this pathway between beats may inhibit the initiation of new motor programs, prevent auditory cues from resetting the cortical timer, and produce the beat-entrained beta activity observed in basal ganglia and elsewhere. In this diagram arrowheads indicate excitatory connections, and solid balls indicate inhibitory connections.

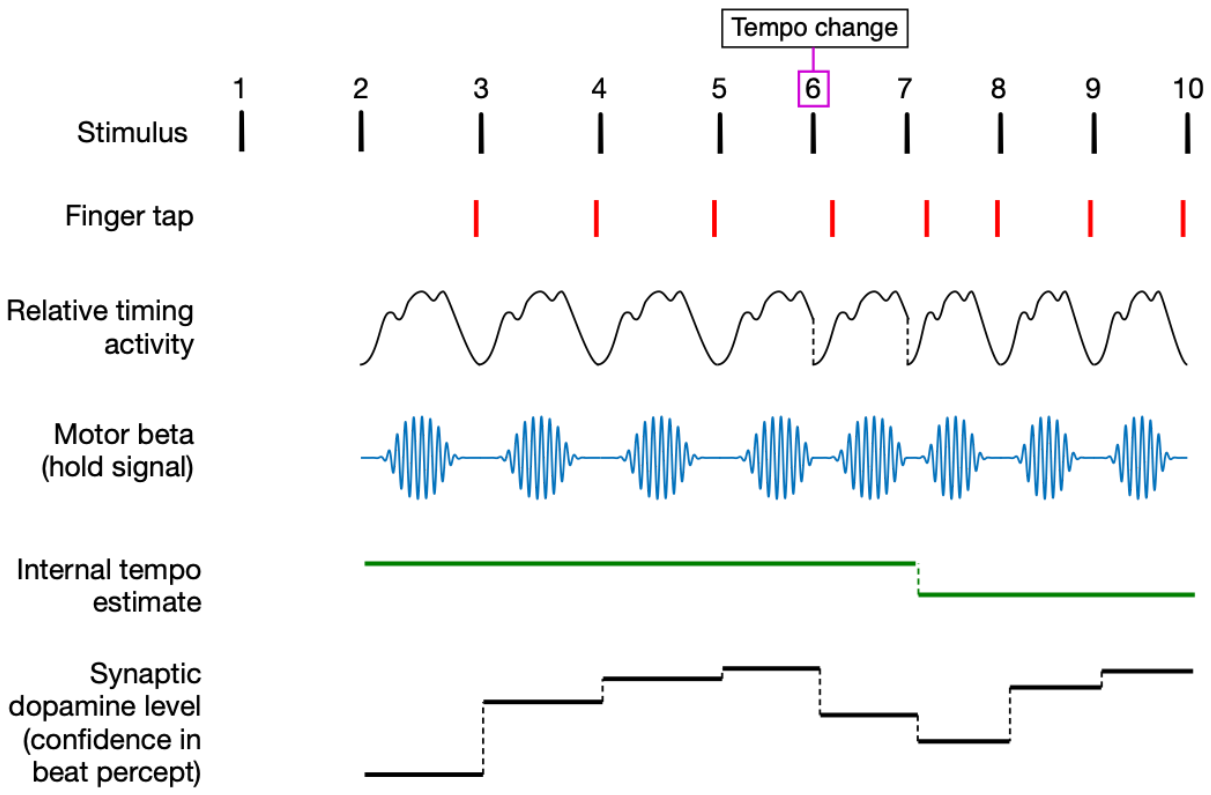

Figure 4: A unified neurodynamic account of tempo change. In this example a metronome changes to a faster tempo (the IOI is shortened) starting at the 6th event. Experiments show that when metronome tempo changes, a subject tapping to the beat first under-corrects their timing, as if to adjust for a single perturbed IOI but without assuming that this change will apply to the following IOIs as well (cf. Figure 1B) (Repp & Keller, 2004). If striatal dopamine serves as an index of confidence in the underlying beat, as we hypothesize, the temporal dynamics of entrainment through a tempo change could be explained by dopaminergic dynamics. Specifically, at the moment of the first inaccurate tap dopamine is still high, so internal tempo (green line) is not updated with new measurements; however, this inaccuracy causes dopamine to drop (lower black line). Since the internal tempo has not been updated, the next tap is also inaccurate, and at this point, low dopamine allows the tempo to be measured and updated. Note that the relative timer's repeating pattern of activity was reset by temporally unexpected events (7 and 8) because the unexpected events occurred near beats, outside of the protective temporal window of elevated beta oscillations between beats.

Box 1: Temporal measurements in the motor system

The inference of tempo from a beat-based stimulus requires an interaction between the stimulus and internally generated timing activity. Perhaps the simplest strategy for interval measurement is for one event to initiate absolute timing activity (as in Fig 1B), and for the state of this activity at the next event to be read by a downstream structure as a measure of the inter-onset interval (IOI). Pre-SMA in particular is involved in perceptual timing (Schwartze et al., 2012), and a greater proportion of cells in pre-SMA are driven by sensory stimuli than in SMA-proper, so this area would be a good place to look for the timing activity necessary for tempo measurement (see also (Macar et al., 2006)).

The cerebellum is a prime candidate for the downstream structure that reads timer activity: it is consistently implicated in interval measurement tasks, and cerebellar degeneration and TMS interfere with motor synchronization and the detection and correction of tempo changes (Del Olmo et al., 2007; Schwartze et al., 2016; Théoret et al., 2001). However, these cerebellar perturbations do not seem to interfere with purely perceptual judgments about a beat-based stimulus (Grube, Cooper, et al., 2010; Grube, Lee, et al., 2010). This ambiguity may be resolved by separating the process of tempo inference from the process of error detection and tempo correction, which shows different spatial activation patterns in fMRI (Cameron, 2016). The olivocerebellar system is not active during initial synchronization, but shows activity in response to deviations from rhythmic timing (Xu et al., 2006). This is consistent with the general picture of the cerebellum as the site of synchronization error correction (Bijsterbosch et al., 2011) and of error-based motor learning (Popa et al., 2016).

Another candidate region to take time measurements at auditory event times is dorsal putamen, which receives significant converging sensory and motor input (Flaherty & Graybiel, 1993; Reig & Silberberg, 2014). A fine-grained fMRI study (Cameron, 2016) showed dorsal putamen activation specifically during beat finding (shifting to ventral putamen once the beat is found, as the stimulus continues), and the Merchant lab observed high firing rates in monkey dorsal putamen just after clicks while monkeys tap to a metronome (with lower rates when

they continue the rhythm in the absence of the stimulus) (Bartolo et al., 2014). In this case, the process of tempo inference would be essentially equivalent to the striatal beat frequency (SBF) model (Matell & Meck, 2004), in which absolute timing activity produced by an impulse resetting a collection of oscillators is read at the next impulse by the striatum.

However, we do not rule out the possibility that the tempo-inferring interaction between stimulus and internal timing activity is more complex: Large et al (Large et al., 2015) show that the activation of resonant dynamics is another plausible mechanism of tempo inference.

Box 2: Implications for Parkinson's Disease

The specific connections between beat-keeping and the motor system proposed here have implications for Parkinson's disease research. Parkinson's patients show impairment in rhythmic timing (Breska & Ivry, 2018; J. A. Grahn & Brett, 2009; Te Woerd et al., 2017), which is linked to the primary symptom of "freezing of gait" (FOG) (Dalla Bella et al., 2017; Leow et al., 2014). The alleviation of FOG and its accompanying neural signatures by dopaminergic medication suggests that this deficit is linked to the reduction of striatal dopaminergic signaling in Parkinson's (Toledo et al., 2014), pointing to a central role for striatal dopamine in rhythmic timing. Our view of dopamine's role in maintaining an internal beat percept offers a concrete mechanism by which reduced striatal dopamine could impair rhythmic timing. Specifically,: reduced dopamine would compromise the systems by which the beat is internally maintained, making the beat percept heavily dependent on auditory input (this could help explain why simply imagining music with a beat doesn't help gait in PD).

One effective treatment for FOG is rhythmic auditory stimulation (RAS) by metronome or beat-based music (Ghai et al., 2018). RAS has been shown to effectively treat Parkinsonian rhythmic impairments beyond FOG (Dalla Bella et al., 2015; Ghai et al., 2018), 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 timing circuits to compensate for impaired timing in basal ganglia circuits (Sen et al., 2010). However, Fischer et al. (Fischer et al., 2018) found that RAS deepened beta modulation in STN during walking in place, suggesting that RAS acts directly on the basal ganglia and on the central beat-keeping system. (See also (Hell et al., 2018)).

Our framework for the motor system's role in beat perception suggests plausible mechanisms for the effect of RAS. One possibility is that the dopamine-depleted striatum cannot easily transmit the signal that allows the end of relative timing activity in SMA to re-initiate relative timing, but pulses of auditory input arriving at striatum at the appropriate moments could

provide sufficient additional excitation for the signal to pass through, inducing a sense of the beat. Once a strong internal beat has been induced, the resulting strong cycle of the beta-oscillatory hold signal could provide clear windows for planning and executing motor programs. If this is indeed a mechanism for the efficacy of RAS, we would expect that all movements along with the beat (not just gait) would be facilitated by RAS and that highly syncopated rhythms with many beats lacking a direct auditory marker would be unhelpful for FOG.

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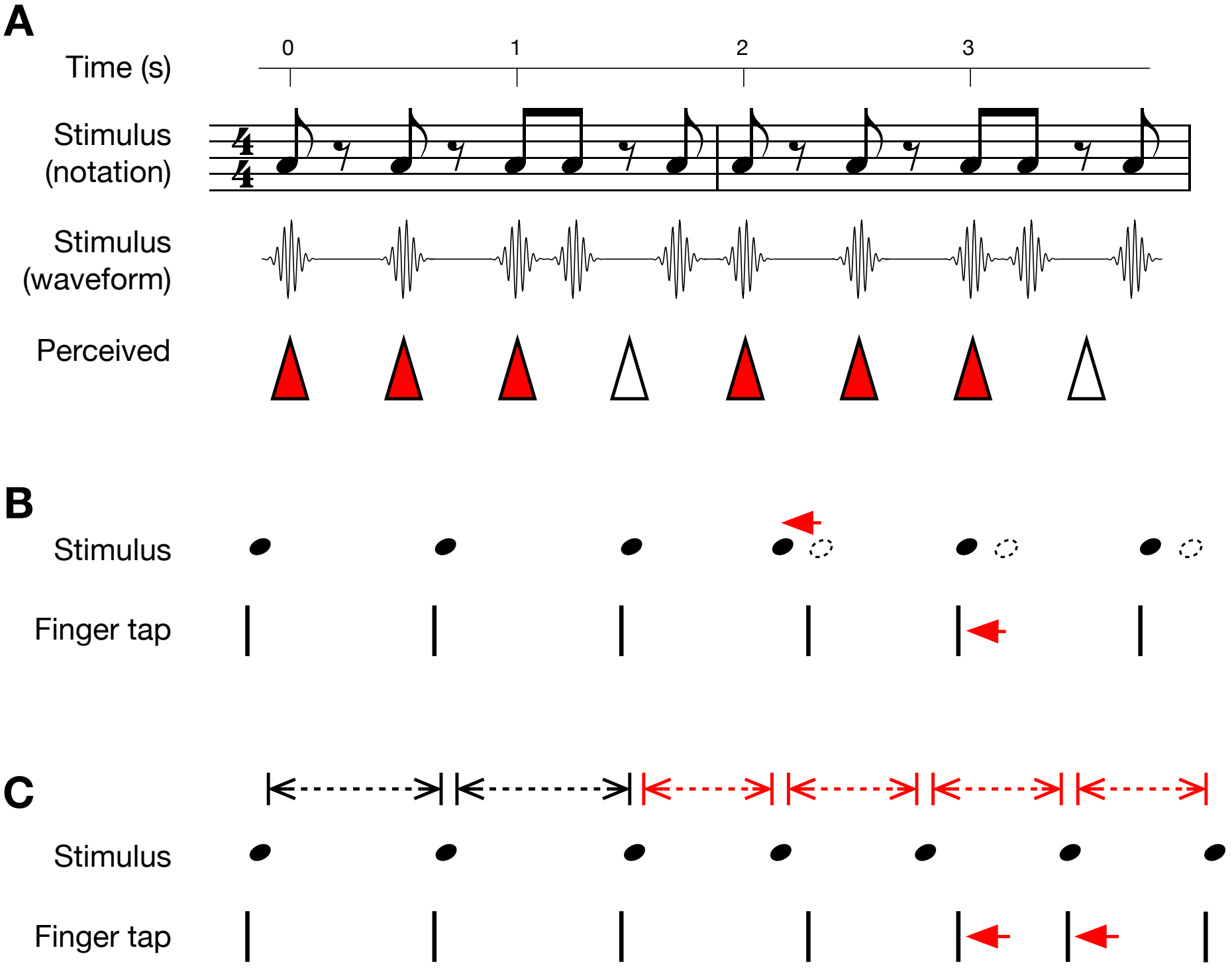
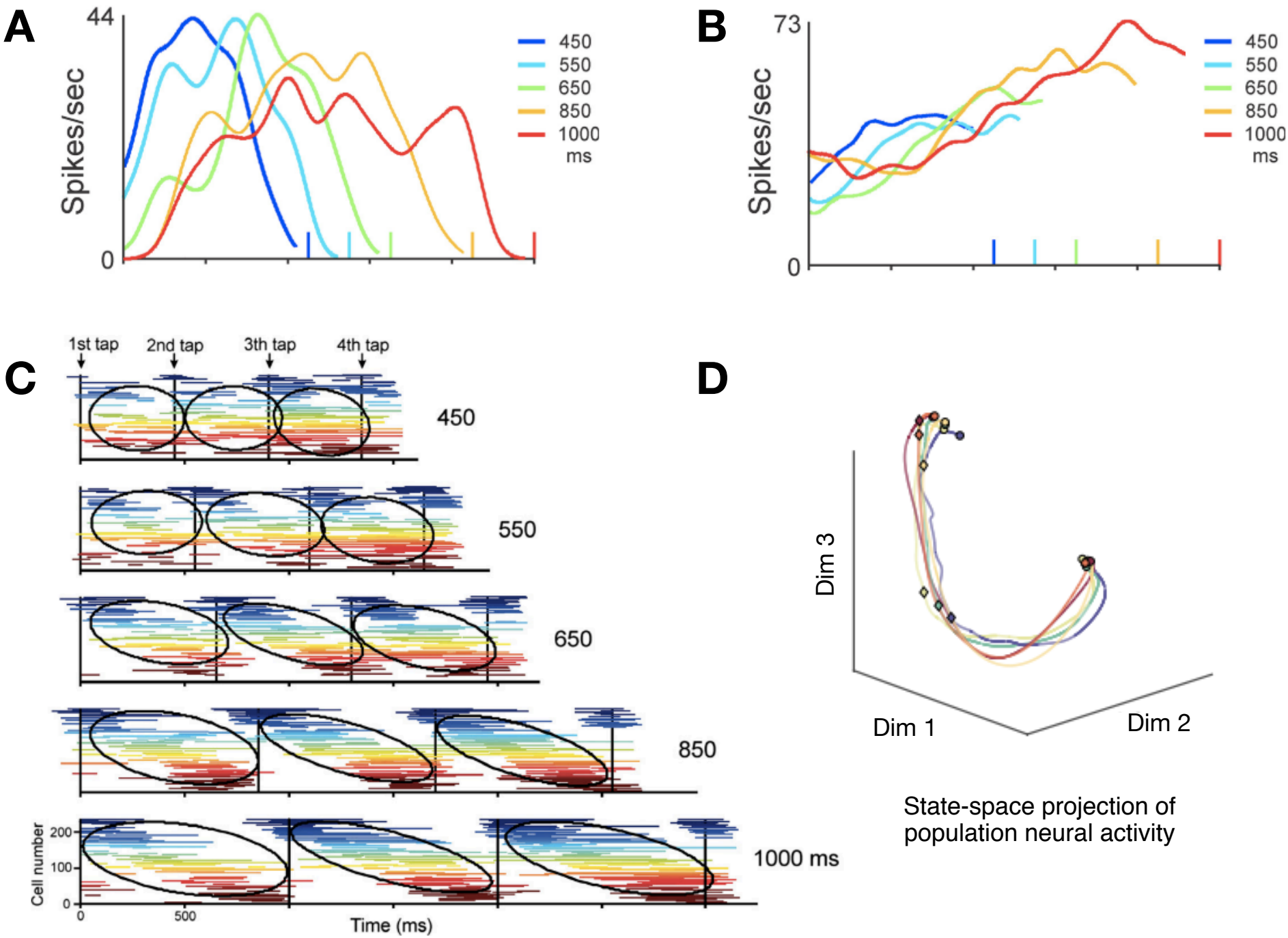
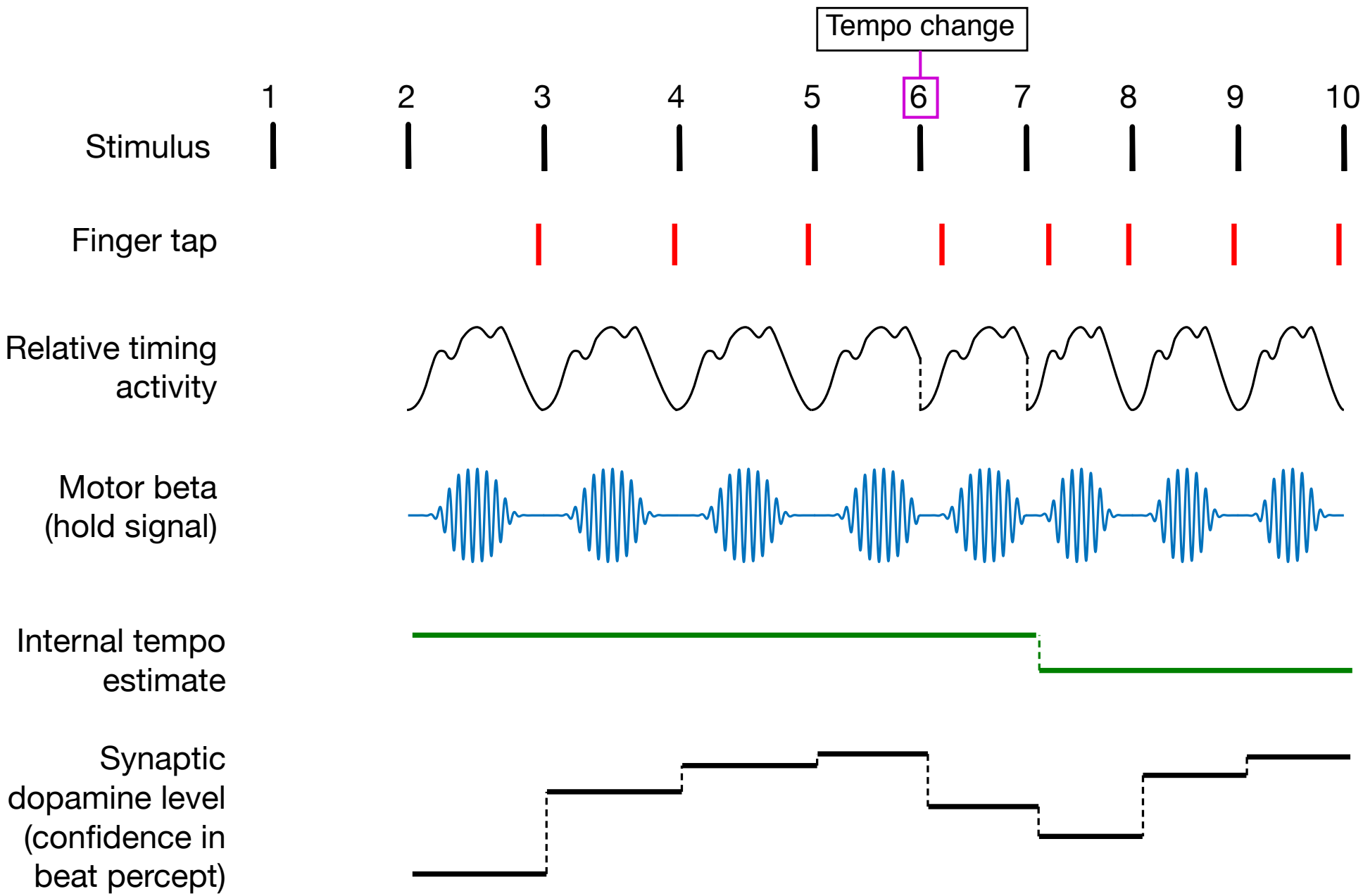
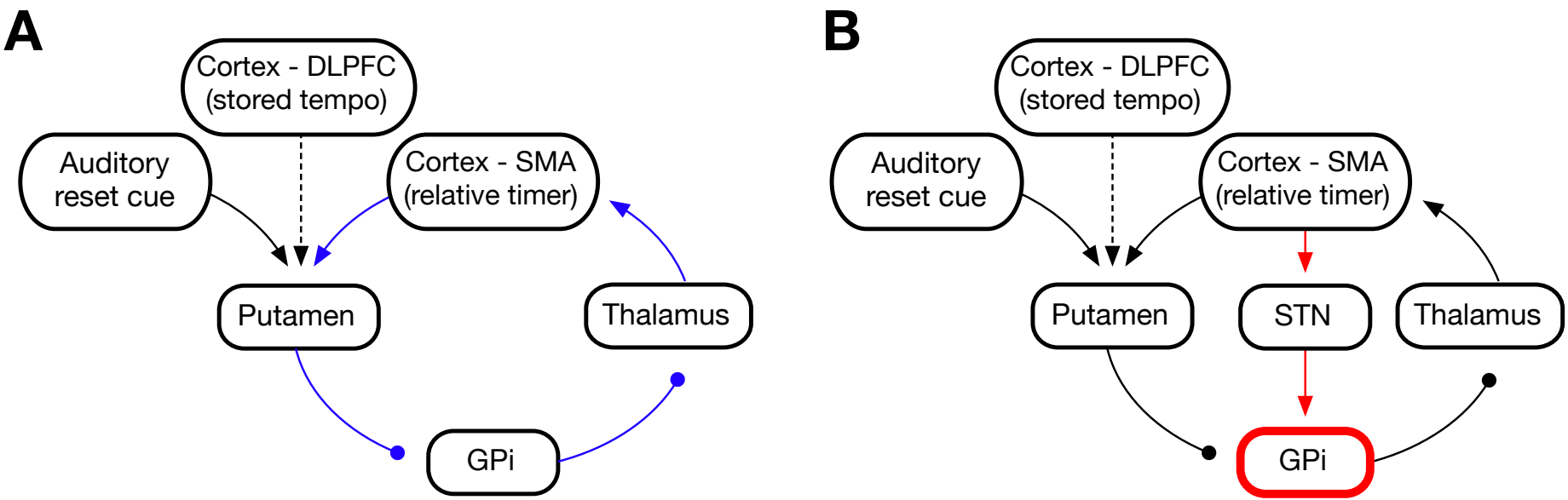

A
Time (s)
0
1
2
3
Stimulus
(notation)
Stimulus
(waveform)
Perceived
B
Stimulus
Finger tap
C
Stimulus
Finger tap


A
44
0
Spikes/sec
450
550
650
850
1000
ms
B
73
0
Spikes/sec
450
550
650
850
1000
ms
C
1st tap
2nd tap
3th tap
4th tap
450
550
650
850
1000 ms
Cell number
200
100
0
0
500
Time (ms)
D
Dim 3
Dim 1
Dim 2
State-space projection of
population neural activity


Tempo change
1
2
3
4
5
6
7
8
9
10
Stimulus
Finger tap
Relative timing activity
Motor beta (hold signal)
Internal tempo estimate
Synaptic dopamine level (confidence in beat percept)


A
Cortex - DLPFC
(stored tempo)
Auditory
reset cue
Cortex - SMA
(relative timer)
Putamen
Thalamus
GPi
B
Cortex - DLPFC
(stored tempo)
Auditory
reset cue
Cortex - SMA
(relative timer)
Putamen
STN
Thalamus
GPi