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People walking side by side spontaneously synchronize their steps on some occasions but not on others, which poses a challenge to theories of perception-action based on interactive dynamic systems. How can action be spontaneously entrained by some sources of perceptual information while others are selectively ignored? The predictive processing framework suggests that saliency factors such as stimulus predictability, consistent deviation, and interactivity of the stimulus control the coupling between the motor system and perceptual information. To test this, we compared entrainment of gait cadence by two interactive auditory stimuli and two noninteractive but predictable, faster than preferred stimuli that were isochronous or statistically matched to gait. One interactive stimulus had properties that are optimal for mutual entrainment as per a mathematical model of interactive periodic processes, the Kuramoto system. In particular, the stimulus was faster than the participant but also adapted its rate to a limited degree as function of phase mismatch with the participant's steps. The second interactive stimulus fully mirrored the gait cycle hence it did not induce mutual synchronization. Furthermore, healthy participants were compared to ones with impaired gait due to Parkinson's disease, a model disorder that makes movement more dependent on external cueing. The mutually interactive condition produced the strongest entrainment, in patients and healthy participants, without differences between groups. The stimulus adapted to each participant's gait while maintaining a consistent lead in phase. Auditory-motor coupling may be enhanced by stimuli that are not only predictable but also interactive in that they align to self-generated movements.

***Keywords**:* dynamic systems, entrainment, gait, predictive processing, sensorimotor synchronization

***Supplemental materials**:* http://dx.doi.org/10.1037/xge0000609.supp

When we walk on an unstable surface, carry liquid in an open container, or manipulate unstable or new tools, our body typically responds in advance thus preparing to cope with possible perturbations. By doing that, we can maintain balance, or avoid letting an object fall, in complex sensory-motor everyday environments. Anticipatory responses constitute a core mechanism for action in a dynamic environment and have received particular attention during the last 2 decades (Burdet, Osu, Franklin, Milner, & Kawato, 2001; Kandel, Schwartz, Jessell, Siegelbaum, & Hudspeth, 2013; Latash, 1996; Turvey, 1990).

The intrinsic readiness of our bodies for anticipating external stimuli might help explain why we oftentimes find ourselves entrained by environmental rhythms. Spontaneous entrainment is apparent when we start tapping our feet to musical beat or when two individuals walking side by side may fall in a synchronous stepping pattern without instruction to do so. Paramount to our understanding of these phenomena is that they do not occur systematically (van Ulzen, Lamoth, Daffertshofer, Semin, & Beek, 2008; Zivotofsky & Hausdorff, 2007). To date, the conditions fostering spontaneous entrainment to an external rhythm are not understood sufficiently.

Accounts grounded in dynamic systems theory (Chemero, 2009; Haken, Kelso, & Bunz, 1985; Kelso, 1995) explain the spontaneous entrainment in terms of the interaction between coupled dynamic systems. Correspondingly, lack of entrainment implies lack of coupling. But we see here a limitation for theories that use dynamic systems as a basis for perception-action. If coupled dynamics explain entrainment then what explains when dynamics of the body and environment are coupled and when not? To deal with this, the predictive processing framework proposes that saliency factors such as predictability are involved in controlling the coupling (Clark, 2015; Friston, 2010). For example, music displaying a strong underlying beat (e.g., marches) is highly salient for a brain built to "predict away" regularities in sensory input (Heilbron & Chait, 2018).

The neural processes that are plausibly involved in these pre- diction mechanisms have received considerable attention. The postsynaptic gain on superficial pyramidal cells is increased when the difference between expected and actual states of the environment have low variance, that is the prediction error is consistent in time (Daw, Niv, & Dayan, 2005; Mumford, 1992). Tone sequences with regular structure produce stronger response in terms of gross neural population activity than tones with irregular structure (Barascud, Pearce, Griffiths, Friston, & Chait, 2016). Auditory rhythms induce spontaneous neuronal entrainment (Nozaradan, Peretz, & Mouraux, 2012). Importantly, sensory prediction partially overlaps with motor planning (Friston, Daunizeau, Kilner, & Kiebel, 2010), allowing the brain to separate self-generated from extrinsic stimulation (Bäß, Jacobsen, & Schröger, 2008; Blakemore, Wolpert, & Frith, 2000). Temporal anticipation relies on oscillatory networks that, among others, involve motor subcortical regions such as basal ganglia and cerebellum (Kotz, Schwartze, & Schmidt-Kassow, 2009; Schwartze, Keller, Patel, & Kotz, 2011; Schwartze & Kotz, 2013). Evidence is accumulating that humans and other mammals use a motor-to-auditory efferent mapping to compare sensory events with anticipatory dynamic signals from the motor system (Schneider & Mooney, 2018), a processed described as covert active sensing (Rimmele, Morillon, Poeppel, & Arnal, 2018). In sum, anticipation by way of sensory- motor interactions is a fundamental aspect of brain function: brains predictively process sensory information with the objective of steering action, and vice versa, brains steer action to be able to predict sensory stimulation (Clark, 2015).

Mutual Synchronization

Next to predictability, an important factor of saliency is stimulus interaction. Interaction with a dynamic stimulus enables the anticipatory response (Friston & Frith, 2015). This is because dynamic systems synchronize more easily if they are reciprocally coupled (Pikovsky, Rosenblum, & Kurths, 2003; Strogatz, 2000, 2003). Interpersonal interaction has emerged as an important topic of research in the context of dyadic tasks where two (or more) people act together (Marsh, Richardson, & Schmidt, 2009; Schilbach et al., 2013; Sebanz, Bekkering, & Knoblich, 2006). In a joint action task, however, it is more difficult to manipulate interactivity experimentally while keeping constant other aspects of the task. Here, we studied the role of interactivity over and above predict- ability in encouraging spontaneous entrainment with a quasiperiodic stimulus. The degree of interactivity of the stimulus could be manipulated experimentally in accordance with a specific theory of mutual synchronization.

Gait is a suitable model for sensory-motor interactions because of its fundamental role in animal movement and because it has a preferred cadence, meaning that entrainment of gait is not a trivial phenomenon. Walking has a degree of adaptability but is mostly an autonomous spinally controlled process (Dimitrijevic, Gerasimenko, & Pinter, 1998; Pearson & Gordon, 2000) and is dominated by the dynamics of the body which imposes a preferred rate of stepping and a relatively smooth cycle of kinetic and potential energy (Kugler & Turvey, 1987). Mathematically, the gait cycle can be seen as a phase oscillator that has a preferred speed at which phase rotates like the arrows of a clock but can also adapt this speed to some extent under the influence of an external stimulus that tends to run at a different speed.

A periodic stimulus can also be seen as a phase oscillator that produces an auditory signal every time phase crosses zero. The interaction between two (or more) such periodic processes has been studied extensively in biology and neuroscience by way of the Kuramoto system[1] (Breakspear, Heitmann, & Daffertshofer, 2010; Strogatz, 2003; Strogatz & Stewart, 1993) and even in altered form to address different theoretical issues in the cueing of gait (Hove, Suzuki, Uchitomi, Orimo, & Miyake, 2012; Miyake, 2009; Uchitomi, Ota, Ogawa, Orimo, & Miyake, 2013). The model of two coupled[2] phase oscillators,

$$\begin{aligned}\dot{\theta}_{stim} &= \omega_{0,stim} + k_{stim} sin(\theta_{gait} - \theta_{stim}) \\ \dot{\theta}_{gait} &= \omega_{0,gait} + k_{gait} sin(\theta_{stim} - \theta_{gait})\end{aligned}, \qquad (1)$$

consists of the phases, θ_{stim} and θ_{gait}, the intrinsic frequencies $\omega_{0,stim}$ and $\omega_{0,gait}$, and the coupling gains k_{stim} and k_{gait}, which describe how much each oscillator is forced to speed up or slow down to compensate for the phase difference with the other. The time of $\theta_{gait} = 0$ corresponds to a footfall and $\theta_{stim} = 0$ to a beat. Predictions of this model could be tested in an experiment by measuring in advance each participant's preferred stepping cycle rate $\omega_{0,gait}$, implementing the first line of the model as an interactive periodic stimulus, setting k_{stim} and $\omega_{0,stim}$ (see Appendix A), and coupling the stimulus and the walking participant by way of auditory beats and real-time sensing of footsteps. The only unknown parameter was the participant's responsiveness to the stim- ulus, k_{gait}.

The detailed solution, parameter estimation, and model validation are given in Appendix A. Here it suffices to describe the qualitative predictions of the mathematical theory, supported by an animated video of the simulation.[3] Strogatz (2003) suggested the following intuitive understanding of the Kuramoto system of coupled phase oscillators. Imagine two friends jogging on a track. Position on the circular track is represented as phase, not as metric distance. The starting line corresponds to zero phase and the number of laps is ignored. Only the difference between the two phases is needed to know the two runners' proximity. Each runner advances at her preferred

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[1] $\dot{\theta}_m = \omega_{0,m} + KN^{-1}\sum_{n=1}^{N} sin(\theta_n - \theta_m),\ m = 1, 2, \ldots, N$

[2] The coupling strengths have been multiplied by two here to simplify the presentation.

[3] An animated movie with simulated mutual synchronization between footsteps and auditory cues in a model system is available at https://vimeo.com/297434940.

speed which is given as intrinsic rate of change of phase, called preferred frequency, and is mostly deter- mined by her physical condition. Each runner also has some motivation to speed up or slow down to cancel the difference with the other, represented as coupling strength. The two can run shoulder to shoulder if the slower one is motivated enough to speed up and the faster one is motivated enough to slow down to let her friend catch up. Thus, several scenarios of unilateral, mutual, or impossible synchronization can be treated with sufficient generality using a model with three ingredients: the *phases* of the periodic processes, their preferred frequencies, and their coupling strengths.

To compare interactivity and predictability, we tested two predictable but noninteractive faster stimuli, an interactive stimulus having the tendency to lead in phase, and a stimulus that mirrored the footsteps and thus obviated mutual synchronization. We expected that the interactive stimulus would entrain participants' gait to a higher cadence than the other stimuli.

Rhythmic Auditory Cueing for Parkinson's Disease

Besides being a model task for the study of sensory-motor entrainment (van Ulzen et al., 2008; Zivotofsky & Hausdorff, 2007), gait is also an important component of daily living affected by several motor disorders. Patients with Parkinson's disease (PD) suffer from impaired gait, reduced capacity for adaptation and, interestingly, an increased reliance on external cues for initiating and guiding walking (Jankovic, 2008). The last characteristic makes the disease an interesting model for entrainment of gait. Repeated tones or music with a tempo can improve gait in PD (Spaulding et al., 2013). The effectiveness of cueing is related to the patient's auditory motor synchronization and beat perception abilities (Cochen de Cock et al., 2018; Dalla Bella, Benoit, Farrugia, Schwartze, & Kotz, 2015; Dalla Bella, Dotov, Bardy, & de Cock, 2018; Dalla Bella, Benoit, et al., 2017), suggesting that adaptive cueing strategies could be beneficial (Hove et al., 2012; Uchitomi et al., 2013). Instructed synchronization may be impossible for some patients or, if possible, come at the expense of disadvantageous alteration of the higher order statistics of the stepping cycle (Dotov et al., 2017). Change in the statistics of the interstride intervals (ISIs), namely the long-range autocorrelation also known as long-range dependence, is correlated with PD symptom severity (Warlop et al., 2016). This trade-off can be avoided by adding the natural variability to the stimulus (Dotov et al., 2017). For this reason, a noninteractive stimulus with said variability parameters and stable average interval was included as an instance of a predictable stimulus.

In this study, healthy participants and PD patients with a gait disorder walked along with a rhythmic auditory stimulus. Synchronization was neither instructed nor related to the success of the task. To study to what extent the saliency factors of predictability and interactivity contribute to the spontaneous entrainment of gait to a higher cadence, two interactive and two noninteractive faster conditions were compared: (a) noninteractive rhythmic isochronous cueing that was faster than the individual's preferred, (b) the same stimulus but with added interbeat interval (IBI) variability (same for all participants) the statistics of which matched normal gait, (c) an interactive cueing having the tendency to run at a faster tempo than the individual's preferred, and (d) cueing that mirrored the timing of the participant's steps. See the supplementary video demonstration[3] and Appendix A for detailed specification of the interactive cueing.

Hypotheses

Performance was evaluated in terms of synchronization with the stimulus and change relative to pretest baseline in spatiotemporal parameters of gait such as cadence and the long-range dependence of ISIs. High level of synchronization and spontaneous entrainment were expected with the interactive stimulus. Specifically, the interactive stimulus and gait were expected to phase-lock and meet at a compromise frequency. The participants' responsiveness estimated as the coupling strength k_{gait} in Equation 1 was expected to be greater than zero. High synchronization but without change in cadence was expected with the mirroring cueing. Less synchronization and less entrainment of cadence were expected in the two noninteractive conditions. Finally, based on previous research a trade-off could be expected between level of synchronization and statistical properties of gait such as the amount and long-range dependence of variability of the gait cycle in the noninteractive conditions, especially for

PD patients who have reduced capacities for gait adaptation. In contrast, the two interactive conditions should induce synchronization without sacrifice other aspects of gait. Additional parameters such as stride length, velocity, and variability of the ISI were measured because they are frequently used to characterize gait in the healthy and in PD. Importantly, any potential changes in cadence could come along with compensatory changes in stride length.

Method

Participants

Twenty nondemented PD patients with gait disorders but no freezing were recruited at the neurological department of the Beau Soleil Clinic and the Department of Neurology of the Montpellier University Regional Hospital, Centre Hospitalier Universitaire (both in Montpellier, France), see Table 1 for details. Patients were examined by movement disorder specialists (Christian Geny and Valérie Cochen de Cock). The clinical diagnosis of PD was based on the Queen Square Brain Bank criteria (Hughes, Daniel, Kilford, & Lees, 1992), excluding patients with dementia (Dalrymple-Alford et al., 2010; Emre et al., 2007).

Hoehn and Yarh stage and Movement Disorder Society–Unified Parkinson's disease Rating Scale (Martinez-Martin et al., 2013) were obtained in "ON" condition. The levodopa equivalent daily dose (LEDD) was calculated (both dopamine agonist LEDD and total LEDD; Tomlinson et al., 2010). Sex-, age-, and education-level- matched members of the general population, without history of neurological or psychiatric disorders, hearing or gait impairment were recruited as healthy controls. All participants gave written informed consent and received financial compensation. The protocol was ap- proved by the National Ethics Committee (CPP Sud Méditérannée III, Nîmes, France, ID-RCB: 2014-A00021-46) in conformity with the Declaration of Helsinki.

Materials and Apparatus

The hardware and software for signal processing, step detection, and auditory feedback was developed as part of a system for interactive cueing of gait in PD based on previously tested apparatus for running (Moens et al., 2014, 2017). An ambulatory system for the analysis of gait used inertial measurement units (6 degrees of freedom) strapped with elastic Velcro bands over the left and right phalanges of the feet, anterior side of left and right tibia, and sternum, to record accelerations and rotations at 128 Hz and extract relevant performance measures offline (APDM Inc., Portland, OR). An additional inertial measurement unit recorded the vibrations of a speaker which reproduced the stimulus in parallel with the participant's head- phones. In this way the gait analysis system captured the stimulus reliably as heard by the participant and with zero delay.

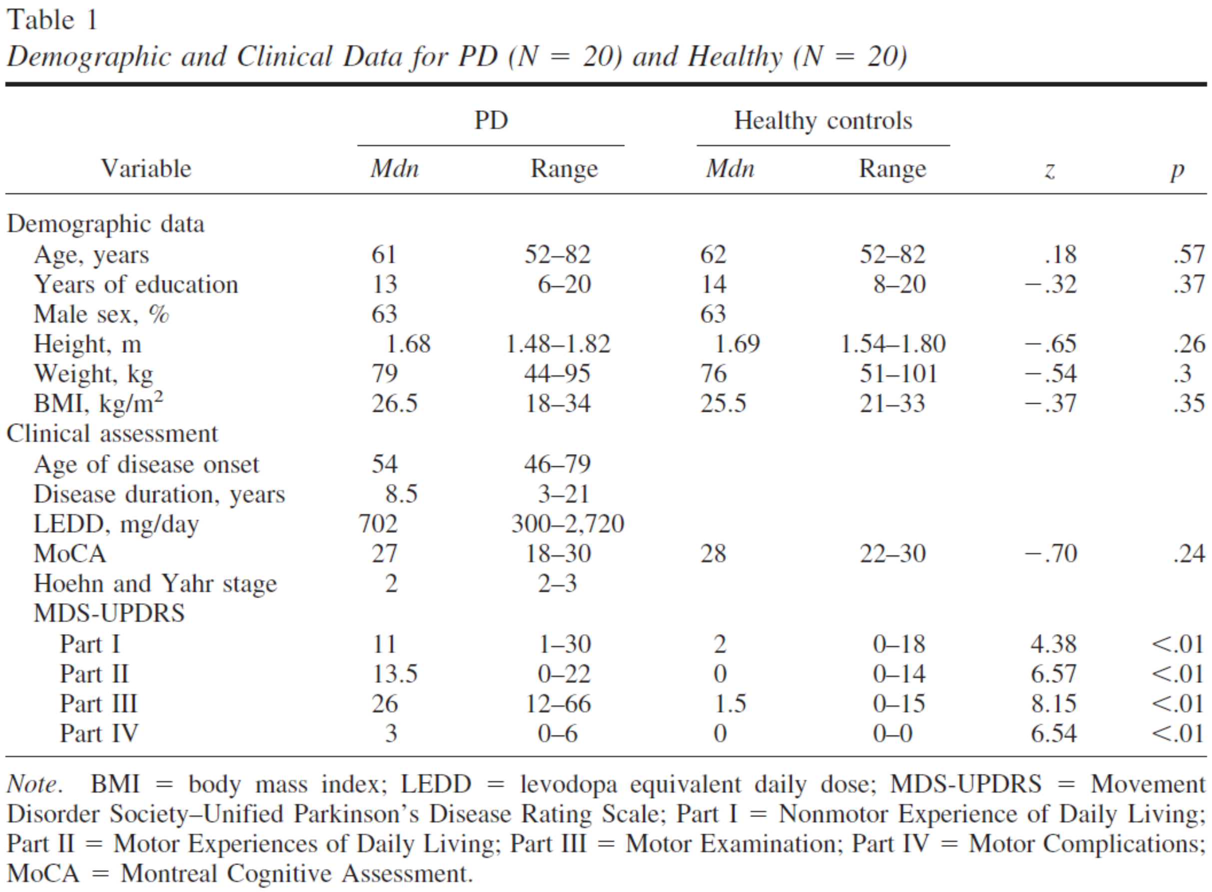

Table 1

Demographic and Clinical Data for PD (N = 20) and Healthy (N = 20)

	PD		Healthy controls			
Variable	*Mdn*	Range	*Mdn*	Range	*z*	*p*
Demographic data						
Age, years	61	52–82	62	52–82	.18	.57
Years of education	13	6–20	14	8–20	−.32	.37
Male sex, %	63		63			
Height, m	1.68	1.48–1.82	1.69	1.54–1.80	−.65	.26
Weight, kg	79	44–95	76	51–101	−.54	.3
BMI, kg/m^2	26.5	18–34	25.5	21–33	−.37	.35
Clinical assessment						
Age of disease onset	54	46–79				
Disease duration, years	8.5	3–21				
LEDD, mg/day	702	300–2,720				
MoCA	27	18–30	28	22–30	−.70	.24
Hoehn and Yahr stage	2	2–3				
MDS-UPDRS						
Part I	11	1–30	2	0–18	4.38	<.01
Part II	13.5	0–22	0	0–14	6.57	<.01
Part III	26	12–66	1.5	0–15	8.15	<.01
Part IV	3	0–6	0	0–0	6.54	<.01

Note. BMI = body mass index; LEDD = levodopa equivalent daily dose; MDS-UPDRS = Movement Disorder Society–Unified Parkinson's Disease Rating Scale; Part I = Nonmotor Experience of Daily Living; Part II = Motor Experiences of Daily Living; Part III = Motor Examination; Part IV = Motor Complications; MoCA = Montreal Cognitive Assessment.

Types of sounds for rhythmic auditory cueing. Cueing consisted either of a metronome with triangle timbre or four musical excerpts such as Mozart's Turkish March adapted for piano. Metronome ticks corresponded to the beats in the musical tracks. Excerpts were selected for salient, unambiguous, regular beat structure, high familiarity in the target population, and positive emotional connotation as assessed in a pilot study. The stimuli make part of a previously the original pieces. A MATLAB script produced the needed tempo by first quantizing each score to a constant IBI and then scaling tempo. To produce variable stimuli, each IBI was stretched (see details below).

Sensors and online stimulus processing and delivery. The processing unit was a tablet computer (7-in. Toughpad FZ-M1, Panasonic Corp., Kadoma, Japan) running MAX/Msp (Cycling ’74, San Francisco, CA), two iPods (fourth generation, Apple Inc., Cupertino, CA) worn just above the ankles, and headphones connected to the tablet. The iPods transmitted their sensor signals (60-Hz three-dimensional gyroscope data) to the tablet via a wire- less network. The tablet, worn by the participant in a running backpack, was controlled and monitored remotely by the experimenters. The dedicated wireless network operated on an empty channel to reduce potential interference.

The custom software played auditory tracks prepared in advance and paired with metainformation files annotated with beat times. In the case of the two interactive conditions the program also applied online stimulus adaptation. To this end, a phase vocoder time- stretching algorithm[4] modulated the song tempo without producing audible deformations of pitch. Time-stretching was controlled by the interactive stimulus oscillator described below using cadence computed online from the latest detected footfalls.

Variability and interactivity of stimulus timing. All participants performed trials in each of the following conditions of stimulus timing interactivity: (a) noninteractive fast isochronous cueing (ISO), (b) noninteractive fast variable cueing with theoretically ideal long-range dependence (VAR), (c) interactive cueing for mutual synchronization (MUT; Equation 1), and (d) cueing that reported study (Dotov et al., 2017). Metronome and music tracks were generated using a software synthesizer from the edited MIDI scores mirrored the timing of footsteps (MIR). Each individual participant’s preferred cadence, the baseline, was determined from the average interstep intervals in the pretest trial (Arias & Cudeiro, 2008; Dalla Bella, Benoit, et al., 2017; Hausdorff et al., 2007; McIntosh, Brown, Rice, & Thaut, 1997).

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[4] See *élastique efficient* by ZPlane, http://www.zplane.de.

Noninteractive isochronous stimulus (ISO). The beats of the metronome and the musical stimuli were isochronous and 10% faster than the participant's baseline.

Noninteractive quasi-periodic stimulus with long-range dependence (VAR). Beat timing was quasi-periodic and on average 10% faster than the participant's baseline. IBIs followed a fractional Gaussian random distribution with long-range dependence ($ex = 1$) and scaled for coefficient of variation (CV) = 2% (standard deviation divided by the mean; Dotov et al., 2017).

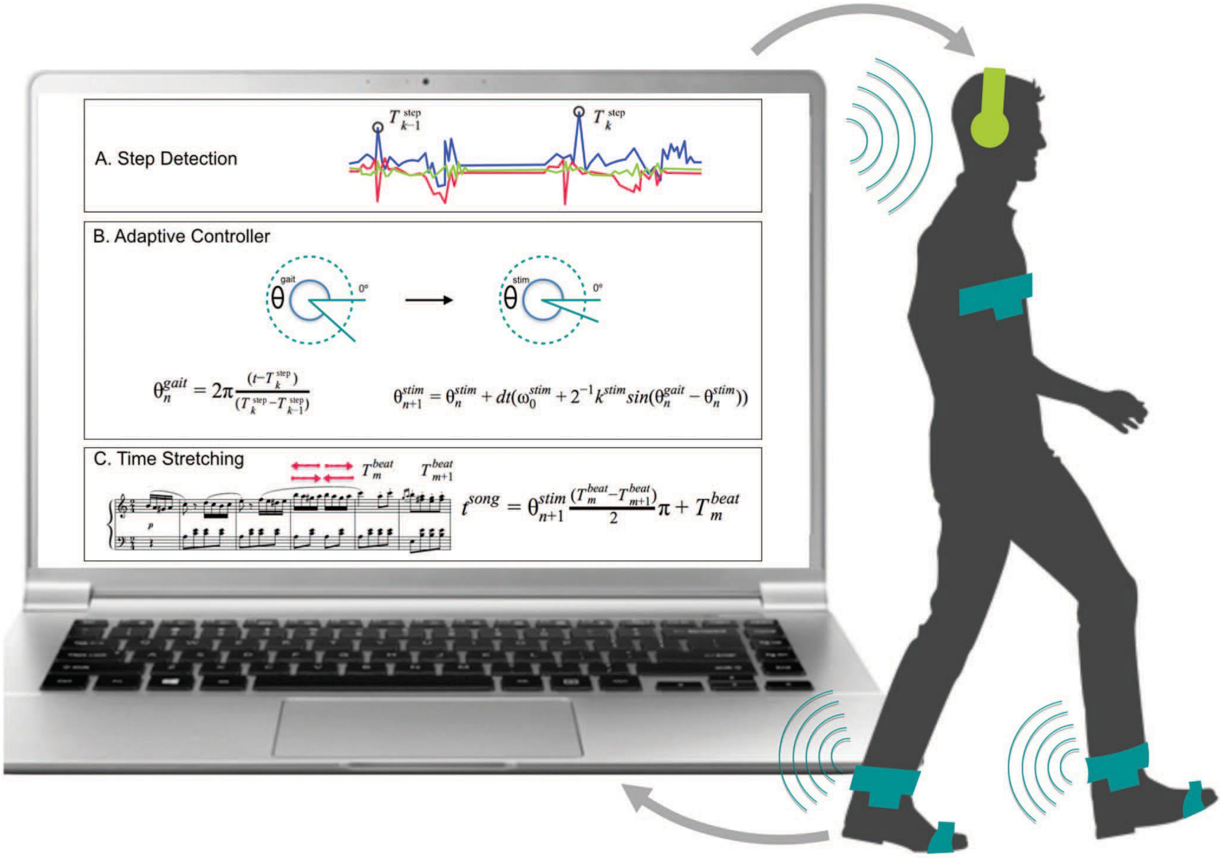


Figure 1. Interactive cueing of walking. Sensors placed on the feet are streamed to a computer and the stimulus is streamed back via wireless headphones. Time-stretching (C) adapts stimulus tempo 100 times per second. The tempo controller is a phase oscillator (B); in its coupling term it uses the gait cycle phase, extrapolated from the most recent footfalls (A). For a noninteractive stimulus, Steps A and B can be canceled and instead a preset sequence of interbeat intervals used to control time-stretching. For a mirroring stimulus, a second lever of adaptation is added by adjusting w_{stim} each cycle to equal the participant's most recent w_{gait}. See the online article for the color version of this figure.

Mutual synchronization (MUT). The interactive stimuli were sound files from the ISO condition played and time-stretched in real-time (Max/MSP, see Figure 1C) by using a numerically integrated phase oscillator as time controller. Beat times were locked to zero phase (Figure 1B). This oscillator was coupled to the phase of gait which was extrapolated from the last two footfall times. Footfalls were detected by streaming angular velocities and accelerations from sensors on the lower limbs and tracking in real-time and with minimal delay characteristic peaks of events such as midswing and initial contact, see Figure 1A (Fraccaro, Coyle, Doyle, & O'Sullivan, 2014). See Appendix A for more details on how the model Equation 1 was implemented in a real-world system.

The stimulus parameters made it interactive but also left enough space for the participant to adapt, that is to encourage mutual synchronization. After having a pretest and before starting cueing trials the intrinsic frequency of the stimulus was set to 120% faster than the participant's baseline, ensuring that the compromise frequency where stimulus and gait met would be anywhere between 100 and 120% of baseline, where 110% was the tempo in the noninteractive conditions. We used the model-derived formula (Equation A4) to set the stimulus coupling strength to the minimum necessary for synchronization even if the participant did not respond to the stimulus.

Mirroring synchronizing system (MIR) added a second level of stimulus adaptation and a high coupling strength (see Appendix A and Equation A6). Instead of having an intrinsic frequency the frequency of the stimulus was updated online to match the participant's calculated from the four most recent footfalls. As a result, the stimulus synchronized with any gait so effectively that the beats coincided with the footsteps (see Figure 2D).

Design

Participants performed one pretest trial without auditory cues and a trial in each cueing condition in a fully crossed within- subject design consisting of stimulus type (metronome and music) and stimulus timing interactivity (ISO, VAR, MUT, and MIR). Stimulus type was blocked and counterbalanced across participants (all music trials followed by all metronome trials or vice versa); the order of the four timing conditions within each block was randomized.

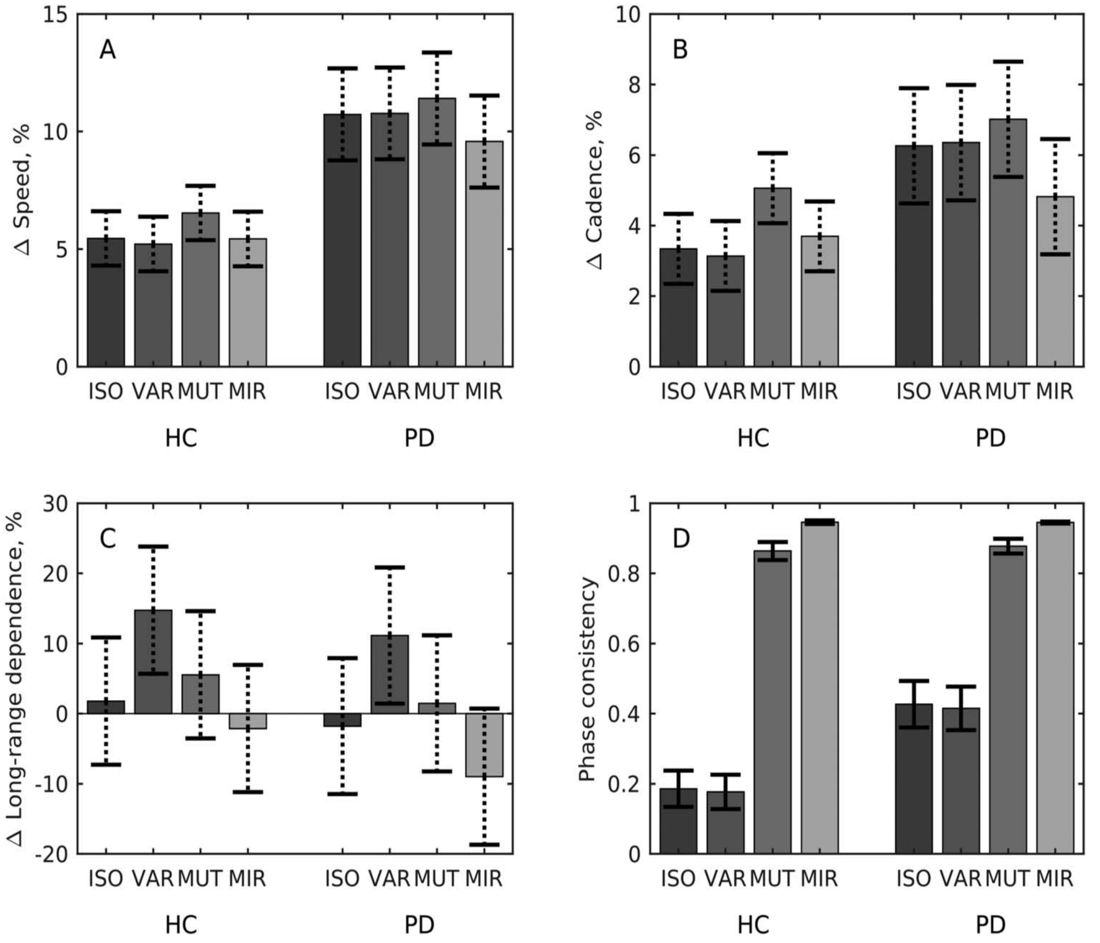


Figure 2. Mean percent change relative to pretest in speed (A), cadence (B), and long-range dependence (C), averaged over music and metronome trials, shown separately for each group of participants. (D) Phase consistency, a measure of synchronization (no baseline). There are two noninteractive conditions: strictly periodic (isochronous [ISO]) and quasi-periodic with statistically matched variability (VAR), and two interactive conditions: weakly interactive inducing mutual synchronization (MUT) and strongly interactive resulting in unilateral synchronization (mirrored [MIR]). Dotted error bars in (A)–(C) are confidence intervals for within- subject comparisons between conditions (not between groups; Masson & Loftus, 2003). Error bars in (D) are standard errors. PD = Parkinson's disease; HC = healthy control.

Procedure

Testing took place in the rehabilitation facility of the Centre Hospitalier Universitaire where participants walked around an elliptical area (6 X 3.6 m). Turning direction was opposite to the patient's clinically assessed laterality and replicated for his or her healthy match. In this way, patients had their more severely affected side on the outer side of the walking path which was the most challenging configuration because the more affected side is also the one that moves more slowly. In the baseline noncued trial participants were asked to walk at their natural comfortable cadence. Next, participants were familiarized to the auditory stimuli during one practice turn around the room. In the subsequent cueing trials participants were asked to walk comfortably. No explicit instructions to synchronize footsteps with the stimulus beat were given. Trials lasted three minutes and a break was given between blocks. The session lasted approximately 30 min.

Measures

Spatiotemporal parameters of gait. A proprietary algorithm (APDM Inc., Portland, OR) applied to the accelerometer and gyroscope data was used to extract left and right footfall times detected as acceleration impulses, ISIs, CV of ISIs (CV_{ISI}, standard deviation divided by the mean ISI), and trial-averaged spatiotemporal gait parameters, namely stride length (in meters), and speed (in meters per second). Cadence (steps per minute) is re- ported here instead of average ISI for easier interpretation. A zero-velocity update method integrated the inertial measurement signals and computed stride length and speed (Peruzzi, Della Croce, & Cereatti, 2011; Yang & Li, 2012; Yun, Bachmann, Moore, & Calusdian, 2007). This uses the signal from the two sensors strapped over the phalanges to detect the stationary stance phase of each foot and remove integration drift by subtracting error on a stride-by-stride basis. In a separate pilot study we verified that the trial-averaged stride length and speed obtained with this method agree with a ground truth measurement with optical motion capture.

The so-called long-range dependence exponent alpha was computed for ISIs using detrended fluctuation analysis (Hausdorff et al., 1996). Contrary to a purely random process, stride-to-stride control of gait tends to exhibit a persistent trend in time, meaning that each stride cycle influences the subsequent stride cycles. This persistence is reduced in PD (Goldberger et al., 2002; Hausdorff, 2007) and also if the synchronization with an isochronous stimulus is an explicit requirement (Dotov et al., 2017).

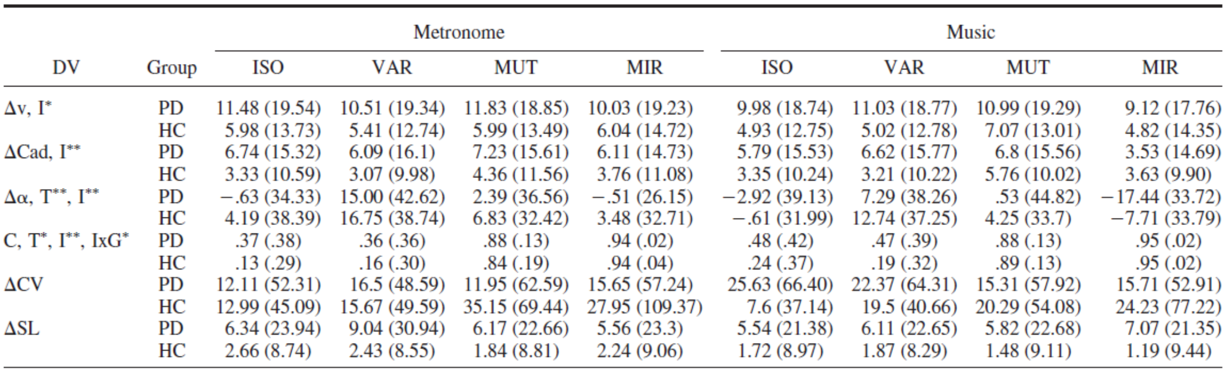
Synchronization: Phase-locking between steps and beats. Synchronization was estimated from the relative phase ($\varphi = \theta_{stim} - \theta_{gait}$) sampled at the time of beats, hence $\varphi_T = \theta_T^{gait}$ at the time T of beats when $\theta_n^{stim} = 2\pi = 0$ (Rosenblum, Pikovsky, Kurths, Schafer, & Tass, 2003). If the phases of the stimulus and stepping are shown as arrows of a clock (see Figure 1B and the video in the online supplemental materials) then the position of the arrow for stepping is sampled every time the stimulus arrow crosses zero. This is similar but not the same as a beat-step asynchrony normalized by the IBI. Consistent relative phase in this representation means that the arrow for stepping is always leading or lagging the stimulus arrow by the same amount. In circular statistics consistency, which here we will call *C*, is the resultant vector length of all φ_T and ranges from zero (no synchronization) to one (perfectly consistent alignment; Jammalamadaka & Sengupta, 2001). Synchronization consistency has proven sensitive to individual differences in synchronization skills in a variety of populations (Bégel et al., 2017; Dalla Bella, Farrugia, et al., 2017; Puyjarinet, Bégel, Lopez, Dellach- erie, & Dalla Bella, 2017; Sowin´ski & Dalla Bella, 2013). The logit transformation was applied before statistical analyses (Falk, Müller, & Dalla Bella, 2015).

Results

Table 2 and Figure 2 summarize the average scores and effects which are listed in detail below.

Table 2

Means (SD) of Gait Parameters, Expressed as Percent Change Relative to Pretest, and Phase Synchronization Consistency



DV	Group	Metronome				Music			
		ISO	VAR	MUT	MIR	ISO	VAR	MUT	MIR
Δv, I*	PD	11.48 (19.54)	10.51 (19.34)	11.83 (18.85)	10.03 (19.23)	9.98 (18.74)	11.03 (18.77)	10.99 (19.29)	9.12 (17.76)
	HC	5.98 (13.73)	5.41 (12.74)	5.99 (13.49)	6.04 (14.72)	4.93 (12.75)	5.02 (12.78)	7.07 (13.01)	4.82 (14.35)
ΔCad, I**	PD	6.74 (15.32)	6.09 (16.1)	7.23 (15.61)	6.11 (14.73)	5.79 (15.53)	6.62 (15.77)	6.8 (15.56)	3.53 (14.69)
	HC	3.33 (10.59)	3.07 (9.98)	4.36 (11.56)	3.76 (11.08)	3.35 (10.24)	3.21 (10.22)	5.76 (10.02)	3.63 (9.90)
$\Delta\alpha$, T**, I**	PD	−.63 (34.33)	15.00 (42.62)	2.39 (36.56)	−.51 (26.15)	−2.92 (39.13)	7.29 (38.26)	.53 (44.82)	−17.44 (33.72)
	HC	4.19 (38.39)	16.75 (38.74)	6.83 (32.42)	3.48 (32.71)	−.61 (31.99)	12.74 (37.25)	4.25 (33.7)	−7.71 (33.79)
C, T*, I**, IxG*	PD	.37 (.38)	.36 (.36)	.88 (.13)	.94 (.02)	.48 (.42)	.47 (.39)	.88 (.13)	.95 (.02)
	HC	.13 (.29)	.16 (.30)	.84 (.19)	.94 (.04)	.24 (.37)	.19 (.32)	.89 (.13)	.95 (.02)
ΔCV	PD	12.11 (52.31)	16.5 (48.59)	11.95 (62.59)	15.65 (57.24)	25.63 (66.40)	22.37 (64.31)	15.31 (57.92)	15.71 (52.91)
	HC	12.99 (45.09)	15.67 (49.59)	35.15 (69.44)	27.95 (109.37)	7.6 (37.14)	19.5 (40.66)	20.29 (54.08)	24.23 (77.22)
ΔSL	PD	6.34 (23.94)	9.04 (30.94)	6.17 (22.66)	5.56 (23.3)	5.54 (21.38)	6.11 (22.65)	5.82 (22.68)	7.07 (21.35)
	HC	2.66 (8.74)	2.43 (8.55)	1.84 (8.81)	2.24 (9.06)	1.72 (8.97)	1.87 (8.29)	1.48 (9.11)	1.19 (9.44)

Note. DV = dependent variable; ISO = isochronous cueing; VAR = variable cueing; MUT = mutual synchronization; MIR = mirrored cueing; PD = Parkinson's disease; HC = healthy participants; v = speed; Cad = cadence; SL = stride length; α = long-range dependence; CV = coefficient of variation; C = phase synchronization consistency.

* $p < .05$, ** $p < .01$; T, main effect of stimulus type; I, main effect of timing interactivity; I×G, interaction between group and timing interactivity.

Baseline Group Comparisons

The between-subjects group comparisons of the baselines from the pretest trials showed that some parameters of gait scored worse in PD than in healthy controls, as expected from the clinical diagnosis. Speed (*M* = 1.14, *SD* = .15 vs. *M* = 1.26, *SD* =

.13) and stride length (*M* = 1.23, *SD* = .15 vs. *M* = 1.40, *SD* = .09) were lower (all $p < .05$) and CV (*M* = 2.42, *SD* = .92 vs. *M* = 1.88, *SD* = .49) was higher ($p < .05$). On the other hand, alpha (*M* = .74, *SD* = .17 vs. *M* = .65, *SD* = .14) and cadence (*M* = 112.06, *SD* = 11.08 vs. *M* = 108.14, *SD* = 7.99) tended to be higher in PD than in healthy participants but not significantly so ($p = .065$ and $p = .23$, respectively).

Overall Effects of Cueing

The overall effectiveness of cueing in general, without recourse to its specific conditions, was evaluated by comparing against zero the percent change from pretest to cueing trials and also comparing between the two groups (mixed-design analyses of variance). As expected by the very design of the stimuli, cadence increased with cueing both in PD (*M* = 6.11, *SD* = 15.08) and healthy (*M* = 3.81, *SD* = 10.26), the effect of cueing being significant, $F(1, 36) = 5.73$, $p < .05$, $\eta_p^2 = .14$, while the effect of group not ($F < 1$). In accord with the overall increase in cadence, cueing also increased speed both in PD (*M* = 10.62, *SD* = 18.50) and healthy participants (*M* = 5.66, *SD* = 13.19) and this effect was significant, $F(1, 36) = 9.77$, $p < .01$, $\eta_p^2 = .21$. The group comparison was not significant ($F < 1$), which is surprising to some extent because one could have expected that PD patients would have a decreased capacity to adapt their gait. Stride length also appeared to increase in PD (*M* = 6.46, *SD* = 23.23) and healthy (*M* = 1.93, *SD* = 8.69) but neither the effect of cueing nor of group were significant, $F(1, 36) = 2.26$, $p = .14$, $\eta_p^2 = .06$, and $F < 1$, respectively. Interestingly, the ISIs were not stabilized by the rhythmic cueing but instead *CV* increased in PD (*M* = 16.90, *SD* = 56.82) and healthy (*M* = 20.42, *SD* = 63.51), which constituted a significant effect of cueing, $F(1, 36) = 5.38$, $p < .05$, $\eta_p^2 = .13$, and not of group ($F < 1$). Alpha did not change in PD (*M* = .47, *SD* = 37.43) nor in healthy participants (*M* = 4.99, *SD* = 34.92), as both effects were not significant (*F*s < 1).

Multivariate Tests of Cueing Conditions

To find whether the manipulations of cueing affected gait we applied a multivariate analysis of variance (multivariate analysis of variance) to synchronization consistency and percent change of cadence, speed, CV, and alpha. The factors were the within-subject stimulus type (metronome vs. music) and stimulus timing (ISO, VAR, MUT, MIR), and the between-subjects group. Stride length was not included in the multivariate analysis of variance because of its correlation with cadence and speed.

Stimulus type had a significant effect on gait parameters and synchronization (Wilk's Λ = .674), *F*(5, 32) = 3.10, $p < .05$, η_p^2 = .33, and, as expected, stimulus timing also had a significant effect (Wilk's Λ = .11), *F*(5, 287.5) = 23.30, $p < .001$, η_p^2 = .52. Surprisingly, group did not have a significant effect, indicating that overall PD patients' gait responded to cueing in the same way as healthy participants (Wilk's Λ = .88), *F*(5, 32) = .87, $p = .51$, η_p^2 = .12. A significant interaction between stimulus timing and group was observed (Wilk's Λ = .77), *F*(15, 287.5) = 1.94, $p < .05$, 'η_p^2 = .09. An interaction between timing and type and stimulus was also observed (Wilk's Λ = .77), *F*(15, 287.5) = 1.87, $p < .05$, η_p^2 = .08. The interaction between stimulus type and group (Wilk's Λ = .85), *F*(5, 32) = 1.14, $p = .36$, η_p^2 = .15, and the three-way interaction (Wilk's Λ = .90), *F*(15, 287.5) = .73, $p = .75$, η_p^2 = .03, were not significant. These effects are decomposed below in terms of univariate tests and pairwise comparisons.

Univariate Tests

Analyses of variance and pairwise comparisons with correction for multiple tests were used to decompose any multivariate effects and interactions. For brevity only the statistically significant effects are reported here.

Cadence was affected by stimulus timing, *F*(3, 108) = 5.01, $p < .01$, η_p^2 = .12. In particular, cadence was higher in the interactive condition MUT relative to the noninteractive and faster ISO and VAR, and the mirroring MIR conditions (all *p*s < .05). This means that the largest entrainment effect on gait was produced by the stimulus promoting mutual synchronization, exceeding stimuli that had a fixed, faster than baseline tempo, and the stimulus that was so effective at synchronizing with footsteps that it avoided the need for mutual synchronization.

Speed was affected by stimulus timing, *F*(3, 108) = 3.08, $p < .05$, η_p^2 = .08. The pattern of differences partially repeated that of cadence. In particular, speed was significantly higher in MUT than in MIR ($p < .05$), and marginally higher than in VAR (*p* =

.066) but not in ISO ($p = .132$, Holm–Bonferroni correction).

Phase synchronization consistency was very high in the interactive conditions MUT and MIR, see Figure 2D. As expected, synchronization consistency was affected by stimulus timing, $F(3, 108) = 127.60$, $p < .001$, $\eta_p^2 = .78$, and it was much higher in MUT and MIR than in ISO and VAR (ps < .001). In addition, due to an interaction between group and stimulus timing, $F(3, 108) = 4.76$, $p < .01$, $\eta_p^2 = .12$, healthy participants synchronized more in MIR than in MUT ($p < .05$), which also explains the observed interaction between stimulus timing and group in the multivariate test. This is an expected but a nontrivial pattern of results because it validates our model-based approach for spontaneous entrainment. Solving the model made it possible to tune the parameters of the interactive stimulus to the individual participant (see Appendix A) in such a way that both a stable synchronization and a consistent phase lag were maintained, inducing the participants to in- crease their cadence, see Figure 3.

The long-range dependence of ISIs was affected by stimulus timing, $F(3, 108) = 10.67$, $p < .001$, $\eta_p^2 = .23$. Alpha was higher in VAR relative to ISO ($p < .01$) and MIR ($p < .001$), marginally higher in VAR than in MUT ($p = .08$), and higher in MUT relative to MIR ($p < .05$). This is to be expected given that VAR was a stimulus with optimal long-range dependence.

The only variables with an effect of the distinction between music and metronome were long-range dependence and synchronization consistency. Alpha was higher with music than with metronome, $F(1, 36) = 8.48$, $p < .01$, $\eta_p^2 = .19$. Synchronization consistency was higher with metronome than with music, $F(1, 36) = 6.64$, $p < .05$, $\eta_p^2 = .16$.

CV was not affected by any of the stimulus types and timings and by group (all ps = n.s.), and the same was true for stride length (all ps = n.s.). These null effects are nontrivial because they imply that there were no hidden adaptations of gait to compensate for changes in cadence.

Discussion

Driven by the concern that dynamic systems accounts of perception-action need to explain how coupling with external stimuli can be selective, we examined the role of interactivity in addition to predictability as factors of saliency. We hypothesized that bidirectional coupling between walking and an auditory beat would induce spontaneous entrainment to a faster cadence and could overcome a degree of initial dissimilarity between gait and stimulus. In keeping with our hypothesis, the highest increase of cadence relative to pretest was observed in the interactive condition MUT. MUT involved a rhythmic auditory stimulus designed as a unit of the Kuramoto system, a fundamental model of mutual synchronization. This model-based approach allowed us to estimate a coupling parameter for gait and show that k_{gait} was greater than zero, confirming that participants were induced to actively contribute to synchronization. In short, when a specific stimulus responds to one's movement, effectively shadowing it with a delay, the motor system is more likely to respond.

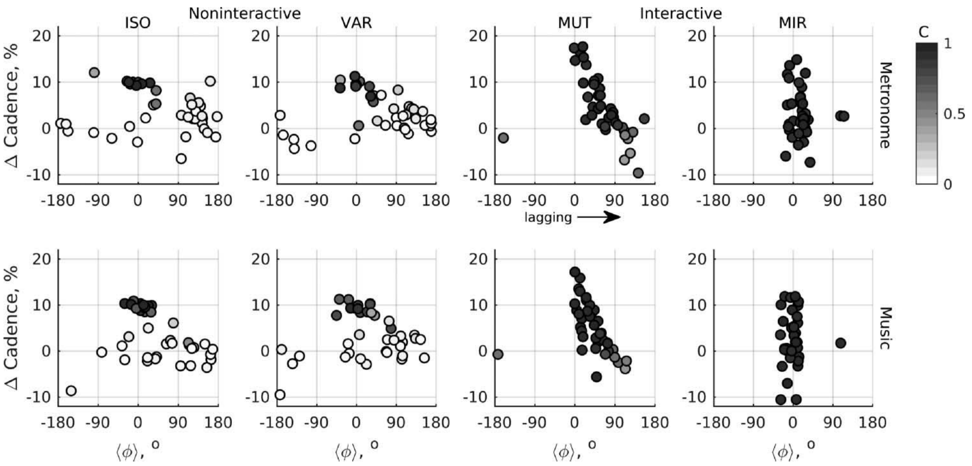


Figure 3. Parkinson's disease and healthy participants' relative phases and change of cadence from pretest to cueing, averaged separately within each condition (trial). For easy interpretation, the abscissa is such that c. is positive when steps are lagging behind beats. The level of synchronization also needs to be indicated— color- coded Phase Consistency *C*—because the average relative phase is meaningless if the processes are not synchronized at all (light gray and white circles).

Although small, the effect sizes associated with the MUT versus ISO and VAR comparisons are important because these stimuli were fixed at a cadence that was already higher than baseline. One's preferred cadence is biomechanically constrained and moving away from it has even an energetic cost (Holt, Jeng, Ratcliffe, & Hamill, 1995). The effect on cadence was equally strong in healthy participants and PD patients with impaired gait. This implies that at the early to moderate stage of the disease at which we sampled patients their movement can be compromised but their use of sensory stimulation is not so different. Indeed, the overreliance on external cueing may be a characteristic advanced symptom when patients have trouble even in initiating action and action switching (Jankovic, 2008).

The effect of MUT is remarkable because participants were not instructed to synchronize nor were they purposefully trying to match their steps to the stimulus beat. The latter is implied by the fact that phase consistency was much lower in the two noninteractive conditions. Furthermore, cadence and velocity were lower in the strongly interactive condition MIR, ruling out the possibility that the effect observed in MUT trials was merely due to the motivating role of synchronous action. Hence, the present study demonstrated unintentional entrainment, a phenomenon that is widely discussed but rarely observed (Van Dyck et al., 2015; Varlet, Coey, Schmidt, & Richardson, 2012) because synchronization paradigms in human motor behavior often involve in- structed or presupposed synchronization.

Historically, we have had the tendency to focus on effects of passive stimuli on behavior and cognitive processing (the majority of psychophysics, reaction time paradigms, etc.). Cognitive neuroscience, following after experimental psychology and movement science, is beginning to acknowledge that mutually interactive processes between body and surroundings or between individuals are fundamental to our abilities for acting in a complex environment and for social interaction (Hasson & Frith, 2016; Pezzulo & Cisek, 2016). Still, the notion of interaction often receives too general of a treatment in the literature. Along with other recent work (Raffard et al., 2018; Słowin´ski et al., 2016), we show that the role of the causal linkage from movement to stimulus can be studied and that this interactivity can be manipulated for the sake of experimental control. The stimulus in condition MUT only implemented half of the model system (the first line of Equation 1). The other half described the gait cycle theoretically. This assumption allowed us to constrain the parameters of the interactive stimulus. A qualitative confirmation of the model came in the form of three effects of MUT: It entrained gait to a cadence higher than the walker’s preferred, MUT was more effective than noninteractive conditions with 10% faster tempo, and was equally effective in PD patients with impaired gait. A quantitative confirmation was given numerically (see Appendix A). The agreement was very high between empirical in MUT and simulated trials based on known trial parameters and model-based estimates of gait responsiveness k_{gait}.

The stimulus for mutual synchronization promises to increase the benefits of the well-known rhythmic auditory cueing of gait in PD. The interactive strategy allows the stimulus to be individualized and to optimally combine synchronization and entrainment across a range of tempo changes, thus responding to patients with different capacities (Dalla Bella et al., 2018). Yet, the noninteractive variable stimulus had one advantage in that it promoted an increase in long-range dependence, arguably an important statistical parameter of gait variability. The practical benefit of cueing strategies depends on the priorities assigned to different dimensions of gait dynamics.

In the present study a rich musical stimulus which was rated as pleasant and uplifting by the same population of participants made no difference from a dull metronome. This null effect is somewhat surprising but also very telling. The acoustic and structural properties of the stimulus might be less important in inducing spontaneous synchronization than the affordance for synchronization that it provides by virtue of its being interactive. Again, this is important because it implies the need to shift from studying pure stimulus properties to studying how the stimulus relates to the participant.

The Auditory Consequences of Self-Generated Action Such as Footsteps

Why do repetitive tones tend to induce spontaneous rhythmic movements and what was the mechanism by which MUT entrained gait to a higher cadence? The mechanism by which the brain parses external from self-generated sensory stimulation may provide a clue to this effect. Typically, research has suggested the existence of an efference copy of motor commands used by the central nervous system to “predict out” sensory input resulting from self-induced motion (Clark, 2015). A compelling demonstration is our inability to self-tickle (Blakemore et al., 2000). The sound of our own footsteps is another example of self-generated but effectively suppressed sensory stimulation. If we are to speculate, when a beat-based stimulus closely mimics or shadows gait it becomes difficult for the auditory system to differentiate be- tween the stimulus and the expected sensory consequences of stepping. This confusion may interfere with gait because the motor system is poised to compensate for anticipated and actual sensory consequences of action (Friston & Frith, 2015). Note that stable relative phase in the mutual synchronization model is proportional to the difference between the intrinsic frequency of the stimulus and the effective frequency of synchronization; the more the stimulus slows down the more it tends to lead in phase (see Figures 1 and A1). For example, if the effective frequency is at the participant's then the stimulus leads by 90° and if it is at the preferred frequency of the stimulus then relative phase is zero.

Interestingly, low-frequency acoustic content below 500 Hz mediates the identification of gait events and walking style (Ekimov & Sabatier, 2006) and low-frequencies are preferred by the human auditory system for extracting rhythmic structure and entraining to music (Hove, Marie, Bruce, & Trainor, 2014; Stupacher, Hove, Novembre, Schütz-Bosbach, & Keller, 2013; Varlet, Williams, & Keller, 2018). The brain may be geared for using stepping sounds in the low end of the spectrum, called a *hyperprior* in the Bayesian terminology, because it provides ecologically stable auditory information about gait. Indeed, the control of walking is affected by experimental manipulations of the self- generated stepping sounds (Tajadura-Jiménez et al., 2015). Furthermore, action-relevant stepping sounds have a stronger effect than pure tones (Rodger, Young, & Craig, 2014; Young, Shreve, Quinn, Craig, & Bronte-Stewart, 2016). To conclude, it is worth considering some other theoretical implications of the present work. Predictive processing tries to avoid the dichotomy of internal models and embodied interaction with the environment by implementing two provocative proposals in the same formal framework. First, the nonlinear dynamics of embodied action in a physical world allow the moving body to partly take care of its own organization (Kelso, 1995). In the context of locomotion the pendulum dynamics of gait mostly takes care of its own timing (Kugler & Turvey, 1987). Second, the brain does not control action in a strict sense but only minimizes the discrepancy between anticipated and actual sensory consequences of action (Friston, 2010; Friston, Kilner, & Harrison, 2006). The body is the first layer of synchronizing with the environment while the second layer, the central nervous system, needs to deal with what is left, namely unexpected sensory events, and couple action to salient aspects of the environment. Ethologically, it makes sense for an animal to possess the capacity for selective coupling because action would break down if it were coupled to all available streams of perceptual information.

PD patients do not readily synchronize to a stimulus with a faster tempo and if they do they need to negotiate a trade-off between synchronization and the natural statistics of the gait cycle (Dotov et al., 2017). The present procedure for optimal gain on stimulus adaptation takes into account the individual participant's preferred cadence. The mutually interactive stimulus in our study had the necessary flexibility to synchronize with all participants, irrespective of their individual capacities, while entraining them to a varying degree. In contrast, the strongly interactive, mirroring condition was very effective in synchronizing with footsteps but not in entraining cadence. It employed phase- and frequency- modulation of the stimulus, similar to the previously proposed WalkMate (Hove et al., 2012; Uchitomi et al., 2013) and DJogger (Moens et al., 2014). Strongly interactive strategies are useful in advanced stage PD with severely impaired interactive capacity. Furthermore, the cadence difference in the model-based approach proposed here can be reversed so that the stimulus tends to be slower than baseline. This manipulation which remains to be tested could be potentially useful in accommodating patients with festination which is characterized by unusually high cadence.

Context of the Research

Synchronization with a moving partner requires the ability to anticipate the partner's dynamics. Dancing or practicing a musical instrument in an ensemble may improve motor capacities and even counter the effects of motor disabilities such as stroke and PD (Altenmüller, Marco-Pallares, Münte, & Schneider, 2009; Hackney & Earhart, 2009; Patel, 2011; Schneider, Schönle, Altenmüller, & Münte, 2007; Sparks, Helm, & Albert, 1974; Wan, Zheng, Marchina, Norton, & Schlaug, 2014). Bidirectional coupling schemes can improve performance in the context of musical listening and performance (Demos, Carter, Wanderley, & Palmer, 2017; Nakata & Trainor, 2015). Mutual synchronization applied as a principle for the design of cueing strategies for neurodegenerative disorders such as PD also suggests how to tackle the important issue of stimulus difficulty. Stimulus interactivity facilitates performance but should not make the task too easy because rehabilitation is more effective if the surviving capacities are being challenged (Merzenich, 2013; Whitall & Byl, 2004). This calls for an individualized approach taking into account each patient's level of performance.

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(*Appendices follow*)

Appendix A

Model-Based Parameter Estimation and Model Validation

Stable synchronization with interactive cueing could be due either to the stimulus, the participant, or both. It is difficult to determine the effective role of each part of the system in a closed feedback loop. In comparison, the noninteractive paradigms that have dominated experimental psychology since its inception have the advantage that all changes in performance measures are due to the participant. Our objective was to work out a method for estimating the participants' adaptation over and above the adaptation of the stimulus. In the Kuramoto-based model of mutual synchronization, Equation A1, this is quantified by the effective coupling strength k_{gait}. Having a reasonably good model, however, could partially circumvent this issue (Schiff, 2010).

The current model has two rate parameters, two coupling parameters, and two phases.

$$\begin{aligned} \dot{\theta}_{stim} &= \omega_{0,stim} + 2^{-1} k_{stim} sin(\theta_{gait} - \theta_{stim}) \\ \dot{\theta}_{gait} &= \omega_{0,gait} + 2^{-1} k_{gait} sin(\theta_{stim} - \theta_{gait}) \end{aligned} \qquad \text{(A1)}$$

Here, θ_{stim} and θ_{gait} are the phases, in radians, winding on a circular domain at rates $\omega_{0,stim}$ and $\omega_{0,gait}$, in rad/s, plus a forcing function of relative phase, the difference of their phases. This means that a unit slows down or speeds up depending on whether its phase is running ahead or lagging behind, respectively. k_{stim} and k_{gait} are the coupling strengths in s^{-1}. Synchronization in this context is defined as phase-locking, that is constant relative phase $\varphi = \theta_{gait} - \theta_{stim}$ = const of reciprocally coupled oscillators (Pikovsky et al., 2003). The relative phase is stable if

$$\dot{\phi} = \omega_{0,gait} - \omega_{0,stim} - 2^{-1}(k_{gait} + k_{stim}) sin(\phi) \qquad \text{(A2)}$$

has a single stable fixed-point φ_{stable}, which is the root of

$$\omega_{0,gait} - \omega_{0,stim} - 2^{-1}(k_{gait} + k_{stim}) sin(\phi) = 0 \qquad \text{(A3)}$$

and that satisfies the inequality $-2^{-1}(k_{gait} + k_{stim})\cos(\varphi_{stable}) < 0$. A necessary constraint for phaselocking is that the total coupling is strong enough to overcome the frequency difference $\delta = \omega_{0,stim} - \omega_{0,gait}$. Specifically, the condition is $k_{stim} + k_{gait} > 2|\delta|$, where the critical coupling strength is

$$k_{critical} = k_{stim} + k_{gait} = 2\,|\,\delta\,|\,. \qquad \text{(A4)}$$

Hence, the relative balance of frequency difference and total coupling strength results in several different scenarios. Figure B1 illustrates the predicted relative phase, Equation A2, and the fixed points, Equation A3, in scenarios where the relative contribution of gait and stimulus varied and also the total coupling was lower, equal, or higher than the critical coupling strength, Equation A4.

The degree to which the frequency of each oscillator changes under the driving force of the other oscillator is a measure of its coupling strength. For example, when coupling is reciprocal, $k_{stim} = k_{\mathrm{gait}}$, the two oscillators will meet at the midpoint between their intrinsic frequencies. In contrast, a unit with relatively high coupling strength will be driven closer to the unit with relatively low coupling strength.

Note that Equation A3 can be solved for k_{gait} and the known values substituted in the right-hand side to obtain a model-based estimate of the gain on participant's adaptation,

$$k_{gait} = 2(\omega_{0,gait} - \omega_{0,stim})/sin(\phi_{stable}) - k_{stim}. \qquad \text{(A5)}$$

The two stimulus parameters are known by design, $\omega_{0,gait}$ is the baseline measured, at pretest from the participant's preferred rate of stepping, and φ_{stable} was the mean relative phase between steps and beats at the moment of footfalls, that is $\varphi_{stable} = \theta_T^{stim}$ at the time T of zero phase of gait $\theta_{gait} = 2\pi = 0$.

Several additional problems had to be solved to implement this model in a real-world system. Beat timing was set by a stimulus phase oscillator. To this end, the first line of Equation A1 was solved numerically (Euler integration, steps dt = 10 ms): $\theta_{n+1}^{stim} = \theta_n^{stim} + dt(\omega_0^{stim} + 2^{-1}\, k_{stim}\, sin(\theta_n^{gait} - \theta_n^{stim}))$. After each integration step, the updated stimulus phase θ_{n+1}^{stim} was mapped to song time $t^{song} = \theta_{n+1}^{stim}\,(T_m^{beat} - T_{m+1}^{beat})/2\pi + T_m^{beat}$ by setting the time-stretching parameter of the vocoder, where T_m^{beat} and T_{m+1}^{beat} were the beat times preceding and following the current song time, respectively, and beat onset was at $\theta^{stim} = 2\pi = 0$ rads. Gait phase at time t was the interstep time linearly extrapolated from the times of the previous footfalls, ($\theta_n^{gait} = 2\,\pi\,(t - T_k^{step})/(T_k^{step}$ –

T_{k-1}^{step}). Extrapolating the phase of gait like this was a small departure from the model but, as results show, this did not appear to alter the predicted behavior. The frequency difference and coupling were introduced in a thirty-second linear ramp at the beginning of the trial to avoid initial transient effects.

The right balance between coupling strength and frequency mismatch in the experimental trials was achieved by finding the critical coupling strength using the individual participant's baseline stepping rate and the given mismatch $\delta = \omega_0^{stim} - \omega_0^{gait} = .2\omega_0^{gait}$ rads *where* $\omega_0^{stim} = 1.2\omega_0^{gait}$ *rads/s,* $\omega_0^{stim} = 2\pi/IBI$*, and* minimum necessary for synchronization in the worst scenario, that is if the participant did not respond to the stimulus, $k^{gait} = 0$. Stimulus coupling was just above the critical coupling, $k^{stim} = 1.1k^{crit}$, where $k^{crit} = 2|\delta|$, and the total coupling $K = k^{stim} + k^{gait}$. As a result, the effective frequency of synchronization could be anywhere between ω_0^{gait} and $1.2\omega_0^{gait}$ depending on the responsiveness of the given participant (see Figure B1C and B1D).

To evaluate model validity, we compared the empirical and model-based estimations of a parameter that was not used in the estimation of k_{gait}. The average gait frequency $\langle\omega_{gait}\rangle$ in each trial of the MUT condition was compared to the simulated average gait frequency ω^gait. Equation A1 was integrated numerically (Euler method with $dt = .01$ and duration of 18,000 steps) using the known trial parameters k_{stim} and $\omega_{0,stim}$, the empirical $\omega_{0,gait}$, and the k_{gait} estimated from Equation A5. Nine trials, five from PD patients and four from healthy controls, were excluded from the comparisons because average cadence was lower than at pretest, a scenario that the model cannot account for and probably relates to fatigue. The simulations resulted in very good agreement with empirical data, $r(68) = .94$, $p < .001$, and slope of the fit $b = 1.02$(see Figure C1).

Having the analytical expressions for various parameters made it possible to estimate the participants' coupling strength. The grand mean of the gait adaptation parameter k_{gait} was significantly larger than zero, $F(1, 38) = 13.85$, $p < .01$, which is further evidence for mutual synchronization between stimulus and participant in MUT trials. PD patients tended to have higher scores in both metronome ($M = .88$, $SD = 1.68$) and music ($M = .83$, $SD = 1.3$) trials relative to control participants ($M = .66$, $SD = 1.51$

and *M* = .82, *SD* = 1.20, respectively). The differences were not statistically significant as neither group, *F*(1, 38) = .07, *p* = .792, nor stimulus type, *F*(1, 38) = .114, *p* = .738, resulted in statistically significant differences, and there was no interaction, *F*(1, 38) = .458, *p* = .502.

For control purposes a strongly interactive system was implemented such that it effectively mirrored the footsteps.

$$\begin{gathered}\dot{\theta}_{stim} = \omega_{n,stim} + k_{stim} sin(\theta_{gait} - \theta_{stim}) \\ \dot{\theta}_{gait} = \omega_{0,gait} + k_{gait} sin(\theta_{stim} - \theta_{gait}) \\ \omega_{n,stim} = \omega_{n-1,gait}\end{gathered} \qquad \text{(A6)}$$

Instead of having a predetermined intrinsic frequency, every cycle the stimulus updated its rate to match the most recent stepping frequency, ω_{n+1}^{stim} = ω_{n}^{stim} = $2\pi/(T_{n}^{step}$ - T_{n-1}^{step}) rad/s. This additional level of adaptation resulted in unilateral rather than mutual synchronization.

Appendix B

Coupling Scenarios for the Two-Unit Kuramoto Model of Auditory-Motor Synchronization

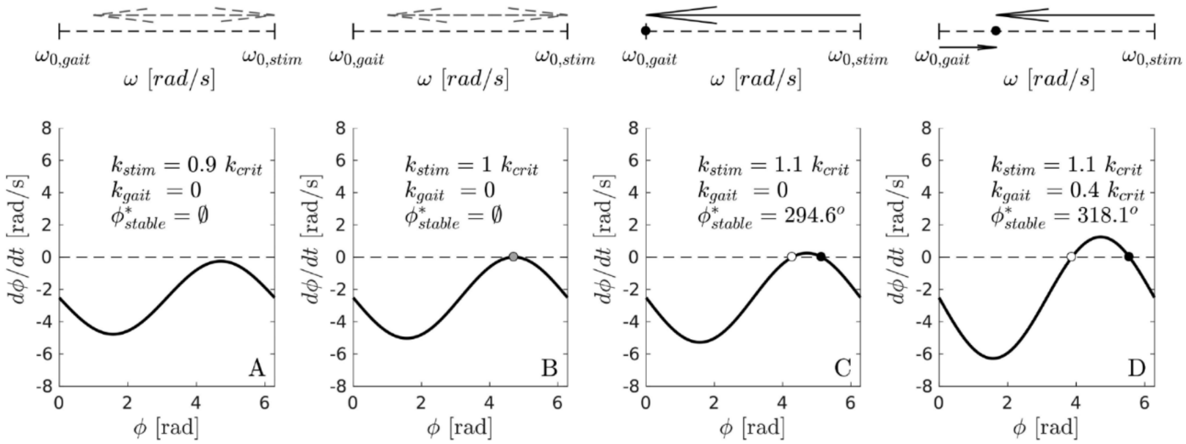

Figure B1. The behavior of the model for mutual synchronization for different coupling scenarios. The sinusoids are given by Equation A2 which is the solution of Equation A1 for the relative phase c., the difference between the two oscillators. Successful synchronization means that relative phase does not change across time, $d\varphi/dt = 0$, the two units maintain the same relation to each other. For example, in (A), the coupling is insufficient in both directions and as a result $d\varphi/dt$ is always negative, meaning that the relative phase constantly decreases because the one oscillator is always running faster than the other. Correspondingly, the dashed arrow in the upper inset in (A) shows that the rotation rate of the stimulus oscillator may fluctuate and come closer to that of the unresponsive gait, yet the two will not match. The intersection between the sinusoid and $d\varphi/dt = 0$ also shows if stable synchronization resisting perturbations is possible and at what specific phase relation (black circles for stable and white circles and gray circles for unstable). (A) insufficient coupling; (B) critical coupling; (C) sufficient coupling with no responsiveness from the participant; (D) sufficient stimulus coupling and coupling on the participant's side. Each panel indicates the corresponding coupling strengths k_{stim} and k_{gait} and the phase difference φ^*_{stable} at which synchronization is maintained if possible. The preferred tempos were 120 spm for gait ($\omega_{0,gait}$ = 12.6 rad/s) and 144 bpm for stimulus ($\omega_{0,stim} = 1.2\omega_{0,gait}$ = 15.8 rad/s). The dashed arrows in (A) and (B) indicate that the stimulus fluctuates without locking to gait. The black arrow in (C) indicates that the stimulus tempo converges to that of gait (120 bpm). In (D), both parties adapt (black arrows) and meet at a compromise tempo (126.05 bpm, 13.2 rad/s).

Appendix C Model Validation

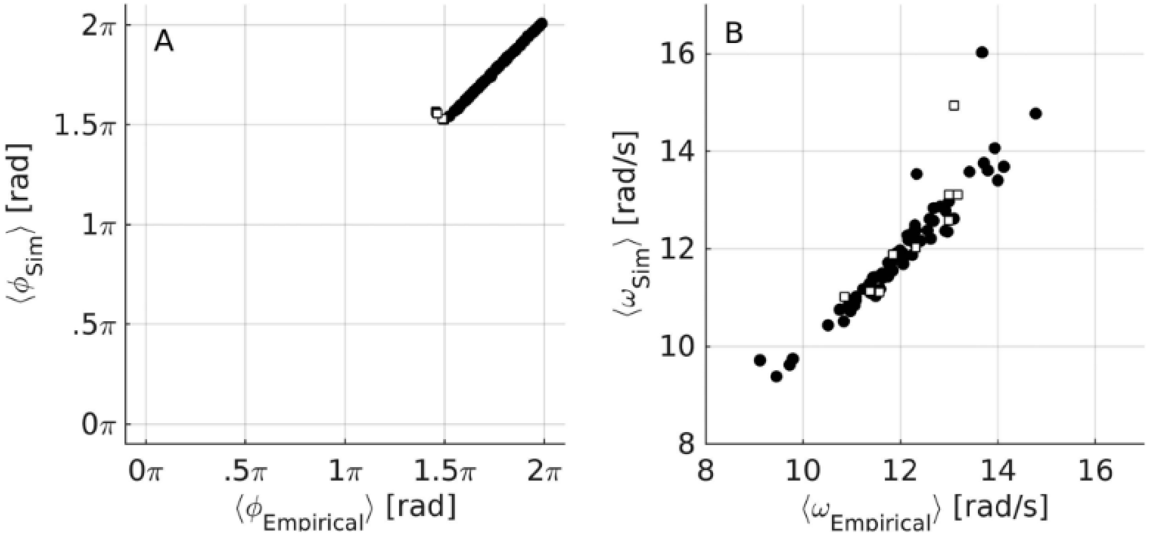

Figure C1. Gait parameters estimated from empirical trials in mutual synchronization were compared to simulated trials. (A) As expected, the empirical relative phase that was part of the simulation parameters was matched almost perfectly by the simulated relative phase. (B) The empirical stepping rate was not an input in the simulations but also was matched well.