Are we in time? How predictive coding and dynamical systems explain musical synchrony

To appear in *Current Directions in Psychological Science*

Preprint DOI: 10.31219/osf.io/8enxy

Caroline Palmer¹ and Alexander P Demos²

¹McGill University

²University of Illinois at Chicago

Contact Information:

Caroline Palmer, Professor

Department of Psychology, McGill University

1205 Dr. Penfield Ave

Montreal, QC Canada H3A 1B1

Caroline.palmer@mcgill.ca

514 398 6128

Abstract

Humans tend to anticipate events when they synchronize their actions with sound (such as clapping to music), which has puzzled scientists for decades. What accounts for this anticipation? We review two theoretical mechanisms for synchrony: predictive coding and dynamical systems. Both theories are grounded in neural activation patterns, but with important distinctions. We contrast their assumptions, computations, and musical applications to explaining anticipatory synchronization.

Keywords

Anticipatory synchronization; coupling; dynamical systems; internal models; predictive coding

Introduction

Some of the most intricate temporal sequences that humans produce are the sounds they use to communicate, including speech and music. People precisely coordinate their movements with sound; speakers prepare for their turn to talk, and musicians time their productions to synchronize or align with sound. Even young toddlers spontaneously drum or sway in response to auditory rhythms, suggesting that humans are predisposed to synchronize movement with sound. Because movement preparation is often slower (100-250 ms) than the rate of musical events (up to 8-10 tones/s), individuals must anticipate future events in order to prepare their movements. A striking feature of musical synchronization is the tendency to act sooner than the sound with which one intends to synchronize; musicians produce tones about 30-50 ms sooner than a regular auditory beat, and nonmusicians anticipate even sooner (50-80 ms) (Repp & Siu, 2015). We refer to this as *anticipatory synchronization*, a cornerstone of human synchrony.

Several key variables influence our ability to synchronize actions with musical sound. One is musical training which reduces the anticipatory synchrony, defined as negative mean asynchrony (when listeners' produced actions precede stimulus onsets, such as claps preceding musical tone onsets). Another factor is sensory feedback; the more feedback available from self-generated and external auditory outcomes, the smaller the asynchrony (Repp & Siu, 2015). A third factor is the predictability of auditory sequences; the more regular the sequence, the smaller the asynchrony variability. Mean and variance measures of asynchrony are used by synchronization models in different ways, as we shall see below.

Two prominent theories offer relevant mechanisms for musical synchronization. One is predictive coding (PC) and the other is dynamical systems (DS). We compare these explanations applied to anticipatory synchronization in the next section, and discuss their assumptions, computations, and limitations.

Predictive Coding

Origins. Originating as early as Helmholtz' proposal of learning based on hierarchical layers of representation (cited in Friston 2009), more recent precursors to predictive coding include internal models of motor commands (Wolpert et al, 1995) and mental simulations of partners' joint actions (Sebanz & Knoblich, 2009). Each proposes internal modeling of future events, based on representations of the mapping between

one's perceptions and actions (Clark, 2013). Internal models have been proposed in motor control that predict the sensory consequences of actions by simulating behavior and compensating for time delays in sensorimotor systems (Wolpert & Flanagan, 2001). Internal models have been applied to poor pitch singing via emulations of vocal fold tension compared with auditory feedback from resulting pitches (Pfordresher & Mantell, 2014). Extensions to interpersonal or joint action propose that a partner's actions are simulated through the use of internal models to generate predictions for upcoming events (Sebanz & Knoblich, 2009). A musical application of joint action combines simulation of actions for oneself and partners, as well as imagining sounds produced by partners, with error correction (van der Steen & Keller, 2013).

Recent PC models compute the difference between an internal model and perceived events with a goal to minimize the entropy (the inverse of predictability) of predictions relative to future observed outcomes (Friston, 2009, 2018). Influenced by neurophysiological evidence of cascading processes among hierarchical levels in the visual system (Rao & Ballard, 1999), recent PC models rely on Bayesian inference to update internal models and have been applied to explain binocular rivalry and bistable visual percepts (see Clark, 2013 for a review). PC applications to auditory perception have recently been assessed (Denham & Winkler, 2020; Heilbron & Chait, 2018).

Assumptions: One key assumption is the use of an internal model to predict future behavior. Perceptual input is compared with the prediction, generating a difference (prediction error) used to adjust the internal model and then discarded. There is no need to store the original perceptual input or the prediction error, and thus the required representation is parsimonious. A second assumption is a hierarchical organization in which lower areas receive sensory input that is projected to higher cortical areas. A hierarchy is formed by forward excitatory connections from sensory areas to association areas, and backward inhibitory connections downward, as well as lateral interactions between units within layers. The hierarchical system permits the computation of prediction error at one level while updating the internal model at another level; the computations occur in a cascaded fashion. Although the temporal properties of this cascade of forward, backward, and lateral connections are not well-specified, the spatial projections are proposed to include the auditory network from brainstem to cortex (Koelsch et al., 2019).

Computations: To create accurate predictions of future states, prediction error is minimized over iterations, based on Bayesian inference. The bottom layer of the hierarchy contains error units that sense the incoming information and compute the prediction error which is sent to higher layers. The top layer encodes prior probabilities that a given sensory input corresponds to a predicted state; this is the internal model. State units in the top layer (actively) generate the prediction signal and send it downward to the error units. In addition, lateral connections connect units within levels. Error units and state units have bidirectional signals: forward connections convey prediction error to state units, and reciprocal backward connections send the predictions to error units. These top-down and bottom-up messages serve to optimize the use of "free energy" (Friston, 2009). Minimizing free energy corresponds to maximizing the probability that the sensory input matches the predicted outcome, given the internal model. Over successive iterations, the state units' prior probabilities (existing beliefs before new evidence is introduced) become closer to the error units' posterior probabilities (updated beliefs after new evidence is introduced). Eventually, when prior probabilities match posterior probabilities, the internal model is stable.

Music Applications: Vuust and Witek (2014) proposed a PC model to explain perception of musical syncopation. Syncopation or the occurrence of musical tones in unexpected metrical locations, typical of "groove" music, often causes listeners to move, sway, or dance. Musical meter, a hierarchy of regular pulses that form patterns of strong and weak beats, provides the prior experience that tones will occur more often on strong beats. An internal model of meter generates predictions that include the movements needed to produce the syncopated rhythm, while suppressing overt action. This suppressed tendency to move arises from predictions of when the beat is expected to occur (see Koelsch et al., 2019 for related neurophysiological evidence). Prediction errors have two important parameters: the mean value, and the variance associated with the mean. In Vuust et al. (2018), high amounts of syncopation were associated with high variance in prediction error (low precision). The more precise the prediction error, the more impact that error has. Only prediction errors associated with small variances cause the higher-level predictions to be adjusted, while prediction errors with large variances are ignored (Vuust et al, 2018), a claim that is testable in synchronization tasks.

Two studies have tested PC models of anticipatory synchronization. The first (Heggli et al., 2019b) tested dyadic partners' internal models as they synchronized with each other while they tapped identical duration patterns. Each partner heard over headphones either the same metrical context as their partner (creating similar shared internal models with matched top-down predictions) or different metrical contexts (creating dissimilar internal models with unmatched top-down predictions) that manipulated the top-down prior beliefs for where their taps should occur. Different contexts created polyrhythms (3 participant taps against 4 context beats) that could be perceived as ambiguous, and auditory feedback was manipulated across conditions. Small mean negative asynchronies were observed across conditions. Asynchrony variability worsened when the two partners' metrical contexts differed (although partners recovered quickly within trials), interpreted as evidence for prediction errors resulting from the discrepancy in the partners' different internal models.

The second study (Elliott et al., 2014) presented individuals with two auditory cues that created ambiguous percepts with which they tried to synchronize. The two cues were altered in their asynchrony (relative phase) and temporal regularity. Large mean negative asynchronies decreased (toward 0) as the two cues' relative phase increased. Participants used different strategies: they synchronized to the integrated (combined) cues when the cues' phase difference was small, but they synchronized with one cue or the other when the phase difference was large. Model fits to asynchrony variabilities provided support for a Bayesian causal inference model with 4 free parameters that captured prior probabilities associated with the auditory cues; prediction errors indicated participants' strategies to minimize the variance and extract a temporally regular beat.

Remaining issues: PC applications to musical synchrony to date have targeted ambiguous percepts, in order to demonstrate the internal model's impact based on prior probabilities. One question is whether PC models can predict anticipatory synchrony (mean behavior). Another is whether an internal model can change only in the presence of prediction error (contextual information), or will it change in the absence of novel information (for example, toward a stable state). A final question is what the time costs are of implementing a hierarchy that relies on several steps between layers before prediction error is computed (upward) and sent downwards.

Dynamical Systems

Origins. DS theories, which explain how systems change over time, have their origins in analysis of physical synchrony among pendulum clocks (Huygens, 1665; described in Pikovksy, Rosenblum & Kurths, 2001) as well as biological synchrony in circadian rhythms, cardiac rhythms, and motor coordination (Haken, Kelso, & Bunz, 1985; Winfree, 1967). Synchronization arises when oscillators (alternating waveforms that repeat) that are self-sustaining (continue in the absence of external input) share information via coupling, causing them to adapt to each other or to a stimulus. Their self-sustaining nature is supported by neural (MEG) representations of musical pulse that continue at the stimulus rate in its absence (Tal et al., 2017). When an oscillator is momentarily disturbed by input, it soon returns to its original frequency, its stable state of minimum energy expenditure. An oscillator will resonate to a stimulus (adapt its phase and/or frequency) when its natural frequency is close to the stimulus frequency, *or* when the coupling between oscillator and stimulus is high. Linear oscillators synchronize 1:1 with stimulus events; nonlinear oscillators additionally synchronize at higher resonances (1:2; 1:3). The perception of hierarchical meter thus arises from higher-order resonances – internal models are not required (Large, 2008).

Anticipatory synchronization arises in delay-coupled systems when a driven oscillator (affected by external input) compares its own time-delayed memory of a previous state to the current input (Voss, 2000). Delay-coupling refers to models in which the coupling term between two or more oscillators is modulated by time delay from at least one oscillator. Stepp and Turvey (2010) describe this delay-coupling approach as "strong" anticipation: anticipated future states are based on present and past information already in the system without the need for internal models. Machado and Matias (2020) demonstrated the biological plausibility of delay-coupled models by simulating delay-coupling in spike neuronal populations that lead to bistable visual percepts. Time delays in DS models have been implemented to account for intra-brain synchronization dynamics (Deco et al., 2009; 2011) as well as interpersonal synchronization (Varlet et al., 2012).

Assumptions: DS theories of human synchrony assume that behavior arises in a system composed of coupled subsystems of oscillators whose emergent processes explain perception and cognition. Individual oscillations arise from the joint activity between coupled excitatory and inhibitory neurons and are modeled

either at the biophysical level or, more commonly, by using oscillator models with simplifying assumptions. Oscillatory time series arise from neuronal interactions, as well as from neurons interacting with external quasi-periodic stimuli such as musical sequences. Most DS theories assume continuous change over time, but they can also be modeled discretely as in the case of musical pulse (Large, 2008). Time-delay in DS models, often implemented as a constant for simplicity, is assumed to represent synaptic transmission rate in a neural system (Machado & Matias, 2020).

Computations: Delay-coupling DS models (incorporating time delay and coupling terms) have been proposed to account for anticipatory synchronization. Based on self-sustaining oscillators, the coupling term is often adapted from the Kuramoto model (Strogatz, 2000) which assumes each oscillator has an intrinsic frequency that can be tuned during development via Hebbian learning (Tichko et al., 2021). Oscillators adapt their phase based on how much they differ from incoming stimulus onsets, modulated by the coupling strength; higher coupling means more phase correction and faster synchronization. Time delay compares the oscillator's past (at a constant delay) with the current input (Voss, 2000), thus providing a type of self-feedback. Most critical is that the oscillator's past incorporates the past of the stimulus; thus, the oscillator (passively) reacts to present events as a function of present and past states of both stimulus and oscillator.

Music Applications: Roman et al. (2019) tested synchronization patterns of individuals who tapped to a metronome, using a single Hopf oscillator with time-delay to represent unidirectional coupling with the metronome. The model, designed to mimic neural oscillations and adapt its frequency, simulated the neural delays necessary to account for the observed tappers' negative mean asynchrony. The model successfully predicted the difference in the degree of anticipatory synchronization between musicians and nonmusicians who tapped at a range of metronome rates.

Demos et al. (2019) used a bidirectional delay-coupled model, adapted from Kuramoto, to model the more complex case of asymmetric anticipatory synchronization between musical duet partners. Each partner was modeled as a simple oscillator with separate parameters for time delay, coupling, and intrinsic frequency. Each oscillator could be driven by or could drive the other oscillator, based on which partner(s) received auditory feedback. The model accounted for anticipatory synchrony under experimental conditions that

manipulated auditory feedback to shift the oscillators from bidirectional to unidirectional information transmission. The use of delay-coupling terms successfully predicted the driven-partner's mean anticipatory synchronization (performing earlier than their driver-partner) when the driver-partner could not hear the driven-partner; this was the first delay-coupling implementation to extend beyond single-person models of musical synchrony to interpersonal interaction.

Heggli et al. (2019a) examined how partners alter their synchronization in a tapping task, using bidirectional coupling but with no time delay. Two oscillators modeled each individual's perception and action; between-individual bidirectional coupling linked one person's action to the partner's perception. The model captured different patterns of synchronization variability, such as when pairs show mutual adaptation (increased coupling) or when both partners try to lead at the same time (reduced coupling). Similar coupled oscillator networks without time delay can produce anticipatory synchronization (Pyragiené & Pyragas, 2015).

Remaining issues: The delay-coupling term in DS models accounts for both individual and dyadic anticipatory synchronization. One question is how time delays map to neural features, such as synaptic transmission (Machado & Matias, 2020) and functional properties of neural networks (Deco et al., 2011). Another question is whether the delay is constrained per individual, task, or social context. Finally, how can these parameters be interpreted and connected back to behavior given the complexity of their nonlinear interactions?

Model Comparisons: Although assumptions and computations differ between PC and DS models, they have similarities too. Both models rely on interconnections between excitatory and inhibitory neurons. The primary differences include the role of time and the organizational architecture: the hierarchical representations (PC) include several layers, more types of nodes (excitatory, inhibitory; modulatory - PC only), and more connections than the bottom-up DS oscillations based on excitatory-inhibitory interactions. These computational distinctions, represented by the number and direction of connections within the excitatory neurons, suggest the models diverge in parsimony. These distinctions parallel differences in the synchrony behaviors accounted for: the PC models' Bayesian properties accounting for synchrony variability, the DS models' delay-coupled differential equations accounting for mean (directional) synchrony. While not mutually exclusive, important

paradigmatic and architectural differences prevent an easy merger of these theories: PC models evolved from information theory / systems neuroscience with top-down/bottom-up distinctions (such as mismatched internal models of musical partners), whereas DS models evolved from physics / mathematical biology with interactions across multiple spatio-temporal scales (such as unidirectional and bidirectional coupling within and across ensemble musicians). In short, predictive coding explains synchrony by *generating predictions* based on prior learning; dynamical systems explains synchrony by *coupling already-existing oscillations* without a need to generate predictions.

Conclusions

Predictive coding and dynamical systems models of musical synchronization share similarities, including the goal to minimize energy; computing differences between expected and observed outcomes; and grounding in neurophysiological models of excitatory and inhibitory activation. The models have important differences in their reliance on prior knowledge about the resulting output; how previous adaptations to stimuli are retained; and their use of mean or variability estimates of synchrony. To date, only DS theories have successfully modeled anticipatory synchronization.

Future directions include modeling noisy conditions; explaining roles of contextual learning, musical pleasure and reward; and scaling up to larger groups. Advances are likely to be assisted by machine learning and other mathematical tools for capturing musical synchrony.

Box 1. Key Concepts of Predictive Coding and Dynamical Systems.

Predictive Coding	Dynamical Systems
Oscillation: Often refers to waves of excitation / inhibition arising at different hierarchical levels and frequencies among neurons (for example, prediction errors propagated via gamma-frequency oscillations; predictions propagated via beta-frequency oscillations (Heilbron & Chait, 2018).	Oscillation: refers to a periodic, recurring time series (like a metronome) with an associated amplitude and frequency (Pikovsky et al., 2001). Often self-sustaining (continuing in the absence of input), oscillations are modeled with mathematical equations.
Predictive timing: Often contrasted with “reactive timing”, assumes the use of past information to generate an internal model capable of anticipating future events (Ravignani et al, 2014).	Anticipatory synchronization: Often called “Strong anticipation”, assumes the presence of coupled oscillations with time delays capable of anticipating future events of a stimulus or partner in the absence of internal models (Stepp & Turvey, 2010).
Free energy: Based on thermodynamics principles, refers to (expendable) energy available for a system to perform work or cause change. Referred to as a PC / information theory measure that constrains surprise arising from model-based prediction (Friston, 2009)	Energy expenditure: Refers to amount of energy used to implement change. States of least energy expenditure define steady (stable) states to which a system returns (Strogatz, 1994), such as runners’ preferred rates.
Prior (probability): In Bayesian inference, refers to expected probability of a hypothesized outcome before it is known. Different writings use alternate terms following <i>prior</i> : probability, distribution (or statistical information), belief, knowledge, assumption, or expectancy. Often refers to internal <i>a priori</i> “knowledge accumulated through experience” (p 3, Vuust & Witek 2014).	Phase: Position within one cycle of a periodic oscillation. The phase relationship between two oscillations is often measured relative to the period (1 / frequency) of the oscillations (hence the term phase (frequency) locking; Balanov et al., 2009).
Posterior (probability): In Bayesian inference, refers to the updated probability after the outcome is known, based on how well the hypothesis predicts the output multiplied by the prior probability of the hypothesis (Denham & Winkler, 2020). “Posterior” is often followed by probability, distribution, belief, knowledge, assumption, or expectancy.	Coupling: A parameter that defines how oscillators influence each other (share information), or how a stimulus influences an oscillator. Coupling can lead oscillators to phase-lock or frequency-match or both (Pikovsky et al., 2001).
Prediction Error: The divergence of the sensory input from the expectation (i.e., priors) used to update the prior probabilities (Clark, 2013).	Delay-coupling: An oscillator model that incorporates a coupling term combined with a time delay, implemented in differential equations (Voss, 2000). The time delay can refer to different functional properties (transmission delay; delay of one’s own feedback) of the oscillator.

Acknowledgements

This work was funded by NSERC Grant 298173 and a Canada Research Chair to C. Palmer. We thank Janeen Loehr, Kerry Marsh, Peter Pfordresher, Paula Silva, and Tim Sparer for comments and Jocelyne Chan for assistance.

References

- Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences*, 36, 181-204. <https://doi.org/10.1017/S0140525X12000477>
- Deco, G., Jirsa, V., McIntosh, A.R., Sporns, O., & Kotter, R. (2009) Key role of coupling, delay, and noise in resting brain fluctuations. *Proc Natl Acad Sci*, 29, 106:10302–10307.
- Deco, G., Jirsa, V.K., & McIntosh, A.R. (2011) Emerging concepts for the dynamical organization of resting-state activity in the brain. *Nature Reviews Neuroscience*, doi:10.1038/nrn2961.
- Demos, A. P., Layeghi, H., Wanderley, M. M., & Palmer, C. (2019). Staying together: A bidirectional delay-coupled approach to joint action. *Cognitive Science*, 43, e12766. <https://doi.org/10.1111/cogs.12766>
- Denham, S.L., & Winkler, I (2020). Predictive coding in auditory perception: Challenges and unresolved questions. *European Journal of Neuroscience*, 51, 1151-1160.
- Elliott, M. T., Wing, A. M., & Welchman, A. E. (2014). Moving in time: Bayesian causal inference explains movement coordination to auditory beats. *Proceedings of the Royal Society B*, 281, 20140751. <https://doi.org/10.1098/rspb.2014.0751>
- Friston, K. (2009). The free-energy principle: A rough guide to the brain? *Trends in Cognitive Sciences*, 13, 293-301. <https://doi.org/10.1016/j.tics.2009.04.005>
- Friston, K. (2018). Does predictive coding have a future? *Nature Neuroscience*, 21, 1019-1021. <https://doi.org/10.1038/s41593-018-0200-7>
- Heggli, O. A., Cabral, J., Konvalinka, I., Vuust, P., & Kringelbach, M. L. (2019a). A Kuramoto model of self-other integration across interpersonal synchronization strategies. *PLoS Computational Biology* 15, e1007422. <https://doi.org/10.1371/journal.pcbi.1007422>
- Heggli, O. A., Konvalinka, I., Kringelbach, M. L., & Vuust, P. (2019b). Musical interaction is influenced by underlying predictive models and musical expertise. *Scientific Reports*, 9, 11048. <https://doi.org/10.1038/s41598-019-47471-3>
- Heilbron, M., & Chait, M. (2018) Great expectations: Is there evidence for predictive coding in auditory cortex? *Neuroscience*, 389, 54-73.

- Koelsch, S., Vuust, P., & Friston, K. (2019). Predictive processes and the peculiar case of music. *Trends in Cognitive Sciences*, 23, 63-77. <https://doi.org/10.1016/j.tics.2018.10.006>
- Large, E. W. (2008). Resonating to musical rhythm: Theory and experiment. In S. Grondin (Ed.), *The Psychology of Time* (pp. 189-232). Emerald.
- Machado, J. N., & Matias, F. S. (2020). Phase bistability between anticipated and delayed synchronization in neuronal populations. *Physics Review E*, 102, 032412. <https://doi.org/10.1103/PhysRevE.102.032412>
- Pfordresher, P. Q., & Mantell, J. T. (2014). Singing with yourself: Evidence for an inverse modeling account of poor pitch singing. *Cognitive Psychology*, 70, 31-57. <https://doi.org/10.1016/j.cogpsych.2013.12.005>
- Pikovsky, A., Rosenblum, M., & Kurths, J. (2001). *Synchrony: A universal concept in nonlinear sciences*. Cambridge: Cambridge University Press.
- Pyragienė, T., & Pyragas, K. (2015). Anticipating synchronization in a chain of chaotic oscillators with switching parameters. *Physics Letters A*, 379, 3084-3088. <https://doi.org/10.1016/j.physleta.2015.10.030>
- Rao, R. P. N., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive field effects. *Nature Neuroscience*, 2, 79–87. <https://doi.org/10.1038/4580>
- Ravignani, A., Bowling, D.L., & Fitch, W.T. (2014) Chorusing, synchrony, and the evolutionary functions for rhythm. *Frontiers in Psychology*, 5, 1118, doi: 10.3389/fpsyg.2014.01118.
- Repp, B. H., & Siu, Y.-H. (2015). Sensorimotor synchronization: A review of recent research (2006-2012). *Psychonomic Bulletin and Review*, 20, 403-452. <https://doi.org/10.3758/s13423-012-0371-2>
- Roman, I. R., Washburn, A., Large, E. W., Chafe, C., & Fujioka, T. (2019). Delayed feedback embedded in perception-action coordination cycles results in anticipation behavior during synchronized rhythmic action: A dynamical systems approach. *PLoS Computational Biology*, 15, e1007371. <https://doi.org/10.1371/journal.pcbi.1007371>
- Sebanz, N., & Knoblich, G. (2009). Prediction in joint action: What, when, and where. *Topics in Cognitive Science*, 1, 353-367. <https://doi.org/10.1111/j.1756-8765.2009.01024.x>
- Stepp, N., & Turvey, M. T. (2010). On strong anticipation. *Cognitive Systems Research*, 11, 148–164. <https://doi.org/10.1016/j.cogsys.2009.03.003>

- Strogatz, S.H. (2000) From Kuramoto to Crawford: exploring the onset of synchronization in populations of coupled oscillators. *Physica D*, 143, 1-20.
- Strogatz, S.H. (1994). *Nonlinear dynamics and chaos*. Reading, MA: Addison-Wesley.
- Tal, I., Large, E. W., Rabinovitch, E., Wei, Y., Schroeder, C. E., Poeppel, D., & Zion Golumbic, E. (2017). Neural entrainment to the beat: The “Missing Pulse” phenomenon. *The Journal of Neuroscience*, 37, 6331–6341. <https://doi.org/10.1523/JNEUROSCI.2500-16.2017>
- Tichko, P., Kim, J.C. & Large, E.W. (2021). Bouncing the network: A dynamical systems model of auditory-vestibular interactions underlying infants’ perception of musical rhythm. To appear in *Developmental Science*.
- Varlet, M., Marin, L, Raffard, S, Schmidt, R.C., Capdevielle, D., Boulenger, J.P., Del-Monte, J., & Bardy, B.G. (2012). Impairments of social motor coordination in schizophrenia. *PLoS One* 7(1): e29772.
- Van der Steen, M. C., & Keller, P. E. (2013). The ADaptation and Anticipation Model (ADAM) of sensorimotor synchronization. *Frontiers in Human Neuroscience*, 7, 253. <https://doi.org/10.3389/fnhum.2013.00253>
- Voss, H. U. (2000). Anticipating chaotic synchronization. *Physical Review E*, 61, 5115-5119. <https://doi.org/10.1103/PhysRevE.61.5115>
- Vuust, P., & Witek, M. A. (2014). Rhythmic complexity and predictive coding: A novel approach to modeling rhythms and meter perception in music. *Frontiers in Psychology*, 5, 1111. <https://doi.org/10.3389/fpsyg.2014.01111>
- Vuust, P., Dietz, M. J., Witek, M., & Kringelbach, M. L. (2018). Now you hear it: A predictive coding model for understanding rhythmic incongruity. *Annals of the New York Academy of Sciences*, 1423, 19-29. <https://doi.org/10.1111/nyas.13622>
- Winfrey, A. (1967) Biological rhythms and the behavior of populations of coupled oscillators. *Journal of Theoretical Biology*, 16, 15-42.
- Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science*, 269, 1880-1882. doi: 10.1126/science.7569931. PMID: 7569931
- Wolpert, D.M, & Flanagan, J.R. (2001). Motor prediction. *Current Biology*, 11, 729-732.

Recommended Readings

A comprehensive, accessible overview of predictive coding:

Bubic, A., Von Cramon, D. Y., & Schubotz, R. I. (2010). Prediction, cognition and the brain. *Frontiers in Human Neuroscience*, 4, 25. <https://doi.org/10.3389/fnhum.2010.00025>

An easy-to-read introduction to synchronization theory from a dynamical systems perspective:

Balanov, A., Janson, N., Postnov, D., & Sosnovtseva, O. (2009) *Synchronization: From simple to complex*. Heidelberg: Springer.

A foundational overview of dynamical systems in human behavior:

Kelso, S.A.J. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge: MIT Press.

A recent synthesis of predictive coding in musical joint action:

Keller, P. E., Novembre, G., & Loehr, J. (2016). Musical ensemble performance: Representing self, other, and joint action outcomes. In S. S. Obhi & E. S. Cross (Eds.), *Shared representations: Sensorimotor foundations of social life* (pp.280-310). Cambridge, UK: Cambridge University Press.

A recent extension of dynamical systems to human-machine interaction:

Washburn, A., Kallen, R. W., Lamb, M., Stepp, N., Shockley, K., & Richardson, M. J. (2019). Feedback delays can enhance anticipatory synchronization in human-machine interaction. *PLoS One*, 14(8), e0221275. <https://doi.org/10.1371/journal.pone.0221275>